

**Examining variability in positive social engagement and functional brain connectivity in
the default mode network in young infants**

Olivia Allison

Charlottesville, VA

A predissertation research project presented to the
graduate faculty of the University of Virginia

in candidacy for the Degree of

Master of Arts

Department of Psychology

University of Virginia

August 2024

Advisor: Tobias Grossmann, Ph.D.

Second Reader: Amrisha Vaish, Ph.D.

Abstract

Positive social engagement relies upon the motivation to attend to, take pleasure in, and maintain social interactions. The default mode network (DMN) comprises superior temporal and medial prefrontal brain regions previously shown to be involved in infants' processing of emotionally expressive and smiling faces in the first year, and longitudinally predicting increased sociability in the second year. It is currently unknown whether and how positive social engagement in young infants relates to variability in functional connectivity in the DMN. The current study tested the pre-registered hypothesis that variability in positive social engagement predicts functional connectivity in the DMN among 5-month-old infants using functional near infrared spectroscopy (fNIRS). Neuroimaging results showed that infants displayed greater functional connectivity in the right than in the left hemisphere of the DMN, indicating faster long-range connectivity development in the right hemisphere. Contrary to our prediction, there were no significant associations between positive social engagement and DMN functional connectivity in 5-month-old infants. However, an exploratory analysis showed that higher levels of infants' smiling and laughter during daily interactions with their caregivers positively predicted DMN functional connectivity in the left hemisphere. This suggests that, already by 5 months of age, infants' functional connectivity in a brain network implicated in a host of social and cognitive functions, is associated with variability in infants' positive affect displayed during social interactions in close relationships.

Introduction

Humans are ultra-social beings (Tomasello, 2014), possessing unique social-cognitive skills and motivations (Tomasello, 2020). From birth, newborns prefer looking at faces rather than other objects (Farroni et al., 2002). Within the first few months of life, infants engage with and develop special bonds with the people and family members around them (Ainsworth, 1969). The cultural intelligence hypothesis posits that humans possess a specialized set of social-cognitive skills that emerge early in infancy promoting the complex learning and development underpinning cultural cognition (Herrmann et al., 2007). Among these early social-cognitive skills is a unique motivation to interact with others. Specifically, social motivation is considered a set of psychological and biological processes that help humans function in collaboration with others through orienting to the social world, finding pleasure in social interactions, and maintaining social relationships (Chevallier et al., 2012). On the behavioral level, social engagement is a manifestation of the underlying social motivation of an individual (Chevallier et al., 2012; Over, 2016). Infants' early social engagement behaviors predict initiating joint attention later in infancy (Salley et al., 2016) as well as social-emotional and behavioral outcomes in childhood (Van Hecke et al., 2007). Much of the research to date has focused on the associations between early social engagement and social, behavioral, and cognitive outcomes. However, little research has focused on the brain-behavior relationship between functional connectivity among social brain regions and social engagement in young infants, making this an important avenue for additional research.

Recently, studies have shown that bidirectional interactions with caregivers lay the foundation of neural architecture and social function in the developing brain (Stern et al., 2024). The default mode network, containing the medial prefrontal cortex (mPFC) and superior

temporal cortex (STC), is involved in social cognition and is one of the first higher-order functional networks to fully develop during infancy (Gao et al., 2009). Neuroimaging studies with infants indicate that cortical brain regions respond preferentially to faces (superior temporal cortex) and positively-valenced social stimuli (medial prefrontal cortex) very early in life (L. J. Powell et al., 2018). Specifically, Powell and colleagues (2018) posited that activation of the medial prefrontal cortex during social interactions may guide the organization of cortical face areas, such as the superior temporal cortex, in young infants.

From birth, infants show enhanced responses to and preferentially look at direct gaze over averted gaze (Farroni et al., 2002), preferentially look at upright faces over inverted faces (Turati et al., 2002), and preferentially attend to infant-directed over adult-directed speech (Cooper & Aslin, 1990; Schachner & Hannon, 2011). Infants' social orienting rapidly increases within the first year of life (Thiele et al., 2021) and continues throughout early childhood (Dubey et al., 2022). There is also evidence suggesting young infants take pleasure in social interaction, such as sequentially vocalizing and smiling with social others (Trevvarthen & Aitken, 2001) and smiling towards upright faces as early as two months of age (Spelke, 2022; Spitz, 1946). During the second half of the first year, infants' smiling and laughter reliably increases in social contexts (Messinger & Fogel, 2007; Sroufe & Waters, 1976). Additionally, research demonstrating the early emergence of prosocial behaviors is indicative of infants' preference for positive social interactions and outcomes (Bloom, 2014; Hamlin et al., 2007; Hamlin & Wynn, 2011; Over, 2016; Warneken & Tomasello, 2006). By 7 months, infants can reliably distinguish between happy and fearful faces and voices (Grossmann, 2013) and studies suggest oxytocin, a neurohormone administered through increased breastfeeding, plays a specific role in facilitating infants' processing of positive emotions and interactions (Krol et al., 2014, 2015).

The medial prefrontal cortex (mPFC), involved in emotion and reward processing in adults, has been shown in infants to selectively respond to viewing smiles compared to frowns, hearing infant-directed speech compared to adult-directed speech, and both hearing and viewing one's own mother compared to another female (Grossmann, 2013; Krol & Grossmann, 2020; Naoi et al., 2012; Saito et al., 2007). The mPFC may reflect infants' interpretations of smiles as a positive communicative signal (Grossmann et al., 2008), supported by research demonstrating that the mPFC preferentially responds to positively valenced social stimuli early in life and continues into toddlerhood (Grossmann, 2013; L. J. Powell et al., 2018; Richardson et al., 2021). Importantly, recent research suggests that dorso-medial prefrontal cortex responses to social smiles, and not social frowns, at 11 months longitudinally predict social motivation behaviors at 18 months (Grossmann & Allison, 2024). Overall, converging evidence suggests the medial prefrontal cortex plays an important role in developing social brain function very early in life and may promote preferences for positive social engagement.

It has also been shown that newborn infants engage superior temporal regions when viewing dynamic faces (Farroni et al., 2013), and by five months, bilaterally engage posterior superior temporal regions in response to social video clips (Lloyd-Fox et al., 2014). Importantly, activation of superior temporal regions while viewing dynamic social stimuli increases with age, indicating the role of face-to-face engagement in developing social function of this bilateral region (Farroni et al., 2013). Recent research suggests that right superior temporal cortex responses to changing faces at 7 months longitudinally predict social motivation behaviors, which are defined as seeking out and taking pleasure in social interactions with others at 18 months (Grossmann, 2024). Overall, converging evidence suggests the superior temporal cortex

plays an important functional role in guiding infants' attention towards social others and may promote social engagement.

