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Sensitive infant care tunes a frontotemporal interbrain network in adolescence

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Caregiving plays a critical role in children's cognitive, emotional, and psychological well-being. In the current longitudinal study, we investigated the enduring effects of early maternal behavior on processes of interbrain synchrony in adolescence. Mother-infant naturalistic interactions were filmed when infants were 3-4 months old and interactions were coded for maternal sensitivity and intrusiveness with the Coding Interactive Behavior Manual. In early adolescence (Mean = 12.30, SD = 1.25), mother-adolescent interbrain synchrony was measured using hyperscanning EEG during a naturalistic interaction of positive valence. Guided by previous hyperscanning studies, we focused on interbrain connections within the right frontotemporal interbrain network. Results indicate that maternal sensitivity in early infancy was longitudinally associated with neural synchrony in the right interbrain frontotemporal network. Post-hoc comparisons highlighted enhancement of motheradolescent frontal-frontal connectivity, a connection that has been implicated in parent-child social communication. In contrast, maternal intrusiveness in infancy was linked with attenuation of interbrain synchrony in the right interbrain frontotemporal network. Sensitivity and intrusiveness are key maternal social orientations that have shown to be individually stable in the mother-child relationship from infancy to adulthood and foreshadow children's positive and negative socialemotional outcomes, respectively. Our findings are the first to demonstrate that these two maternal orientations play a role in enhancing or attenuating the child's interbrain frontotemporal network, which sustains social communication and affiliation. Results suggest that the reported long-term impact of maternal sensitivity and intrusiveness may relate, in part, to its effects on tuning the child's brain to sociality.

Keywords Social neuroscience, Hyperscanning, EEG, Synchrony, Social development, Mother-child relationships, Maternal sensitivity

From the moment infants are born they depend on their caregivers to fulfil their basic physiological needs and acquire the necessary social skills to prepare their brain and behavior for participation in the social world. The caregiver's social behavior plays a critical role in the infant's cognitive, social, and emotional development^{1–5} and in the formation of brain structure and functions^{6–9}. This renders early caregiving a key contributor to the maturation of brain and behavior throughout life.

Extant research pointed to the associations between positive developmental outcomes and sensitive caregiving. Maternal sensitivity was first described within the attachment theory framework as the mother's ability to recognize the infant's signals, accurately interpret them, and respond in an appropriate and timely manner¹⁰. Sensitive parenting is characterized by awareness of the infant's state, reciprocity, and appropriate stimulation that considers the infant's social signals^{11–15}. Empirical and meta-analytic studies have confirmed the importance of sensitive caregiving in the first months of life for the development of children's social-emotional competencies in both normative and high-risk populations^{2,16–20}. Longitudinal studies have shown that maternal sensitivity in infancy shapes the development of secure attachment^{21–23}, social competencies^{24–28}, emotion regulation and social adjustment^{29–33}, and cognitive and executive function^{34,35} across childhood^{28,35,36}, adolescence^{22,24,31,34,37,38}, and adulthood^{23,25}.

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In contrast, researchers have described maternal intrusiveness as an orientation that is diametrically opposite to the sensitive style and is characterized by maternal overriding and impingement, forceful behavior, overstimulation, and disregard of the child's state, signals, and social initiation^{15,39,40}. The mother's intrusive style in early life was found to predict insecure attachment⁴¹, behavior problems and social maladjustment^{39,42,43}, difficulties in emotion regulation⁴⁴ and executive function^{45,46}, and language delays⁴⁷. Longitudinal studies have indicated that both sensitivity and intrusiveness are individually stable from infancy to adolescence and young adulthood^{12,37,38,48}. As the mother's sensitive-synchronous and intrusive-overriding styles are stable over time, they are considered to function as resilience and risk factors, respectively, for child well-being and development⁴⁹.

The mechanisms by which maternal sensitivity and intrusiveness exert their long-term effects on the developing brain are not fully clear. Studies suggest that the repeated experience of well-adapted versus nonmatched parenting behaviors impacts the maturation of neural systems implicated in social, emotional and cognitive functioning^{6,50–55}. Indeed, several longitudinal studies demonstrated the effects of early maternal sensitivity and intrusiveness on brain development and functioning. An EEG study reported that mother-infant interactions characterized by positive affect and less physical stimulation at the age of 5 months predicted higher frontal resting EEG power (alpha and theta band) at 10 and 15 months, suggesting that a more sensitive and less intrusive maternal style facilitate brain development⁵⁶. Structural magnetic resonance imaging (MRI) studies linked maternal sensitivity and support in early childhood with higher gray matter volume⁶, larger hippocampal volume⁵⁷and smaller amygdala volume at school age⁵⁸. A functional MRI (fMRI) study found that maternal behavior characterized by awareness of the infant's mental states, appropriate response, and autonomy support at 13 and 15 months predicted functional connectivity between the default mode network and salience network at 10 years, pointing to the effect of maternal behavior on maturation of networks involved in social cognition, affect cognition, and cognitive control⁹. Another fMRI study found that stability of the mother's sensitive style from infancy to adolescence predicted young adults' amygdalar and insular sensitivity to others' emotions⁴⁸. Greater mother sensitivity and child social engagement in infancy was found to predict a more consolidated response to attachment cues in adulthood⁵⁹. Using magnetoencephalography (MEG), maternal sensitivity in infancy predicted a more robust neural emphatic response to others' distress⁶⁰ and to attachment cues in adolescence⁶¹.

In addition to the long-term effects of maternal sensitivity on the developing brain, intrusive mothering in infancy has similarly been shown to carry long-term negative effects on brain development. Intrusive parenting at 9 months predicted aberrant neural response to others' pain⁶² and disrupted default mode network connectivity in adolescence^{63,64}. Overall, these studies demonstrate the long-term effects of the mother's sensitive and intrusive style on social brain functioning in adolescence.

