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Received: 31 August 2025

Accepted: 22 April 2026

Cite this article as: Schwartz, L., Shilo, C., Hayut, O. *et al.* Inter-brain processes during *Live* and *Represented* social moments are inter-related and shaped by behavioral synchrony. *Commun Psychol* (2026). <https://doi.org/10.1038/s44271-026-00468-x>

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## **Inter-brain Processes during *Live* and *Represented* Social Moments are Inter-related and Shaped by Behavioral Synchrony**

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Keywords: Social Neuroscience, Hyperscanning, EEG, Synchrony

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**Abstract**

Inter-brain synchrony has recently emerged as core mechanism of brain functioning. Two approaches distinctly measure cross-brain processes; during live social exchanges or passive observation of social stimuli, but are the two underpinned by similar processes? Guided by the *biobehavioral synchrony* frame, we utilized hyperscanning EEG and a paradigm developed for the current study to explore the linkage between inter-brain synchrony during *Live* and *Represented* social experiences. In Study 1 (n=130) mother-adolescent dyads engaged in free interaction, coded for behavioral synchrony, and then observed this interaction in separate rooms. Greater neural synchrony across the fronto-temporal inter-brain network emerged during live social participation than passive observation of represented social moments, and the two were inter-related and predicted by behavioral synchrony. Study 2 (n=54) tested the generalizability of the findings in unfamiliar adults and similarly found linkage between neural synchrony during live and represented experiences, both associated with behavioral synchrony. Shared social experiences create lasting neural synchrony that can be reactivated during subsequent invocation and depends on relationship quality and familiarity. Findings highlight the role of live social moments and their retention in memory in shaping the social brain and have implications for the integration of the third- and second-person perspectives in social neuroscience.

## 1. Introduction

Humans are fundamentally social beings whose survival and success depend on the ability to navigate complex social environments, understand others' intentions, and coordinate behavior with others<sup>1,2</sup>. From the earliest moments of life, humans must rapidly acquire the skills for effective interpersonal functioning, including reading emotional expressions, understanding social hierarchies, and predicting others' behavior<sup>3,4</sup>. These social competencies emerge through two primary social learning mechanisms: actively participating in social interactions and passively observing others' social behavior<sup>5-7</sup>. Despite their natural co-occurrence and joint role in social learning, neuroscience research has traditionally examined these processes in isolation, creating a critical gap in our understanding of how the brain integrates social information acquired through active participation and passive observation of represented social experiences.

### ***Divergent methodological approaches into the brain basis of social learning***

The methodological divide has resulted in two distinct traditions that approach social cognition from fundamentally different perspectives. Decades of neuroimaging research on passive observation of social interactions have pinpointed activations within the fronto-temporal network across two core systems. The mentalizing network, anchored in areas such as the medial prefrontal cortex (mPFC) and temporal-parietal junction (TPJ), processes mental states, beliefs, and intentions from a third-person perspective<sup>8,9</sup>, and the social perception network, centered on the superior temporal sulcus (STS), processes biological motion and social cues<sup>10,11</sup>.

In contrast, hyperscanning studies measure how brains align during live social exchanges, focusing on how brains participate in active social moments and create shared neural networks across two brains in real time. These studies have similarly demonstrated neural synchronization within these same fronto-temporal regions across a variety of social interaction tasks, including cooperation<sup>12-14</sup>, joint attention<sup>15,16</sup>, and naturalistic conversations<sup>17-</sup>

<sup>19</sup>. Neural coupling has shown to be strongest between attachment partners<sup>20</sup>, particularly mother-child pairs who display strong fronto-temporal inter-brain network activation in studies spanning infancy, childhood, and adolescence <sup>19,21–28</sup>.

### ***Convergent neural substrate, divergent mechanisms***

While these methodologically distinct approaches converge on the fronto-temporal network as their common neural substrate, a system involved in social cognition, social attention, mental state inference, theory of mind and social semantic knowledge<sup>8–11,29–31</sup>, further research is needed to directly evaluate the neural underpinnings of active and passive social experiences within the same experimental design. This critically limits our understanding of the overlapping or distinct neural mechanisms that operate across live and represented or invoked social experiences and combine the third- and second-person perspectives in social neuroscience. Existing evidence hints at a differential engagement of this network, suggesting that live social conditions elicit enhanced activations in temporal brain regions, such as the right STS, which reflect greater neural engagement and physiological arousal during live social moments compared to observational conditions <sup>32</sup>. Similarly, the mere belief in participation in a live social interaction enhances activations in temporal brain regions as compared to viewing recorded interactions <sup>33</sup>. However, these single-brain results do not shed light on how two brains align during active participation versus passive observation of the same social content.

### ***Developmental foundations of dual-pathway social learning***

To understand the inter-brain mechanisms that underpin social learning, it is particularly important to adopt a developmental perspective, due to the fact that fronto-temporal networks follow a protracted maturational trajectory and their functional specialization continues across childhood and adolescence. Such extended development may explain why the effects of early social experiences persist over time, as the same networks supporting early social coordination continue to mature and reorganize throughout development <sup>34,35</sup>.

Adopting a developmental framework highlights the mother-child relationship as the foundational context for maturation of the social brain and the importance of the mother's matched, well-attuned behavior as the primary organizer of the child's neural architecture. *Biobehavioral synchrony* refers to the coordinated social behavior between mother and child that creates the template for neural coordination, and tunes infants' neural systems for social participation and shapes their social brain development<sup>36–38</sup>. The profound impact of such neural attunement extends beyond the immediate interaction period and supports lasting neural reorganization. Longitudinal studies demonstrate that sensitive and synchronous maternal care predict enhanced brain development years later, including larger hippocampal volumes<sup>39</sup>, increased gray matter volume<sup>40</sup>, and greater functional connectivity between the default mode and salience networks at school age<sup>41</sup>. Conversely, maternal intrusive behavior disrupts the neural tuning process, leading to aberrant neural responses to social stimuli and disrupted default mode network connectivity in adolescence<sup>42,43</sup>.

Recent hyperscanning research has begun to illuminate how behavioral synchrony patterns translate into neural coordination. Synchronous mother-child behaviors have been associated with greater inter-brain synchrony in fronto-temporal networks during live interactions<sup>19,21,22,24,25,44</sup>. Moreover, behavioral synchrony in infancy was found to predict enhanced neural synchrony in adolescence<sup>24</sup>, demonstrating a lasting effect of behavioral synchrony on the social brain. These findings suggest that behavioral synchrony not only shapes individual social brain development, but also impacts the brain's propensity for interbrain processes and creates enduring neural templates that influence how the fronto-temporal network would respond to social experiences broadly. Given its pervasive impact on social brain development of both the single brain and two-brain coordination, behavioral synchrony may provide a link between neural coordination of the fronto-temporal network during active participation in live social experiences and passive observation of represented social stimuli.

In addition to active social participation, studies have shown that passive observation of social interactions plays an important role in social brain development when infants and children acquire core social knowledge, not only through direct interaction with their caregivers, but also by observing social exchanges around them. Such observational learning engages neural networks that overlap with those involved in direct social interactions, as revealed by fNIRS and EEG studies. Findings demonstrate that infants' motor areas activate when observing live actions<sup>45</sup>, with gamma oscillatory activity in response to direct gaze at 4 months<sup>46</sup> and differential neural responses to emotional expressions by 8 months<sup>47</sup>. Passive observational learning is particularly important for acquiring complex social skills, such as theory of mind, where children must understand others' mental states through observation before they can effectively engage in reciprocal social interactions<sup>48,49</sup>.

The aforementioned studies indicating overlapping neural networks that activate during both active participation and passive observation, combined with evidence that mother-child behavioral synchrony creates enduring neural templates that persist across development lend support to the hypothesis that behavioral synchrony, which enhances inter-brain coordination during live interactions, may engage similar fronto-temporal network patterns when social experiences are passively observed, albeit this engagement may come in a more attenuated format as compared to real-time participation. Together, these findings suggest that the same *biobehavioral synchrony* mechanisms that tune the developing brain to social participation may enable graded reactivation of the shared neural coordination patterns across the two fundamental modes of social learning.

### ***Integrating live and represented social moments***

As seen, there is a critical gap in our understanding of how active and passive social processing interact in real-world contexts. Adding to this complexity, the term "neural synchrony" represents different phenomena across two neuroimaging traditions. In the context

of fMRI studies the term synchrony often refers to the same activation of brain areas and networks in response to the same time-bound stimuli, like a movie or a story<sup>50–52</sup>. On the other hand, in hyperscanning EEG and fNIRS studies, neural synchrony refers to the joint activation of brain areas or neural networks among two partners engaged in a live social interaction or social task<sup>53</sup>. Here, we bridge the two approaches by evaluating inter-brain synchrony both when two people engage in live interaction and when they subsequently observe their own recorded interaction, thereby combining the second-person perspective of active social participation with the third-person perspective of observing represented social experiences.

For the study, we developed a paradigm where people participate in live social interaction and then observe the same interaction from separate rooms while inter-brain synchrony in the fronto-temporal network is assessed. Unlike studies of passive observation that use unfamiliar protagonists, viewing one's own social interactions engages self-referential processing, autobiographical memory retrieval, and likely reactivates mental states associated with the original interaction<sup>54,55</sup>. Our paradigm can therefore tap into mechanisms of neural reinstatement whereby observing one's own social interactions reactivates neural patterns that were active during the original experience and triggered interpersonal neural synchrony<sup>56,57</sup>.

According to our *biobehavioral synchrony* model<sup>36,38,58</sup>, children are tuned to behavioral and neural synchrony within the context of the mother-child attachment. We thus began our exploration of how neural coupling manifests across both live and represented experiences with mothers and adolescents. To assess whether our findings are limited to attachment contexts or feature a human-general phenomenon, we then tested our paradigm in stranger adult pairs.

### ***The current study***

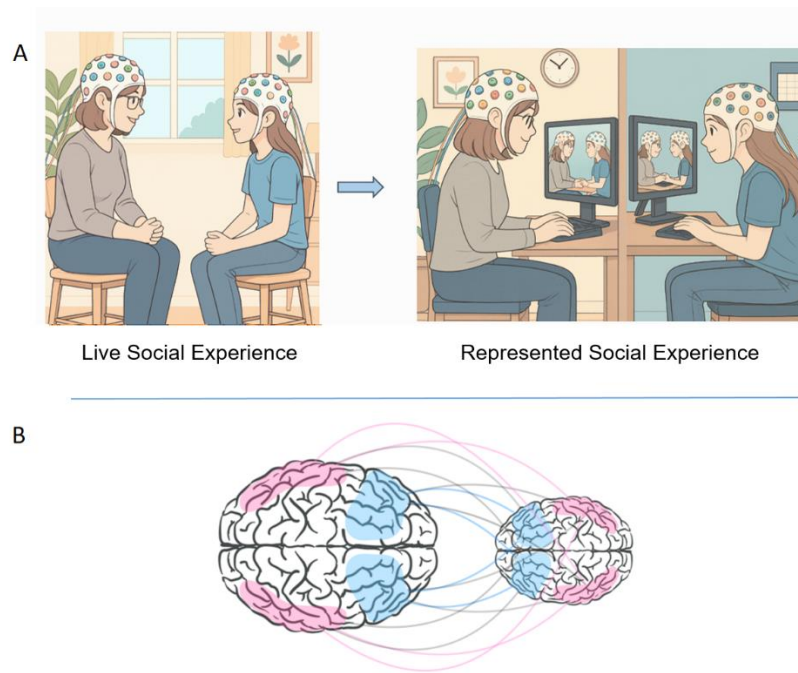
We recorded neural activity from mother-adolescent dyads and stranger dyads while they engaged in face-to-face positively-valenced interaction (*Live Social Experience*) and when they simultaneously viewed videos of their own recorded interaction from separate rooms (*Represented Social Experience*). This design enabled direct comparison of neural coupling



during active participation versus passive observation of the same social content. Three primary hypotheses were formulated. First, we expected to see significant inter-brain synchrony across all paradigms and groups, in both *Live Social Experience* and *Represented Social Experience*, and in both attachment partners and unfamiliar adults.

Second, we expected greater inter-brain synchrony during active participation compared to passive observation, particularly among mother-adolescent dyads. According to our *biobehavioral synchrony* model, participating in matched social dialogue with the mother prepares the child's brain for the possibility of inter-brain synchrony. Whether a stronger activation will be found during participation as compared to observation among stranger adults, once the brain has already been tuned to neural coupling, remained an open research question. We further expected the two processes to be linked in both groups. That is, greater neural synchrony during the live social interaction would predict greater neural synchrony when this interaction is represented, validating the link between neural activity during a social event and during the retrieval of this event from memory with regards to two-brain mechanisms.

Third, the degree of behavioral synchrony during the interaction, the degree to which the partner's signals are acknowledged and reciprocated, and the degree to which the interaction is flowing, positive, and engaged, would be associated with the degree of neural coupling both during the social event and during its invocation in the observation part. This would illuminate how individual differences in dyadic coordination influence neural processing of social memories, pinpointing mechanisms by which interpersonal experiences shape lasting neural representations.