Taken together, research suggests the medial prefrontal cortex and superior temporal cortex: 1) develop social functions within the first few months of life, 2) are positively associated with increased positive social interaction, and 3) are longitudinally associated with overt social behavior within the first two years of life. However, it is currently unclear whether and how the functional connectivity between these brain regions as part of the default mode network are linked to variability in infants' positive social engagement before 7 months. Measures of brain connectivity at rest among infants can inform our understanding of underlying connections between different brain regions. Importantly, individual variability in functional network connectivity has been linked to individual differences in cognitive and behavioral outcomes among infants (Z. Fu et al., 2023; C. M. Kelsey, Farris, et al., 2021). In the cognitive neurosciences, the study of functional brain connectivity is seen to be one of the most promising avenues for understanding brain-behavior relationships (Friston, 2011). In adults, research suggests changes in default mode network connectivity are associated with changes in social behavior (Breukelaar et al., 2020; Li et al., 2014; Mars et al., 2012). Using functional near-infrared spectroscopy (fNIRS), an infant-friendly neuroimaging technique with higher spatial resolution than electrophysiological techniques (Wilcox & Biondi, 2015), the default mode network has been associated with overtly displayed, parent-reported affect and behavior in infants as young as one month of age (C. M. Kelsey, Farris, et al., 2021). In five-month-old infants, maternal sensitivity during a mother-infant free play interaction was associated with greater connectivity in the default mode network using fNIRS, even when accounting for socioeconomic status (Chajes et al., 2022). Given the above, the current study tested our pre-

registered hypothesis (<https://osf.io/3bs4v>) that heightened levels of parent-reported and observed positive social engagement (infant-derived Social Attentiveness, Social Engagement, Social Smiling and Laughter, Social Touch, and Social Approach) are positively associated with resting-state default mode network functional connectivity in 5-month-old infants. To our knowledge, this study is the first to explore the associations between a long-range cortical social brain network at rest and overtly displayed positive social engagement in very young infants.

Methods

Participants. Participating infants were part of a larger longitudinal study of social and emotional development. 121 mother-infant dyads were first recruited from a local hospital when the infants were newborns (for details see Kelsey, Farris, et al., 2021 and Kelsey, Prescott, et al., 2021). To be included, participants had to be born at term, with normal birth weight (>2,500 g), and did not have any hearing or visual impairments. Of the original 121 dyads, 109 families returned to the lab when the infants were 5 months (M age = 5.2 months; SD = 0.68 months; range = 4–7 months; n = 64 male, sex assigned at birth). At the 5-month-old timepoint, infants completed a five-minute free-play session with their mothers following a resting-state fNIRS recording session. Additionally, mothers completed questionnaires that included questions about their infants' behavior. Of the 109 dyads that completed the 5-month visit, 35 were included in the final analytic sample (M age = 5.8 months; SD = 0.44 months; range = 4.9–6.8 months; n = 24 male sex assigned at birth) who had all variables of interest detailed below. 74 participants were excluded from the present analyses for one or more of the following reasons: n = 45 excluded for having more than 50% of fNIRS channels excluded during preprocessing (see below for details); n = 16 excluded due to technical errors; n = 7 excluded because they did not have at least 100 seconds of continuous fNIRS data with no disruptive behaviors (see below); n =

1 excluded because of inaccurate placement of the fNIRS cap (more than 1 cm deviation from proper cap placement); n=21 excluded for not completing item 90 of the IBQ-R short form or answering 'N/A' or 'prefer not to answer'; n=2 excluded for not completing free-play interaction; n=1 excluded for deep sleep or crying for more than 50% of the free play interaction. Parents provided informed consent on behalf of themselves and their infant, all procedures were approved by the authors' institutional review board, and participants received monetary compensation for their participation.

Behavioral coding from free play. Infants' Social Attentiveness, Social Engagement, Social Smiles and Laughter, and Social (active) Touch were assessed using video recordings of mother-infant interactions during the 5-month time point. In order to capture a natural play session, each mother was instructed to interact with her infant as she did at home. Two cameras simultaneously recorded the interaction. One camera captured the face and body of the mother, and the other camera captured the face and body of the infant. Mothers were made aware of the cameras and instructed to remain within view of them. Infants were placed on their backs on a carpet in the center of the playroom and no further instructions were given. The same selection of 4 objects (3 toys and 1 play book) was provided to each mother-infant dyad to assist play. Mothers and infants could freely choose and change the object of interest during the interaction or abandon the objects altogether. Once assembled, the experimenter left the room, and the mother-infant pair was left alone to interact for 5 minutes. Social Attentiveness, Social Engagement, social smiles and laughter, and social (active) touch were behaviorally coded and scored offline using INTERACT software (Mangold International, Arnstorf, Germany), and the exact coding scheme can be accessed through osf (<https://osf.io/preprints/psyarxiv/ym3ne>) (see Grossmann et al., 2018 and Krol et al., 2019 for information on the initial creation of this coding

scheme). Social Attentiveness and Social Engagement were scored on a scale from 1 (not at all) to 5 (very much). Social Attentiveness and Social Engagement were coded separately to acquire more detailed information about infants' behaviors: 1) How attentive was the infant towards the mother? and 2) How engaged was the infant towards the mother? Since scores were strongly correlated (Pearson's $r = 0.57$; Cohen, 1988), Social Attentiveness and Social Engagement scores were combined into one Social Engagement score, consistent with previous work by Grossmann et al., (2018). Social Attentiveness and Social Engagement were double-coded for all videos by two independent raters for reliability. Inter-rater reliability was good for Social Attentiveness (Intraclass correlation coefficient = 0.950; Fleiss Kappa = 0.774) and Social Engagement (Intraclass correlation coefficient = 0.922; Fleiss Kappa = 0.694). Discrepancies were resolved via conferencing. Social (active) touch and social smiles and laughter were scored based on the duration of time infants exhibited the behavior during the five-minute free-play interaction. Specifically, Social Touch only included infant-initiated touch directed at the mother (i.e. proactively touching mother) and social smiles and laughter only included infants' smiles and laughter directed at the mother (i.e. smiling or laughing while looking at mother or as a direct response to mother). Infant social smiles and laughter duration were coded together since infant smiles typically occurred with laughter.

Parental report of infant behavior. Social Approach was measured using the Approach subscale of the parent-reported Infant Behavior Questionnaire- Revised (IBQ-R) short form (Putnam et al., 2014). Mothers completed a series of questionnaires on Qualtrics (Qualtrics, Provo, UT) before each time point of data collection. The Infant Behavior Questionnaire- Revised short form was completed by mothers prior to in-person data collection at the 5-month-old timepoint. Items were rated by mothers on a scale from 1-7 (1 (never) to 7 (always)) with

two additional answer options provided (8 (N/A) and 9 (prefer not to answer)). The following item on the Approach subscale (item 90) was selected: “When familiar relatives/friends visited, how often did the baby get excited?” Although only one item on the Approach subscale represented our Social Approach variable, this item is similar to the Sociability scale items from the Early Childhood Behavior Questionnaire administered between 18 and 36 months of age (Putnam et al., 2006). The Sociability subscale has been used in previous work to capture social motivation behaviors (i.e. seeking out and taking pleasure in social interactions with others; see Grossmann & Allison, 2024). As an exploratory question, we separately included the Smiling and Laughter subscale (6 item composite score) from the IBQ-R short form, defined as smiling and laughter from the child in general caretaking and play situations (Putnam et al., 2014), to increase power of parent-reported positive social engagement (see *Table 1*).