In contrast to studies that describe the effects of early caregiving on the brain, no study to date has tested the longitudinal effects of the parent's relational style in infancy on interbrain synchrony in later life. Interbrain synchrony considers the temporal concordance of neural dynamics between two or more brains^{65–67}. Studies have shown that interbrain synchrony increases when partners are within an attachment bond, including parents and children^{68,69}, romantic partners⁷⁰, close friends⁷¹, and patients and therapists⁷². Mother-child dyads in infancy, childhood, and adolescence, display strong interbrain synchrony across multiple tasks, including free play^{68,73–76}, joint problem-solving tasks^{77–79}, naturalistic face-to-face and video-chat conversations⁸⁰, and cooperative video-games^{65,69,81}.

Interbrain synchrony is sensitive to social behavior and increases when interactions are engaged and reciprocal^{67,68,70,82–86}. Sharing social gaze, joint engagement, empathic resonance, and interpersonal reciprocity enhance interbrain synchrony, particularly during naturalistic, ecologically-valid interactions^{71,80,87}.

According to the biobehavioral synchrony model^{88,89}, children acquire the capacity for brain synchrony within the mother-infant context during sensitive, well-timed social interactions^{88,89}. Consistent with the model, studies have shown that episodes of brain coupling during infancy and early childhood are aligned with the mother's or female stranger's social behavior, including touch, gaze, or vocalizations^{67,85}. As to the two maternal orientations sensitivity and intrusiveness, it was found that maternal sensitivity at 5–9 months was associated with higher mother-infant interbrain synchrony in a frontotemporal network, while maternal intrusiveness was related to attenuated interbrain coupling in that network, pointing to a differential impact of these two styles on mother-child interbrain synchrony within temporal regions⁷⁹, indirectly pointing at the effect of parenting on mother-child interbrain synchrony. Still, to our knowledge, no study to date has examined the long-term effect of parenting on the maturation of interbrain synchrony beyond infancy.

In the current study, we examined the longitudinal associations between early maternal caregiving and the development of interbrain synchrony in adolescence. We focused on maternal sensitivity and intrusiveness during naturalistic interactions in infancy and measured mother-adolescent interbrain synchrony 12 years later using hyperscanning EEG. Our key hypothesis was that maternal sensitivity would predict enhanced interbrain synchrony, while intrusiveness attenuated interbrain synchrony.

We focused on the *interbrain frontotemporal network* that underpins core socio-cognitive functions^{90,91}. Studies of mother-child neural interbrain synchrony have shown that this network plays an important role during face-to-face interactions, as well as in remote interactions of zoom or texting^{80,92}. In infancy, this network has been associated with the mother's sensitive and intrusive style, respectively⁵¹. Specifically, we focused on interbrain synchrony in the right frontotemporal network, and based this hypothesis on the "right hemisphere hypothesis"⁹³. This hypothesis suggests a general dominance of the right hemisphere in processing emotions, and has been supported by numerous studies demonstrating right-hemisphere dominance in multiple emotional functions⁹⁴⁻¹⁰¹. Given its crucial role in survival-related functions and nonverbal communication, right hemisphere dominance is thought to have a more ancient evolutionary origin as well as to mature early in human development¹⁰²⁻¹⁰⁵. As the mother-child context is the first to facilitate synchrony of brain and behavior,

we expected early caregiving to have a more notable impact on the right hemisphere network in connecting the brains of mother and child in adolescence.

We focused on interbrain synchrony in the beta frequency band. Neural oscillations are a pervasive component of neuronal activity and their temporal consistency underpins the dynamic organization of neural functions¹⁰⁶. Oscillations help build a model of self and partner's behavior and guide neural activity towards smooth interpersonal exchanges¹⁰⁷. Beta oscillations are involved in post-synaptic neuronal sensitivity changes that modify predictions and information flow to higher brain regions^{108,109} and are implicated in complex social functions, such as empathy¹¹⁰ and attachment⁶¹. Beta rhythms support active information processing¹⁰⁶, mentalization¹¹¹, prediction of others' actions¹¹², sensory perception and integration¹¹³, and the constant adaptation and updating of predictions¹¹⁴. During social interactions, these beta-modulated functions facilitate the rapid adaptation and mutual entrainment required for effective interbrain coordination¹¹⁵.

Hyperscanning research demonstrated cross-brain synchrony in the beta frequency in social contexts, such as responding to positive gestures¹¹⁶, experiencing compassion¹¹⁷ and cooperation^{118,119} that reflect active thinking, joint focus, and mentalizing processes triggered by coordination dynamics¹²⁰. Individual factors, such as trait empathy, engagement, and joint attention predict interbrain beta synchrony during real-world face-to-face interactions⁸⁷. Beta rhythms sustain natural communication between romantic couples and close friends⁷¹, and between adolescents and their mothers^{80,92}. Based on this large body of work, we focused on interbrain synchrony in the beta band.

Two hypotheses were formulated. First, we expected that the mother-adolescent face-to-face interaction would trigger significant neural synchrony within the *interbrain frontotemporal network*. To ascertain the findings on interbrain synchrony and control for spurious findings, interbrain connectivity was evaluated relative to surrogate data as a validation analysis, consistent with previous studies^{65,77,80,92,121}. We expected interbrain connections of four types: homologue (same area, same hemisphere), same-region cross-hemisphere links (same area, different hemisphere), cross-region same-hemisphere (same hemisphere, different area), and multi-dimensional (cross-region and cross-hemisphere).

Second, guided by the bio-behavioral synchrony model^{49,88}, we hypothesized that significant longitudinal associations will be found between maternal caregiving behaviors in infancy and interbrain synchrony in adolescence. Specifically, we anticipated that higher levels of maternal sensitivity during mother-infant interactions at 3 months would be positively associated with enhanced connectivity in the right *frontotemporal interbrain network* during mother-adolescent interactions 12 years later. This hypothesis was grounded in the understanding that maternal sensitivity promotes secure attachment and optimal social-emotional development, potentially facilitating the maturation of neural circuits involved in social cognition and affiliation. Conversely, we predicted that higher levels of maternal intrusiveness in infancy would be negatively associated with interbrain synchrony in the same network during adolescence. This expectation was based on evidence suggesting that intrusive parenting may impede the development of self-regulatory skills and secure attachment, potentially leading to altered neural processing of social cues and reduced synchrony in parent-child interactions. By examining these longitudinal associations, we aimed to elucidate the potential neurobiological pathways by which early caregiving experiences may shape long-term social-emotional functioning and parent-child interactions.

