Interpersonal Neural Synchrony Across Levels of Interpersonal Closeness and Social Interactivity

Alessandro Carollo[a], Andrea Bizzego[a], Verena Schäfer[b], Carolina Pletti[b], Stefanie Hoehl[b], Gianluca Esposito[a,*]

[a] *Department of Psychology and Cognitive Science, University of Trento, 38068 Rovereto, Italy*

[b] *Department of Developmental and Educational Psychology, University of Vienna, 1010 Vienna, Austria*

Abstract

Interpersonal neural synchrony is a key marker of social interactions, offering insights into the neural mechanisms underlying human connection and developmental outcomes. So far, hyperscanning studies have examined synchrony across diverse dyads and tasks, leading to inconsistencies and limiting cross-study comparability. This variability challenges the establishment of a unified theoretical framework for neural synchrony. This study investigated the effects of interpersonal closeness and social interactivity on neural synchrony using functional near-infrared spectroscopy hyperscanning. We recorded brain activity from 142 dyads (70 close-friend, 39 romantic-partner, and 33 mother-child dyads) across three interaction conditions: video co-watching (passive), a cooperative game (structured active), and free interaction (unstructured active). Neural synchrony was computed between participants' bilateral inferior frontal gyrus (IFG) and temporoparietal junction (TPJ) using wavelet transform coherence. Results showed that true dyads exhibited significantly higher synchrony than non-interacting surrogate dyads ($q < .001$), particularly in combinations involving the right IFG, left IFG, and left TPJ. Mother-child dyads displayed lower synchrony than adult-adult dyads at the global ($p < .001$) and local level of analysis. At the global level, synchrony was highest during video co-watching, followed by the cooperative game and free interaction ($p < .001$). However, left IFG–left IFG and

*Corresponding Author

Email address: gianluca.esposito@unitn.it (Gianluca Esposito)

left IFG–right TPJ synchrony peaked during the cooperative game. These findings highlight the role of brain maturation and social task structure in shaping neural synchrony. By providing an experimental framework, this study lays the groundwork for future hypothesis-driven hyperscanning research, advancing our understanding of the neural mechanisms underlying human social interactions.

Keywords: interpersonal neural synchrony, hyperscanning, functional near-infrared spectroscopy, fNIRS, parental brain, attachment

---

1. Introduction

> "I feel like somehow our hearts have become intertwined. Like when she feels something, my heart moves in tandem. Like we are two boats tied together with a rope. Even if you want to cut the rope, there is no knife sharp enough to do it." (H. Murakami, *Men Without Women*)

Social interactions play a central role throughout human life. From birth, early social interactions scaffold the acquisition of cognitive, emotional, and social skills (Vygotsky, 1978), including language (Kuhl, 2007, 2011), emotional regulation (Bornstein and Esposito, 2023; Hollenstein et al., 2017), and expectations about the social world that allow engaging in effective interactions with significant others throughout life (Bowlby and Holmes, 2012).

Due to the central role of social interactions in human life, understanding and scientifically characterizing their quality has become a key focus in developmental and social research. Extensive literature on human development has emphasized the importance of concepts such as rhythm, reciprocity, and synchrony, all of which are observed in high-quality social interactions (Feldman, 2007; Stern, 2009; Trevarthen, 1998). In particular, the concept of synchrony has been widely applied across various fields to describe the temporal relationship between events, resulting in coordinated states among the individual components of a system (Feldman, 2007; Leclère et al., 2014). In developmental science, synchrony has been especially useful for understanding the attunement between caregiver and child and predicting the child's developmental outcomes (Leclère et al., 2014). Early observational studies revealed that behavioral synchrony depends on both the caregiver's and the child's ability to attune to each other's signals, fostering a reciprocally rewarding interaction (Reyna and Pickler, 2009). Since its introduction, the

concept of synchrony has expanded beyond behavioral events to encompass the coordination of physiological rhythms (Feldman, 2012). More recently, emerging research in human development has extended the concept of bio-behavioral synchrony to include the temporal alignment of neural signals, laying the groundwork for studies on interpersonal neural synchrony (Carollo et al., 2021; Carollo and Esposito, 2024).

The emergence of the second-person neuroscience approach and hyperscanning, especially with functional near-infrared spectroscopy (fNIRS), has significantly advanced research on bio-behavioral synchrony, providing strong evidence for the existence of interpersonal neural synchrony (Carollo et al., 2021; Carollo and Esposito, 2024; Hasson et al., 2012). For instance, in their pioneering work, Cui et al. (2012) demonstrated the benefits of using fNIRS in a hyperscanning paradigm to explore the neural dynamics underlying real-life social interactions. In their study, participants played a cooperative video game side-by-side while their brain activity was monitored via fNIRS. The results revealed that interpersonal neural synchrony in the right superior frontal cortex was higher during the cooperative task compared to the competitive or solo conditions. Furthermore, greater synchrony was associated with better cooperation performance. Following this, other studies using fNIRS hyperscanning have investigated interpersonal neural synchrony in caregiver-child dyads. For example, Azhari et al. (2021) found increased synchrony in prefrontal regions during the co-viewing of animation videos by father-child dyads. Similarly, Nguyen et al. (2020, 2021b) reported higher synchrony in the inferior frontal gyrus and temporoparietal junction during cooperative tasks in mother-child and father-child dyads compared to the individual performance of the same task. In mother-child dyads, higher synchrony during cooperative problem-solving was associated with greater behavioral reciprocity and task success. These findings emphasize interpersonal neural synchrony as a potential biomarker for mother-child interaction quality (Nguyen et al., 2020; Reindl et al., 2018). Consistent with this, a recent electroencephalography (EEG) study by Endevelt-Shapira and Feldman (2023) found that higher sensitivity in maternal caregiving was associated with stronger interpersonal neural synchrony, while higher intrusiveness was linked to lower synchrony.

The literature on bio-behavioral synchrony is by no means limited to caregiver-child dyads. The concept of interpersonal neural synchrony has also been applied to investigate the neural dynamics underlying other types of social bonds, such as romantic partners, close friends, colleagues, and

strangers (Astolfi et al., 2011; Carollo et al., 2025; Feldman, 2017; Gvirts and Perlmutter, 2020; Lim et al., 2024a; Long et al., 2021; Toppi et al., 2016). For example, during a receiver-sender game paradigm, romantic couples demonstrated higher interpersonal neural synchrony in the frontopolar cortex and the right temporoparietal junction compared to stranger dyads (Shao et al., 2023). Similarly, using EEG hyperscanning, Kinreich et al. (2017) observed interpersonal neural synchrony in temporal-parietal regions during naturalistic face-to-face interactions for romantic partners but not for strangers. In close friendships, interpersonal neural synchrony has been linked to prosocial behaviors (Balconi et al., 2019, 2020).

Building on the diversity of dyadic relationships explored in hyperscanning research, studies have employed a wide range of tasks to investigate interpersonal neural synchrony across different contexts. Synchrony has been observed in contexts where individuals simply co-attend to the same stimulus (e.g., watching a video together; Azhari et al. 2019; De Felice et al. 2024b), collaborate on cooperative tasks (e.g., Cui et al. 2012; Liu et al. 2021), or engage in conversational exchanges (e.g., Carollo et al. 2025; Nguyen et al. 2021a). These tasks vary in the degree of interactivity they require from participants. For instance, experimental conditions that involve co-attending to the same sensory stimulus demand minimal active social interaction, as participants are involved in a shared social context without engaging in direct exchanges. In contrast, tasks such as solving cooperative problems or participating in conversations require higher levels of interactivity and active social coordination. Furthermore, highly interactive scenarios can range from constrained, rules-based exchanges to completely free and naturalistic social interactions.

Consistently with the aforementioned literature on hyperscanning and bio-behavioral synchrony, De Felice et al. (2024a) identified two key dimensions central to the study of interpersonal neural synchrony: interpersonal closeness and interactivity. Interpersonal closeness refers to the degree of social proximity between interacting agents, often assessed through measures of relationship duration and/or intimacy. Interactivity, on the other hand, captures the level of reciprocity and the richness of multisensory mutual exchanges during a social interaction. While it is hypothesized that both interpersonal closeness and interactivity positively influence interpersonal neural synchrony, the relative contributions of these dimensions have not yet been directly compared. The existing literature provides limited direct comparisons of bio-behavioral synchrony across different dyads and social tasks. For

instance, Pan et al. (2017) examined variations in neural synchrony across different types of dyads, while Bizzego et al. (2019a) investigated physiological synchrony between strangers, friends, and lovers. Furthermore, Fishburn et al. (2018) compared neural synchrony during tasks involving simple co-exposure to a shared sensory stimulus versus cooperative problem-solving.