DMN measures using fNIRS. Infants sat on their parents’ lap approximately 60 cm from the 23-inch monitor that displayed the resting state video stimulus for a total of up to 7 minutes while fNIRS data were being recorded. The infants wore an fNIRS fabric cap (EasyCap, Germany) which was secured in place using infant overalls and outside netting. Parents were asked to remain quiet throughout the fNIRS recording session. Sessions were video-recorded and a trained research assistant behaviorally coded infants’ behavior during the fNIRS recording offline using the behavior coding scheme from C. M. Kelsey, Farris, et al. (2021). Timepoints were removed if infants were crying, looking at the parent or experimenter, or parents were talking. A primary coder coded all of the videos and an additional trained research assistant coded a selected subsample of videos for reliability (28.4%, $n = 31$). Interrater reliability was excellent (Intraclass correlation coefficient = 0.92). Based on previous work, infants needed a minimum of 100 seconds of disruption-free data to be included (see Chajes et al., 2022).

Following previously published work (C. M. Kelsey, Farris, et al., 2021; C. M. Kelsey, Prescott, et al., 2021), the non-social stimulus was created by selecting non-social video clips (e.g., toys, fruits, and everyday objects) from a popular infant video (Baby Einstein - Kids2 Inc.). The images were accompanied by classical music and the video was segmented into 30 second intervals. The order of video segment presentation was randomized for each infant. Infants' fNIRS data were recorded using a NIRx NIRScoutX system and NIRStar acquisition software. The fNIRS system has 49 channels (approximately 2 cm source-detector distance) covering the frontal, temporal, and parietal brain regions in both hemispheres (see Chajes et al., 2022; Grossmann et al., 2018; C. Kelsey et al., 2019; Krol et al., 2019). The system emits two wavelengths of light, 760 and 850 nm, and captures both oxygenated hemoglobin (oxyHb) and deoxygenated hemoglobin (deoxyHb). The diodes have a power of 25 mW/wavelength and data were recorded at a preset default sampling rate of 3.91 Hz. Following our pre-registered fNIRS data processing plan, custom Matlab scripts and Homer2 were used to preprocess the data in accordance with guidelines outlined in Powell (2020). First, raw intensity data were converted to optical density units and channels with mean intensities outside the system recommended values (enPrunechannels: $d_{min} = 10^{-2}$, $d_{max} = 109$) or high-frequency amplitude changes with over 90% of time points marked as motion (hmrMotionArtifactByChannel_indLambda: tMotion = 1.0, tMask = 1.0, stdThresh = 100, ampThresh = 0.1) were removed. Flexible targeted Principal Component Analysis with up to three iterations (tMotion = 1.0, tMask = 1.0, Std Thresh = 100, Amp Thresh = 0.2, tpcaFilter = 0.97) were used to correct for motion artifacts, and corrected data were band-passed filtered from 0.01–0.08 Hz. Data were converted into oxygenated and deoxygenated hemoglobin concentration change values using a modified Beer Lambert Law assuming a partial path length factor of 5 (hmrOD2Conc). For each infant, a 49x49 correlation

matrix was created depicting all of the associations between all of the channels measured. Finally, the correlation values were standardized using a Fisher Z-transformation. The default mode network was created from an average of select channels that corresponded with regions of interest (Chajes et al., 2022; C. M. Kelsey, Farris, et al., 2021; C. M. Kelsey, Prescott, et al., 2021). Brain areas were named in accordance with anatomical mappings of the 10–20 system in similar age infants. Based on the LONI probabilistic brain atlas (LPBA, Shattuck et al., 2008) using photon propagation simulation with realistic, age-appropriate (6 months) head models (devfOLD; X. Fu & Richards, 2021; Zimeo Morais et al., 2018), brain areas were confirmed at the group level. The default mode network (DMN) left and right oxyHb z-scores were created by averaging the left and right hemisphere correlations between three channels in the medial prefrontal cortex, corresponding with the Fpz electrode (10–20 system) or the superior and middle frontal gyri (LPBA), and three channels in the left and right lateral temporal cortex, corresponding with T7 and T8 electrodes (10–20 system) or the superior and middle temporal gyri (LPBA). Specifically, left DMN resting state functional connectivity network z-scores were created using the three medial prefrontal and three left hemisphere temporal source-detector pairs. Right DMN resting state functional connectivity network z-scores were created using the three medial prefrontal and three right hemisphere temporal source-detector pairs (see *Figure 1*).

Results

Following our pre-registered data analysis plan (<https://osf.io/3bs4v>), multiple linear regression modeling using the entry method was employed to test our main hypothesis that enhanced positive social engagement (Social Attentiveness, Social Engagement, Social Smiling and Laughter, Social Touch, and Social Approach) positively predicts functional connectivity in the DMN. Analyses were carried out in IBM SPSS Statistics (Version 28) and assumptions were

tested using R Studio (Version 2024.04). Before conducting the multiple linear models, we first examined whether DMN connectivity differed between the left and right hemisphere. Results of the paired-samples t -test revealed a significant difference between left ($N = 49$ observations) and right ($N = 54$ observations) DMN connectivity strength ($t[47] = -2.09, p = 0.04$), with the right hemisphere DMN ($M = 0.28, SD = 0.28$) showing significantly greater functional connectivity than the left hemisphere ($M = 0.18, SD = 0.20$) (see *Figure 2*). We therefore tested whether our positive social engagement predictor variables were associated with left and right DMN functional connectivity in two separate multiple linear regression models.

Second, the linearity, normality, homoscedasticity, and absence of multicollinearity assumptions of both left and right hemisphere models were checked. Residuals were examined through diagnostic plots. Right hemisphere DMN showed a negative autocorrelation in the residuals (autocorrelation = -0.44 , D-W statistic = $2.86, p = 0.002$). All other assumption testing indicated that the two models accurately captured the relation between the predictors and the outcome variables and estimated coefficients for predictors were stable and reliable.