**Fig. 1. Experimental procedure for investigating neural synchrony during *Live and Represented Social Experiences*.** A. Study design and procedure. Participants first engaged in a 3-minute naturalistic face-to-face interaction (*Live Social Experience*) while neural activity was recorded via dual EEG hyperscanning. The interaction was video-recorded for subsequent behavioral synchrony coding using the Coding Interactive Behavior (CIB) system. Participants were then separated into different rooms and simultaneously viewed their own previously recorded interaction (*Represented Social Experience*), enabling neural reactivation of shared social memories. This design allowed direct comparison of neural coupling during identical social content experienced through active participation versus passive observation. Study 1:  $n = 65$  mother-adolescent dyads; Study 2:  $n = 27$  stranger dyads. B. Fronto-temporal network architecture. Schematic representation of the four bilateral regions of interest (ROIs) analyzed: left and right frontal (blue) and temporal (pink) areas across both participants. The network comprises 16 total inter-brain connections (4 ROIs per participant  $\times$  4 ROIs of partner). Neural synchrony was quantified using weighted phase lag index (wPLI) for each inter-brain connection.

## 2. Methods

### 2.1 Participants

**Study 1:** 65 mother-adolescent dyads (130 participants) were recruited through community center advertisements and social media platforms. All mothers self-reported as biological mothers and primary caregivers. Mothers' mean age was 43.93 years ( $SD = 4.26$ ), and adolescents' mean age was 12.13 years ( $SD = 1.42$ ), with 29 males and 36 females (gender information was provided by the participants). All participants self-reported being

physically and mentally healthy and all adolescents were enrolled in mainstream public schools. Written informed consent was obtained from mothers for themselves and their children. While only the mothers, being the legal guardians, signed the consent forms, the paradigm was explained to both participants, and both were informed that they may withdraw from the experiment at any moment with no penalty and receive full compensation.

**Study 2:** 27 stranger dyads (54 participants) were recruited through the same channels. Participants' mean age was 27.3 years ( $SD = 4.7$ ), with 37 females and 17 males. Strangers were matched for age ( $\pm 5$  years) and had no prior acquaintance.

For both studies, experimental procedures were explained beforehand, and participants were informed of their right to withdraw while retaining full compensation (\$30/hour). Studies were approved by the Reichman University Institutional Ethics Committee and conducted in accordance with relevant guidelines and regulations.

A preregistration for the broader research project was submitted on October 7, 2020, and is available on OSF (<https://osf.io/swun7/>). However, none of the hypotheses or analyses reported in the current manuscript were preregistered. The preregistration addresses a related but distinct experimental paradigm within the same broader project. The three hypotheses tested in the current study are exploratory and emerged as distinct research questions during the project's development. The overall preregistration is cited solely for transparency.

## **2.2 Sample Specifications and Exclusion Criteria**

Final sample sizes were determined by data quality thresholds and task completion rates. Dyads were excluded if they had fewer than 120 shared clean epochs with at least one other surrogate, the minimum we required for reliable surrogate control generation.

**Study 1:** From 65 recruited mother-adolescent dyads, analytical samples included  $n = 65$  (*Live Social Experience*) and  $n = 62$  (*Represented Social Experience*), with 3 dyads excluded due to insufficient data quality. Mediation analyses examining neural-behavioral

coupling required complete datasets across neural synchrony, and behavioral synchrony, yielding  $n = 58$  dyads, as CIB behavioral coding was unattainable for four dyads.

**Study 2:** From 27 recruited stranger dyads, analytical samples included  $n = 26$  for both conditions, with 1 dyad excluded for insufficient data quality in the *Live Social Experience* paradigm and 1 dyad not completing the *Represented Social Experience* paradigm. Comparison between the two conditions and complete mediation datasets were available for  $n = 25$  dyads.

Quality control procedures ensured robust inter-brain connectivity estimates and reliable statistical comparisons. Listwise deletion maintained complete case analysis across all measures, with final sample sizes reflecting the stringent data quality requirements necessary for dual-brain hyperscanning analyses.

### 2.3 Procedure

Dyads engaged in a 3-minute naturalistic face-to-face interaction (*Live Social Experience*) discussing positive topics (planning activities, trips, or outings), counterbalanced across participants to elicit natural social engagement. During this condition, participants were seated at approximately 45° angles to each other, to enable direct observation of facial expressions and nonverbal behavior, while the interaction was recorded simultaneously by four cameras positioned strategically around the room. Participants were then separated into different rooms and simultaneously viewed a recording of their own previous interaction (*Represented Social Experience*), with footage from the frontal camera providing consistent, optimal frontal views of both participants' facial expressions throughout the *Live Social Experience*.

In Study 1, mother-adolescent dyads also completed a non-social control condition in which they simultaneously viewed a 3-minute neutral nature clip that depicts landscapes and animals accompanied by music (*Nature Movie*) from separate rooms using an identical viewing setup to the *Represented Social Experience* condition.

Each experimental condition lasted 3 minutes, and we selected this duration on the basis of prior work indicating that comparable paradigm lengths reliably detect robust inter-brain synchrony across developmental periods and relationship contexts. Previous hyperscanning studies have successfully employed interaction paradigms of 2-3 minutes to identify significant neural coupling in infancy<sup>25,28</sup>, adulthood<sup>20,59</sup>, and mother-adolescent dyads in both face-to-face and remote interaction contexts<sup>19,21–23</sup>. Neural activity was recorded continuously across all experimental conditions using dual EEG systems with synchronized time-locking (see Fig. 1). Analyses focused on the first two minutes of each condition, consistent with the analytic approach employed in prior hyperscanning studies from our laboratory<sup>19,22–25,28</sup>.

#### **2.4 Dual EEG Data Acquisition**

Neural activity was recorded simultaneously from both participants using a 64-channel BrainAmp amplifier (Brain Products, Germany) with dual 32-electrode BrainCaps arranged according to the international 10/10 system. Continuous EEG data were acquired at 1000 Hz with analog bandpass filtering (0.1–500 Hz). Electrode impedances were maintained below 10 k $\Omega$ , with AFz serving as the ground electrode. To ensure precise temporal synchronization between participants, both EEG caps were connected to a single amplifier, enabling millisecond-level accuracy for inter-brain connectivity analyses.

#### **2.5 EEG Preprocessing**

EEG preprocessing was conducted using Python 3.8 and the MNE software package (v0.17.0). EEG recording of each dyad was separated into two individual files to enable participant-specific preprocessing. Data were re-referenced to Cz and filtered (1-50 Hz) following established hyperscanning protocols. Signals were segmented into 1000 ms epochs with 500 ms overlap for optimal time-frequency resolution. Artifact removal employed a two-stage approach: automated detection using Bayesian optimization algorithms to identify channel-specific artifacts, followed by Independent Component Analysis (ICA) using fastica and CORRMAP implementations<sup>60</sup>. Components reflecting ocular, muscular, and other non-neural

artifacts were manually identified and removed, with standardized templates applied across all participants to ensure consistent preprocessing.

### **2.6 Inter-brain Connectivity Analysis of the Fronto-Temporal Network**

Inter-brain synchrony was quantified using the weighted phase lag index (wPLI), a robust connectivity measure that minimizes volume conduction artifacts while preserving genuine neural coupling<sup>61</sup>. The wPLI emphasizes consistent non-zero phase relationships between neural oscillations across participants, providing reliable estimates of inter-brain coordination in naturalistic settings.

Connectivity analysis focused on beta-band oscillations (13.5-29.5 Hz) based on extensive evidence linking beta synchrony to social coordination, empathy, and joint attention across diverse social contexts and relationship types, and have been consistently associated with mentalizing processes, cooperative behavior, and inter-brain coupling during both direct social interaction and shared stimulus processing<sup>19–24,59,62–65</sup>.

Analytic signals were computed using IIR filtering with Hamming windows, followed by Hilbert transformation. The analysis targeted four bilateral fronto-temporal regions of interest (ROIs): left frontal (F3, F7), right frontal (F4, F8), left temporal (T7, P7), and right temporal (T8, P8). Electrode regions are referenced by their approximate cortical correspondence (e.g., 'frontal', 'temporal') following the 10-20 system conventions, so that our terminology reflects scalp topography, not precise source localization. For each inter-brain ROI pair, wPLI values were calculated between all electrode combinations and averaged, yielding 16 possible inter-brain connectivity links across participants. Following validation of uniform effects across ROIs, connectivity values were averaged across all fronto-temporal links to provide a comprehensive measure of inter-brain network synchrony.

### **2.7 CIB coding**

Behavioral synchrony during face-to-face interactions was assessed using the Coding Interactive Behavior (CIB) manual<sup>66</sup>, a validated observational system with over 300 published

applications across diverse populations and contexts, and has been successfully implemented in hyperscanning research<sup>19–22,25</sup>. The CIB employs 52 codes rated on 5-point scales that are aggregated or averaged into theoretically-based constructs. This study utilized the Behavioral Synchrony construct, adapted for each sample's relational context.

In adolescence, during interaction with their parents that involves different ages and power imbalance, *Behavioral synchrony* comprises the following codes: mutual affectionate touch, child involvement and positive affect and maternal involvement and positive affect, joint regulation, expansion and reciprocity, openness, and mother allowing child to lead conversation. For adults, the interaction between two people of roughly the same age and equal status, *Behavioral Synchrony* included: empathy, understanding the other's perspective, supportive presence, openness, containment, reciprocity, and relaxed mood. The CIB uses different scales to evaluate synchrony at different ages. In adolescence, the mother-adolescent relationship still involves power imbalance and children still depend on their mothers during the interaction. In adulthood, where there's no power imbalance, the degree two interactors can share, empathize, flow, and see each other's perspective are the key components of adult synchrony.

Coding was performed by trained raters blind to study hypotheses. Inter-rater reliability was established on 20% of interactions, with all codes achieving >90% agreement (ICC = 0.93, range = 0.89-0.99). Behavioral measures were subsequently analyzed in relation to neural synchrony to examine brain-behavior coupling mechanisms.

## **2.8 Statistical Analysis**

### **2.8.1 Validation Analysis**

Neural synchrony specificity was validated by comparing real dyad connectivity against surrogate controls for each experimental condition. Surrogate data were generated by pairing participants across different dyads (mother from dyad A with adolescent from dyad B, or participant 1 from dyad A with participant 2 from dyad B), creating all possible cross-dyad

combinations. Only surrogate pairs meeting the 120 clean epoch threshold were included, ensuring equivalent data quality between real and surrogate comparisons.

Surrogate connectivity values were computed using identical wPLI procedures. For each original dyad, connectivity values from all possible surrogate combinations were averaged to create a single representative surrogate value, ensuring robust baseline estimates. Validation employed repeated-measures ANOVA with Data Type (real vs. surrogate) and ROI (16 inter-brain link combinations) as within-subject factors, establishing genuine inter-brain coupling above chance-level connectivity.

### **2.8.2 Comparing Inter-brain Synchrony across Social Experience Types**

Direct comparisons of neural coupling between *Live* and *Represented Social Experiences* assessed differences in inter-brain synchrony by comparing the increase in inter-brain connectivity relative to surrogate data ( $\Delta wPLI$ ) across the fronto-temporal network in each condition. Repeated-measures ANOVA with Condition (*Live* vs. *Represented Social Experience*) and ROI (16 inter-brain link combinations) as within-subject factors quantified differential neural synchrony patterns across active participation versus passive observation of identical social content. When statistical assumptions were violated, appropriate corrections (such as Greenhouse-Geisser (GG) correction) were applied.

### **2.8.3 Brain-Behavior Analysis**

Mediation analyses examined whether behavioral synchrony mediates the relationship between *Live Social Experience* neural synchrony (predictor) and *Represented Social Experience* neural synchrony (outcome), testing how behavioral synchrony during the *Live* face-to-face interaction influences subsequent neural reactivation during *Represented* social processing.

Analyses were conducted using Python 3.8 with pandas and statsmodels packages on complete case samples (Study 1:  $n = 58$ ; Study 2:  $n = 25$ ). Prior to the mediation testing,



Pearson correlations assessed relationships between all variables to establish prerequisite associations for mediation analysis.

The mediation framework followed standard procedures using ordinary least squares regression: (1) total effect of *Live Social Experience* neural synchrony on predicting *Represented Social Experience* neural synchrony (path *c*), (2) effect of *Live Social Experience* neural synchrony on predicting behavioral synchrony (path *a*), (3) full model with both *Live Social Experience* neural synchrony and behavioral synchrony predicting *Represented Social Experience* neural synchrony (paths *c'* and *b*), and indirect effect calculation via bootstrap estimation (20,000 iterations). Bootstrap resampling provided empirical confidence intervals and significance tests without distributional assumptions, particularly advantageous for smaller samples where normality violations may occur. Proportion mediated was calculated as the ratio of indirect to total effect, quantifying the percentage of the relationship explained through behavioral pathways.