Despite the insights gained from previous research, a systematic exploration of how interpersonal closeness and interactivity interact to shape and influence interpersonal neural synchrony remains an open question. This gap limits the cross-comparability of hyperscanning studies and, ultimately, challenges the establishment of a unified theory of synchrony. This study seeks to address this gap by examining how interpersonal neural synchrony varies according to *(i)* the level of interpersonal closeness and *(ii)* the degree of interactivity required by the experimental task. To achieve this, we employed fNIRS hyperscanning to monitor brain activity in three types of dyads: close friends, romantic partners, and mother-child pairs. These dyads participated in three tasks designed to vary in interactivity: video co-exposure, a rules-based cooperative game, and free verbal interaction. By systematically varying both interpersonal closeness and task interactivity, this study aims to identify the factors that foster interpersonal neural synchrony and provide a deeper understanding of the underlying mechanisms of human social interactions. Based on the bio-behavioral synchrony literature (De Felice et al., 2024a; Feldman, 2017), we hypothesized that:

- Interpersonal neural synchrony would be higher in dyads with greater interpersonal closeness, with the order being mother-child pairs having the highest synchrony, followed by romantic partners, and then close friends.

- Interpersonal neural synchrony would be influenced by the level of interactivity in the task, with lower synchrony observed in passive tasks (video co-exposure), higher synchrony in constrained social interactions (rules-based cooperative game), and the highest synchrony during more free-form interactions (free verbal interaction).

2. Methods

2.1. Study Design

All data for this study were collected using a hyperscanning approach, where dyads of participants took part in the experimental tasks while their

brain activity was simultaneously monitored using fNIRS.

To examine the impact of interpersonal closeness on interpersonal neural synchrony, the study included three types of dyads: close friends, romantic partners, and mother-child pairs. Data collection for close friends and romantic partners took place in Italy at the University of Trento, while data for mother-child dyads was collected at the University of Vienna in Austria.

In the experiment, dyads of participants completed three distinct social tasks: video co-exposure, rules-based cooperative game, and free verbal interaction. These tasks were designed to vary the levels of interactivity, ranging from structured, passive activities to spontaneous, active exchanges.

The study was approved by the Ethics Committees of the University of Trento (ref. 2022-052) and the University of Vienna (ref. 00732). The conduction of the experiment followed the guidelines provided by the Declaration of Helsinki. Informed consent was obtained from all participants, and for the children involved, consent was provided by their primary caregivers.

2.2. Participants

A total of 284 participants (142 dyads) took part in the study. Specifically, the sample consisted of 70 dyads of close friends (29 male-male dyads, 23 female-female dyads, and 18 male-female dyads; Mean age = 21.60 ± 2.06 years), 39 heterosexual romantic partner dyads (Mean age = 23.45 ± 3.08 years), and 33 mother-child dyads (20 female children, Mean age mother = 38.59 ± 4.66 years, Mean age children = 5 years 6 months $\pm$ 3 months). A total of two close friend dyads, one romantic partner dyad, and two mother-child dyads were excluded for technical issues during the experiment.

To participate in the data collection as close friends, each dyad needed to have a friendship with no current or past romantic relationship between the two individuals. For romantic partner dyads, only heterosexual couples with an ongoing romantic relationship were included in the study. Finally, for the mother-child dyads, only mothers of children aged 5 years old were eligible for enrollment in the study. All participants reported no history of known or diagnosed health or neurological conditions, particularly those that could affect the oxygen-binding capacity of the blood.

Close friend and romantic partner dyads were recruited through convenience and snowball sampling via social media platforms and the University of Trento's participant management and recruitment system (SONA). Mother-child dyads were recruited from a pre-existing database of volunteers at the University of Vienna. While close friend and romantic partner dyads

did not receive monetary compensation, mother-child dyads were compensated with €6 (equivalent to the cost of two round-trip journeys on public transportation in Vienna) and a small toy for the child (i.e., a €6 Lego set).

2.3. Experimental Tasks

For all dyads, the experiment began with a resting-state measurement (2 minutes for adult dyads and 1 minute for mother-child dyads), which served as a baseline neural activity assessment. Additionally, mother-child dyads had a 1-minute resting-state measurement between each task.

The experiment consisted of three experimental tasks: video co-exposure, rules-based cooperative game, and free verbal interaction. These conditions were designed to explore the effect of interactivity levels on interpersonal neural synchrony, ranging from highly structured (video co-exposure) to semi-structured (rules-based cooperative game) to unstructured (free verbal interaction) social interactions.

In the video co-exposure condition, a 3-minute, language-free animated video was presented to the dyads on a monitor positioned in front of them. The video was carefully selected to ensure consistency across experiments conducted in two different countries, thereby avoiding potential confounding variables related to language. It was also chosen for its appropriateness for both adult and child participants, making it suitable for all dyadic groups involved in the study. During this condition, dyads were instructed to simply attend to the video without interacting with each other. This setup allowed for the measurement of interpersonal neural synchrony driven by the shared sensory experience of the video in a social setting, without the influence of direct social interaction.

The rules-based cooperative condition involved a 5-minute session of cooperative Jenga. A Jenga tower was constructed and placed on a table between the participants, who were instructed to play according to the provided rules. Dyads were asked to take turns removing one block at a time and placing it on top of the tower. To maintain consistent difficulty across all dyads, participants were instructed to remove only one block per layer, starting from the bottom of the tower. In cases where the tower collapsed, participants were allowed to rebuild it and continue playing to ensure that the total duration of the task remained consistent for all dyads. This rule-based task was included to provide a semi-structured social interaction, ensuring a consistent level of predictability of the social exchange.

In the free verbal interaction condition, participants sat facing each other and were free to engage in verbal interaction as they preferred for a duration of 5 minutes. This unstructured task allowed for natural, spontaneous communication between the dyads.

The order of the experimental conditions was randomized for each dyad to mitigate potential order effects on the results. For the current work, we did not analyze the resting-state phases.

2.4. Acquisition of Neural Data

fNIRS hyperscanning was used across all experimental tasks to monitor participants' brain activity. Each participant wore a cap equipped with eight LED sources emitting light at wavelengths of 760 nm and 850 nm, along with eight detectors arranged to capture brain activity from the bilateral inferior frontal gyri (IFG) and bilateral temporoparietal junctions (TPJ), following previous research protocols (Nguyen et al., 2020).

The cap configurations differed slightly across data collections. In the close friends and romantic partners studies conducted in Italy, one detector was dedicated to collecting signals from eight short-distance channels, resulting in a total of 14 fNIRS channels per participant. In contrast, for the mother-child dyads study conducted in Vienna, short-distance channels were not available. Instead, the eighth detector was used to add two long-distance channels, leading to a total of 16 fNIRS channels per participant.

For the data analysis, fNIRS channels were aggregated into four regions of interest: left IFG, right IFG, left TPJ, and right TPJ. The cap setup for the close friends and romantic partners studies was optimized using the fNIRS Optodes' Location Decider (fOLD) to maximize sensitivity in the target regions of interest (Zimeo Morais et al., 2018) (see Figure S1A in the Supplementary Materials). Due to logistical constraints in the laboratory in Austria, the cap setup for the mother-child dyads study was designed based on previous adult-child studies (Nguyen et al., 2020, 2021a,b) (see Figure S1B in the Supplementary Materials).

For the experiment, channel placement followed the international 10-20 EEG system. In the data collection conducted in Italy, optode stabilizers ensured that the distance between sources and detectors never exceeded 3 cm, maintaining a high signal-to-noise ratio. Additionally, different fNIRS devices were used across locations: a NIRSport2 device (NIRx Medical Technologies LLC) with a sampling rate of 10.17 Hz was used in Italy, while a NIRSport

device (NIRx Medical Technologies LLC) with a sampling rate of 7.81 Hz was used in Austria.