Third, as an exploratory analysis, a series of Spearman's rho correlations was used to identify significant associations between the main variables of interest. Correlations revealed that the Social Engagement combined score (Social Attentiveness + Social Engagement) was positively associated with touch duration ($r[33] = 0.36, p = 0.03$) and smiling and laughing duration ($r [33] = 0.59, p = 0.0002$). Surprisingly, our parent-reported Social Approach score was not significantly correlated with any of the behavior-based positive social engagement variables coded from free play. Additionally, we tested whether any of the demographic and fNIRS data quality measures, including signal-to-noise ratio for wavelength 1/760 nm (SNR 1; $M = 10.70, SD = 6.30$), signal-to-noise ratio for wavelength 2/850 nm (SNR 2; $M = 9.84, SD = 7.51$), included

channels ($M=38.53$, $SD= 6.77$), and included time ($M= 343.61$, $SD= 96.33$), were associated with left and right DMN functional connectivity. Of these measures, only SNR 1 ($r [42] = 0.35$, $p < 0.05$) and SNR 2 ($r [42] = 0.43$, $p < 0.01$) were significantly positively associated with left default mode network connectivity. SNR 1 and SNR 2 were strongly positively correlated ($r [43] = 0.80$, $p < 0.001$). We employed two models to test whether positive social engagement predictor variables were positively associated with functional connectivity of the DMN, one for the left and another for the right hemisphere. We ran these models without and with including SNR 2 as a covariate. SNR 2 for wavelength 850 nm was chosen as the covariate because the higher wavelength (lower frequency) best reflects signal changes related to oxyHb, which was the fNIRS measure used to compute DMN functional connectivity.

Results of the multiple linear models revealed that none of the predictor variables (Social Attentiveness, Social Engagement, Social Smiling and Laughter, Social Touch, and Social Approach) significantly predicted DMN functional connectivity in the left hemisphere, $F(4, 30) = 0.23$, $p = 0.92$, explaining only 3% of the variance ($R^2 = .03$, Adjusted $R^2 = -.10$), or in the right hemisphere, $F(4, 30) = 0.40$, $p = 0.81$, explaining only 5% of the variance ($R^2 = .05$, Adjusted $R^2 = -.08$). When controlling for signal-to-noise ratio, positive social engagement predictor variables remained not significantly associated with DMN functional connectivity in the left hemisphere, $F(4, 30) = 0.98$, $p = 0.43$, explaining only 12% of the variance ($R^2 = .12$, Adjusted $R^2 = -.002$), and DMN functional connectivity in the right hemisphere, $F(4, 30) = 0.93$, $p = 0.46$, explaining only 11% of the variance ($R^2 = .11$, Adjusted $R^2 = -.009$). Additionally, we employed a Bayesian regression analysis in JASP (Version 0.18.3). Corresponding to the results using the linear regression approach reported above, the Bayesian analysis showed greater support for the null

hypothesis than our alternative hypothesis for all predictor variables in both models, with and without including SNR 2 as a covariate (see *Supplementary Materials*).

As an exploratory analysis, we conducted multiple linear regressions corresponding to the ones reported above but with the IBQ-R-derived Smiling and Laughing scores as an additional predictor variable to test whether parent-reported smiling and laughing during daily interactions predicted left and right hemisphere DMN functional connectivity. Results of this exploratory analyses revealed a significant positive relation between parent-reported Smiling and Laughing scores and left DMN functional connectivity ($F[5, 29] = 3.16, p = .02$, accounting for approximately 35% of the variance ($R^2 = .35$, Adjusted $R^2 = .24$, see *Figure 3*), but not right DMN oxyHb ($F(5, 29) = 0.78, p = .57$, accounting for approximately 12% of the variance ($R^2 = .12$, Adjusted $R^2 = -.03$) (note that this analysis controlled for SNR 2 as a covariate). To test the extent of this association, we employed a Bayesian regression analysis in JASP (Version 0.18.3; Kelter, 2020). The Bayesian regression analysis revealed a $BF_{10} = 1.00$ for Smiling and Laughing scores without SNR 2 as a covariate and $BF_{10} = 2.02$ for Smiling and Laughing scores with SNR 2 as a covariate, showing greater support for our hypothesis than the null hypothesis. Together, the parent-reported measures, Smiling and Laughing scores and Social Approach item scores, revealed the greatest support for our alternative hypothesis compared to the null hypothesis for functional connectivity of the DMN in the left hemisphere as the outcome variable ($BF_{10} = 3.91$ with SNR2 covariate) (see *Supplementary Materials*). None of the predictors revealed greater support for the alternative hypothesis than the null hypothesis for functional connectivity of the DMN in the right hemisphere as the outcome variable. Surprisingly, parent-reported Smiling and Laughing scores were not significantly correlated with behaviorally-coded smiling and laughing duration (Spearman's $r[33] = 0.11, p = 0.49$), or any other observed positive

social engagement behaviors during the mother-infant free play interaction. However, parent-reported smiling and laughing was significantly correlated with parent-reported Social Approach (Spearman's $r[86] = 0.27, p < 0.01$).

Discussion

The current study examined the association between positive social engagement behaviors and resting-state DMN functional connectivity in 5-month-old infants. Individual differences in positive social engagement were measured using parental report (Social Approach and Smiling and Laughter) as well as through behavioral observation from mother-infant free play (Social Attentiveness, Social Engagement, Social Smiling and Laughter, and Social Touch). Contrary to our pre-registered hypothesis, our results failed to reveal a positive association between behaviorally coded positive social engagement and resting-state DMN functional connectivity. However, results from an exploratory analysis show that higher parent-reported levels of infants' smiling and laughter during daily interactions with their caregivers positively predicted DMN functional connectivity in the left hemisphere. This suggests that, already by 5 months of age, infants' functional connectivity in a long-range brain network implicated in a host of social and cognitive functions in adults (Breukelaar et al., 2020; Li et al., 2014; Mars et al., 2012), is associated with variability in infants' positive affect displayed during social interactions in close relationships. Furthermore, results of a Bayesian regression analysis indicate that infants displaying higher levels of parent-reported social approach and smiling/laughter show greater functional connectivity of the DMN in the left hemisphere. Together, this pattern of findings provides preliminary evidence for the notion that some aspects of infants' positive affective engagement and Social Approach behavior are linked to functional connectivity in the DMN.

While the current study was unable to provide evidence for the pre-registered hypothesis, the findings still advance our understanding of the relation between positive social engagement and functional brain connectivity early in human development. The current exploratory findings, indexing a positive association between infants' positive affective engagement in social interactions, are consistent with prior work demonstrating the early developmental emergence of brain systems involved in promoting the formation of positive social relationships (Grossmann, 2024; Grossmann & Allison, 2024; Grossmann & Wood, 2023). Moreover, the current results extend previous findings of a link between enhanced DMN connectivity and behaviors that facilitate positive social relationships across the lifespan (Li et al., 2014; Yeshurun et al., 2021), into early infancy. In line with our findings, it has also been shown that infant-caregiver coupling in DMN regions, especially within medial prefrontal cortex, is associated with positive social engagement behaviors, including smiling during social interactions with caregivers among older infants (Piazza et al., 2020). Furthermore, our findings may also relate to previous research with adults proposing a so-called extended social-affective default-mode network (Amft et al., 2015). Interestingly, brain regions involved in adults' extended social-affective DMN at rest such as the medial prefrontal and the lateral temporal cortex are consistently recruited during social-affective engagement in infants and toddlers (Grossmann, 2013; L. J. Powell et al., 2018; Richardson et al., 2021). Considering our findings show that functional connectivity at rest, precisely between these medial prefrontal and lateral temporal brain regions, is predicted by infants' positive affect displayed during social interactions, raises the possibility that this association reflects early developing connectivity in the extended social affective DMN. Thus, future research would benefit from measuring task-related functional connectivity during social interactions in addition

to the rest-state functional connectivity in infancy to examine this possibility and to better understand the exact nature of the observed effect.