#### 2.8.4 - Statistical Power — Sensitivity Analysis

Sensitivity power analyses were conducted to determine the minimum effect sizes detectable at  $\alpha = 0.05$  with 80% power, given the study's sample sizes. For the primary condition comparison (repeated-measures ANOVA, *Live Social Experience* vs. *Represented Social Experience*), the mother-adolescent sample ( $n = 62$ ) could detect effects as small as  $\eta^2p = 0.12$ , while the stranger sample ( $n = 25$ ) could detect effects as small as  $\eta^2p = 0.25$ . For the three-way condition comparison (*Live Social Experience* vs. *Represented Social Experience* vs. *Nature Movie*;  $n = 58$ ), the minimum detectable effect was  $\eta^2p = 0.05$ . Validation analyses comparing real versus surrogate dyads were powered to detect effects of  $\eta^2p = 0.11$  for the mother-adolescent sample ( $n = 62$ – $65$ ) and  $\eta^2p = 0.25$  for the strangers sample ( $n = 26$ ), values that were well below the observed effects in both samples ( $\eta^2p = 0.52$ – $0.87$ ).

For the Pearson correlation analyses, the mother-adolescent sample ( $n = 60$ – $64$ ) could detect correlations of  $r \geq 0.34$ , so that all three observed correlations ( $r = 0.35$ – $0.59$ ) fell at or

above the relevant threshold. The stranger sample ( $n = 27-28$ ) required larger effects ( $r \geq 0.50$ ) for adequate power, indicating that the marginally significant interaction between *Live Social Experience* and Behavioral Synchrony ( $r = 0.35$ ) was underpowered, while the *Represented Social Experience* and Behavioral Synchrony correlation ( $r = 0.54$ ) was adequately powered.

For the regression-based mediation analyses, the mother-adolescent sample ( $n = 58$ ) could detect model effects of  $R^2 \geq 0.12$  (for a single predictor) and  $R^2 \geq 0.15$  (for two predictors), and the stranger sample ( $n = 25$ ) required  $R^2 \geq 0.26$  (single predictor) and  $R^2 \geq 0.31$  (two predictors). The full mediation models in both samples exceeded these thresholds ( $R^2 = 0.45$  and  $R^2 = 0.37$ , respectively). Between-group Welch's t-tests ( $n = 62$  vs.  $n = 25$ ) could detect differences of Cohen's  $d \geq 0.67$ . The observed effect for *Live Social Experience* ( $d = 0.76$ ) exceeded this threshold, while the *Represented Social Experience* comparison ( $d = 0.51$ ) fell below it, though the effect was nonetheless statistically significant ( $p = 0.014$ ). The complete sensitivity calculations are reported in Supplementary Table 2.

### ***Data visualization and figures***

All figures in this manuscript were created by the authors or were generated using custom scripts available at - <https://osf.io/57m94/overview>.

### ***Declaration of generative AI and AI-assisted technologies in the writing process***

During the preparation of this work, we employed AI tools only to improve the language and readability of the paper, and to generate illustrations for the dyads throughout the interactions. After using this tool, humans reviewed and edited the content as needed, and take full responsibility for the content of the publication.

### 3. Results

#### Study 1

##### 3.1 Neural synchrony validation: evidence for genuine inter-brain coupling

To establish that observed neural activity reflected genuine inter-brain coupling rather than spurious connectivity, we compared real mother-adolescent dyads to surrogate controls across all experimental conditions using separate repeated measures ANOVAs with Data Type (real vs. surrogate) and ROI (16 combinations) as factors for each experimental condition.

Real dyads demonstrated significantly greater neural synchrony than surrogate controls across both social conditions: during *Represented Social Experience* ( $F(1, 61) = 87.95, p < 0.001, \eta^2p = 0.59, 95\% \text{ CI} = [0.42, 0.69]$ ) and during *Live Social Experience* ( $F(1, 64) = 70.49, p < 0.001, \eta^2p = 0.52, 95\% \text{ CI} = [0.35, 0.64]$ ). ROI effects were non-significant during *Represented Social Experience* ( $F(15, 915) = 1.6, p = 0.069, \eta^2p = 0.025, 95\% \text{ CI} = [0.001, 0.04]$ , (GG-corrected  $p = 0.11, \varepsilon = 0.621$ )) and during *Live Social Experience* ( $F(15, 960) = 1.495, p = 0.1, \eta^2p = 0.02, 95\% \text{ CI} = [0.00, 0.03]$ , (GG-corrected  $p = 0.134, \varepsilon = 0.686$ )). Data Type  $\times$  ROI interactions were also non-significant in both conditions (*Represented Social Experience*:  $F(15, 915) = 1.22, p = 0.25, \eta^2p = 0.02, 95\% \text{ CI} = [0.00, 0.02]$ , (GG-corrected  $p = 0.279, \varepsilon = 0.651$ ); *Live Social Experience*:  $F(15, 960) = 0.82, p = 0.66, \eta^2p = 0.01, 95\% \text{ CI} = [0.00, 0.03]$ , (GG-corrected  $p = 0.62, \varepsilon = 0.697$ )). This pattern indicates robust neural coupling enhancement across the fronto-temporal network during both *Live Social Experience* and *Represented Social Experience* (see Table 1). The results of the *Nature Movie Control* condition are reported in Supplementary Fig. 1 and Supplementary Table 1.

**Table 1. Inter-brain synchrony values (wPLI) across fronto-temporal network links during *Live* and *Represented Social Experience*: Real mother-adolescent dyads versus surrogate controls (n = 65 for *Live Social Experience*, n = 62 for *Represented Social Experience*)**

| ROI | Real Data<br>(M $\pm$ SE) | Real Data<br>95% CI | Surrogate<br>(M $\pm$ SE) | Surrogate<br>Data<br>95% CI |
|-----|---------------------------|---------------------|---------------------------|-----------------------------|
|-----|---------------------------|---------------------|---------------------------|-----------------------------|

| <b><i>Represented Social Experience (Mother-adolescent dyads)</i></b> |               |                |               |                |
|-----------------------------------------------------------------------|---------------|----------------|---------------|----------------|
| LF-LF                                                                 | 0.109 ± 0.003 | [0.103, 0.115] | 0.075 ± 0.003 | [0.069, 0.081] |
| LF-LT                                                                 | 0.109 ± 0.003 | [0.103, 0.115] | 0.075 ± 0.003 | [0.069, 0.081] |
| LF-RF                                                                 | 0.108 ± 0.003 | [0.101, 0.114] | 0.075 ± 0.003 | [0.069, 0.081] |
| LF-RT                                                                 | 0.112 ± 0.003 | [0.106, 0.118] | 0.075 ± 0.003 | [0.069, 0.081] |
| LT-LF                                                                 | 0.105 ± 0.003 | [0.099, 0.111] | 0.075 ± 0.003 | [0.069, 0.081] |
| LT-LT                                                                 | 0.104 ± 0.003 | [0.098, 0.11]  | 0.075 ± 0.003 | [0.069, 0.081] |
| LT-RF                                                                 | 0.108 ± 0.003 | [0.102, 0.115] | 0.076 ± 0.003 | [0.07, 0.082]  |
| LT-RT                                                                 | 0.111 ± 0.003 | [0.105, 0.117] | 0.076 ± 0.003 | [0.07, 0.082]  |
| RF-LF                                                                 | 0.104 ± 0.003 | [0.098, 0.11]  | 0.075 ± 0.003 | [0.069, 0.081] |
| RF-LT                                                                 | 0.106 ± 0.003 | [0.1, 0.112]   | 0.075 ± 0.003 | [0.069, 0.081] |
| RF-RF                                                                 | 0.106 ± 0.003 | [0.1, 0.112]   | 0.075 ± 0.003 | [0.069, 0.081] |
| RF-RT                                                                 | 0.108 ± 0.003 | [0.102, 0.114] | 0.076 ± 0.003 | [0.07, 0.082]  |
| RT-LF                                                                 | 0.107 ± 0.003 | [0.101, 0.113] | 0.075 ± 0.003 | [0.069, 0.081] |
| RT-LT                                                                 | 0.109 ± 0.003 | [0.103, 0.115] | 0.076 ± 0.003 | [0.069, 0.082] |
| RT-RF                                                                 | 0.11 ± 0.003  | [0.104, 0.116] | 0.075 ± 0.003 | [0.069, 0.082] |
| RT-RT                                                                 | 0.109 ± 0.003 | [0.103, 0.116] | 0.075 ± 0.003 | [0.069, 0.082] |
| <b><i>Live Social Experience (Mother-adolescent Dyads)</i></b>        |               |                |               |                |
| LF-LF                                                                 | 0.117 ± 0.004 | [0.109, 0.124] | 0.077 ± 0.004 | [0.07, 0.085]  |
| LF-LT                                                                 | 0.12 ± 0.004  | [0.112, 0.127] | 0.078 ± 0.004 | [0.071, 0.086] |
| LF-RF                                                                 | 0.118 ± 0.004 | [0.111, 0.126] | 0.078 ± 0.004 | [0.07, 0.085]  |
| LF-RT                                                                 | 0.118 ± 0.004 | [0.11, 0.125]  | 0.079 ± 0.004 | [0.072, 0.087] |
| LT-LF                                                                 | 0.12 ± 0.004  | [0.112, 0.128] | 0.078 ± 0.004 | [0.07, 0.085]  |
| LT-LT                                                                 | 0.122 ± 0.004 | [0.114, 0.129] | 0.079 ± 0.004 | [0.071, 0.087] |
| LT-RF                                                                 | 0.123 ± 0.004 | [0.115, 0.13]  | 0.078 ± 0.004 | [0.07, 0.085]  |
| LT-RT                                                                 | 0.118 ± 0.004 | [0.111, 0.126] | 0.079 ± 0.004 | [0.071, 0.087] |
| RF-LF                                                                 | 0.116 ± 0.004 | [0.108, 0.124] | 0.077 ± 0.004 | [0.07, 0.085]  |
| RF-LT                                                                 | 0.12 ± 0.004  | [0.112, 0.127] | 0.079 ± 0.004 | [0.071, 0.086] |
| RF-RF                                                                 | 0.119 ± 0.004 | [0.111, 0.127] | 0.077 ± 0.004 | [0.07, 0.085]  |
| RF-RT                                                                 | 0.12 ± 0.004  | [0.112, 0.127] | 0.079 ± 0.004 | [0.071, 0.087] |
| RT-LF                                                                 | 0.118 ± 0.004 | [0.11, 0.125]  | 0.077 ± 0.004 | [0.07, 0.085]  |
| RT-LT                                                                 | 0.122 ± 0.004 | [0.115, 0.13]  | 0.079 ± 0.004 | [0.071, 0.086] |
| RT-RF                                                                 | 0.119 ± 0.004 | [0.111, 0.126] | 0.078 ± 0.004 | [0.07, 0.086]  |
| RT-RT                                                                 | 0.123 ± 0.004 | [0.115, 0.13]  | 0.079 ± 0.004 | [0.072, 0.087] |

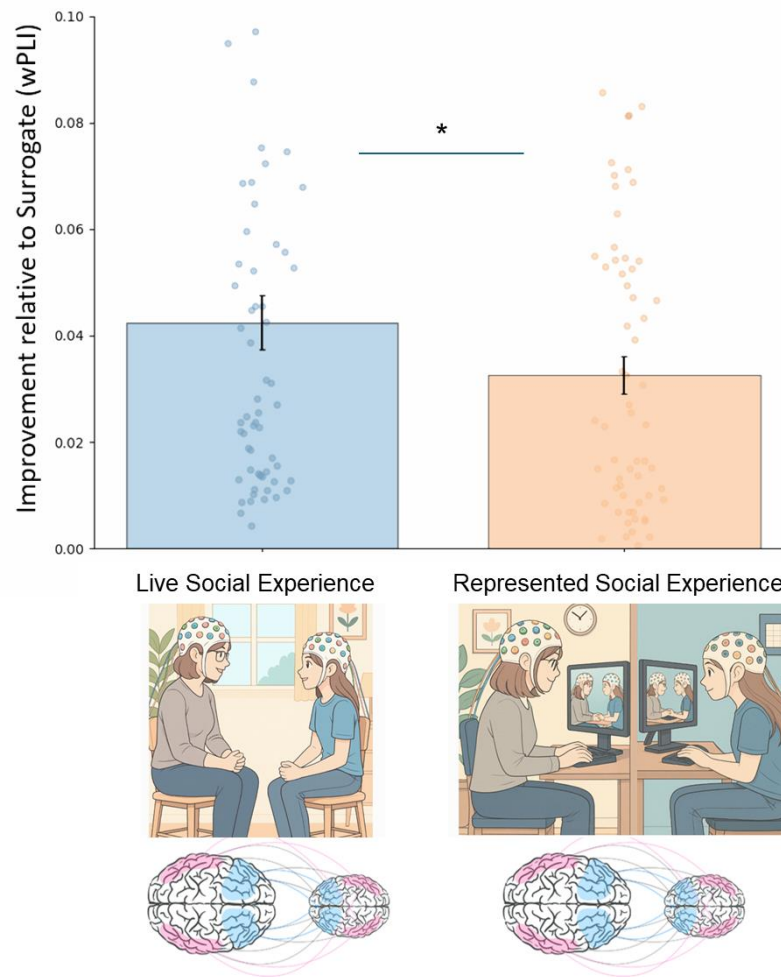
### ***3.2 Neural synchrony during Live Social Experience elicits greater neural coupling than Represented Social Experience***

We next assessed differences in inter-brain synchrony between *Live Social Experience* and *Represented Social Experience*, comparing the increase in inter-brain connectivity relative to surrogate data ( $\Delta wPLI$ ) across the fronto-temporal network in each condition.