2.5. Processing of Neural Data

Pre-processing and synchrony analyses were conducted using *pyphysio* (Bizzego et al., 2019b). The fNIRS raw intensity signals were first converted to changes in optical density. To ensure consistency in the length of data across experimental conditions, the optical density data were segmented to include only the first 3 minutes of each condition. Signal quality was assessed using a convolutional neural network model trained to classify the quality of fNIRS segments (Bizzego et al., 2021, 2022). The processed data were then resampled to 10 Hz and converted into oxygenated (HbO) and deoxygenated hemoglobin (HbR) values using the modified Beer-Lambert law (Delpy et al., 1988). For the statistical analyses, we focused exclusively on HbO values, consistent with previous studies (e.g., Lim et al. (2024a,b); see the results on HbR values in the Supplementary Materials). Finally, temporal autocorrelations and physiological noise in the neural data were removed by whitening the signals through an autoregressive model (Barker et al., 2013). The use of an autoregressive filter to pre-whiten the signals before the analysis has been shown to reduce the false discovery rate when estimating the coherence between signals (Santosa et al., 2017).

2.6. Interpersonal Neural Synchrony

Interpersonal neural synchrony was calculated on a channel-by-channel basis between participants using wavelet transform coherence (WTC) (Grinsted et al., 2004). WTC allows estimating the coherence between fNIRS time series considering both frequency and time dimensions, while also accounting for both in-phase and phase-lagged correlations (Nguyen et al., 2020). In this way, WTC facilitates a comprehensive analysis of global coherence patterns in brain activity.

For each pair of good quality channels in every experimental task, WTC was calculated over a frequency range of 0.01 to 0.20 Hz, following the approach of previous works (Carollo et al., 2025; Lim et al., 2024a,b). To obtain the final WTC value, coherence scores were averaged across the entire frequency spectrum. This approach ensured an unbiased analysis, as no specific frequency bands were hypothesized *a priori* (Carollo et al., 2025).

To obtain a random level of synchrony between participants who did not interact directly with one another but did the same experimental task, we also

computed WTC between surrogate dyads (i.e., randomly paired participants taken from different real dyads). As in Carollo et al. (2025), we performed a single permutation of the dyads, resulting in the same number of data points as the true dyads. To ensure that the surrogate dyads maintained the same experimental conditions and fNIRS channels as the real dyads, we created these pairs by randomly matching participants who were originally from different dyads. Specifically, for each fNIRS channel, we took the data segment from one participant in a given dyad and paired it with the corresponding channel's data segment from a participant in another dyad, while keeping the task condition (e.g., video co-exposure) the same. For example, if participant A from dyad 001 had fNIRS data recorded from channel X during the video co-exposure task, we paired it with the fNIRS data from channel X of participant B from dyad 002 during the same task.

2.7. Data Analysis

The data analysis for the current study is organized into three main steps:

1. Identifying the combinations of brain regions between the two participants where a statistically significant difference in WTC scores exists between true and surrogate dyads;
2. Outline the effect of interpersonal closeness and social interactivity on overall interpersonal neural synchrony across all combinations of regions of interest between the two participants;
3. Outline the effect of interpersonal closeness and social interactivity on interpersonal neural synchrony in specific combinations of brain regions between the two participants.

Across analytical steps, we used linear mixed models (Bates et al., 2005). Before conducting the analyses, we created two types of region combination IDs: one that identified combinations of brain regions regardless of their order (e.g., treating region X in participant A–region Y in participant B and region Y in participant A–region X in participant B as equivalent) and another that accounted for the specific order of the combination (e.g., treating region X in participant A–region Y in participant B and region Y in participant A–region X in participant B as distinct). Subsequently, we conducted:

1. A separate linear mixed model for each combination of regions of interest (independently from their order) between the two participants, with WTC scores as the dependent variable and dyad type (true *vs.*

surrogate dyads) as the fixed effect. Dyadic relationships (i.e., close friends, romantic partners, mother-child dyads), experimental conditions (i.e., video co-exposure, rules-based cooperative game, free verbal interaction), and dyad IDs were included as random effects. For models based on synchrony data from combinations of non-homologous brain regions, we also included the order-dependent region combination IDs as a random effect. A Bonferroni correction was applied to control the false positive rate arising from multiple comparisons.

2. A single linear mixed model using data from all brain region combinations. This model was designed to examine the overall effect of interpersonal closeness and social interactivity on interpersonal neural synchrony, using only data from true dyads. WTC scores in true dyads served as the dependent variable, while dyadic relationships and experimental tasks were included as fixed effects. The model also included the two types of region combination IDs (one that is order-independent and one that is order-dependent) and dyad IDs as random effects. *Post-hoc* pairwise comparisons of marginal means were performed to identify significant differences between levels of each significant main factor. A Bonferroni correction was applied to control the false positive rate in *post-hoc* comparisons.
3. A separate linear mixed model with data from each combination of regions of interest (independently from their order) between the two participants. In these models, WTC scores from true dyads were the dependent variable, and dyadic relationships and experimental conditions were used as fixed effects. Additionally, the model included the dyad IDs and, only for models conducted on non-homologous combinations of brain region, the order-dependent region combination IDs as random effects. *Post-hoc* pairwise comparisons of marginal means were performed, with Bonferroni correction applied to control for multiple comparisons and minimize the risk of Type I error.

3. Results

3.1. Neural Synchrony in True Versus Surrogate Dyads

In the first stage of the analysis, we used a linear mixed model to test the differences in interpersonal neural synchrony between true and surrogate dyads for each combination of brain regions between the two participants. The results revealed significant differences in synchrony across all brain region

combinations, with true dyads showing higher levels of synchrony compared to surrogate dyads (i.e., left IFG–left IFG: $t = 12.48$, $p < .001$, $q < .001$; left IFG–right IFG: $t = 18.60$, $p < .001$, $q < .001$; left IFG–left TPJ: $t = 16.48$, $p < .001$, $q < .001$; left IFG–right TPJ: $t = 13.15$, $p < .001$, $q < .001$; right IFG–right IFG: $t = 16.81$, $p < .001$, $q < .001$; right IFG–left TPJ: $t = 19.20$, $p < .001$, $q < .001$; right IFG–right TPJ: $t = 13.77$, $p < .001$, $q < .001$; left TPJ–left TPJ: $t = 11.80$, $p < .001$, $q < .001$; left TPJ–right TPJ: $t = 10.20$, $p < .001$, $q < .001$; right TPJ–right TPJ: $t = 5.42$, $p < .001$, $q < .001$; see Figure 1). This finding suggests that the neural synchrony observed in true dyads is distinct from surrogate, non interacting dyads, supporting the hypothesis that dyadic interactions contribute to meaningful interpersonal neural synchrony. Given these statistical differences, we used all data from true dyads across all combinations of brain regions for subsequent analysis.

3.2. Interpersonal Closeness and Social Interactivity on Neural Synchrony (All Combinations of Regions)

In the second stage of our analysis, we conducted a linear mixed model to examine the effects of interpersonal closeness and levels of social interactivity on interpersonal neural synchrony across all regions of interest. Our results indicate that both interpersonal closeness ($F(2, 131) = 10.54$, $p < .001$; see Figure 2A) and social interactivity ($F(2, 71{,}662) = 201.38$, $p < .001$; see Figure 2B) have a statistically significant effect on interpersonal neural synchrony scores.

Pairwise comparisons of marginal means revealed significant differences in interpersonal neural synchrony between close friend dyads and mother-child dyads (estimate = 0.00583, Standard Error (SE) = 0.00128, $z = 4.56$, $q < .001$), as well as between romantic partners and mother-child dyads (estimate = 0.00463, SE = 0.00143, $z = 3.24$, $q = .004$). However, no significant difference was found between close friend dyads and romantic partners dyads ($q > .05$).

Further *post-hoc* analyses showed significant differences in interpersonal neural synchrony between video co-exposure and rules-based cooperative game (estimate = 0.000453, SE = 0.000130, $z = 3.47$, $q = .002$), video co-exposure and free verbal interaction (estimate = 0.002423, SE = 0.000128, $z = 18.88$, $q < .001$), and rules-based cooperative game and free verbal interaction (estimate = 0.001970, SE = 0.000130, $z = 15.18$, $p < .001$).