Given that positive affect serves as a reward that motivates and reinforces behavior (Shiota et al., 2021), our findings may be taken to suggest that young infants expressing and experiencing positive affect during social interactions with close others may reflect social motivational processes playing a role in the development of DMN, at least in the left hemisphere. The finding that our effect was lateralized to the left hemisphere agrees with research with infants and adults implicating the left hemisphere in positive affect and approach behaviors (Davidson & Fox, 1982). Furthermore, with respect to the lateralization of the effect to the left hemisphere, it is important to note that our results showed that, at the group level, 5-month-old infants displayed greater functional connectivity in the right than in the left hemisphere of the DMN. This group-level effect is in line with prior work showing differential cortical maturation of the two hemispheres during infancy, with the right hemisphere maturing earlier than the left hemisphere during early ontogeny (Thatcher et al., 1987). In the context of the current findings, this may suggest that infants who display greater positive affect and positive engagement develop functional connectivity earlier (faster maturation) than infants showing reduced positive affect and positive engagement. This tentative suggestion clearly requires further investigation, especially by testing infants at older ages using a similar approach as used in the current study.

In summary, the current study provides preliminary evidence that, already by 5 months of age, infants' functional connectivity in a major long-range brain network implicated in a host of socio-affective and cognitive functions, is predicted by variability in infants' positive affect displayed during social interactions in close relationships. The observed association effect is limited to specific behaviors observed by the parents during daily social interactions and not seen

during behavioral observation in the laboratory, suggesting a limited ability of laboratory-based measures to tap into young infants' behavioral variability relevant to the development of this brain network. Moreover, the observed effect is restricted to the left hemisphere, which in agreement with prior research appears to be the hemisphere developing more slowly during infancy and being involved in positive affect and approach. The current findings support the general notion that brain development is intricately connected to positive experiences in close social relationships very early in life.

References

- Ainsworth, M. D. S. (1969). Object Relations, Dependency, and Attachment: A Theoretical Review of the Infant-Mother Relationship. *Child Development, 40*(4), 969–1025.
<https://doi.org/10.2307/1127008>
- Amft, M., Bzdok, D., Laird, A. R., Fox, P. T., Schilbach, L., & Eickhoff, S. B. (2015). Definition and characterization of an extended social-affective default network. *Brain Structure & Function, 220*(2), 1031–1049. <https://doi.org/10.1007/s00429-013-0698-0>
- Bloom, P. (2014). *Just Babies: The Origins of Good and Evil*. Crown.
- Breukelaar, I. A., Griffiths, K. R., Harris, A., Foster, S. L., Williams, L. M., & Korgaonkar, M. S. (2020). Intrinsic functional connectivity of the default mode and cognitive control networks relate to change in behavioral performance over two years. *Cortex, 132*, 180–190.
<https://doi.org/10.1016/j.cortex.2020.08.014>
- Chajes, J. R., Stern, J. A., Kelsey, C. M., & Grossmann, T. (2022). Examining the Role of Socioeconomic Status and Maternal Sensitivity in Predicting Functional Brain Network Connectivity in 5-Month-Old Infants. *Frontiers in Neuroscience, 16*.
<https://www.frontiersin.org/articles/10.3389/fnins.2022.892482>
- Chevallier, C., Kohls, G., Troiani, V., Brodtkin, E. S., & Schultz, R. T. (2012). The Social Motivation Theory of Autism. *Trends in Cognitive Sciences, 16*(4), 231–239.
<https://doi.org/10.1016/j.tics.2012.02.007>
- Cooper, R. P., & Aslin, R. N. (1990). Preference for infant-directed speech in the first month after birth. *Child Development, 61*(5), 1584–1595. <https://doi.org/10.2307/1130766>
- Davidson, R. J., & Fox, N. A. (1982). Asymmetrical brain activity discriminates between positive and negative affective stimuli in human infants. *Science (New York, N.Y.), 218*(4578), 1235–1237.
<https://doi.org/10.1126/science.7146906>

- Dubey, I., Brett, S., Ruta, L., Bishain, R., Chandran, S., Bhavnani, S., Belmonte, M. K., Estrin, G. L., Johnson, M., Gliga, T., & Chakrabarti, B. (2022). Quantifying preference for social stimuli in young children using two tasks on a mobile platform. *PLoS ONE*, *17*(6), e0265587. <https://doi.org/10.1371/journal.pone.0265587>
- Farroni, T., Chiarelli, A. M., Lloyd-Fox, S., Massaccesi, S., Merla, A., Di Gangi, V., Mattarello, T., Faraguna, D., & Johnson, M. H. (2013). Infant cortex responds to other humans from shortly after birth. *Scientific Reports*, *3*(1), 2851. <https://doi.org/10.1038/srep02851>
- Farroni, T., Csibra, G., Simion, F., & Johnson, M. H. (2002). Eye contact detection in humans from birth. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(14), 9602–9605. <https://doi.org/10.1073/pnas.152159999>
- Friston, K. J. (2011). Functional and effective connectivity: A review. *Brain Connectivity*, *1*(1), 13–36. <https://doi.org/10.1089/brain.2011.0008>
- Fu, X., & Richards, J. E. (2021). Age-related changes in diffuse optical tomography sensitivity profiles in infancy. *PloS One*, *16*(6), e0252036. <https://doi.org/10.1371/journal.pone.0252036>
- Fu, Z., Liu, J., Salman, M. S., Sui, J., & Calhoun, V. D. (2023). Functional connectivity uniqueness and variability? Linkages with cognitive and psychiatric problems in children. *Nature Mental Health*, *1*(12), 956–970. <https://doi.org/10.1038/s44220-023-00151-8>
- Gao, W., Zhu, H., Giovanello, K. S., Smith, J. K., Shen, D., Gilmore, J. H., & Lin, W. (2009). Evidence on the emergence of the brain's default network from 2-week-old to 2-year-old healthy pediatric subjects. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(16), 6790–6795. <https://doi.org/10.1073/pnas.0811221106>
- Grossmann, T. (2013). The role of medial prefrontal cortex in early social cognition. *Frontiers in Human Neuroscience*, *7*. <https://www.frontiersin.org/articles/10.3389/fnhum.2013.00340>
- Grossmann, T. (2024). Social Perception in the Infant Brain and Its Link to Social Behavior. *Journal of Cognitive Neuroscience*, 1–9. https://doi.org/10.1162/jocn_a_02165