A repeated measures ANOVA was conducted with Condition (*Live Social Experience*, *Represented Social Experience*) and ROI (16 inter-brain link combinations across four fronto-temporal regions) as within-subject factors. While no significant main effect emerged for ROI ( $F(15, 915) = 0.72$ ,  $p = 0.762$ ,  $\eta^2p = 0.01$ , 95% CI = [0.00, 0.01], (GG-corrected  $p = 0.704$ ,  $\epsilon = 0.676$ )) or the Condition  $\times$  ROI interaction ( $F(15, 915) = 1.34$ ,  $p = 0.163$ ,  $\eta^2p = 0.02$ , 95% CI = [0.00, 0.03], (GG-corrected  $p = 0.189$ ,  $\epsilon = 0.74$ )), the analysis revealed a significant main effect of Condition ( $F(1,61) = 5.71$ ,  $p = 0.02$ ,  $\eta^2p = 0.09$ , 95% CI = [0.001, 0.23]), reflecting that active social participation elicits stronger neural coupling than passive observation of the same social content, even when controlling for identical visual and social information, across the entire fronto-temporal network (see Fig. 2 for main effect).

Following, to rule out the alternative explanation - that inter-brain synchrony in the *Represented Social Experience* condition simply reflects stimulus-driven sensory overlap resulting from watching identical visual content - we compared neural synchrony during both social experiences versus a neutral *Nature Movie* viewing. A repeated measures ANOVA revealed a significant main effect of Condition ( $F(2, 114) = 13.6$ ,  $p < 0.001$ ,  $\eta^2p = 0.19$ , 95% CI = [0.07, 0.31]), with no significant ROI effect ( $F(15, 855) = 0.99$ ,  $p = 0.463$ ,  $\eta^2p = 0.02$ , 95% CI = [0.00, 0.02]) nor significant Condition  $\times$  ROI interaction ( $F(30, 1710) = 1.22$ ,  $p = 0.188$ ,  $\eta^2p = 0.02$ , 95% CI = [0.00, 0.02]). Holm-corrected post-hoc tests showed that both social conditions elicited greater neural synchrony than non-social *Nature Movie* content: *Live Social Experience* ( $t(57) = 5.22$ ,  $p_{Holm} < 0.001$ , Cohen's  $d = 0.6$ , 95% CI = [0.29, 0.91]) and *Represented Social Experience* ( $t(57) = 2.67$ ,  $p_{Holm} = 0.017$ , Cohen's  $d = 0.31$ , 95% CI = [0.02, 0.6]). *Live Social Experience* again elicited significantly greater inter-brain synchrony than *Represented Social Experience* ( $t(57) = 2.54$ ,  $p_{Holm} = 0.017$ , Cohen's  $d = 0.29$ , 95% CI = [0.01, 0.58]). These findings demonstrate that inter-brain synchrony during social content viewing reflects processing of shared social meaning rather than passive co-viewing of identical stimuli, and that active

participation produces stronger neural coupling than observation alone. Full analysis is described in Supplementary Fig 2.



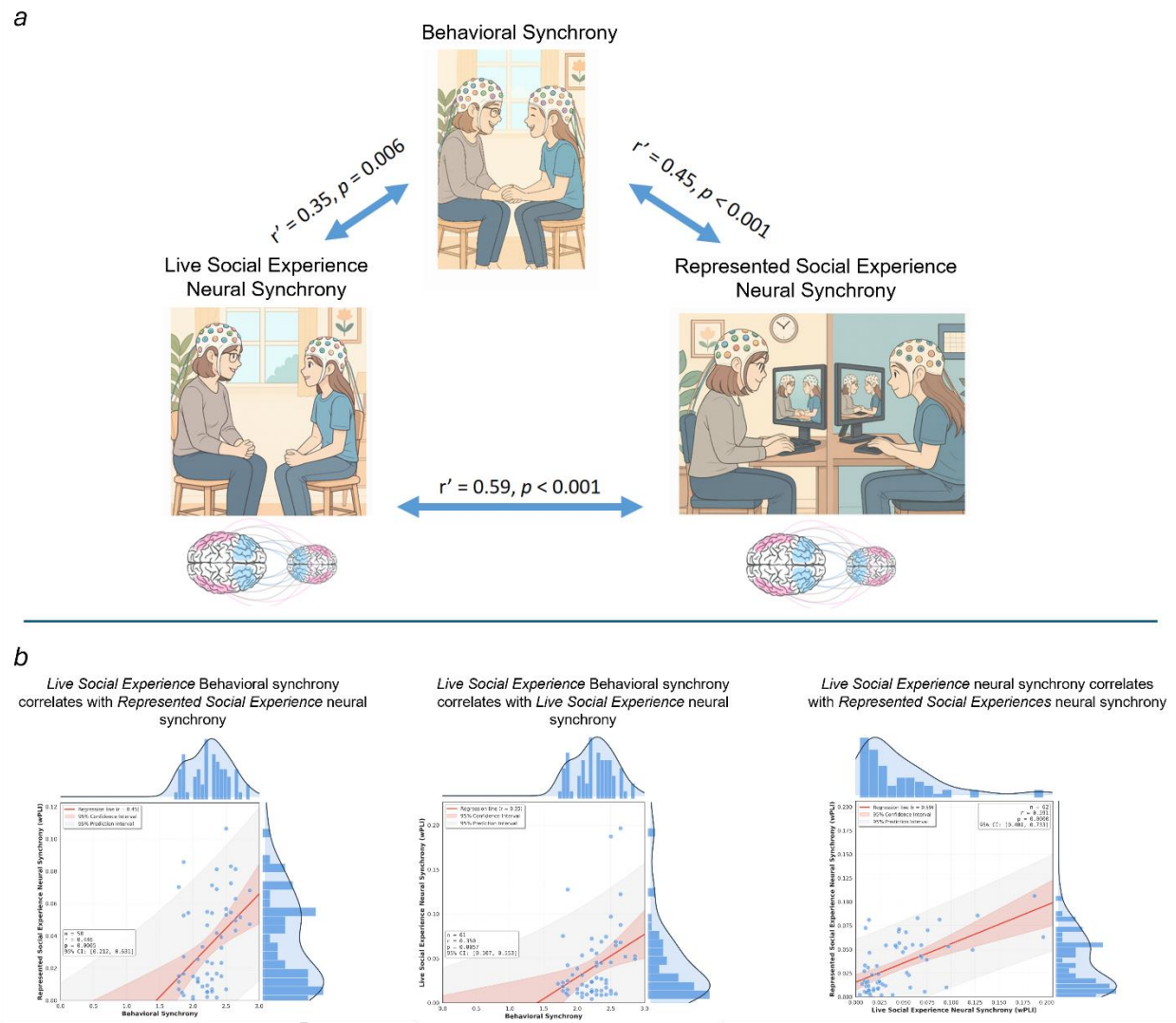
**Fig. 2. Inter-brain synchrony across *Live* and *Represented Social Experiences* relative to Non-social condition in mother-adolescent dyads.** Improvement in neural synchrony ( $\Delta wPLI$ ) relative to surrogate data across fronto-temporal networks during *Live Social Experience* (face-to-face interaction) and *Represented Social Experience* (watching their own recorded interaction). *Live Social Experience* showed significantly greater neural synchrony than *Represented Social Experience* ( $F(1, 61) = 5.71, p = 0.02$ ). Individual data points represent dyad-level synchrony values.  $*p < 0.05$ . Error bars represent standard error of the mean.  $n = 62$  mother-adolescent dyads.

### **3.3 Mediation analysis: Mechanisms underlying neural coupling transfer**

#### **3.3.1 Preliminary correlation analyses**

Prior to examining mediation pathways, we evaluated relationships between key variables using Pearson correlations. All results were Holm-corrected for multiple comparisons of three planned tests.

Strong positive correlations emerged between all variables: *Live Social Experience* Neural Synchrony correlated significantly with Behavioral Synchrony ( $r(59) = 0.35$ ,  $p_{Holm} = 0.006$ , 95% CI = [0.1, 0.55]) and with *Represented Social Experience* Neural Synchrony ( $r(60) = 0.59$ ,  $p_{Holm} < 0.001$ , 95% CI = [0.4, 0.73]), while Behavioral Synchrony also correlated strongly with *Represented Social Experience* Neural Synchrony ( $r(56) = 0.45$ ,  $p_{Holm} < 0.001$ , 95% CI = [0.21, 0.63], see Fig 3). These robust correlations supported subsequent mediation analysis to examine underlying mechanisms of neural coupling transfer from *Live* to *Represented Social Experience*.



**Fig. 3. Neural-behavioral coupling relationships in mother-adolescent dyads. a.** illustration of the three key variables and their pairwise correlations. Illustrations depict the experimental conditions: Behavioral Synchrony (top, center) was coded from a naturalistic face-to-face interaction; *Live Social Experience* Neural Synchrony (left) was measured via dual-EEG hyperscanning during face-to-face interaction; *Represented Social Experience* Neural Synchrony (right) was measured via dual-EEG hyperscanning while dyad members passively co-viewed a video recording of their earlier interaction, from separate rooms. Blue double-headed arrows connecting the three variables display Pearson correlation coefficients ( $r$ ) with Holm–Bonferroni-corrected  $p$ -values (two-tailed). **b.** Scatterplots displaying pairwise associations between the three variables. Left panel: Behavioral Synchrony (x-axis) against *Represented Social Experience* Neural Synchrony (wPLI; y-axis). Centre panel: Behavioral Synchrony (x-axis) against *Live Social Experience* Neural Synchrony (wPLI; y-axis). Right panel: *Live Social Experience* Neural Synchrony (wPLI; x-axis) against *Represented Social Experience* Neural Synchrony (wPLI; y-axis). In each scatterplot, individual dyads are represented by blue circles, the red solid line indicates the ordinary least squares (OLS) regression fit, the pink shaded band surrounding the regression line represents the 95% confidence interval, and the lighter grey shaded band represents the 95% prediction interval. Blue histogram bars along the top and right margins of each panel display marginal frequency distributions for each variable. Statistical annotations within scatterplot panels report unadjusted  $p$ -values; arrow labels in the top panel show Holm-corrected  $p$ -values. wPLI.  $n = 61$  dyads for the *Live Social Experience* Neural Synchrony–Behavioral Synchrony correlation ( $r(59) = 0.35$ ,  $p_{\text{Holm}} =$



0.006);  $n = 62$  dyads for the *Live Social Experience Neural Synchrony–Represented Social Experience Neural Synchrony* correlation ( $r(60) = 0.59$ ,  $p_{Holm} < 0.001$ );  $n = 58$  dyads for the *Behavioral Synchrony–Represented Social Experience Neural Synchrony* correlation ( $r(56) = 0.45$ ,  $p_{Holm} < 0.001$ ).

### 3.3.2 Mediation model testing

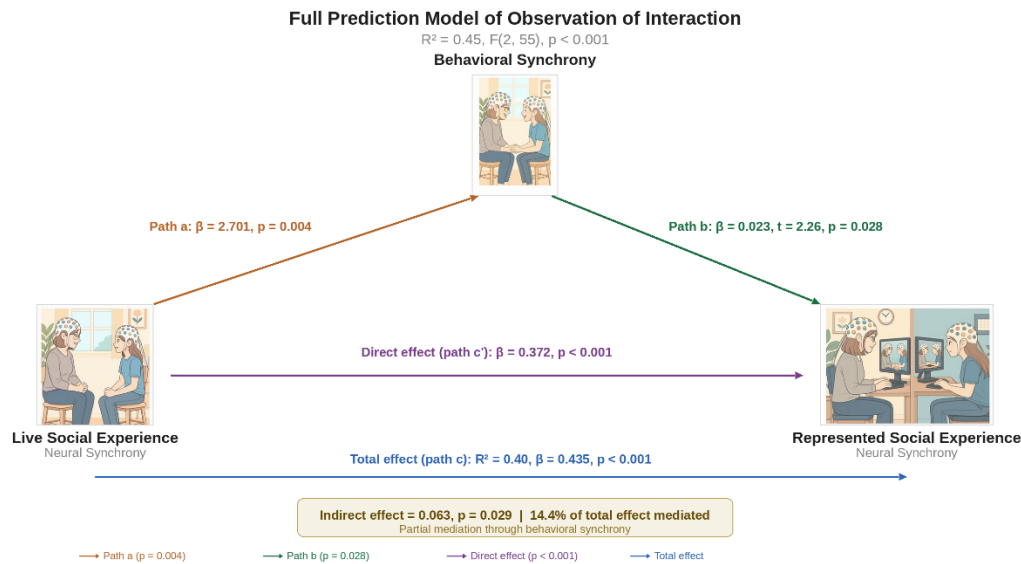
Mediation analysis employed ordinary least squares regression with bootstrap estimation (20,000 iterations) on complete cases ( $n = 58$ ), following standard mediation procedures<sup>67</sup>.