Materials and methods Participants

Participants included 60 individuals, comprising 30 mother-firstborn pairs seen over a span of 12 years. In this study we chose to focus on mothers and their firstborn children, as the transition to motherhood is most profound with a first child, presenting a distinct context for maternal behavior and mother-child interactions. This focus allowed us to examine mother-child dynamics in a context where maternal behavior and its effects may be most pronounced and uninfluenced by prior parenting experiences, and to capture the full extent of maternal behavior's impact on mother-child interbrain synchrony.

Mothers and their infants were initially recruited for the study through ads posted in campus for a study on the transition to parenthood (Time 1). All were the infant's biological mothers, served as the child's primary caregiver, and all children were firstborns. At the first time-point mother-infant dyads were seen when infants were 3–4 months old and 40% of the infants were male. All mothers, whose average age was 28, had completed at least high-school education and 83% finished college and all were of middle to upper-middle socioeconomic status. Based on their self-reports in questionnaires, both the mothers and the children did not suffer from any mental or health problems, infants were all born at term without complications, and 87% were breastfeeding.

In early adolescence (Time 2) the mothers' average age was 41.31 years old (SD = 3.40), and the adolescents' average age was 12.30 years old (SD = 1.25). 40% of the adolescents were males. According to self-reported data, neither the mothers nor the children had any significant physical health conditions. Moreover, there were no reported mental health disorders that could potentially impair the mother-child relationship or maternal caregiving behaviors. Specifically, the mothers did not report symptoms consistent with depression or anxiety disorders, and the children were not reported to exhibit any psychopathological symptoms. All adolescents attended state-controlled typical schools.

The original study during Time 1 was approved by the Bar-Ilan University ethics committee. The Reichman University institutional ethics committee approved the hyperscanning EEG experiment during Time 2, and all experiments were performed in accordance with the relevant guidelines and regulations. All mothers signed a written informed consent form for themselves and their adolescent children. All procedures were explained to the participants prior to the experiment, and the participants were free to leave the experiment at any time with full compensation. Participants were reimbursed for study participation (\$30 per hour).

Procedure

Infancy

Mother-infant dyads were videotaped during a naturalistic interaction. Instructions were "play with your infant as you normally do", and 10 min of free play interaction were filmed for offline coding.

Adolescence

The study utilized hyperscanning dual-EEG during positive-valence interaction. The experimental paradigm was designed to be consistent with and build upon previous behavioral and neuroscience research that has utilized similar paradigms to study dyadic interactions^{48,59–61,70,80,92,122–125}. Mother-adolescent dyads were sitting on chairs in the same room, 50 cm apart from each other, in a face-to-face position and were instructed to discuss a positive topic randomly selected by the researchers. Three possible positive topics were counterbalanced: "plan a fun day to spend together," "plan a camping trip," "plan a visit to an amusement park" (see Fig. 1).

Dual neural and behavioral data acquisition

The EEG activity of both the mother and adolescent was recorded simultaneously and continuously throughout the experiment. The initial two-minute time window of the mother-adolescent interaction was the focus of the analysis in the present study. This methodological approach was adopted for two key reasons. First, the length of the overall mother-adolescent interactions varied to a minor degree across participants, necessitating the selection of a standardized temporal window for analysis to ensure consistency. Second, restricting the analysis to the first two minutes of the interaction aligns with the precedent established by prior research in this domain, which has evaluated the initial two-minute period of naturalistic, positive-valence mother-child interactions as the primary unit of analysis^{68,80,92}. This methodological choice was made to facilitate meaningful comparisons between the current findings and the established literature on the characteristics and dynamics of the interbrain synchrony in positive mother-child interactions. Data acquisition was performed using a 64-channel BrainAmp amplifier from Brain Products Company (Germany). The EEG system was composed of two Brain product standard subtemporal BrainCap with an integrated chin belt. Each cap included 32 electrodes each, buttoned directly to the cap and arranged according to the international 10/10 system, an extension of the standard 10/20 system (See Supplementary Table S1 for full list of electrodes and electrode positions. Theta/Phi coordinates are reported, standardized to a Theta of 90 for the plane through Fpz, T7, T8, Oz). Analog 0.1-500 Hz band-pass was used for filtering, and data was sampled at 1000 Hz. Impedances were maintained below 10 kOhm, and the ground electrode was placed on the AFz electrode. Both helmets were connected to the same amplifier to ensure millisecond-range synchrony between the EEG recording of the mother and adolescent.

EEG preprocessing

Preprocessing was conducted using Spyder 5.05 and Python 3.8, utilizing MNE (v0.17.0). First, the EEG data file of each dyad was separated into two data files, one for the mother and one for the child, so that each file could undergo separate preprocessing. Data were then average-referenced, and a 1–50 Hz bandpass filter was applied to all data files, consistent with prior studies^{68,71,80}. Next, the data were segmented into 1000 ms epochs with 500

Time 1

Mother-Infant (3-month old) free interaction

Time 2

Mother-Adolescent (12-year old) free conversation





Behavioral measures of *Maternal Sensitivity* and *Maternal Intrusiveness* Neural measures of interbrain synchrony focusing on the *right frontotemporal network*

Fig. 1. Procedure and experimental design.