- Grossmann, T., & Allison, O. (2024). Dorso-medial prefrontal cortex responses to social smiles predict sociability in early human development. *Imaging Neuroscience*, 2, 1–8.
https://doi.org/10.1162/imag_a_00129
- Grossmann, T., Johnson, M. H., Lloyd-Fox, S., Blasi, A., Deligianni, F., Elwell, C., & Csibra, G. (2008). Early cortical specialization for face-to-face communication in human infants. *Proceedings of the Royal Society B: Biological Sciences*, 275(1653), 2803–2811.
<https://doi.org/10.1098/rspb.2008.0986>
- Grossmann, T., Missana, M., & Krol, K. M. (2018). The neurodevelopmental precursors of altruistic behavior in infancy. *PLoS Biology*, 16(9), e2005281.
<https://doi.org/10.1371/journal.pbio.2005281>
- Grossmann, T., & Wood, A. (2023). Variability in the expression and perception of positive affect in human infancy. *Social Cognitive and Affective Neuroscience*, 18(1), nsad049.
<https://doi.org/10.1093/scan/nsad049>
- Hamlin, J. K., & Wynn, K. (2011). Young infants prefer prosocial to antisocial others. *Cognitive Development*, 26(1), 30–39. <https://doi.org/10.1016/j.cogdev.2010.09.001>
- Hamlin, J. K., Wynn, K., & Bloom, P. (2007). Social evaluation by preverbal infants. *Nature*, 450(7169), Article 7169. <https://doi.org/10.1038/nature06288>
- Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science (New York, N.Y.)*, 317(5843), 1360–1366. <https://doi.org/10.1126/science.1146282>
- Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews. Neuroscience*, 6(10), 766–774.
<https://doi.org/10.1038/nrn1766>
- Kelsey, C., Dreisbach, C., Alhusen, J., & Grossmann, T. (2019). A primer on investigating the role of the microbiome in brain and cognitive development. *Developmental Psychobiology*, 61(3), 341–349.
<https://doi.org/10.1002/dev.21778>

- Kelsey, C. M., Farris, K., & Grossmann, T. (2021). Variability in Infants' Functional Brain Network Connectivity Is Associated With Differences in Affect and Behavior. *Frontiers in Psychiatry, 12*.
<https://www.frontiersin.org/articles/10.3389/fpsy.2021.685754>
- Kelsey, C. M., Prescott, S., McCulloch, J. A., Trinchieri, G., Valladares, T. L., Dreisbach, C., Alhusen, J., & Grossmann, T. (2021). Gut microbiota composition is associated with newborn functional brain connectivity and behavioral temperament. *Brain, Behavior, and Immunity, 91*, 472–486.
<https://doi.org/10.1016/j.bbi.2020.11.003>
- Kelter, R. (2020). Bayesian alternatives to null hypothesis significance testing in biomedical research: A non-technical introduction to Bayesian inference with JASP. *BMC Medical Research Methodology, 20*(1), 142. <https://doi.org/10.1186/s12874-020-00980-6>
- Krol, K. M., & Grossmann, T. (2020). Impression Formation in the Human Infant Brain. *Cerebral Cortex Communications, 1*(1), tgaa070. <https://doi.org/10.1093/texcom/tgaa070>
- Krol, K. M., Monakhov, M., Lai, P. S., Ebstein, R. P., & Grossmann, T. (2015). Genetic variation in CD38 and breastfeeding experience interact to impact infants' attention to social eye cues. *Proceedings of the National Academy of Sciences of the United States of America, 112*(39), E5434–E5442. <https://doi.org/10.1073/pnas.1506352112>
- Krol, K. M., Puglia, M. H., Morris, J. P., Connelly, J. J., & Grossmann, T. (2019). Epigenetic modification of the oxytocin receptor gene is associated with emotion processing in the infant brain. *Developmental Cognitive Neuroscience, 37*, 100648.
<https://doi.org/10.1016/j.dcn.2019.100648>
- Krol, K. M., Rajhans, P., Missana, M., & Grossmann, T. (2014). Duration of exclusive breastfeeding is associated with differences in infants' brain responses to emotional body expressions. *Frontiers in Behavioral Neuroscience, 8*, 459. <https://doi.org/10.3389/fnbeh.2014.00459>
- Li, W., Mai, X., & Liu, C. (2014). The default mode network and social understanding of others: What do brain connectivity studies tell us. *Frontiers in Human Neuroscience, 8*.
<https://www.frontiersin.org/articles/10.3389/fnhum.2014.00074>

- Lloyd-Fox, S., Richards, J. E., Blasi, A., Murphy, D. G. M., Elwell, C. E., & Johnson, M. H. (2014). Coregistering functional near-infrared spectroscopy with underlying cortical areas in infants. *NeuroPhotonics*, *1*(2), 025006. <https://doi.org/10.1117/1.NPh.1.2.025006>
- Mars, R. B., Neubert, F.-X., Noonan, M. P., Sallet, J., Toni, I., & Rushworth, M. F. (2012). On the relationship between the “default mode network” and the “social brain.” *Frontiers in Human Neuroscience*, *6*. <https://doi.org/10.3389/fnhum.2012.00189>
- Messinger, D., & Fogel, A. (2007). THE INTERACTIVE DEVELOPMENT OF SOCIAL SMILING. In *Advances in Child Development and Behavior* (Vol. 35, pp. 327–366). Elsevier. <https://doi.org/10.1016/B978-0-12-009735-7.50014-1>
- Naoi, N., Minagawa-Kawai, Y., Kobayashi, A., Takeuchi, K., Nakamura, K., Yamamoto, J., & Kojima, S. (2012). Cerebral responses to infant-directed speech and the effect of talker familiarity. *NeuroImage*, *59*(2), 1735–1744. <https://doi.org/10.1016/j.neuroimage.2011.07.093>
- Over, H. (2016). The origins of belonging: Social motivation in infants and young children. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1686). <https://doi.org/10.1098/rstb.2015.0072>
- Piazza, E. A., Hasenfratz, L., Hasson, U., & Lew-Williams, C. (2020). Infant and Adult Brains Are Coupled to the Dynamics of Natural Communication. *Psychological Science*, *31*(1), 6–17. <https://doi.org/10.1177/0956797619878698>
- Powell, L. (2020). *Robust and automated motion correction for real infant fNIRS data*. PsyArXiv. <https://doi.org/10.31234/osf.io/yxcnb>
- Powell, L. J., Deen, B., & Saxe, R. (2018). Using individual functional channels of interest to study cortical development with fNIRS. *Developmental Science*, *21*(4), e12595. <https://doi.org/10.1111/desc.12595>
- Putnam, S. P., Gartstein, M. A., & Rothbart, M. K. (2006). Measurement of fine-grained aspects of toddler temperament: The Early Childhood Behavior Questionnaire. *Infant Behavior and Development*, *29*(3), 386–401. <https://doi.org/10.1016/j.infbeh.2006.01.004>