**Total effect model (Path c).** We first established that *Live Social Experience Neural Synchrony* significantly predicted *Represented Social Experience Neural Synchrony* ( $R^2 = 0.40$ ,  $F(1, 56) = 37.26$ ,  $p < 0.001$ , 95% CI = [0.2, 0.58]), with a strong positive effect ( $\beta = 0.435$ ,  $t = 6.104$ ,  $p < 0.001$ , 95% CI = [0.3, 0.64]), confirming robust neural reinstatement from live interaction to memory reactivation and establishing the prerequisite relationship for mediation analysis.

**Path a.** *Live Social Experience Neural Synchrony* significantly predicted *Behavioral Synchrony* ( $R^2 = 0.14$ ,  $F(1, 56) = 9.095$ ,  $p = 0.004$ , 95% CI = [0.02, 0.33]), indicating that stronger neural coupling facilitates more coordinated behavioral patterns ( $\beta = 2.701$ ,  $t = 3.016$ ,  $p = 0.004$ , 95% CI = [1.04, 4.99]).

**Full mediation model** (Paths c' and b). The full model significantly predicted *Represented Social Experience Neural Synchrony* ( $R^2 = 0.45$ ,  $F(2, 55) = 22.54$ ,  $p < 0.001$ , 95% CI = [0.25, 0.63]). When both predictors were included simultaneously, both *Live Social Experience Neural Synchrony* ( $\beta = 0.372$ ,  $t = 5.021$ ,  $p < 0.001$ , 95% CI = [0.18, 0.58]) and *Behavioral Synchrony* ( $\beta = 0.023$ ,  $t = 2.258$ ,  $p = 0.028$ , 95% CI = [0.003, 0.05]) contributed significantly beyond the influence of the other factor.

**Indirect effect.** Bootstrap analysis revealed significant partial mediation through *Behavioral Synchrony* (indirect effect = 0.063,  $p = 0.029$ , 95% CI [0.005, 0.18]), accounting for 14.4% of the total relationship (95% CI = [0.01, 0.48]). As the direct neural pathway remained significant, indicating dual mechanisms: direct neural reinstatement (85.6%) and indirect behavioral coordination (14.4%, see Fig. 4).



**Fig. 4. Mediation analysis of neural synchrony relationships in mother-adolescent dyads.**

Illustration of the mediation model testing whether Behavioral Synchrony mediates the relationship between *Live Social Experience Neural Synchrony* and *Represented Social Experience Neural Synchrony* ( $n = 58$  dyads). Orange solid arrows indicate Path a (*Live Social Experience Neural Synchrony* → Behavioral Synchrony:  $\beta = 2.701, p = 0.004$ ); green solid arrows indicate Path b (Behavioral Synchrony → *Represented Social Experience Neural Synchrony*:  $\beta = 0.023, p = 0.028$ ); the purple solid arrow indicates the direct effect, Path c' (*Live Social Experience Neural Synchrony* → *Represented Social Experience Neural Synchrony*:  $\beta = 0.372, p < 0.001$ ), which remained significant after inclusion of the mediator, indicating partial mediation. The blue solid arrow below represents the total effect (Path c:  $R^2 = 0.40, \beta = 0.435, p < 0.001$ ) prior to inclusion of the mediator. The amber box displays the indirect effect through Behavioral Synchrony (indirect effect = 0.063,  $p = 0.029$ ), accounting for 14.4% of the total effect. Full model:  $R^2 = 0.45, F(2, 55) = 22.54, p < 0.001$ .

## Study 2

### 3.4 Validation of inter-brain synchrony above surrogate levels

Using the same analytical approach, we compared real stranger dyads to surrogate controls across experimental conditions with separate repeated measures ANOVAs with Data Type (real vs. surrogate) and ROI as factors for each experimental condition.

Real stranger dyads demonstrated significantly greater neural synchrony than surrogate controls across both social conditions: during *Represented Social Experience* ( $F(1, 25) = 76.62, p < 0.001, \eta^2 p = 0.75, 95\% \text{ CI} = [0.54, 0.84]$ ) and during *Live Social Experience* ( $F(1, 25) = 162.51, p < 0.001, \eta^2 p = 0.87, 95\% \text{ CI} = [0.74, 0.91]$ ). ROI effects were non-significant during *Represented Social Experience* ( $F(15, 375) = 0.75, p = 0.74, \eta^2 p = 0.03, 95\% \text{ CI} = [0.00, 0.06]$ ),

(GG-corrected  $p = 0.638$ ,  $\varepsilon = 0.487$ ) and during *Live Social Experience* ( $F(15, 375) = 0.54$ ,  $p = 0.917$ ,  $\eta^2 p = 0.021$ , 95% CI = [0.00, 0.05], (GG-corrected  $p = 0.816$ ,  $\varepsilon = 0.508$ )). Data Type  $\times$  ROI interactions were also non-significant in both conditions (*Represented Social Experience*:  $F(15, 375) = 0.8$ ,  $p = 0.683$ ,  $\eta^2 p = 0.031$ , 95% CI = [0.00, 0.06], (GG-corrected  $p = 0.594$ ,  $\varepsilon = 0.476$ ); *Live Social Experience*:  $F(15, 375) = 0.52$ ,  $p = 0.93$ ,  $\eta^2 p = 0.02$ , 95% CI = [0.00, 0.05], (GG-corrected  $p = 0.826$ ,  $\varepsilon = 0.495$ )). For full values of all ROI links, see Table 2). This pattern indicates robust neural coupling enhancement across the fronto-temporal network during both social experience conditions, replicating the same pattern of consistent, uniform inter-brain synchrony observed in mother-adolescent dyads.

**Table 2. Inter-brain synchrony values (wPLI) across fronto-temporal network links during *Live* and *Represented Social Experience*: Real Stranger dyads versus surrogate controls (n = 26 dyads)**

| ROI                                                          | Real Data<br>(M $\pm$ SE) | Real Data<br>95% CI | Surrogate<br>(M $\pm$ SE) | Surrogate<br>Data<br>95% CI |
|--------------------------------------------------------------|---------------------------|---------------------|---------------------------|-----------------------------|
| <b><i>Represented Social Experience (Stranger Dyads)</i></b> |                           |                     |                           |                             |
| LF-LF                                                        | 0.092 $\pm$ 0.003         | [0.086, 0.098]      | 0.073 $\pm$ 0.003         | [0.068, 0.079]              |
| LF-LT                                                        | 0.092 $\pm$ 0.003         | [0.087, 0.098]      | 0.071 $\pm$ 0.003         | [0.065, 0.077]              |
| LF-RF                                                        | 0.087 $\pm$ 0.003         | [0.082, 0.093]      | 0.071 $\pm$ 0.003         | [0.065, 0.076]              |
| LF-RT                                                        | 0.093 $\pm$ 0.003         | [0.087, 0.099]      | 0.071 $\pm$ 0.003         | [0.065, 0.077]              |
| LT-LF                                                        | 0.091 $\pm$ 0.003         | [0.085, 0.097]      | 0.072 $\pm$ 0.003         | [0.066, 0.077]              |
| LT-LT                                                        | 0.094 $\pm$ 0.003         | [0.089, 0.1]        | 0.07 $\pm$ 0.003          | [0.064, 0.075]              |
| LT-RF                                                        | 0.088 $\pm$ 0.003         | [0.083, 0.094]      | 0.069 $\pm$ 0.003         | [0.063, 0.075]              |
| LT-RT                                                        | 0.092 $\pm$ 0.003         | [0.086, 0.098]      | 0.07 $\pm$ 0.003          | [0.064, 0.075]              |
| RF-LF                                                        | 0.093 $\pm$ 0.003         | [0.087, 0.098]      | 0.071 $\pm$ 0.003         | [0.066, 0.077]              |
| RF-LT                                                        | 0.095 $\pm$ 0.003         | [0.089, 0.1]        | 0.069 $\pm$ 0.003         | [0.064, 0.075]              |
| RF-RF                                                        | 0.09 $\pm$ 0.003          | [0.084, 0.095]      | 0.069 $\pm$ 0.003         | [0.064, 0.075]              |
| RF-RT                                                        | 0.094 $\pm$ 0.003         | [0.089, 0.1]        | 0.069 $\pm$ 0.003         | [0.064, 0.075]              |
| RT-LF                                                        | 0.094 $\pm$ 0.003         | [0.088, 0.1]        | 0.071 $\pm$ 0.003         | [0.065, 0.077]              |
| RT-LT                                                        | 0.093 $\pm$ 0.003         | [0.087, 0.098]      | 0.069 $\pm$ 0.003         | [0.064, 0.075]              |
| RT-RF                                                        | 0.092 $\pm$ 0.003         | [0.087, 0.098]      | 0.069 $\pm$ 0.003         | [0.063, 0.075]              |
| RT-RT                                                        | 0.092 $\pm$ 0.003         | [0.086, 0.097]      | 0.069 $\pm$ 0.003         | [0.064, 0.075]              |
| <b><i>Live Social Experience (Stranger Dyads)</i></b>        |                           |                     |                           |                             |
| LF-LF                                                        | 0.093 $\pm$ 0.002         | [0.088, 0.098]      | 0.071 $\pm$ 0.002         | [0.066, 0.076]              |
| LF-LT                                                        | 0.091 $\pm$ 0.002         | [0.087, 0.096]      | 0.071 $\pm$ 0.002         | [0.066, 0.076]              |
| LF-RF                                                        | 0.092 $\pm$ 0.002         | [0.087, 0.096]      | 0.071 $\pm$ 0.002         | [0.067, 0.076]              |

|       |               |                |               |                |
|-------|---------------|----------------|---------------|----------------|
| LF-RT | 0.092 ± 0.002 | [0.087, 0.097] | 0.071 ± 0.002 | [0.066, 0.075] |
| LT-LF | 0.091 ± 0.002 | [0.086, 0.095] | 0.07 ± 0.002  | [0.066, 0.075] |
| LT-LT | 0.09 ± 0.002  | [0.085, 0.095] | 0.071 ± 0.002 | [0.066, 0.076] |
| LT-RF | 0.087 ± 0.002 | [0.082, 0.091] | 0.071 ± 0.002 | [0.066, 0.075] |
| LT-RT | 0.093 ± 0.002 | [0.088, 0.098] | 0.071 ± 0.002 | [0.066, 0.076] |
| RF-LF | 0.094 ± 0.002 | [0.09, 0.099]  | 0.071 ± 0.002 | [0.066, 0.076] |
| RF-LT | 0.091 ± 0.002 | [0.086, 0.095] | 0.071 ± 0.002 | [0.066, 0.075] |
| RF-RF | 0.093 ± 0.002 | [0.088, 0.097] | 0.07 ± 0.002  | [0.066, 0.075] |
| RF-RT | 0.091 ± 0.002 | [0.086, 0.096] | 0.071 ± 0.002 | [0.066, 0.075] |
| RT-LF | 0.092 ± 0.002 | [0.088, 0.097] | 0.071 ± 0.002 | [0.066, 0.075] |
| RT-LT | 0.09 ± 0.002  | [0.086, 0.095] | 0.072 ± 0.002 | [0.067, 0.076] |
| RT-RF | 0.091 ± 0.002 | [0.087, 0.096] | 0.071 ± 0.002 | [0.066, 0.076] |
| RT-RT | 0.092 ± 0.002 | [0.087, 0.097] | 0.072 ± 0.002 | [0.067, 0.076] |