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ms overlap between epochs. Autoreject v0.1¹²⁶, an unsupervised algorithm with Bayesian optimization as the threshold method, was utilized to remove trials containing transient jumps in isolated EEG channels and artifacts affecting groups of channels. Following AutoReject (AR), a sample of the first 10 epochs of each participant was visually inspected pre- and post-AR correction to verify the algorithm's output. While AR specializes in excluding trials containing transient jumps in specific channels, systematic physiological artifacts that may affect multiple sensors, such as eye blinks or muscular movements are not optimally removed by AR algorithms. Therefore, independent component analysis (ICA) was used to remove artifact components from the data. To that end, MNE's implementations of fastica and CORRMAP¹²⁷ were used to remove systematic physiological artifacts that affected the data. Independent components were manually selected for exclusion and served as templates for selecting and excluding similar components in all other participants. Such components included non-physiological components, eye blinks, eye movements, and muscle artifacts. The removal of muscular movement components was of particular importance, as the face-to-face interactions include artifacts of speech, facial expressions, and eye movements. (Examples of excluded components are presented in Supplementary Fig. S1).

Overall, following preprocessing and cleaning procedures, an average of 110.08 (SD = 54.31) epochs per dyad remained in the face-to-face condition. Following preprocessing, dyads that did not share a minimum of 30 common epochs were excluded from the following connectivity analysis, resulting in the exclusion of one dyad.

Connectivity analysis

Interbrain synchrony was calculated using the weighted phase lag index (wPLI), an interbrain connectivity method that has been used in various previous studies of naturalistic social interactions^{68,80,92,128}. Interbrain connectivity values were calculated for the beta rhythm (13.5–29.5 Hz).

Consistent with prior research, we divided the EEG cap into pre-defined areas of interest based on the research hypotheses^{71,80,92,129}, resulting in a total of 4 ROIs that were examined in this study. Each ROI consisted of 3 electrodes: right frontal (RF - Fp2, F4, F8), left frontal (LF - Fp1, F3, F7), right temporal (RT - T8, TP10, P8), and left temporal (LT - T7, TP9, P7). Notably, we were particularly interested in the right frontal and temporal areas. The grouping of channels was used to enhance the reliability of region specification and provide a more meaningful and realistic interpretation of the results¹³⁰. Overall, a total of 4 ROIs were measured in each brain, resulting in 16 possible links between the mother's and adolescent's ROIs in the comparison to surrogate data (control) analysis. The respective wPLI value of the partners' ROIs was calculated as the mean connectivity value of each of the 3 electrodes in one target ROI with each of the 3 electrodes in the second target ROI, resulting in a total of 9 connectivity values averaged for each interbrain link between 2 ROIs.

Of the 30 dyads participating in the experiment, one dyad did not share sufficient common epochs following AutoReject and independent component rejection, so connectivity could not be measured, resulting in a total of 29 dyads that were included in the analysis.

Behavioral coding

Mother-infant interaction was coded offline using the Coding Interactive Behavior manual¹³¹. The CIB is a well-validated rating system used for coding social interactions that has yielded over 200 publications across multiple cultures, age range, and pathological conditions (for review, see^{68,132}), including hyper-scanning research^{68,71,80,92}. The CIB yields 52 codes, each rated on 5-point scales that aggregate into theoretically-based constructs. Here, we used the two central constructs of maternal behavior. *Maternal sensitivity* comprised the following scales: parent gaze, vocal appropriateness, reciprocity, enthusiasm (alpha=0.91). *Maternal intrusiveness* included the following scales: overriding, imitation, anxiety, constriction (alpha=0.89). Coding was conducted by trained coders who were blind to study hypotheses with inter-rater reliability for 20% of the interactions exceeding 90% on all codes (intra-class r=0.93, range=0.89–99).

Statistical analysis

Comparing interbrain synchrony during social interaction vs. surrogate data

First, we conducted a validation analysis of the interbrain connectivity values of the face-to-face relative to a control condition of surrogate data. Our goal was to evaluate whether face-to-face interaction resulted in increased interbrain connectivity values relative to the surrogate data control, consistent with previous literature on two-brain research^{65,77,80,121}. This analysis was conducted on the fronto-temporal network, resulting in 4 areas of interest (RT, LT, RF, LF) in each brain, leading to 16 possible interbrain links between the mother and child brains.

To establish a statistical baseline for comparison, we created surrogate data representing the neural connectivity patterns between mothers and unrelated adolescents. This approach allowed us to differentiate the interbrain synchrony observed in authentic mother-adolescent dyads from that which would be expected by chance between randomly paired individuals.

The surrogate data was generated as following: First, we computed the interbrain connectivity, quantified using weighted Phase Lag Index (wPLI), between each mother and an adolescent from a different dyad. This process was repeated for every possible combination of mother and non-matching adolescent across all dyads in the study, resulting in 28 unique surrogate mother-other-adolescent pairs for each of the 29 mothers. This yielded a total of 812 surrogate pairs.

Next, we averaged the 28 surrogate connectivity values computed for each mother, resulting in a single "average surrogate" connectivity score for each authentic mother-adolescent dyad. This step ensured that each real dyad had a corresponding surrogate comparator.

Finally, we directly compared the actual interbrain connectivity observed within each real mother-adolescent dyad to the surrogate connectivity values generated for that dyad. This allowed us to determine whether the

neural synchrony present in the true dyadic interactions differed significantly from what would be expected by chance pairing of individuals that participated in the same task, but did not interact with each other. Notably, by creating and analyzing these surrogate datasets, we were able to establish a robust statistical baseline to evaluate the specificity of the neural synchrony patterns observed in the authentic mother-adolescent relationships under investigation.

The analysis itself was conducted using "eelbrain", an open source Python module for accessible statistical analysis of MEG and EEG data (v0.31.7). A non-parametric permutation test with mass-univariate was utilized as this test uses the distribution derived from permuting the observed scores of the data and to avoid multiple comparisons¹³³.

The permutation test was used to compute the F value for each of the ROI pairs in order to compare connectivity patterns between the real connectivity scores and the surrogate data. The same procedure was repeated in 1000 random permutations, shuffling the condition labels of the data (face-to-face, control). For each permutation, the largest F value was retained to form the nonparametric estimate of the distribution under the null hypothesis that condition labels are exchangeable. The p-value was computed for each ROI pair as the proportion of permutations that yielded a comparison with a larger F value than the comparison under question. Following the permutation tests, only ROIs that reached a p-value of 0.05 or smaller following the algorithm build-in correction for multiple comparisons are reported in the results section.