These findings suggest that both the nature of the relationship between individuals and the type of social interaction they engage in play crucial roles

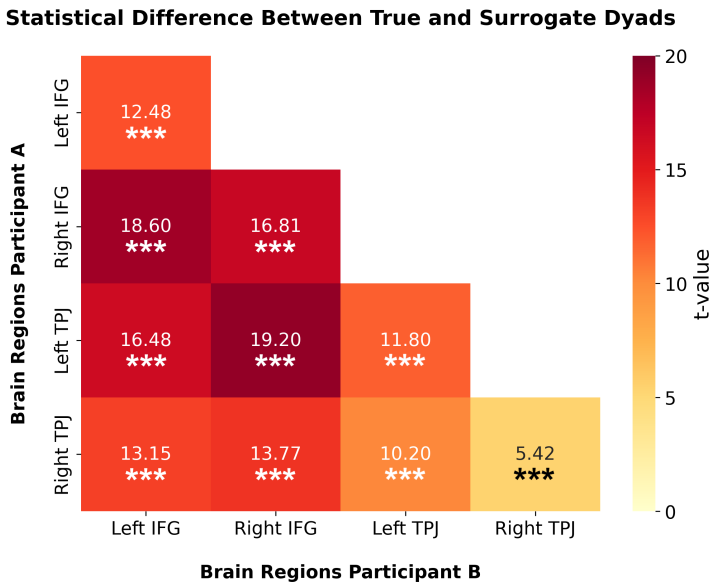

Figure 1: Statistical difference between true and surrogate dyads in terms of interpersonal neural synchrony. For each combination of brain regions (i.e., bilateral inferior frontal gyri (IFG) and bilateral temporoparietal junctions (TPJ)) between the two participants involved in the experiment, we report the t-value and its significance level. A linear mixed model was used with wavelet transform coherence scores as the dependent variable and dyad type (true *vs.* surrogate) as the fixed effect. Dyadic relationships, experimental conditions, and dyad IDs were included as random effects. In the models conducted on non-homologous combinations of brain regions, we included the order-dependent region combination ID as a random effect. Bonferroni correction was applied to adjust the alpha level for multiple comparisons. (*** $q < .001$).

in modulating interpersonal neural synchrony.

3.3. Interpersonal Closeness and Social Interactivity on Neural Synchrony (Individual Combinations of Regions)

In the third stage of our analysis, we conducted a linear mixed model to examine the effects of interpersonal closeness and social interactivity on interpersonal neural synchrony across individual combinations of regions of interest. Our results indicate that both interpersonal closeness and social interactivity had a statistically significant effect on synchrony scores in the following brain region pairs: left IFG–left IFG (interpersonal closeness: $F(2, 130.20) = 8.31$, $p < .001$, $q = .008$; social interactivity: $F(2, 5581.10) = 37.42$, $p < .001$, $q < .001$), left IFG–right IFG (interpersonal closeness: $F(2,$

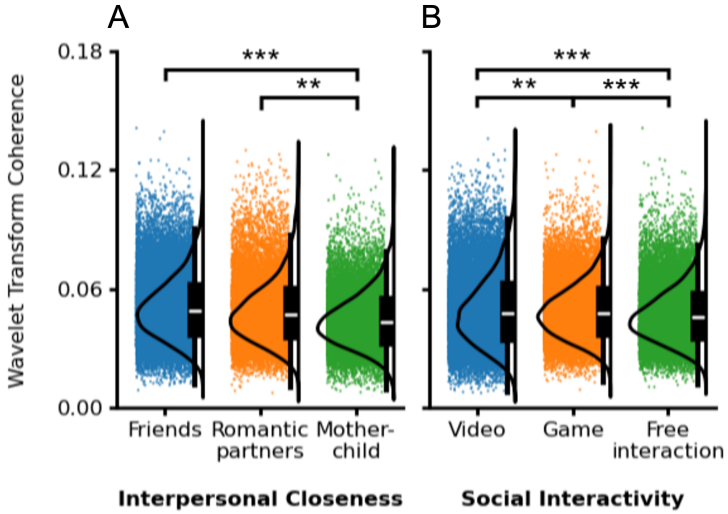

Figure 2: **A**. Comparison of overall interpersonal neural synchrony scores across levels of interpersonal closeness (i.e., close friends, romantic partners, and mother-child dyads). **B**. Comparison of overall interpersonal neural synchrony scores across levels of social interactivity (i.e., video co-exposure, rules-based cooperative game, and free verbal interaction). (** $q < .01$; *** $q < .001$).

132.40) = 20.98, $p < .001$, $q < .001$; social interactivity: $F(2, 11{,}072.30) = 51.95$, $p < .001$, $q < .001$), left IFG–left TPJ (interpersonal closeness: $F(2, 131.80) = 7.54$, $p < .001$, $q = .016$; social interactivity: $F(2, 11{,}012.80) = 22.45$, $p < .001$, $q < .001$), right IFG–right IFG (interpersonal closeness: $F(2, 131.20) = 20.44$, $p < .001$, $q < .001$; social interactivity: $F(2, 5390.50) = 55.16$, $p < .001$, $q < .001$), right IFG–left TPJ (interpersonal closeness: $F(2, 132.20) = 14.51$, $p < .001$, $q < .001$; social interactivity: $F(2, 10{,}838.90) = 66.97$, $p < .001$, $q < .001$), and right IFG–right TPJ (interpersonal closeness: $F(2, 127.50) = 9.75$, $p < .001$, $q = .002$; social interactivity: $F(2, 6451.60) = 7.66$, $p < .001$, $q = .010$).

Conversely, social interactivity—but not interpersonal closeness—had a statistically significant effect on synchrony in the following brain region pairs: left IFG–right TPJ (interpersonal closeness: $F(2, 121.30) = 4.86$, $p = .009$, $q > .05$; social interactivity: $F(2, 6603) = 29.80$, $p < .001$, $q < .001$), left TPJ–left TPJ (interpersonal closeness: $F(2, 128.70) = 0.84$, $p > .05$, $q > .05$; social interactivity: $F(2, 5337.30) = 36.71$, $p < .001$, $q < .001$), left TPJ–right TPJ (interpersonal closeness: $F(2, 128.80) = 1.11$, $p > .05$, $q > .05$; social interactivity: $F(2, 6435.10) = 13.50$, $p < .001$, $q < .001$), and

right TPJ–right TPJ (interpersonal closeness: $F(2, 119.14) = 0.35$, $p > .05$, $q > .05$; social interactivity: $F(2, 2014.71) = 13.06$, $p < .001$, $q < .001$).

Pairwise comparisons of marginal means revealed that close friends exhibited significantly higher interpersonal neural synchrony than mother-child dyads in the left IFG–left IFG, left IFG–right IFG, left IFG–left TPJ, right IFG–right IFG, right IFG–left TPJ, and right IFG–right TPJ. Moreover, romantic partners showed significantly higher brain synchrony than mother-child dyads in the left IFG–right IFG, right IFG–right IFG, right IFG–left TPJ, and right IFG–right TPJ. The complete results of these analyses are presented in Table 1 and represented in Figure 3. These findings suggest that interpersonal neural synchrony is generally stronger among close friends and romantic partners compared to mother-child dyads, as found in the analysis presented in Section 3.2.