### 3.5 Participation versus observation in stranger dyads

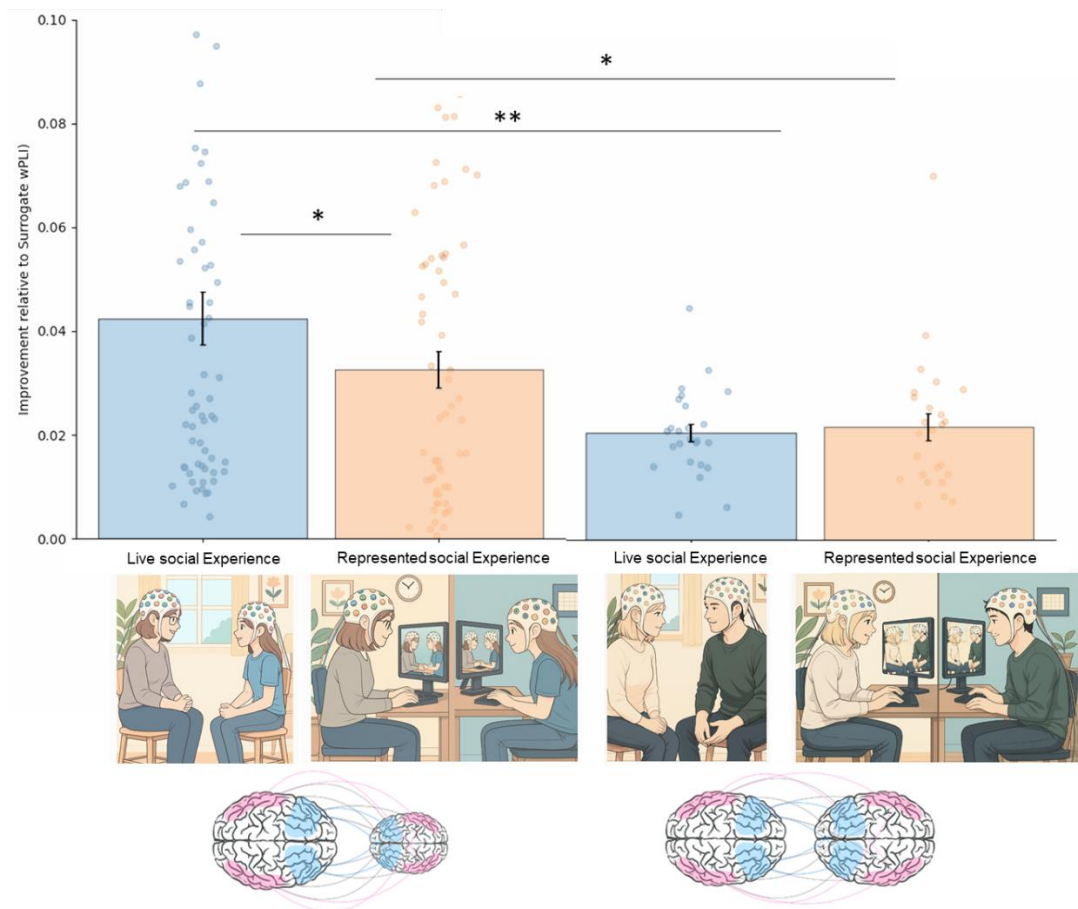
A repeated measures ANOVA examined differences in inter-brain synchrony between *Live Social Experience* and *Represented Social Experience*, comparing neural coupling enhancement relative to surrogate data ( $\Delta wPLI$ ) across the fronto-temporal network in stranger dyads. Unlike mother-adolescent dyads, stranger dyads exhibited no significant difference in inter-brain synchrony between the two social experiences ( $F(1, 24) = 0.27, p = 0.606, \eta^2 p = 0.011, 95\% CI = [0.00, 0.19]$ ). No significant ROI effects ( $F(15, 360) = 0.65, p = 0.832, \eta^2 p = 0.026, 95\% CI [0.00, 0.02]$ , (GG-corrected  $p = 0.736, \varepsilon = 0.541$ )) and no significant Condition  $\times$  ROI interactions ( $F(15, 360) = 0.68, p = 0.804, \eta^2 p = 0.028, 95\% CI = [0.00, 0.02]$  (GG-corrected  $p = 0.705, \varepsilon = 0.523$ ), were observed.

### 3.6 Neural coordination across social experience types and relationship contexts

To examine how neural coupling varies across different social experiences and relationship types, we compared the improvement in inter-brain connectivity relative to surrogate controls ( $\Delta wPLI$ ) between mother-adolescent and stranger dyads during both *Live* and *Represented Social Experience*. Levene's test indicated significant violations of equal variance assumptions for both conditions ( $p < 0.001$ ), necessitating the use of Welch's t-tests with Holm correction for multiple comparisons.

Mother-adolescent dyads exhibited significantly stronger neural coordination than stranger dyads during both *Live Social Experience* ( $M = 0.042$  vs.  $M = 0.021$ , Welch's  $t(72.73) = 4.089$ ,  $p_{Holm} = 0.002$ , Cohen's  $d = 0.757$ , 95% CI = [0.27, 1.24]) and *Represented Social Experience* ( $M = 0.033$  vs.  $M = 0.022$ , Welch's  $t(82.12) = 2.507$ ,  $p_{Holm} = 0.014$ , Cohen's  $d = 0.509$ , 95% CI = [0.04, 0.98]).

Finally, to evaluate whether the improvement in neural synchrony from *Represented* to *Live Social Experience* differed by relationship type, we compared the magnitude of change across the fronto-temporal network between samples. Mother-adolescent dyads showed significantly greater neural synchrony during *Live* compared to *Represented Social Experience* ( $M = 0.042$  &  $M = 0.033$ , respectively,  $t(61) = 2.39$ ,  $p = 0.020$ , Cohen's  $d = 0.30$ , 95% CI = [0.05, 0.56]), whereas stranger dyads showed equivalent neural synchrony across both conditions ( $M = 0.021$  &  $M = 0.022$ , respectively,  $t(24) = -0.52$ ,  $p = 0.606$ , Cohen's  $d = -0.11$ , 95% CI = [-0.5, 0.29]). This difference in improvement between *Represented* to *Live social experience* between the two samples was significant ( $t(84.69) = 2.28$ ,  $p = 0.025$ , Cohen's  $d = 0.45$ , 95% CI [-0.03, 0.91]), indicating that the improvement in neural synchrony during *Live* interaction relative to *Represented Social Experience* was significantly stronger in mother-adolescent dyads than in stranger dyads. This indicates that while attachment relationships enhance neural coupling across both active and memory-based social experiences, this biological advantage is most pronounced during live social coordination (see Fig. 5).



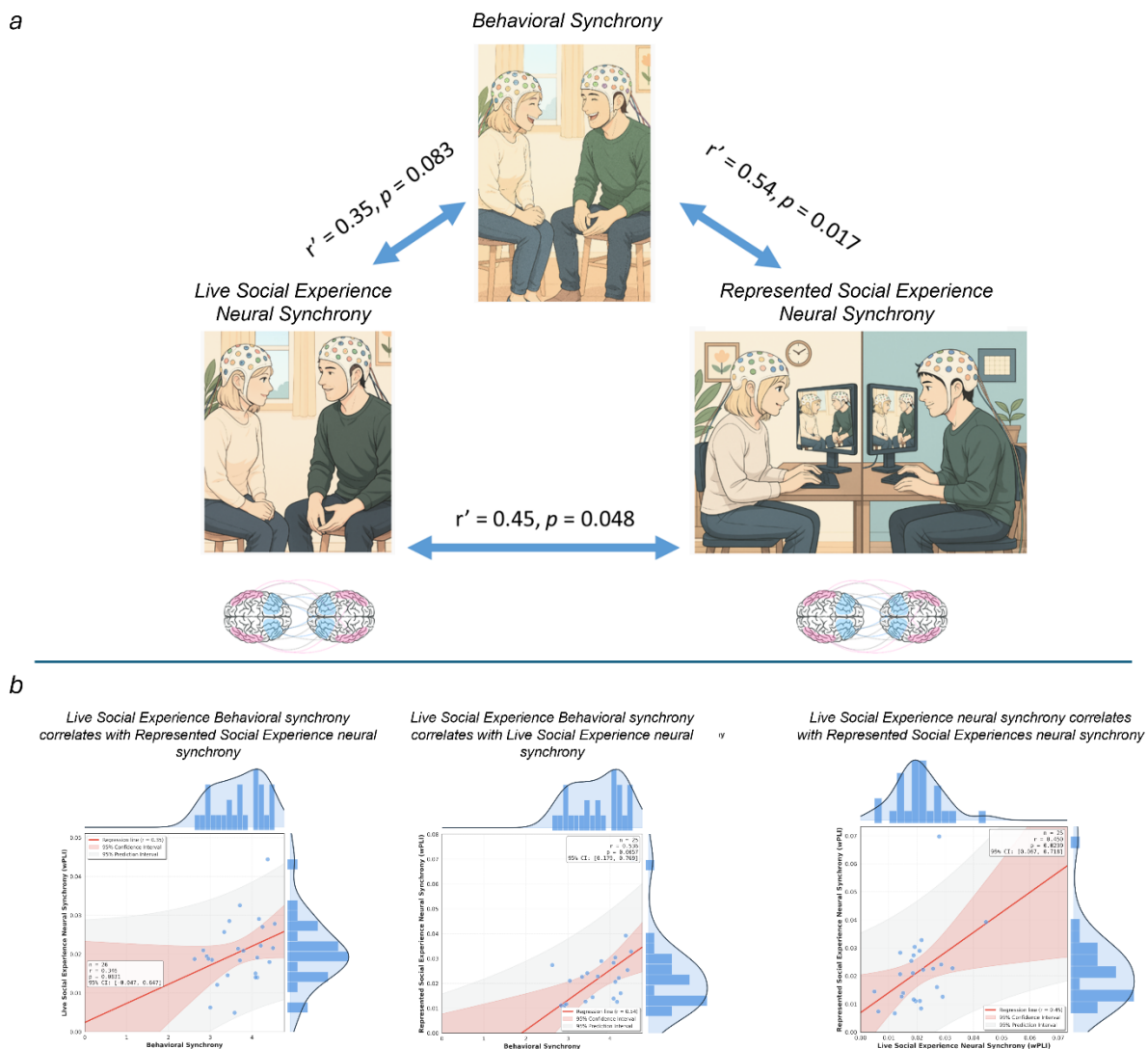
**Fig. 5. Inter-brain synchrony across *Live* and *Represented Social Experiences* in mother-adolescent and stranger dyads.** Neural synchrony ( $\Delta wPLI$ ) relative to surrogate data across fronto-temporal networks during *Live Social Experience* (face-to-face interaction) and *Represented Social Experience* (passive observation). Due to violations of equal variance assumptions (Levene's test,  $p < 0.001$ ), Welch's t-tests with Holm correction were used for comparisons. Mother-adolescent dyads showed significantly higher neural coordination than stranger dyads during both *Live Social Experience* ( $M = 0.042$  vs.  $M = 0.021$ ,  $p_{Holm} = 0.002$ ) and *Represented Social Experience* ( $M = 0.033$  vs.  $M = 0.022$ ,  $p_{Holm} = 0.014$ ). The coordination advantage was stronger during *Live Social Experience*, indicating that attachment relationships enhance neural coupling across both engagement modes, with the biological advantage most pronounced during real-time social interaction. \* $p < 0.05$ , \*\* $p < 0.005$ . Error bars represent standard error of the mean.  $n = 62$  mother-adolescent dyads,  $n = 25$  stranger dyads.

### 3.7 Mediation analysis in stranger dyads: Mechanisms underlying neural coupling transfer

#### 3.7.1 Preliminary correlation analyses

Prior to examining mediation pathways in stranger dyads, we evaluated relationships between key variables using Pearson correlations. Results were Holm-corrected for multiple comparisons. *Live Social Experience* Neural Synchrony correlated marginally with Behavioral

Synchrony ( $r(24) = 0.35$ ,  $p_{Holm} = 0.083$ , 95% CI = [-0.05, 0.65]) and significantly with *Represented Social Experience Neural Synchrony* ( $r(23) = 0.45$ ,  $p_{Holm} = 0.048$ , 95% CI = [0.07, 0.72]). Behavioral Synchrony also correlated with *Represented Social Experience Neural Synchrony* ( $r(23) = 0.54$ ,  $p_{Holm} = 0.017$ , 95% CI = [0.18, 0.77]; see Fig. 6). These correlations supported subsequent mediation analysis to examine underlying mechanisms of neural coupling transfer in unacquainted dyads.



**Fig. 6. Neural-behavioral coupling relationships in stranger dyads. a.** Schematic illustration of the three key variables and their pairwise correlations. Illustrations depict the experimental conditions: Behavioral Synchrony (top, center) was coded from a naturalistic face-to-face interaction; *Live Social Experience Neural Synchrony* (left) was measured via dual-EEG hyperscanning during face-to-face interaction; *Represented Social Experience Neural Synchrony* (right) was measured via dual-EEG

hyperscanning while dyad members passively co-viewed a video recording of their earlier interaction, from separate rooms. Blue double-headed arrows connecting the three variables display Pearson correlation coefficients ( $r$ ) with Holm–Bonferroni-corrected  $p$ -values (two-tailed). **b.** Scatterplots displaying pairwise associations between the three variables. Left panel: Behavioral Synchrony (x-axis) against *Live Social Experience* Neural Synchrony (wPLI; y-axis). Centre panel: Behavioral Synchrony (x-axis) against *Represented Social Experience* Neural Synchrony (wPLI; y-axis). Right panel: *Live Social Experience* Neural Synchrony (wPLI; x-axis) against *Represented Social Experience* Neural Synchrony (wPLI; y-axis). In each scatterplot, individual dyads are represented by blue circles, the red solid line indicates the ordinary least squares (OLS) regression fit, the pink shaded band surrounding the regression line represents the 95% confidence interval, and the lighter grey shaded band represents the 95% prediction interval. Blue histogram bars along the top and right margins of each panel display marginal frequency distributions for each variable. Statistical annotations within scatterplot panels report unadjusted  $p$ -values; arrow labels in the top panel show Holm-corrected  $p$ -values. wPLI, weighted phase lag index.  $n = 26$  dyads for the *Live Social Experience* Neural Synchrony–Behavioral Synchrony correlation ( $r(24) = 0.35$ ,  $p_{\text{Holm}} = 0.083$ );  $n = 25$  dyads for the *Live Social Experience* Neural Synchrony with *Represented Social Experience* Neural Synchrony correlation ( $r(23) = 0.45$ ,  $p_{\text{Holm}} = 0.048$ );  $n = 25$  dyads for the Behavioral Synchrony with *Represented Social Experience* Neural Synchrony correlation ( $r(23) = 0.54$ ,  $p_{\text{Holm}} = 0.017$ ).