Brain-behavior correlations

Following, brain-behavior Pearson correlations were used to examine whether maternal behavior during infancy affected neural synchrony in adolescence. Here, we chose to focus on two well-known and validated constructs – maternal sensitivity and maternal intrusiveness¹³². Consistent with previous research describing the advantage of the right hemisphere in infancy^{103,134}, the brain-behavior correlations focused on the right hemisphere network, and were computed between the maternal behavior during the child's infancy and the interbrain connectivity values. Notably, interbrain synchrony values were calculated as the increase in interbrain connectivity relative to control (wPLI of face-to-face interaction – wPLI of surrogate data = Δ wPLI).

In Time 1, Mother and their 3-months old firstborns were videotaped during a naturalistic interaction, and were instructed to play with their infant as they normally do. Offline CIB coding later assessed maternal Intrusiveness and Sensitivity. In Time 2, the study utilized hyperscanning dual-EEG during positive-valence interaction. Mothers and their now adolescents were sitting on chairs in the same room, in a face-to-face position and were instructed to discuss a positive-valenced topic. EEG connectivity at the frontotemporal network has been assessed.

Results

Comparing neural synchrony during face-to-face relative to surrogate data

We first compared neural synchrony during face-to-face interaction and the control condition (surrogate data) by using nonparametric permutation test with mass-univariate analysis of variance (ANOVA) based on one-way repeated-measures ANOVA designed to detect effects stemming from the face-to-face interaction compared to control on wPLI scores. The results revealed a significant main effect for the face-to-face condition compared to control (F(1,61) = 23.83, p < 0.001). (See Fig. 2A and B).

Significant (p < 0.05) interbrain connections were observed in every one of the possible 16 links of the frontotemporal network (Fig. 2B; Table 1). The greater interbrain synchrony in the face-to-face interaction compared to the control condition comprised four sub-groups of interbrain connections: (a) *Homologous connections within mother-adolescent frontotemporal network*, (b) *same-hemisphere cross-region connections within motheradolescent frontotemporal network*, (c) *cross-hemisphere same-region connections within motheradolescent frontotemporal network*, (d) *cross-hemisphere cross-region linkage within mother and child's frontotemporal network*.

- (a) Homologous connections within mother-adolescent frontotemporal network the homolog links included the left-frontal-left-frontal link (F(1,28)=15.8, p = 0.001, $\eta_p^2 = 0.36$), the right-frontal-right-frontal link (F(1,28)=12.26, p = 0.011, $\eta_p^2 = 0.3$), the left-temporal-left-temporal link (F(1,28)=10.8, p = 0.017, $\eta_p^2 = 0.28$), and the right-temporal-right-temporal link (F(1,28)=13.99, p = 0.001, $\eta_p^2 = 0.33$).
- (b) Same-hemisphere cross-region connections within mother-adolescent frontotemporal network comprised four links; two in the left hemisphere: between the mother's left frontal region and the adolescent's left temporal region (F(1,28) = 23.1, p < 0.001, η²_p = 0.45), and the mother's left temporal region with the adolescent's left frontal region (F(1,28) = 13.9, p = 0.001, η²_p = 0.33). Two links were also found in the right hemisphere: between the mother's right frontal region and the adolescent's right temporal region (F(1,28) = 12.1, p = 0.011, η²_p = 0.3), and the mother's right temporal region with the adolescent's right frontal region (F(1,28) = 12.1, p = 0.011, η²_p = 0.31).
 (c) Cross-hemisphere same-region connections within mother-adolescent frontotemporal network included four
- (c) Cross-hemisphere same-region connections within mother-adolescent frontotemporal network included four links: between the mother's left frontal region and the adolescent's right frontal region (F(1,28)=10.9, p=0.016, $\eta^2_{p}=0.28$), between the mother's right frontal and the adolescent's left frontal region (F (1,28)=11.1, p=0.016, $\eta^2_{p}=0.28$), between the mother's left temporal region and the adolescent's right temporal region (F(1,28)=14.9, p=0.001, $\eta^2_{p}=0.35$), and between the mother's right temporal region and the adolescent's right temporal region (F(1,28)=14.9, p=0.001, $\eta^2_{p}=0.35$), and between the mother's right temporal region and the adolescent's right temporal region (F(1,28)=16.8, p<0.001, $\eta^2_{p}=0.38$).
- (d) Cross-hemisphere cross-region connections within mother-adolescent frontotemporal network. This included four links: between the mother's left frontal region and the adolescent's right temporal region (F(1,28)=12.9, p=0.007, $\eta^2_p=0.32$), between the mother's right frontal region and the adolescent's left temporal region (F(1,28)=15.2, p=0.001, $\eta^2_p=0.35$), between the mother's left temporal region and the adolescent's right



Fig. 2. Visualization of validation analysis conducted on face-to-face relative to control (surrogate data): Higher interbrain synchrony was detected during the face-to-face interactions relative to control (surrogate data). (**A**) Visualization of the surrogate data (left) compared to the real connectivity values (right). Each node represents a different ROI in the mother and child brains. RT – right temporal, LT – left temporal, RC – right central, LC - left central, RF – right frontal, LF - left frontal. M and C refer to the mother and child, respectively. Darker shades represent greater values of interbrain connectivity (wPLI scores). (**B**) Visualization of the significant links found in the face-to-face interaction relative to control. A permutation test based on repeated-measures ANOVA revealed a significant advantage for the face-to-face interaction compared to the control condition in facilitating interbrain synchrony in the frontotemporal network (p < 0.001). Further analysis revealed this effect was evident in every possible link between the mother and child frontotemporal network. (**C**) Visualization of interbrain increase in the face-to-face interaction compared to control, with each dot representing a dyad. Both the overall interbrain across the entire frontotemporal network and the right hemisphere network showed increased synchrony relative to control (p < 0.001).