Contrast	**Estimate**	**Standard Error**	**z-ratio**	***q***
Left inferior frontal gyrus – left inferior frontal gyrus				
Close friends–Romantic partners	0.00222	0.0013	1.68	> .05
Close friends–Mother-child	0.00579	0.0014	4.06	< .001 ***
Romantic partners–Mother-child	0.00357	0.0016	2.25	> .05
Left inferior frontal gyrus – right inferior frontal gyrus				
Close friends–Romantic partners	0.00147	0.0013	1.16	> .05
Close friends–Mother-child	0.00878	0.0014	6.40	< .001 ***
Romantic partners–Mother-child	0.00730	0.0015	4.77	< .001 ***
Left inferior frontal gyrus – left temporoparietal junction				
Close friends–Romantic partners	0.00173	0.0013	1.39	> .05
Close friends–Mother-child	0.00524	0.0014	3.88	< .001 ***
Romantic partners–Mother-child	0.00351	0.0015	2.33	> .05
Right inferior frontal gyrus – right inferior frontal gyrus				
Close friends–Romantic partners	0.00046	0.0016	0.29	> .05
Close friends–Mother-child	0.01080	0.0018	6.13	< .001 ***
Romantic partners–Mother-child	0.01034	0.0020	5.27	< .001 ***
Right inferior frontal gyrus – left temporoparietal junction				
Close friends–Romantic partners	0.00074	0.0015	0.51	> .05
Close friends–Mother-child	0.00825	0.0016	5.23	< .001 ***
Romantic partners–Mother-child	0.00751	0.0018	4.26	< .001 ***
Right inferior frontal gyrus – right temporoparietal junction				
Close friends–Romantic partners	0.00142	0.0013	1.09	> .05
Close friends–Mother-child	0.00618	0.0014	4.40	< .001 ***
Romantic partners–Mother-child	0.00476	0.0016	3.03	.007 **

Table 1: Results of the *post-hoc* pairwise comparisons examining the effect of interpersonal closeness on interpersonal neural synchrony across different brain region combinations. For each combination, we report the estimated contrast between two levels of interpersonal closeness, along with the standard error, z-ratio, and corrected q-value. (** $q < .01$; *** $q < .001$).

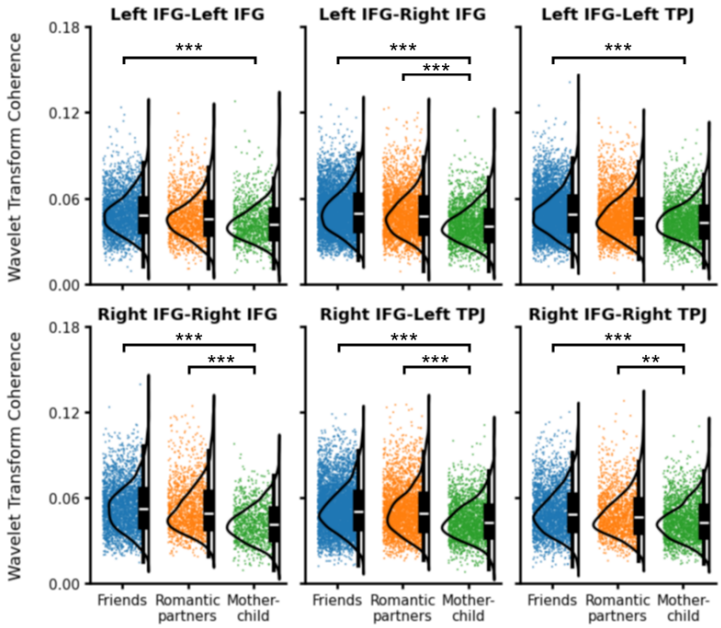

Figure 3: Effect of interpersonal closeness on interpersonal neural synchrony across combinations of regions of interest (i.e., bilateral inferior frontal gyri (IFG) and bilateral temporoparietal junctions (TPJ)). (** $q < .01$; *** $q < .001$).

Furthermore, regarding the effect of social interactivity, pairwise comparisons of marginal means revealed distinct synchrony patterns across different brain region pairs. Notably, the video co-exposure condition exhibited significantly greater synchrony than the other experimental tasks in the following combinations: right IFG–right IFG, right IFG–left TPJ, left TPJ–left TPJ, and left TPJ–right TPJ. In contrast, the rules-based cooperative game condition demonstrated the highest synchrony for left IFG–left IFG and left IFG–right TPJ. Additionally, both the video co-exposure and rules-based cooperative game conditions showed greater synchrony than free interaction in the following region pairs: left IFG–right IFG, left IFG–left TPJ, right IFG–right TPJ, and right TPJ–right TPJ. Overall, across all experimental tasks, free interaction consistently exhibited the lowest level of interpersonal neural synchrony. The full results detailing the effect of interactivity levels on neural synchrony are provided in Table 2 and represented in Figure 4.

Contrast	Estimate	Standard Error	z-ratio	q
Left inferior frontal gyrus – left inferior frontal gyrus				
Video–Cooperative game	-0.00203	0.0004	-4.73	< .001 ***
Video–Free interaction	0.00166	0.0004	3.91	< .001 ***
Cooperative game–Free interaction	0.00369	0.0004	8.64	< .001 ***
Left inferior frontal gyrus – right inferior frontal gyrus				
Video–Cooperative game	-0.000403	0.0003	-1.23	> .05
Video–Free interaction	0.002624	0.0003	8.15	< .001 ***
Cooperative game–Free interaction	0.003027	0.0003	9.32	< .001 ***
Left inferior frontal gyrus – left temporoparietal junction				
Video–Cooperative game	-0.000124	0.0003	-0.40	> .05
Video–Free interaction	0.001758	0.0003	5.61	< .001 ***
Cooperative game–Free interaction	0.001882	0.0003	5.94	< .001 ***
Left inferior frontal gyrus – right temporoparietal junction				
Video–Cooperative game	-0.00251	0.0004	-6.25	< .001 ***
Video–Free interaction	0.00032	0.0004	0.81	> .05
Cooperative game–Free interaction	0.00284	0.0004	7.09	< .001 ***
Right inferior frontal gyrus – right inferior frontal gyrus				
Video–Cooperative game	0.00220	0.0005	4.70	< .001 ***
Video–Free interaction	0.00484	0.0005	10.49	< .001 ***
Cooperative game–Free interaction	0.00264	0.0005	5.66	< .001 ***
Right inferior frontal gyrus – left temporoparietal junction				
Video–Cooperative game	0.00253	0.0003	7.47	< .001 ***
Video–Free interaction	0.00379	0.0003	11.38	< .001 ***
Cooperative game–Free interaction	0.00127	0.0003	3.76	< .001 ***
Right inferior frontal gyrus – right temporoparietal junction				
Video–Cooperative game	-0.000583	0.0004	-1.36	> .05
Video–Free interaction	0.001057	0.0004	2.50	.037 *
Cooperative game–Free interaction	0.001640	0.0004	3.85	< .001 ***
Left temporoparietal junction – left temporoparietal junction				
Video–Cooperative game	0.003630	0.0005	7.93	< .001 ***
Video–Free interaction	0.003039	0.0005	6.74	< .001 ***
Cooperative game–Free interaction	-0.000591	0.0005	-1.29	> .05
Left temporoparietal junction – right temporoparietal junction				
Video–Cooperative game	0.001644	0.0004	3.94	< .001 ***
Video–Free interaction	0.002009	0.0004	4.89	< .001 ***
Cooperative game–Free interaction	0.000365	0.0004	0.88	> .05
Right temporoparietal junction – right temporoparietal junction				
Video–Cooperative game	-0.000603	0.0007	-0.86	> .05
Video–Free interaction	0.002724	0.0007	3.94	< .001 ***
Cooperative game–Free interaction	0.003327	0.0007	4.77	< .001 ***

Table 2: Results of the *post-hoc* pairwise comparisons examining the effect of social interactivity levels on interpersonal neural synchrony across different brain region combinations. For each combination, we report the estimated contrast between two levels of social interactivity, along with the standard error, z-ratio, and corrected q-value. (* $q < .05$; *** $q < .001$).