### 3.7.2 Mediation analysis - stranger dyads

Mediation analysis employed ordinary least squares regression with bootstrap estimation (20,000 iterations) on complete cases ( $n = 25$ ).

**Total effect model** (Path c). We first established that *Live Social Experience* Neural Synchrony significantly predicted *Represented Social Experience* Neural Synchrony ( $R^2 = 0.203$ ,  $F(1, 23) = 5.849$ ,  $p = 0.024$ , 95% CI = [0.02, 0.48]), with a positive effect ( $\beta = 0.715$ ,  $t = 2.419$ ,  $p = 0.024$ , 95% CI = [0.17, 1.41]), confirming neural reinstatement from live interaction to memory reactivation even in stranger dyads.

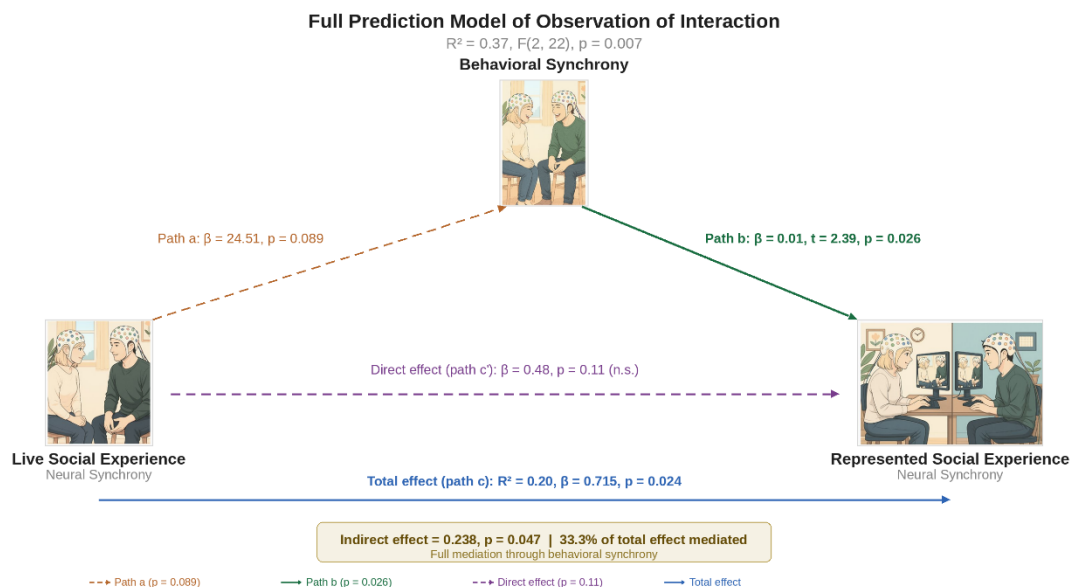
**Path a.** *Live Social Experience* Neural Synchrony showed a marginally significant relationship with Behavioral Synchrony ( $R^2 = 0.120$ ,  $F(1, 23) = 3.149$ ,  $p = 0.089$ , 95% CI = [0.003, 0.33]), suggesting weaker neural-behavioral coupling in unfamiliar dyads ( $\beta = 0.4514$ ,  $t = 1.775$ ,  $p = 0.089$ , 95% CI = [3.15, 43.63]).

**Full mediation model** (Paths  $c'$  and b). The full model significantly predicted *Represented Social Experience* Neural Synchrony ( $R^2 = 0.367$ ,  $F(2, 22) = 6.377$ ,  $p = 0.007$ , 95% CI = [0.11, 0.68]). When both predictors were included simultaneously, *Live Social Experience* Neural Synchrony no longer showed a significant direct effect ( $\beta = 0.477$ ,  $t = 1.661$ ,



$p = 0.111$ , 95% CI = [0.07, 0.98]), while Behavioral Synchrony demonstrated a significant effect beyond the influence of neural synchrony ( $\beta = 0.010$ ,  $t = 2.389$ ,  $p = 0.026$ , 95% CI = [0.001, 0.02]; see Fig. 7).

**Indirect effect.** Bootstrap analysis revealed that behavioral synchrony mediated the relationship between *Live* and *Represented Social Experience* neural synchrony (indirect effect = 0.238,  $p = 0.047$ , 95% CI [0.002, 0.64]), accounting for 33.3% of the total relationship. The direct effect became non-significant ( $\beta = 0.477$ ,  $p = 0.111$ , 95% CI = [0.002, 0.64]), suggesting the relationship operates primarily through behavioral pathways in unfamiliar dyads.



**Fig. 7. Mediation analysis of neural synchrony relationships in stranger dyads.** Illustration of the mediation model testing whether Behavioral Synchrony mediates the relationship between *Live Social Experience* Neural Synchrony and *Represented Social Experience* Neural Synchrony ( $n = 25$  dyads). Orange dashed arrows indicate Path *a* (*Live Social Experience* Neural Synchrony → Behavioral Synchrony:  $\beta = 24.51$ ,  $p = 0.089$ , marginal); green solid arrows indicate Path *b* (Behavioral Synchrony → *Represented Social Experience* Neural Synchrony:  $\beta = 0.01$ ,  $p = 0.026$ ); the grey dashed arrow indicates the direct effect, Path *c'* (*Live Social Experience* Neural Synchrony → *Represented Social Experience* Neural Synchrony:  $\beta = 0.48$ ,  $p = 0.11$ , n.s.), which became non-significant after inclusion of the mediator, suggesting full mediation. The blue solid arrow below represents the total effect (Path *c*:  $R^2 = 0.20$ ,  $\beta = 0.715$ ,  $p = 0.024$ ) prior to inclusion of the mediator. The amber box displays the indirect effect through Behavioral Synchrony (indirect effect = 0.238,  $p = 0.047$ ), accounting for 33.3% of the total effect. Solid arrows denote statistically significant paths ( $p < 0.05$ ); dashed arrows denote non-significant or marginal paths. Full model:  $R^2 = 0.37$ ,  $F(2, 22) = 6.38$ ,  $p = 0.007$ .

### 3.7.3 Comparing the mediation of behavioral synchrony

Finally, to test whether the mediation patterns differed between relationship types, we compared the proportion of the neural coupling transfer mediated by behavioral synchrony using a Z-test for independent proportions. Behavioral synchrony mediated a larger proportion of the neural transfer in stranger dyads (33.3%, SE = 0.094,  $n = 25$ ) compared to mother-adolescent dyads (14.4%, SE = 0.046,  $n = 58$ ), a 2.3-fold difference that was marginally significant ( $Z = 1.80$ ,  $p = 0.071$ , Cohen's  $h = 0.44$ , 95% CI  $[-0.03, 0.91]$ ). As indicated in sections 3.3.2 and 3.7.2, both indirect effects were individually significant (Stranger dyads: indirect effect = 0.238,  $p = .047$ , 95% CI  $[0.002, 0.64]$ ; Mother-adolescent dyads: indirect effect = 0.063,  $p = .029$ , 95% CI  $[0.004, 0.18]$ ), confirming that behavioral synchrony operates as a significant mediator across both relationship types. However, despite the marginal statistical significance of the sample difference, which likely stems from the smaller stranger sample, the 2.3-fold difference in mediation strength coupled with significant effects in both samples suggests a mechanistic variation: stranger dyads may rely more heavily on observable behavioral coordination to transfer neural coupling patterns from *live* to *represented* experiences, whereas mother-adolescent dyads may demonstrate stronger direct neural reinstatement that is less dependent on behavioral mediation.

## 4. Discussion

### ***Bridging active participation and passive observation in social neuroscience***

Humans learn to navigate the social world through active participation and passive observation of social experiences, two fundamental yet complementary pathways for social learning. To date, different disciplines in neuroscience employed distinct methodological approaches that artificially separate these interconnected learning modes. Single-brain fMRI studies characterized how brain networks respond to passive viewing represented social stimuli by identifying activation in distributed fronto-temporal regions. In parallel, hyperscanning research examined how two or more brains coordinate during live interactions, revealing neural

coupling across the same fronto-temporal regions. Our study integrated these two schools in a single experimental design.

Four important insights emerged from our study. First, we found significantly stronger neural synchronization during *Live Social Experience* compared to *Represented Social Experience* in mother-adolescent dyads, but not in the stranger dyads, providing support for relationship-dependent neural mechanisms. Second, mother-adolescent dyads had significantly greater overall neural synchrony than stranger dyads across both conditions, indicating that attachment relationships trigger stronger neural coordination. Third, we found robust associations between neural synchrony during *Live Social Experience*, the degree of *behavioral synchrony* during the interaction, and the neural synchrony during *Represented Social Experience* across both relationship types, suggesting conserved coordination mechanisms that could reflect the "hypersociality" of our species<sup>68,69</sup>. Fourth, the mediation analyses revealed relationship-dependent coordination strategies where established bonds rely more on direct neural pathways while interactions with strangers depend more heavily on behavioral synchrony when reactivating shared representations.

#### ***Neural reinstatement in social memory: Evidence from inter-brain coupling***

A core theoretical contribution of this study lies in the evidence it provides to neural reinstatement mechanisms that operate simultaneously across two brains. Neural reinstatement, the reactivation of neural processes during memory retrieval that mirror the processes that took place during active encoding, has been documented in individual memory systems<sup>55,56</sup>. Our findings extend this principle to interpersonal neural networks and show that representing our own just-experienced social interactions reactivates neural alignment patterns within the same fronto-temporal networks that synchronized during the original lived experience.

The mechanism described here charts a unique form of distributed neural reinstatement, where memory reactivation occurs across the neural systems of both partners simultaneously. The persistence of inter-brain synchrony during passive observation of the just-lived interaction,

when partners are physically separated so that no social cues could transfer between them, suggests that memories of shared social moments are encoded as shared neural representations that can be jointly reactivated<sup>52,57</sup>. Unlike the typical passive observation of social interactions of unfamiliar protagonists in fMRI studies, viewing one's own social interactions engages self-referential processing and reactivates mental states associated with the original interaction<sup>54,55</sup>.

### ***Biobehavioral synchrony and relationship-dependent neural coordination***

Our findings may lend empirical support to the *biobehavioral synchrony framework*, which describes how repeated mother-infant interactions create stable neural templates that facilitate coordination through specialized neural circuits<sup>36–38,70</sup>. The enhanced neural synchrony during *Live Social Experience* compared to *Represented Social Experience*, was observed exclusively in mother-adolescent dyads, but not in stranger dyads. This suggests that relationship familiarity alters the neural mechanisms that underpin social coordination and memory reactivation.

According to the *biobehavioral synchrony* theory, the mother-child relationship serves as the foundational context for social brain development, where maternal matched and sensitive behavior acts as the primary organizer of the infant's neural architecture<sup>37,38</sup>. The greater overall neural synchrony in mother-adolescent dyads compared to stranger dyads provides neurobiological evidence for this theoretical framework, suggesting that thousands of hours of coordinated mother-infant interactions create deeply ingrained coordination patterns that fundamentally distinguish attachment relationships from social encounters with strangers. The relationship-dependent nature of neural coordination aligns with theories of distributed cognition, which proposes that while social cognition can emerge as a property of coupled dynamic systems, the degree of coupling critically depends on relationship familiarity and pre-established coordination patterns<sup>71</sup>.

### ***Evidence for conserved social coordination mechanisms***

Despite relationship-dependent differences in neural synchrony levels, a key finding emerged from our analysis of the links between neural synchrony during *Live Social Experience*, behavioral synchrony during the interaction, and neural synchrony during *Represented Social Experience*. All three factors showed strong correlations across both relationship types and these correlations persisted even in the stranger dyads, despite the absence of a main effect for *Live* versus *Represented Social Experience*.

This pattern of results may suggest that the neural-behavioral link represents a conserved mechanism that operates independent of specific relational contexts. Such mechanism may reflect the "hypersociality" of our species, the innate capacity for social coordination underlying human cooperation and communication<sup>68,69</sup>. The robust correlations across relationship types support evolutionary perspectives suggesting that social synchrony serves as a fundamental "social glue" that enables rapid social learning, behavioral mimicry, and prosocial behavior even among strangers<sup>72-76</sup>, and reflect coupling mechanisms that operate at multiple levels of biological organization from neural oscillations to social behaviors to mental representations<sup>36,37,77</sup>.

### ***Differential mediation pathways: From behavioral scaffolding to direct neural coupling and developmental implications***

The mediation analyses revealed intriguing relationship-dependent differences in how neural synchrony during *Live Social Experience* relates to neural synchrony during *Represented Social Experience*. In mother-adolescent dyads, while the mediation was significant, behavioral synchrony accounted for only 14.4% of the total effect, with the direct neural pathway remaining strongly significant. However, in stranger dyads, behavioral synchrony explained 33.3% of the relationship between *Live* and *Represented Experience*, with the direct neural pathway becoming non-significant when behavioral synchrony was included.