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frontal region (F(1,28) = 10.1, p = 0.02, $\eta^2_{p} = 0.27$), and finally between the mother's right temporal region and the adolescent's left frontal region ((F(1,28) = 10.7, p = 0.017, $\eta^2_{p} = 0.28$). (See Fig. 2B; Table 1).

Following the findings that mother-child face-to-face interactions facilitated greater interbrain synchrony relative to control across all links, we assessed our next hypothesis on the association between maternal behavior in infancy and interbrain synchrony in adolescence.

Brain-behavior coupling

Increase in interbrain connectivity within the right hemisphere network is related to maternal sensitivity and intrusiveness

Focusing on the right hemisphere, we then assessed the advantage of the right hemisphere interbrain network over control (averaged across all 4 links that are specific to the right hemisphere – RF-RF, RT-RT, RF-RT, RT-RF). A repeated-measures ANOVA revealed greater right network synchrony in the face-to-face interaction relative to control (F(1,28) = 18.47, p < 0.001, $\eta^2_p = 0.4$) (See Fig. 2C). Following, we investigated the association between maternal sensitivity and intrusiveness and the index of increased right hemisphere interbrain connectivity in the face-to-face condition compared to control (wPLI of face-to-face interaction – wPLI control = Δ wPLI).

Maternal sensitivity predicts greater synchrony in the right frontotemporal interbrain network

The results revealed that maternal sensitivity strongly correlated with the improvement in face-to-face interbrain synchrony relative to control (N=29, r=0.41, p=0.026, see Fig. 3A). Following this finding, we next sought to shed light on the links that sustained this correlation within the right hemisphere network in a set of posthoc tests. Results indicate that maternal sensitivity correlated with both the right frontal homolog link (N=29, r=0.41, p=0.029) and the mother-right-frontal adolescent-right-temporal link (N=29, r=0.47, p=0.01). The

Interbrain link	wPLI face-to-face (SD)	wPLI surrogate (SD)	F	<i>p</i> value
Mother left frontal - child left frontal	0.138 (0.05)	0.107 (0.03)	15.75	0.001***
Mother left frontal - child right frontal	0.134 (0.05)	0.106 (0.03)	10.93	0.016*
Mother left frontal - child left temporal	0.139 (0.05)	0.109 (0.03)	23.06	< 0.001***
Mother left frontal - child right temporal	0.136 (0.05)	0.109 (0.03)	12.89	0.007**
Mother right frontal - child left frontal	0.132 (0.05)	0.107 (0.03)	11.06	0.016*
Mother right frontal - child right frontal	0.132 (0.05)	0.108 (0.03)	12.26	0.011*
Mother right frontal - child left temporal	0.140 (0.05)	0.110 (0.03)	15.24	0.001***
Mother right frontal - child right temporal	0.135 (0.05)	0.110 (0.03)	12.05	0.011*
Mother left temporal - child left frontal	0.137 (0.05)	0.110 (0.03)	13.86	0.001***
Mother left temporal - child right frontal	0.134 (0.05)	0.108 (0.03)	10.13	0.02*
Mother left temporal - child left temporal	0.138 (0.05)	0.111 (0.03)	10.79	0.017*
Mother left temporal - child right temporal	0.134 (0.05)	0.109 (0.03)	14.9	0.001***
Mother right temporal - child left frontal	0.131 (0.05)	0.109 (0.03)	10.74	0.017*
Mother right temporal - child right frontal	0.138 (0.05)	0.109 (0.03)	12.57	0.01**
Mother right temporal - child left temporal	0.140 (0.05)	0.110 (0.03)	16.75	< 0.001***
Mother right temporal - child right temporal	0.131 (0.04)	0.110 (0.03)	13.99	0.001***

Table 1. Increased interbrain synchrony following face-to-face interactions relative to control. Reported hereare the significant interbrain links emerging following nonparametric permutation test with mass-univariateanalysis of variance (ANOVA) to detect differences on wPLI connectivity measures during face-to-faceinteractions relative to control. All results were corrected to accommodate multiple comparisons. Interbrainsynchrony was found in each link of the frontotemporal network. *P < 0.05 **P < 0.01, ***P < 0.001.



Fig. 3. Visualization of brain-behavior correlations with the improvement in interbrain synchrony during the face-to-face interaction. The improvement in interbrain synchrony in the face-to-face interaction relative to control (calculated as Δ wPLI) is shown on the Y-axis. (A) Improvement in interbrain synchrony in the right hemisphere network is correlated positively with maternal sensitivity (r=0.41, p=0.026), and negatively with maternal intrusiveness (r = -0.37 p = 0.049). (B) The improvement in interbrain synchrony in the mother-left-frontal child-right-temporal is correlated positively with maternal sensitivity (r=0.42 p=0.022), and negatively with maternal intrusiveness (r = -0.49 p = 0.007).

remaining links in the right network did not correlate with maternal sensitivity (see Supplementary Table 2) (see Fig. 3A).

Next, to evaluate the achieved power, we examined the correlation using a regression model, with the maternal sensitivity (measured when the children were 3-motths) to predict the frontotemporal interbrain synchrony in the right hemisphere network. The results indicate that for effect size of F^2 =0.22, with α =0.05, and a total sample size of N=29, with one predictor, the power was 0.688.

Maternal intrusiveness predicts lower synchrony in the right frontotemporal interbrain network

The results revealed that the maternal intrusiveness correlated negatively with the improvement in interbrain synchrony in the face-to-face interaction relative to control (N=29, r = -0.37 p = 0.049) (see Fig. 3A). Following this finding, we next sought to shed light on the links that sustained this correlation within the right network in a set of post-hoc tests, and revealed that maternal intrusiveness negatively correlated the mother-right-frontal adolescent-right-temporal link (N=29, r = -0.43, p = 0.02). The remaining links in the right network did not correlate with maternal intrusiveness (see Supplementary Table 3) (see Fig. 3A).