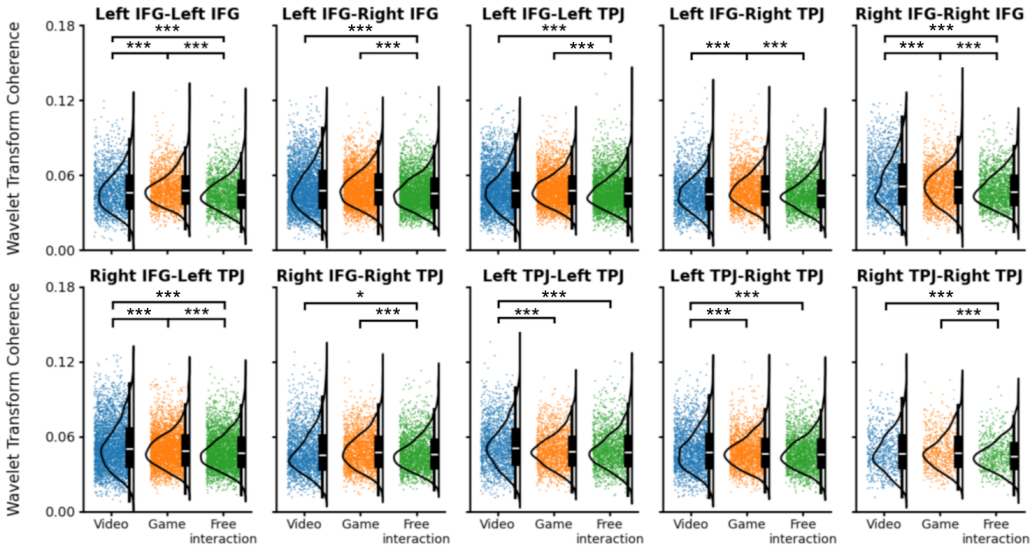

Figure 4: Effect of social interactivity on interpersonal neural synchrony across combinations of regions of interest (i.e., bilateral inferior frontal gyri (IFG) and bilateral temporoparietal junctions (TPJ)). (* $q < .05$; *** $q < .001$).

4. Discussion

In this study, we conducted an fNIRS hyperscanning experiment with 142 dyads to examine how interpersonal closeness and social interactivity levels affect interpersonal neural synchrony. To manipulate interpersonal closeness, we recruited dyads from three relationship types: close friends, romantic partners, and mother-child pairs. Additionally, each dyad participated in an experimental session involving social interactions at varying levels of interactivity. Specifically, they engaged in three conditions: video co-exposure (passive condition, no direct interaction), rules-based cooperative game (active condition, structured interaction), and free interaction (active condition, unstructured interaction). Based on previous research (De Felice et al., 2024a; Feldman, 2017), we hypothesized that both greater interpersonal closeness (mother-child > romantic partners > close friends) and higher levels of social interactivity (free interaction > cooperative game > video co-exposure) would be associated with increased interpersonal neural synchrony between participants.

To test these hypotheses, we initially examined patterns of neural synchrony across different brain regions and compared real dyads to surrogate,

non-interacting dyads. Our results revealed higher-than-random levels of interpersonal neural synchrony across all brain region pairs involving the bilateral IFG and TPJ in both participants. Notably, the strongest statistical difference between real and surrogate dyads emerged in synchrony scores between one participant's left IFG and the other's right IFG, as well as between the right IFG and left TPJ. Hence, social interactions appear to strongly induce interpersonal neural synchrony between one participant's right IFG and the other's left fronto-temporal regions, highlighting the role of these areas in social cognitive processing. The IFG is a key region of the mirror neuron system (Aziz-Zadeh et al., 2006), which plays a crucial role in action understanding and imitation by enabling the brain to simulate observed actions (Aziz-Zadeh et al., 2006; Carr et al., 2003; Iacoboni, 2005; Lyons et al., 2006). Mirror neurons are thought to establish a bridge between passive action observation and social perception encoding (Lyons et al., 2006). Studies on brain modulation have demonstrated that the left IFG is essential for social perception (Keuken et al., 2011). A meta-analysis of 485 functional imaging studies on the IFG conducted by Liakakis et al. (2011) identified four functionally distinct clusters in this brain region. In the left hemisphere, one cluster was linked to empathy, another to semantic and phonological processing, and a third to working memory. A fourth cluster, associated with fine movement control, was located in the right hemisphere. The presence of strong INS between the left and right IFG suggests a connection between action execution and action simulation/social perception, reinforcing the role of mirror neuron mechanisms in interactive and coordinated behaviors. Similarly, the TPJ is a key hub for mentalizing and perspective-taking, allowing individuals to infer the thoughts, beliefs, and intentions of others (Gallagher et al., 2000; Samson et al., 2004; Van Overwalle, 2009). Synchrony between the right IFG and left TPJ may indicate dynamic interactions between action execution and higher-order social cognition.

Building on these findings, we further examined how interpersonal closeness and social interactivity modulate neural synchrony across different brain region combinations. When conducting the analyses on all possible brain region combinations altogether, we observed that both interpersonal closeness and social interactivity influence interpersonal neural synchrony. However, contrary to our hypotheses, close friends and romantic partners exhibited significantly higher synchrony than mother-child dyads. Similarly, in contrast to our expectations, passive social interactions (video co-exposure) elicited higher synchrony than both active, structured interactions (rules-based co-

operative game) and active, unstructured interactions (free exchange).

The pattern in interpersonal closeness effects persisted when analyzing specific brain region pairs, all involving the IFG. As observed on physiological synchrony by Bizzego et al. (2019a), interpersonal closeness appears to have a negative association with synchrony, with more distant interpersonal relationships being supported by stronger bio-behavioral synchrony. Together with interpersonal closeness, developmental differences may contribute to our findings. In fact, the neural rhythms and functional dynamics of children's brains might not yet be fully comparable to those of adults (Meng et al., 2022). Brain regions involved in social cognition, such as the IFG and TPJ, continue to mature well into adolescence and early adulthood (Gweon et al., 2012; Kolk and Rakic, 2022; Wang et al., 2020). This prolonged development may affect the efficiency and coordination of neural activity during social interactions, leading to differences in interpersonal neural synchrony between children and adults. Moreover, myelination, synaptic pruning, and changes in connectivity across cortical networks influence the way information is processed and integrated over time. As a result, the mother-child dyads in our study may exhibit lower neural synchrony not necessarily due to weaker social bonds but rather due to ongoing maturation of brain mechanisms that support shared attention, perspective-taking, and interpersonal attunement in children. Another possible explanation of the difference between adult-adult and mother-child dyads could relate to the different devices that were used to collect the brain data in Italy and in Austria. In fact, Bizzego et al. (2024) showed that different devices and different labs collect brain signals with different intrinsic characteristics beyond signal quality *per se*.

Finally, we observed distinct patterns across different brain region pairs regarding the effect of social interactivity on interpersonal neural synchrony. While some regions (i.e., right IFG–right IFG, right IFG–left TPJ, left TPJ–left TPJ, left TPJ–right TPJ) followed the previously described trend–showing the highest synchrony during video co-exposure, followed by the cooperative game and the lowest during free interaction–other regions (i.e., left IFG–left IFG, left IFG–right TPJ) displayed the opposite pattern, with cooperative game interactions eliciting the highest synchrony, followed by video co-exposure, and the lowest synchrony occurring during free interaction. These latter combinations of brain regions reflect mirror mechanisms that involve the left IFG as well as attention control and theory of mind processes that are typically, but not exclusively, observed in the right portion of the TPJ (Krall et al., 2015). These diverging trends suggest that different neural mecha-

nisms may be engaged depending on the nature of the interaction. In brain regions where synchrony peaks during video co-exposure, neural alignment may be predominantly driven by shared sensory input in a social context, as both participants passively experience the same audiovisual stimuli. In contrast, regions where the cooperative game leads to the highest synchrony may be more involved in joint action coordination, strategic thinking, and shared goal pursuit, processes that require active engagement and real-time behavioral alignment.

5. Limitations

One consideration in our study is the slight variation in data collection methods across participant groups. Specifically, data from adult-adult dyads and mother-child interactions were collected in different countries, which may have introduced some cultural and contextual differences. Additionally, these sessions were conducted using different devices, which could have led to minor variations in the measurement of interpersonal neural synchrony. However, these methodological choices were made to align with the expertise and facilities available in each research lab. While these factors do not compromise the overall validity of our findings, they may introduce slight differences that affect the direct comparability of results across groups.

Another limitation is that our study focused exclusively on the bilateral IFG and TPJ, without monitoring other brain areas, such as the medial portions of the prefrontal cortex, which are also relevant for social cognition and interpersonal synchrony. This constraint was primarily due to the number of available fNIRS optodes, which limited our ability to capture a more comprehensive neural representation of social interactions. Future research could benefit from broader brain region coverage to provide a more complete understanding of the neural mechanisms underlying interpersonal synchrony.