- Putnam, S. P., Helbig, A. L., Gartstein, M. A., Rothbart, M. K., & Leerkes, E. (2014). Development and assessment of short and very short forms of the infant behavior questionnaire-revised. *Journal of Personality Assessment, 96*(4), 445–458. <https://doi.org/10.1080/00223891.2013.841171>
- Richardson, H., Taylor, J., Kane-Grade, F., Powell, L., Bosquet Enlow, M., & Nelson, C. A. (2021). Preferential responses to faces in superior temporal and medial prefrontal cortex in three-year-old children. *Developmental Cognitive Neuroscience, 50*, 100984. <https://doi.org/10.1016/j.dcn.2021.100984>
- Saito, Y., Kondo, T., Aoyama, S., Fukumoto, R., Konishi, N., Nakamura, K., Kobayashi, M., & Toshima, T. (2007). The function of the frontal lobe in neonates for response to a prosodic voice. *Early Human Development, 83*(4), 225–230. <https://doi.org/10.1016/j.earlhumdev.2006.05.017>
- Salley, B., Sheinkopf, S. J., Neal-Beevers, A. R., Tenenbaum, E. J., Miller-Loncar, C. L., Tronick, E., Lagasse, L. L., Shankaran, S., Bada, H., Bauer, C., Whitaker, T., Hammond, J., & Lester, B. M. (2016). Infants' early visual attention and social engagement as developmental precursors to joint attention. *Developmental Psychology, 52*(11), 1721–1731. <https://doi.org/10.1037/dev0000205>
- Schachner, A., & Hannon, E. E. (2011). Infant-directed speech drives social preferences in 5-month-old infants. *Developmental Psychology, 47*(1), 19–25. <https://doi.org/10.1037/a0020740>
- Shattuck, D. W., Mirza, M., Adisetiyo, V., Hojatkashani, C., Salamon, G., Narr, K. L., Poldrack, R. A., Bilder, R. M., & Toga, A. W. (2008). Construction of a 3D Probabilistic Atlas of Human Cortical Structures. *NeuroImage, 39*(3), 1064–1080. <https://doi.org/10.1016/j.neuroimage.2007.09.031>
- Shiota, M. N., Papies, E. K., Preston, S. D., & Sauter, D. A. (2021). Positive affect and behavior change. *Current Opinion in Behavioral Sciences, 39*, 222–228. <https://doi.org/10.1016/j.cobeha.2021.04.022>
- Spelke, E. S. (2022). Core Social Cognition. In E. S. Spelke (Ed.), *What Babies Know: Core Knowledge and Composition Volume 1* (p. 0). Oxford University Press. <https://doi.org/10.1093/oso/9780190618247.003.0008>

- Spitz, R. A. (1946). The smiling response: A contribution to the ontogenesis of social relations. *Genetic Psychology Monographs*, *34*, 57–125.
- Sroufe, L. A., & Waters, E. (1976). The ontogenesis of smiling and laughter: A perspective on the organization of development in infancy. *Psychological Review*, *83*(3), 173–189.
- Stern, J. A., Kelsey, C. M., Yancey, H., & Grossmann, T. (2024). Love on the developing brain: Maternal sensitivity and infants' neural responses to emotion in the dorsolateral prefrontal cortex. *Developmental Science*, *n/a*(*n/a*), e13497. <https://doi.org/10.1111/desc.13497>
- Thatcher, R. W., Walker, R. A., & Giudice, S. (1987). Human cerebral hemispheres develop at different rates and ages. *Science (New York, N.Y.)*, *236*(4805), 1110–1113.
<https://doi.org/10.1126/science.3576224>
- Thiele, M., Hepach, R., Michel, C., & Haun, D. (2021). Infants' Preference for Social Interactions Increases from 7 to 13 Months of Age. *Child Development*, *92*(6), 2577–2594.
<https://doi.org/10.1111/cdev.13636>
- Tomasello, M. (2014). The ultra-social animal. *European Journal of Social Psychology*, *44*(3), 187–194.
<https://doi.org/10.1002/ejsp.2015>
- Tomasello, M. (2020). The adaptive origins of uniquely human sociality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1803), 20190493.
<https://doi.org/10.1098/rstb.2019.0493>
- Trevarthen, C., & Aitken, K. J. (2001). Infant intersubjectivity: Research, theory, and clinical applications. *Journal of Child Psychology and Psychiatry, and Allied Disciplines*, *42*(1), 3–48.
- Turati, C., Simion, F., Milani, I., & Umiltà, C. (2002). Newborns' preference for faces: What is crucial? *Developmental Psychology*, *38*(6), 875–882.
- Van Hecke, A. V., Mundy, P. C., Acra, C. F., Block, J. J., Delgado, C. E. F., Parlade, M. V., Neal, A. R., Meyer, J. A., & Pomares, Y. B. (2007). Infant Joint Attention, Temperament, and Social Competence in Preschool Children. *Child Development*, *78*(1), 53–69.
<https://doi.org/10.1111/j.1467-8624.2007.00985.x>

- Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science (New York, N.Y.)*, *311*(5765), 1301–1303. <https://doi.org/10.1126/science.1121448>
- Wilcox, T., & Biondi, M. (2015). fNIRS in the developmental sciences. *Wiley Interdisciplinary Reviews. Cognitive Science*, *6*(3), 263–283. <https://doi.org/10.1002/wcs.1343>
- Yeshurun, Y., Nguyen, M., & Hasson, U. (2021). The default mode network: Where the idiosyncratic self meets the shared social world. *Nature Reviews. Neuroscience*, *22*(3), 181–192. <https://doi.org/10.1038/s41583-020-00420-w>
- Zimeo Morais, G. A., Balardin, J. B., & Sato, J. R. (2018). fNIRS Optodes' Location Decider (fOLD): A toolbox for probe arrangement guided by brain regions-of-interest. *Scientific Reports*, *8*(1), 3341. <https://doi.org/10.1038/s41598-018-21716-z>

Item #	Infant Behavior Questionnaire- Revised short form Smiling and Laughing Subscale Items
40	When being dressed or undressed during the last week, how often did the baby smile or laugh?
42	When put into the bath water, how often did the baby smile?
43	When put into the bath water, how often did the baby laugh?
65	When face was washed, how often did the baby smile or laugh?
11	How often during the last week did the baby smile or laugh after accomplishing something (e.g., stacking blocks, etc.)?
12	How often during the last week did the baby smile or laugh when given a toy?