Then, to evaluate the achieved power, we examined the correlation using a regression model. The results indicate that for effect size of $F^2 = 0.16$, with $\alpha = 0.05$, and a total sample size of N = 29, with one predictor, the power was 0.55.

Cross-hemisphere frontotemporal connections associated with maternal sensitivity and intrusiveness

Finally, based on previous findings⁵¹, which revealed that the mother-left-frontal infant-right-temporal connection correlated negatively with maternal intrusiveness in real-life interactions, the same link has been evaluated in our study. The results indicated that in our study the mother-left-frontal child-right-temporal link also correlated negatively with maternal intrusiveness (N=29, r = -0.49 p = 0.007). The same cross-hemisphere connection also correlated positively with maternal sensitivity (N=29, r=0.42 p = 0.022), (see Fig. 3B)

Maternal sensitivity and intrusiveness did not affect synchrony in the left frontotemporal interbrain network

Finally, while not hypothesized in advance, we further evaluated whether maternal intrusiveness or sensitivity affected interbrain synchrony in the left frontotemporal interbrain network during face-to-face interactions relative to control. The results indicate that neither maternal sensitivity (N=29, r=0.27 p=0.15), nor maternal intrusiveness (N=29, r = -0.2 p=0.3) correlated with mother-adolescent left frontotemporal interbrain synchrony in this study.

Discussion

Maternal care provides the basis for the child's future development, well-being, social competencies, and brain functioning^{1,2,135-137}. This study adds to the existing literature by demonstrating, for the first time, the long-term neurobiological impact of early caregiving styles on mother-adolescent interbrain synchrony. We examined how maternal sensitivity and intrusiveness in infancy each predicts a distinct pattern of interbrain coupling in adolescence, and found compelling evidence for the importance of the right *frontotemporal interbrain network* in parent-child social communication. Specifically, we found that maternal sensitivity enhances connectivity of this interbrain network, while intrusiveness attenuates it.

Several important findings are highlighted by our data. First, we found significant interbrain synchrony between the mother and adolescent's brains during free interactions relative to control, consistent with previous literature on mother-child interbrain synchrony from infancy to adulthood^{68,69,71,77,79–81,138}. Notably, greater interbrain synchrony was observed across the entire frontotemporal interbrain network, with each possible link connecting the mother and the adolescent frontal and temporal areas. These interbrain connections included homologous same-region-same-hemisphere connections, as well as same-hemisphere-different-region connections, same-region-different-hemisphere connections, and frontal-to-temporal or temporal-to-frontal different hemisphere connections.

Second, our findings reveal significant long-term associations between maternal caregiving in infancy and interbrain synchrony in adolescence. We found that this effect was specific to the right hemisphere network. While the entire frontotemporal network activated between the two brains, only the right frontotemporal interbrain network was longitudinally connected to maternal behaviors in infancy. Maternal behavior characterized by more attuned caregiving to the infant's cues linked with greater interbrain synchrony 12 years later, while maternal behavior marked by overriding the infant's signals was associated with lower interbrain synchrony. These findings point to the possibility that sensitivity and intrusiveness may have lingering effects on children's capacity for interbrain synchrony, particularly of the right hemisphere, and suggest a potential two-brain mechanism by which early caregiving experiences shape social-emotional development.

A deeper investigation of the correlation between maternal sensitivity and the increase in interbrain synchrony utilizing post-hoc tests revealed that the correlation stemmed from two connections. The first is the mother-child right-frontal-right-frontal connection, a link that has been found in multiple studies of parent-child interbrain synchrony^{65,80,139}. The second is the mother's right-frontal region and the child's right-temporal region, a link that is consistent with previous mother-child interbrain studies^{80,92}.

The right hemisphere plays a crucial role in social cognition and emotional processing, with its specialization evident from early infancy. Studies have shown that infants as young as 2–3 months demonstrate right hemispheric activation in response to faces¹⁴⁰, and by 6 months show greater activation in the right frontotemporal cortex when exposed to their mother's face¹⁴¹. This hemispheric advantage extends to emotional processing¹⁴² and

is critical for various social functions, including empathy¹⁴³, emotional processing^{144,145}, theory of mind¹⁴⁶, and understanding others¹⁴⁷. The right hemisphere's importance in interpersonal emotional communication is particularly evident in early mother-infant interactions¹⁴⁵, where non-verbal cues form the basis for attachment. Through sensitive caregiving, mothers regulate their infants' emotions, a process dependent on right-hemispheric functions in both individuals. These early interactions are suggested to facilitate the maturation of the infant's social and emotional functions, including the development of relevant brain regions such as the right temporoparietal junction (TPJ)¹⁴⁸.

Our findings may suggest that the joint activation of the right-hemisphere network begins in early infancy and extends into adolescence. Possibly, the maternal right brain influences the development of the infant's right brain, resulting in a consistent pattern of right-lateralized processing years after infancy. This pattern is dependent on the mother's ability to respond to and regulate the child's brain throughout development.

Our findings underscore the centrality of the right frontal areas to mother-child interbrain coupling and their association with maternal sensitivity. The frontal-frontal connection between parents and children has been well-established across multiple studies using both hyperscanning EEG and fNIRS methodologies. Mother-child fNIRS studies reported right frontal-frontal synchrony during recovery as compared to a frustration tasks¹³⁸, during cooperation tasks⁸¹, and in both cooperation and competition tasks¹³⁹. In addition, mother-child dyads exhibited greater right frontal-frontal synchrony as compared to stranger-child dyads in both competition and cooperation tasks⁶⁹. The frontal areas implicate higher-order social functions, including social cognition, mental state knowledge, and social decision-making^{149,150}, abilities that are known to develop in the context of maternal care¹⁵¹. Overall, our findings add to the existing literature and suggest that the mother's frontal areas play an important role in monitoring, adjusting, and regulating the two-brain dynamics with her child and adjust in real-time to the child's signals and needs. This tunes the developing brain to social life, partly through interbrain synchrony mechanisms^{49,152}.