6. Conclusion

In the current study, we employed an fNIRS hyperscanning approach to investigate how interpersonal closeness and social interactivity modulate interpersonal neural synchrony, analyzing data from a diverse sample of 284 participants. To systematically vary interpersonal closeness, we recruited close friends, romantic partners, and mother-child dyads, while social interactivity was manipulated through three conditions: a video co-exposure, a

rules-based cooperative game, and a free interaction. Our results highlight that interpersonal neural synchrony exhibited the most pronounced statistical differences when computed between one participant's right IFG and the other's left fronto-temporal regions. Additionally, we identified a robust trend across multiple levels of analysis, indicating that neural synchrony diminishes with interpersonal closeness. Furthermore, video co-exposure elicited the strongest synchrony across brain regions, while the cooperative game enhanced synchrony between the left IFG and the other person's left IFG and right TPJ, underscoring the role of active social interactions in shaping neural alignment in regions involved in the mirror neurons system and supporting theory of mind processes.

These findings contribute to the growing evidence that interpersonal neural synchrony reflects the dynamics of social bonds and shared experiences (Carollo et al., 2025; Lim et al., 2024a,b), with potential implications for developmental neuroscience. Understanding how different types of relationships and interactive contexts shape interpersonal neural synchrony may provide valuable insights into social cognition, cooperative behavior, and even therapeutic approaches for individuals with social challenges (e.g., autism spectrum disorder). Future research should explore how individual differences in personality or social skills, as well as relationship quality, further modulate neural synchrony. Furthermore, by providing an experimental framework, this study establishes a foundation for future hypothesis-driven hyperscanning research, facilitating a more systematic investigation of the neural mechanisms underlying human social interactions. This study reinforces the idea that human connection is deeply embedded in and supported by behavioral, physiological, and neural mechanisms.

Authors contribution

Conceptualization: AC, GE; Methodology: AC, AB; Formal analysis: AC, AB; Investigation: AC, VS; Data Curation: AC, AB; Writing – Original Draft: AC; Writing – Review & Editing: AC, AB, VS, CP, SH, GE; Supervision: SH, GE. All authors have read and agreed to the published version of the manuscript.

Supplementary Materials

Supplementary Material 1: Functional Near-Infrared Spectroscopy Cap. **Supplementary Material 2**: Analysis on Deoxygenated Hemoglobin.

Data availability statement

The data used for the present study are available upon request to the corresponding author.

Conflict of interests

The authors declare no conflict of interest.

Funding

The authors received no specific funding for this work.

References

Astolfi, L., Toppi, J., Borghini, G., Vecchiato, G., Isabella, R., Fallani, F. D. V., Cincotti, F., Salinari, S., Mattia, D., He, B., et al. (2011). Study of the functional hyperconnectivity between couples of pilots during flight simulation: an eeg hyperscanning study. In *2011 Annual International Conference of the IEEE Engineering in Medicine and Biology Society*, pages 2338–2341. IEEE.

Azhari, A., Bizzego, A., and Esposito, G. (2021). Father-child dyads exhibit unique inter-subject synchronization during co-viewing of animation video stimuli. *Social neuroscience*, 16(5):522–533.

Azhari, A., Leck, W. Q., Gabrieli, G., Bizzego, A., Rigo, P., Setoh, P., Bornstein, M. H., and Esposito, G. (2019). Parenting stress undermines mother-child brain-to-brain synchrony: A hyperscanning study. *Scientific reports*, 9(1):11407.

Aziz-Zadeh, L., Koski, L., Zaidel, E., Mazziotta, J., and Iacoboni, M. (2006). Lateralization of the human mirror neuron system. *Journal of Neuroscience*, 26(11):2964–2970.

Balconi, M., Fronda, G., and Vanutelli, M. E. (2019). Donate or receive? social hyperscanning application with fnirs. *Current Psychology*, 38:991–1002.

Balconi, M., Fronda, G., and Vanutelli, M. E. (2020). When gratitude and cooperation between friends affect inter-brain connectivity for eeg. *BMC neuroscience*, 21:1–12.

Barker, J. W., Aarabi, A., and Huppert, T. J. (2013). Autoregressive model based algorithm for correcting motion and serially correlated errors in fnirs. *Biomedical optics express*, 4(8):1366–1379.

Bates, D. et al. (2005). Fitting linear mixed models in r. *R news*, 5(1):27–30.

Bizzego, A., Azhari, A., Campostrini, N., Truzzi, A., Ng, L. Y., Gabrieli, G., Bornstein, M. H., Setoh, P., and Esposito, G. (2019a). Strangers, friends, and lovers show different physiological synchrony in different emotional states. *Behavioral Sciences*, 10(1):11.

Bizzego, A., Battisti, A., Gabrieli, G., Esposito, G., and Furlanello, C. (2019b). pyphysio: A physiological signal processing library for data science approaches in physiology. *SoftwareX*, 10:100287.

Bizzego, A., Carollo, A., Lim, M., and Esposito, G. (2024). Effects of individual research practices on fnirs signal quality and latent characteristics. *IEEE Transactions on Neural Systems and Rehabilitation Engineering*.

Bizzego, A., Gabrieli, G., and Esposito, G. (2021). Deep neural networks and transfer learning on a multivariate physiological signal dataset. *Bioengineering*, 8(3):35.

Bizzego, A., Neoh, M., Gabrieli, G., and Esposito, G. (2022). A machine learning perspective on fnirs signal quality control approaches. *IEEE Transactions on Neural Systems and Rehabilitation Engineering*, 30:2292–2300.

Bornstein, M. H. and Esposito, G. (2023). Coregulation: A multilevel approach via biology and behavior. *Children*, 10(8):1323.

Bowlby, J. and Holmes, J. (2012). *A secure base*. Routledge.

Carollo, A. and Esposito, G. (2024). Hyperscanning literature after two decades of neuroscientific research: A scientometric review. *Neuroscience*, 551:345–354.

Carollo, A., Lim, M., Aryadoust, V., and Esposito, G. (2021). Interpersonal synchrony in the context of caregiver-child interactions: A document co-citation analysis. *Frontiers in psychology*, 12:701824.

Carollo, A., Stella, M., Lim, M., Bizzego, A., and Esposito, G. (2025). Emotional content and semantic structure of dialogues are associated with interpersonal neural synchrony in the prefrontal cortex. *NeuroImage*, 121087.

Carr, L., Iacoboni, M., Dubeau, M.-C., Mazziotta, J. C., and Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proceedings of the national Academy of Sciences*, 100(9):5497–5502.

Cui, X., Bryant, D. M., and Reiss, A. L. (2012). Nirs-based hyperscanning reveals increased interpersonal coherence in superior frontal cortex during cooperation. *NeuroImage*, 59(3):2430–2437.

De Felice, S., Chand, T., Croy, I., Engert, V., Goldstein, P., Holroyd, C. B., Kirsch, P., Krach, S., Ma, Y., Scheele, D., et al. (2024a). Relational neuroscience: insights from hyperscanning research. *Neuroscience & Biobehavioral Reviews*, page 105979.

De Felice, S., Hakim, U., Gunasekara, N., Pinti, P., Tachtsidis, I., and Hamilton, A. (2024b). Having a chat and then watching a movie: how social interaction synchronises our brains during co-watching. *Oxford Open Neuroscience*, 3:kvae006.

Delpy, D. T., Cope, M., van der Zee, P., Arridge, S., Wray, S., and Wyatt, J. (1988). Estimation of optical pathlength through tissue from direct time of flight measurement. *Physics in Medicine & Biology*, 33(12):1433.

Endevelt-Shapira, Y. and Feldman, R. (2023). Mother–infant brain-to-brain synchrony patterns reflect caregiving profiles. *Biology*, 12(2):284.

Feldman, R. (2007). Parent–infant synchrony: Biological foundations and developmental outcomes. *Current directions in psychological science*, 16(6):340–345.

Feldman, R. (2012). Parent-infant synchrony: A biobehavioral model of mutual influences in the formation of affiliative bonds. *Monographs of the Society for Research in Child Development*, 77(2):42–51.

Feldman, R. (2017). The neurobiology of human attachments. *Trends in cognitive sciences*, 21(2):80–99.