Table 1. This table lists the six items taken from the IBQ-R short form used to determine the Smiling and Laughing subscale score in the current study.

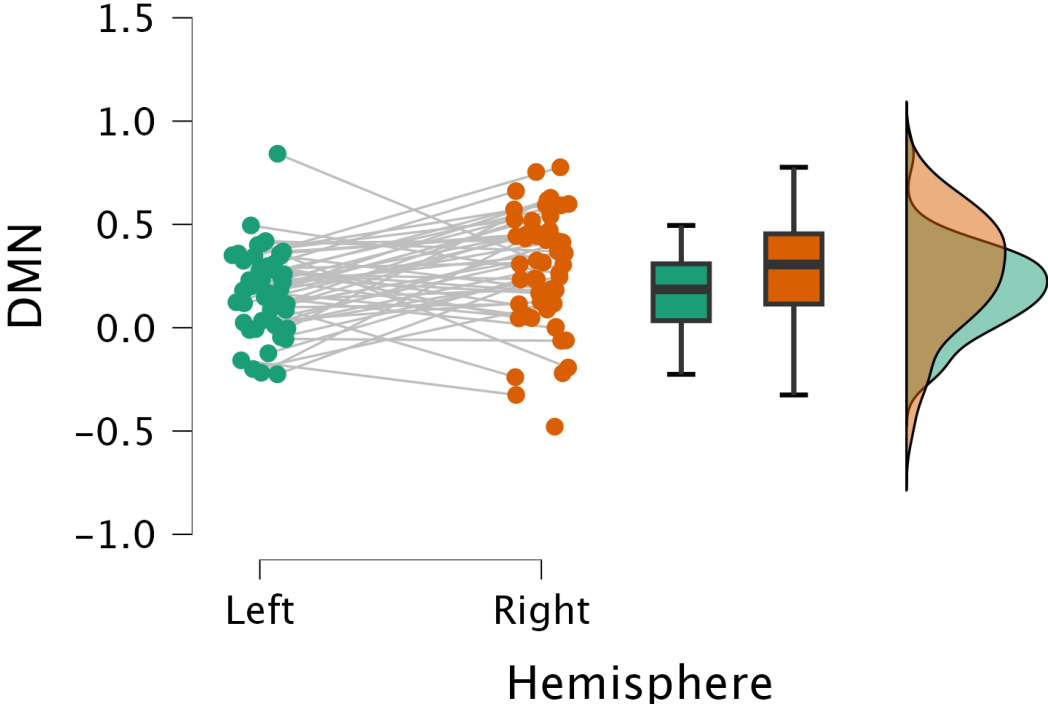


Figure 2. This raincloud plot shows the difference in functional connectivity in the DMN between the left and the right hemisphere.

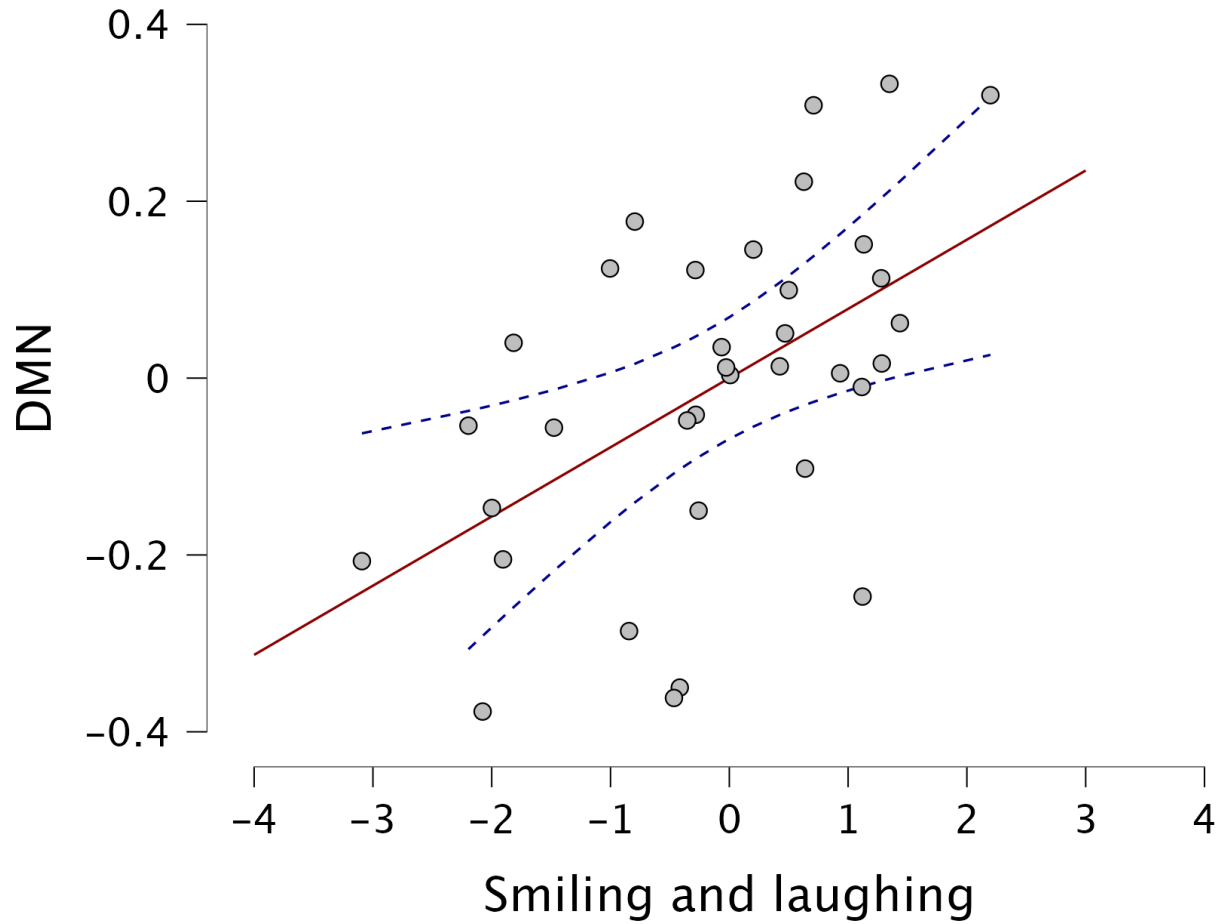


Figure 3. This scatter plot shows the results of the regression modeling revealing a positive association between the residuals of the parent-reported Smiling and Laughing scores using the IBQ and the residuals of default mode network functional connectivity in the left hemisphere controlling for the signal-to-noise ratio.

Supplementary Materials

Supplementary materials for this paper have been posted to OSF and are publicly available at this link: <https://osf.io/3bs4v/files/osfstorage>

Data Availability

Data have been posted on OSF and are publicly available at this link:

<https://osf.io/3bs4v/files/osfstorage>