The association between maternal intrusiveness and reduced interbrain synchrony observed in our study aligns with and extends previous research on the detrimental effects of intrusive parenting. Existing literature has demonstrated that maternal intrusiveness in early life predicts a range of negative outcomes, including insecure attachment⁴¹, behavior problems and social maladjustment^{39,42,43}, as well as difficulties in emotion regulation⁴⁴. Our findings suggest a potential neural mechanism underlying these adverse effects. The observed reduction in interbrain synchrony associated with maternal intrusiveness may indicate a "shutting down" response in the child's neural systems. This diminished synchrony could represent a defensive adaptation to overstimulating or unpredictable maternal behavior, whereby the child's brain becomes less responsive to maternal cues as a means of self-protection. Consequently, this neural disengagement may hinder the child's ability to synchronize effectively in social interactions, not only with the mother but potentially in broader social contexts. This impaired capacity for neural synchronization could, in turn, contribute to the social difficulties and maladjustment observed in children of intrusive mothers. By linking early maternal intrusiveness to reduced interbrain synchrony in later child development, our study provides a neurobiological perspective on the long-term impact of parenting styles and offers a potential explanatory mechanism for the social and emotional challenges faced by children exposed to intrusive caregiving.

Our findings indicate interbrain synchrony of beta rhythms. This aligns with extensive research pointing to the crucial role of beta rhythm in parent-child interactions and attachment processes^{61,80,92,153,154}. Beta rhythms are also involved in higher social functions related to the frontotemporal network and to right-hemisphere functions, including empathy¹¹⁰, mentalization¹¹¹, the prediction of others' behavior¹¹², and active information processing¹⁰⁶. Consistent with the theory that mothers adjust their behavior in real-time to match their child's cues and regulate the child through sensitive caregiving, the beta frequency is further linked with continuous adaptation and updating of predictions¹¹⁴. Overall, we propose that the interbrain synchrony in the beta frequency observed here may be related to the ongoing adaptation and mutual adjustment of the mother-child dyad, processes that are essential for interbrain coordination¹¹⁵.

Across development from infancy to adolescence the brain undergoes significant changes, particularly in regions involved in social functions, such as the prefrontal cortex (PFC) and the posterior superior temporal sulcus (pSTS)¹⁵⁵. In our study, we identified a network of interconnections between the mother's and child's right and left frontal and temporal regions in various combinations. Their joint activations across a variety of connections suggests that this frontotemporal network supports joint socio-cognitive functions^{90,91}. Despite the rapid maturation and changes these regions experience during adolescence, we found that the neural coherence of the dyad correlated with maternal behaviors measured years earlier. Our findings are consistent with previous hyperscanning studies that have reported frontotemporal interbrain synchrony during social interactions^{80,156–158}, and further extend the existing literature by showing that increased connectivity in the right frontotemporal network during face-to-face interactions could be predicted by maternal behavior measured many years earlier.

Finally, our study represents the first investigation into the long-term effects of maternal behaviors on interbrain synchrony, building upon a previous research and extending their findings⁵¹, which demonstrated specific real-time connections between brain activity and behavior, such as the left-frontal to right-temporal link. We sought to determine whether these connections persisted over a 12-year span, from infancy to adolescence. Our results indeed confirm that this left-frontal to right-temporal link continues to play a role in interbrain synchrony during adolescence and is associated with both maternal sensitivity and intrusiveness measured in infancy. Although this particular connection is not part of the right hemisphere network that has been the focus of the study, its significance in our findings suggests that broader neural processes may be involved in the long-term effects of maternal caregiving on mother-child brain synchrony.

This discovery further implies that the impact of early maternal behavior on neural synchrony may extend beyond the predominantly right-lateralized social-emotional processing network. The persistence of this cross-

hemispheric connection over more than a decade underscores the enduring nature of early caregiving influences on brain function and mother-child interactions.

It is important to acknowledge the limitations of our study, particularly the relatively small sample size, as observed by our power analysis. This constraint may have precluded the detection of smaller effects that could potentially be observed in a larger cohort, such as a possible involvement of the left-hemisphere network. Nevertheless, our results provide compelling evidence for a substantial impact of early maternal behavior on the development of the right hemisphere network, as reflected in interbrain synchrony patterns during adolescence. These findings underscore the enduring influence of early caregiving experiences on neural synchrony and suggest a potential mechanism through which maternal behavior may shape long-term socialemotional development. Future research with larger sample sizes may further elucidate the full spectrum of these associations and potentially uncover additional effects not detected in the current study. Furthermore, our results highlight the need for a more comprehensive approach to studying parent-child interbrain synchrony considering both hemispheric specialization and inter-hemispheric connections. Future investigations should aim to elucidate the full extent of these neural networks involved in parent-child interactions and how they are shaped by early caregiving experiences. Additionally, longitudinal studies with larger sample sizes and more frequent assessment points could provide deeper insights into the developmental trajectory of these brainbehavior links. Such research could potentially uncover how these neural patterns evolve over time and how they relate to various aspects of social-emotional development and parent-child relationship quality across childhood and adolescence. Studies should also examine the longitudinal impact of fathering and of early difficulties to bonding, in conditions such as postpartum depression, premature birth, or environmental adversity. Our study points to the potential enduring effects of early maternal behavior on the development of interbrain synchrony processes. Much further research is needed to explore these longitudinal links and shed light on the mechanisms by which maternal behavior tunes the child's brain to the social world.

Data availability

The data generated during the current study are not publicly available due to participants' privacy but are available from the corresponding author on reasonable request.

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LS -conceptualization, study design, wrote the main manuscript, performed statistical analysis, and run the experiment at timepoint 2.OH - conceptualization, study design, wrote the main manuscript, performed statistical analysis, and run the experiment at timepoint 2. J. L - Conceptualization, experimental designI. G - Conceptualization, study design, running experiment at timepoint 1R. F - Conceptualization, writing, study design, statistical analysis, supervision.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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