Fishburn, F. A., Murty, V. P., Hlutkowsky, C. O., MacGillivray, C. E., Bemis, L. M., Murphy, M. E., Huppert, T. J., and Perlman, S. B. (2018). Putting our heads together: interpersonal neural synchronization as a biological mechanism for shared intentionality. *Social cognitive and affective neuroscience*, 13(8):841–849.

Gallagher, H. L., Happé, F., Brunswick, N., Fletcher, P. C., Frith, U., and Frith, C. D. (2000). Reading the mind in cartoons and stories: an fmri study of 'theory of mind'in verbal and nonverbal tasks. *Neuropsychologia*, 38(1):11–21.

Grinsted, A., Moore, J. C., and Jevrejeva, S. (2004). Application of the cross wavelet transform and wavelet coherence to geophysical time series. *Nonlinear processes in geophysics*, 11(5/6):561–566.

Gvirts, H. Z. and Perlmutter, R. (2020). What guides us to neurally and behaviorally align with anyone specific? a neurobiological model based on fnirs hyperscanning studies. *The Neuroscientist*, 26(2):108–116.

Gweon, H., Dodell-Feder, D., Bedny, M., and Saxe, R. (2012). Theory of mind performance in children correlates with functional specialization of a brain region for thinking about thoughts. *Child development*, 83(6):1853–1868.

Hasson, U., Ghazanfar, A. A., Galantucci, B., Garrod, S., and Keysers, C. (2012). Brain-to-brain coupling: a mechanism for creating and sharing a social world. *Trends in cognitive sciences*, 16(2):114–121.

Hollenstein, T., Tighe, A. B., and Lougheed, J. P. (2017). Emotional development in the context of mother–child relationships. *Current opinion in psychology*, 17:140–144.

Iacoboni, M. (2005). Neural mechanisms of imitation. *Current opinion in neurobiology*, 15(6):632–637.

Keuken, M. C., Hardie, A., Dorn, B., Dev, S., Paulus, M., Jonas, K., Van Den Wildenberg, W., and Pineda, J. (2011). The role of the left inferior frontal gyrus in social perception: an rtms study. *Brain research*, 1383:196–205.

Kinreich, S., Djalovski, A., Kraus, L., Louzoun, Y., and Feldman, R. (2017). Brain-to-brain synchrony during naturalistic social interactions. *Scientific reports*, 7(1):17060.

Kolk, S. M. and Rakic, P. (2022). Development of prefrontal cortex. *Neuropsychopharmacology*, 47(1):41–57.

Krall, S. C., Rottschy, C., Oberwelland, E., Bzdok, D., Fox, P. T., Eickhoff, S. B., Fink, G. R., and Konrad, K. (2015). The role of the right temporoparietal junction in attention and social interaction as revealed by ale meta-analysis. *Brain Structure and Function*, 220:587–604.

Kuhl, P. K. (2007). Is speech learning 'gated'by the social brain? *Developmental science*, 10(1):110–120.

Kuhl, P. K. (2011). Early language learning and literacy: Neuroscience implications for education. *Mind, brain, and education*, 5(3):128–142.

Leclère, C., Viaux, S., Avril, M., Achard, C., Chetouani, M., Missonnier, S., and Cohen, D. (2014). Why synchrony matters during mother-child interactions: a systematic review. *PloS one*, 9(12):e113571.

Liakakis, G., Nickel, J., and Seitz, R. (2011). Diversity of the inferior frontal gyrus—a meta-analysis of neuroimaging studies. *Behavioural brain research*, 225(1):341–347.

Lim, M., Carollo, A., Bizzego, A., Chen, A. S., and Esposito, G. (2024a). Culture, sex and social context influence brain-to-brain synchrony: an fnirs hyperscanning study. *BMC psychology*, 12(1):350.

Lim, M., Carollo, A., Bizzego, A., Chen, A. S., and Esposito, G. (2024b). Synchrony within, synchrony without: establishing the link between interpersonal behavioural and brain-to-brain synchrony during role-play. *Royal Society Open Science*, 11(9):240331.

Liu, T., Duan, L., Dai, R., Pelowski, M., and Zhu, C. (2021). Team-work, team-brain: exploring synchrony and team interdependence in a nine-person drumming task via multiparticipant hyperscanning and inter-brain network topology with fnirs. *NeuroImage*, 237:118147.

Long, Y., Zheng, L., Zhao, H., Zhou, S., Zhai, Y., and Lu, C. (2021). Interpersonal neural synchronization during interpersonal touch underlies affiliative pair bonding between romantic couples. *Cerebral Cortex*, 31(3):1647–1659.

Lyons, D. E., Santos, L. R., and Keil, F. C. (2006). Reflections of other minds: how primate social cognition can inform the function of mirror neurons. *Current opinion in neurobiology*, 16(2):230–234.

Meng, X., Sun, C., Du, B., Liu, L., Zhang, Y., Dong, Q., Georgiou, G. K., and Nan, Y. (2022). The development of brain rhythms at rest and its impact on vocabulary acquisition. *Developmental science*, 25(2):e13157.

Nguyen, T., Schleihauf, H., Kayhan, E., Matthes, D., Vrtička, P., and Hoehl, S. (2020). The effects of interaction quality on neural synchrony during mother-child problem solving. *cortex*, 124:235–249.

Nguyen, T., Schleihauf, H., Kayhan, E., Matthes, D., Vrtička, P., and Hoehl, S. (2021a). Neural synchrony in mother–child conversation: Exploring the role of conversation patterns. *Social Cognitive and Affective Neuroscience*, 16(1-2):93–102.

Nguyen, T., Schleihauf, H., Kungl, M., Kayhan, E., Hoehl, S., and Vrtička, P. (2021b). Interpersonal neural synchrony during father–child problem solving: an fnirs hyperscanning study. *Child development*, 92(4):e565–e580.

Pan, Y., Cheng, X., Zhang, Z., Li, X., and Hu, Y. (2017). Cooperation in lovers: an f nirs-based hyperscanning study. *Human brain mapping*, 38(2):831–841.

Reindl, V., Gerloff, C., Scharke, W., and Konrad, K. (2018). Brain-to-brain synchrony in parent-child dyads and the relationship with emotion regulation revealed by fnirs-based hyperscanning. *NeuroImage*, 178:493–502.

Reyna, B. A. and Pickler, R. H. (2009). Mother-infant synchrony. *Journal of Obstetric, Gynecologic & Neonatal Nursing*, 38(4):470–477.

Samson, D., Apperly, I. A., Chiavarino, C., and Humphreys, G. W. (2004). Left temporoparietal junction is necessary for representing someone else's belief. *Nature neuroscience*, 7(5):499–500.

Santosa, H., Aarabi, A., Perlman, S. B., and Huppert, T. J. (2017). Characterization and correction of the false-discovery rates in resting state connectivity using functional near-infrared spectroscopy. *Journal of Biomedical Optics*, 22(5):055002–055002.

Shao, C., Zhang, X., Wu, Y., Zhang, W., and Sun, B. (2023). Increased interpersonal brain synchronization in romantic couples is associated with higher honesty: An fnirs hyperscanning study. *Brain sciences*, 13(5):833.

Stern, D. N. (2009). *The first relationship*. Harvard University Press.

Toppi, J., Borghini, G., Petti, M., He, E. J., De Giusti, V., He, B., Astolfi, L., and Babiloni, F. (2016). Investigating cooperative behavior in ecological settings: an eeg hyperscanning study. *PloS one*, 11(4):e0154236.

Trevarthen, C. (1998). The concept and foundations of infant intersubjectivity. In Bråten, S., editor, *Intersubjective communication and emotion in early ontogeny*, pages 15–46. Cambridge University Press.

Van Overwalle, F. (2009). Social cognition and the brain: a meta-analysis. *Human brain mapping*, 30(3):829–858.

Vygotsky, L. S. (1978). *Mind in society: The development of higher psychological processes*, volume 86. Harvard university press.

Wang, J., Yang, Y., Zhao, X., Zuo, Z., and Tan, L.-H. (2020). Evolutional and developmental anatomical architecture of the left inferior frontal gyrus. *NeuroImage*, 222:117268.

Zimeo Morais, G. A., Balardin, J. B., and 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.