This differential pattern may suggest that established attachment relationships rely more heavily on direct neural coupling pathways operating largely independent of observable behavioral coordination, whereas social interactions with strangers seem to depend more heavily on visible behavioral synchrony to achieve neural synchronization during later reactivation. This biological distinction may explain why social interactions with attachment partners feel effortless and automatic, while coordination with unfamiliar individuals requires more conscious attention to behavioral cues and social signals. The enhanced reliance on behavioral pathways in stranger dyads may reflect the need for explicit coordination mechanisms when pre-established neural templates are absent. These findings align with the biobehavioral synchrony framework, which posits that repeated mother-infant interactions create stable neural templates facilitating automatic coordination through specialized neural circuits and attachment-related brain networks<sup>22,24,25,36,37,70,78</sup>.

### ***Developmental foundations and neural plasticity***

Building on this framework, our findings may point to the ways by which early-established neural templates, such as found in mother-child bonds, create lasting developmental trajectories. These relationship-dependent differences in neural coordination are consistent with longitudinal studies demonstrating that sensitive maternal care predicts enhanced brain development years later, including larger gray matter volume and greater functional connectivity<sup>24,40,41,79,80</sup>. Conversely, maternal intrusiveness disrupts these neural tuning processes<sup>24,25</sup>, leading to aberrant neural responses in adolescence<sup>42,43</sup>. Our findings extend this literature by demonstrating that synchronous mother-child behavior leads to greater inter-brain synchrony during both *Live* and *Represented Social Experiences*.

The persistence of these early-established coordination patterns in our adolescent sample could reflect the scaffolding role early neural templates play in brain development<sup>37,38</sup>. As fronto-temporal networks continue their functional specialization through adolescence<sup>34,35</sup>, stable coordination templates from early mother-child interactions remain actively influential in

guiding neural development<sup>78,81</sup>. The robust direct neural coupling in mother-adolescent dyads may reflect the consolidation of repeated coordination experiences into stable neural circuits that serve as scaffolds for learning new coordination patterns throughout life.

### ***Game theory and the evolution of cooperation***

From a game theory perspective, our findings on the significant inter-brain synchrony across all social experiences, both *Live* and *Represented*, relative to control are particularly noteworthy. Participants in the stranger sample received no instructions to cooperate, reach common goals, or maintain future interactions, conditions that typically promote strategic cooperation according to rational choice models<sup>82,83</sup>, but still displayed significant interbrain coupling. While mother-adolescent dyads showed markedly greater neural synchronization, findings that are in line with evolutionary theories on parent-offspring cooperation<sup>84,85</sup>, stranger dyads still showed significant inter-brain synchrony relative to control, despite having no immediate benefits or expectations of future interaction. This pattern suggests that interbrain synchronization reflects automatic coordination mechanisms rather than strategic social investment and lend support to theories that perceive humans as fundamentally prosocial beings whose default mode of relatedness is cooperation rather than competition<sup>86,87</sup>. The robust neural-behavioral correlations in stranger dyads provide evidence for "strong reciprocity", the tendency to cooperate even when costly<sup>83,88</sup>, representing a crucial evolutionary adaptation that enabled large-scale cooperation beyond kinship networks.

### ***Fronto-temporal networks as neural substrates for social memory and communication***

Our findings of neural synchrony specifically within the fronto-temporal network provide insights into the biological substrates underlying both real-time social coordination and social memory processes. This distributed system represents one of the most well-characterized networks in social neuroscience<sup>8,89,90</sup>, with these fronto-temporal regions consistently

supporting social cognition, attention, mentalizing processes and social semantic knowledge <sup>8-11,29-31</sup>.

The maintenance of synchronized activity within these networks during both live interaction and subsequent memory retrieval suggests they serve as biological repositories for shared social experiences, enabling transmission of social knowledge across time and context. The persistence of synchrony during *Represented Social Experience* demonstrates these regions' capacity for reactivating shared neural processes that emerged during live interactions. This extends previous hyperscanning literature showing fronto-temporal areas as critical neural hubs facilitating inter-brain alignment during social interaction <sup>91</sup> providing evidence that these regions maintain neural coupling even when partners are physically separated. This capacity suggests a fundamental biological mechanism for maintaining and reactivating shared neural representations, enabling transfer of coordination patterns learned in one context to future social encounters.

### ***Evaluating Alternative Explanations***

Several alternative explanations for our findings warrant further consideration. First, the *stimulus-driven sensory overlap* suggests that neural synchrony during the *Represented Social Experience* could reflect passive co-viewing of identical visual stimuli rather than memory-based reinstatement. Notably, our Nature Movie control condition directly contradicts this hypothesis. While passive co-viewing of neutral content from separate rooms did elicit significant inter-brain synchrony compared to surrogate baseline (Supplementary Fig. 1), the inter-brain synchrony was significantly lower than both the *Live* and *Represented Social Experience* conditions (Supplementary Fig. 2). Critically, the non-social Nature Movie condition involved identical viewing setup, duration, and continuous visual stimulation, yet yielded little neural coupling compared to the social content conditions. These findings demonstrate that passive co-viewing establishes baseline neural coordination, which is specifically enhanced when viewing shared social experiences.



Second, the *self-related processing* hypothesis suggests that the enhanced inter-brain synchrony results from the participants viewing themselves in the recorded interaction, which activates self-referential neural networks rather than reactivating social memories. However, this cannot explain our different pattern of results across samples, as mother-adolescent dyads showed significantly greater *Live* than *Represented* differences while the strangers exhibited minimal effects in the opposite direction, with different mediation patterns. If self-viewing were the primary mechanism, we would expect similar patterns across both samples, regardless of relationship history. Our findings therefore suggest that relationship context and behavioral coordination history are important determinants of neural coupling patterns during the representation of social content.

Third, emotional or attentional re-engagement mechanisms suggest that the salience or emotional content of viewing one's own interaction could drive neural synchrony rather than memory reinstatement processes. However, participants remained attentive during the *Nature Movie* and the *Represented Social Experience* viewing conditions; yet the non-social *Nature Movie* control yielded significantly lower synchrony. Moreover, the relationship-dependent mediation patterns, in which behavioral synchrony showed a stronger effect in strangers versus familiar dyads, cannot be explained by attentional engagement.

These converging lines of evidence may provide support for our interpretation that the *Represented Social Experience* reflects memory-driven neural reinstatement of shared social experiences, with reactivation strength depending on relationship familiarity and behavioral coordination quality during the original interaction. While no study can exclude all alternative mechanisms, the convergent pattern across our control condition, relationship-dependent effects, and differential mediation pathways strongly supports this interpretation.

### ***Clinical and methodological considerations and study limitations***

Understanding the neural mechanisms that underpin social participation and observation has important implications for clinical populations. Individuals with autism spectrum conditions,

social anxiety, or attachment difficulties may show different patterns of brain-behavior coupling, potentially explaining why social interactions feel more effortful for these populations<sup>92,93</sup>. The finding that behavioral synchrony can mediate neural coordination provides potential intervention targets, suggesting that training programs focused on enhancing behavioral coordination skills might strengthen social communication competence.

Several methodological considerations warrant discussion. First, while dual-EEG hyperscanning provides unique insights with excellent temporal resolution, laboratory settings may limit ecological validity. Second, our focus on fronto-temporal synchrony in the beta band captures only one aspect of the complex multi-frequency neural dynamics that underpin social interactions.

Several limitations warrant consideration when interpreting the findings. The current research originally focused on mother-adolescent dyads as the primary population of interest, with Study 1 designed to test our core hypotheses regarding neural and behavioral synchrony during *Live versus Represented Social Experiences* within attachment relationships. Study 2 with the stranger dyads was subsequently conducted as an exploratory investigation to evaluate whether similar effects emerged in unfamiliar adult pairs and whether the observed patterns generalized beyond attachment contexts. This exploratory design resulted in substantially different sample sizes between studies, with the stranger dyad study comprising a smaller sample ( $n = 25$  complete cases) than the mother-adolescent study ( $n = 58$  complete cases). Sensitivity analysis indicated that the mother-adolescent sample could detect condition effects as small as  $\eta^2p = 0.12$ , whereas the stranger sample required effects of at least  $\eta^2p = 0.25$ . The observed condition effect in mother-adolescent dyads ( $\eta^2p = 0.09$ ) fell below the detectable threshold, though the effect was significant. In stranger dyads, the minimal condition effect ( $\eta^2p = 0.011$ ) trended in the opposite direction to our hypothesis. Detecting such a small, reversed effect as statistically significant would require approximately 720 dyads, and critically, the trend favored *Represented over Live Social Experience*, contrary to our predicted direction. These

findings suggest a meaningful absence of differential neural responses in unfamiliar dyads, rather than a statistical limitation.

Critically, the smaller stranger sample nonetheless detected significant effects where predicted. Between-group comparisons were adequately powered (minimum detectable  $d = 0.67$ ), confirming that mother-adolescent dyads show reliably stronger neural coupling than stranger dyads during *Live Social Experience* (observed  $d = 0.76$ ). The mediation analyses revealed significant behavioral mediation in both samples, with stronger mediation in stranger dyads (33.3% vs. 14.4%), an inverse pattern that cannot be attributed to power constraints, as such constraints would not yield larger effects in the smaller sample.

Nevertheless, given the exploratory nature of Study 2, future well-powered studies with larger stranger samples are needed to better establish these mechanistic differences between familiar and unfamiliar relationship. Furthermore, we suggest future research should further explore how individual-level neural pattern reinstatement relates to dyadic-level inter-brain synchrony, and encourage employing multimodal neuroimaging approaches during both *Live* and *Represented Social Experiences* at both the inter- and intra-brain coupling levels, which would provide more comprehensive characterization of neural systems supporting *Live* versus *Represented Social Experience*.

### **Conclusions**

Our findings contribute to understanding how social interactions create lasting neural representations that can be collectively reactivated across two brains. The results reveal patterns consistent with conserved biological mechanisms that underpin human social coordination and relationship-specific adaptations that optimize coordination efficiency.

Our findings that behavioral synchrony partially mediates the relationship between neural coordination during *Live* and *Represented Social Experience* through fundamentally different pathways in attachment partners versus strangers provide insight into the biological mechanisms that may sustain social brain evolution. The persistence of neural-behavioral

correlations across both relationship types, despite differential neural coupling strengths, suggests that social coordination capacity represents a fundamental biological mechanism operating across different relationship contexts. These findings are consistent with theories that view humans as an inherently "hypersocial" species who are equipped with specialized neural systems for rapid social coordination that may have facilitated our unique evolutionary trajectory.

The differential mediation patterns illuminate how social familiarity shapes distinct neural coordination strategies: established attachment relationships rely primarily on direct neural coupling mechanisms, while social encounters with strangers depend more heavily on behavioral synchrony pathways. These findings shed light on how early social experiences create lasting templates for social communication that persist throughout development that tunes the brain to establish coordination with unfamiliar partners. Our findings highlight the dual capacity of the human brain to create complex social experiences and transmit them across generations.

**Resource Availability Statement**

Any requests for further information and resources that would not compromise the participants' privacy should be directed to and will be fulfilled by the corresponding author.

**Data Availability Statement**

The anonymized, aggregated data used to generate all tables and figures is available at - <https://osf.io/57m94/overview>. Additional data generated in this study cannot be made publicly available due to participant privacy protections under our ethical approval (IRB) protocol. Requests to access further anonymized, aggregated data may be directed to the corresponding author and will be evaluated on a case-by-case basis. Data sharing requests must include: (1) a research proposal outlining intended use, (2) confirmation of institutional ethics approval, and (3) a data use agreement. Requests will be fulfilled within 30 days where feasible and compliant with privacy regulations.

**Code Availability Statement**

All analysis code is publicly available at - <https://osf.io/57m94/overview> and <https://github.com/Yoavshapira1/FelmanLabEEGpipeline>. The repository includes preprocessing scripts, neural synchrony analysis pipelines, statistical analysis code, and visualization functions.

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Conceptualization: L.S., J.L., and R.F.; methodology: L.S., and R.F.; investigation and data curation: L.S., C.S., J.B., and O.H.; formal analysis, L.S., J.B., and I.P.; writing: L.S., and R.F.; writing - review and editing: R.F., C.S., and O.H.

**Competing interests**

The authors declare no competing interests.

**Acknowledgments**

The study was supported by the Simms/Mann Foundation Chair to Ruth Feldman and by the Bezos Family Foundation. The funders had no role in study design, data collection and analysis, decision to publish or preparation of the manuscript.

**Editor Summary:**

Measuring synchrony between two brains during live social interaction versus passive viewing of the same event shows greater interbrain synchrony during live than represented experiences, both shaped by the behavioral coordination between partners.

**Peer Review Information:**

*Communications Psychology* thanks the anonymous reviewers for their contribution to the peer review of this work. Primary Handling Editors: David Pascucci and Jennifer Bellingtier. A peer review file is available.