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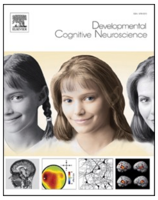

Epigenetic modification of the oxytocin receptor gene is associated with child-parent neural synchrony during competition

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ABSTRACT

Interpersonal neural synchrony (INS) occurs when neural electrical activity temporally aligns between individuals during social interactions. It has been used as a metric for interpersonal closeness, often during naturalistic child-parent interactions. This study evaluated whether other biological correlates of social processing predicted the prevalence of INS during child-parent interactions, and whether their observed cooperativity modulated this association. Child-parent dyads ($n = 27$) performed a visuospatial tower-building task in cooperative and competitive conditions. Neural activity was recorded using mobile electroencephalogram (EEG) headsets, and experimenters coded video-recordings post-hoc for behavioral attunement. DNA methylation of the oxytocin receptor gene (*OXTR*m) was measured, an epigenetic modification associated with reduced oxytocin activity and socioemotional functioning. Greater INS during competition was associated with lower child *OXTR*m, while greater behavioral attunement during competition and cooperation was associated with higher parent *OXTR*m. These differential relationships suggest that interpersonal dynamics as measured by INS may be similarly reflected by other biological markers of social functioning, irrespective of observed behavior. Children's self-perceived communication skill also showed opposite associations with parent and child *OXTR*m, suggesting complex relationships between children's and their parents' social functioning. Our findings have implications for ongoing developmental research, supporting the utility of biological metrics in characterizing interpersonal relationships.

1. Introduction

1.1. Background

Interpersonal interaction, an innate human drive, is associated with physiological effects across cardiovascular, respiratory, endocrine, and other autonomically regulated systems (Baumeister and Leary, 1995; Helm et al., 2018). The neurohormone oxytocin (OT) is widely regarded as a modulator of socio-emotional behavior and affiliative processes in humans and other animals (Buchheim et al., 2009; Feldman, 2012a). Such processes include pair bonding (Bosch and Young, 2017; Ross et al., 2009; Young et al., 2011), maternal (Insel and Shapiro, 1992; Marlin et al., 2015) and anxiety-related behaviors (Ayers et al., 2011; Blume et al., 2008; Windle et al., 1997), as well as social cognition (Dluzen et al., 1998; Kirsch et al., 2005; Lancaster et al., 2015). OT activity depends on binding to its receptor (OXTR), the expression of which is epigenetically regulated (i.e., reduced) via DNA methylation of the OT receptor gene (*OXTR*m; Jack et al., 2012; Puglia et al., 2015). *OXTR*m varies across the lifespan in response to one's unique experiences, and thus presents an opportunity to interrogate individual functional variability in the endogenous OT system and its implications for social processing. Another proposed biological marker of social processes is *interpersonal neural synchrony (INS).* INS refers to the temporal coupling of neural activity between social partners and is considered a metric for real-time social interactional closeness (Helm et al., 2018; Zaki and Ochsner, 2009). INS has been studied using various

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neuroimaging modalities and analytic frameworks, resulting in primarily convergent results that support its proposed social implications (Koole et al., 2020; Nastase et al., 2020). However, literature in this area is relatively sparse.

Child-parent interactions in particular often elicit strong physiological effects (Feldman, 2007, 2012b; Golds et al., 2022). Both oxytocinergic activity (Cecil et al., 2020; Gordon et al., 2011; Maud et al., 2018) and INS (Feldman et al., 2007; Feldman, 2012b) have been examined in the context of child-parent relationships. However, this study is among few to compare these biological measures of social functioning measured during interactions between parents and their typically-developing children. We leverage known social implications of *OXTR*m alongside observable behavior to characterize mechanisms and effects of INS. Concurrently, we examine associations between observational and neural measures of *situational* social processing and *long-term* socioemotional capacities linked to *OXTR*m.

1.2. Socioemotional processing and OT

The neurohormone OT plays a role in regulating a wide range of social behaviors and cognitive processes. Studies examining the effects of artificially increasing endogenous OT have supported its potential involvement at typical levels in processes related to social behaviors of multiple valences and across contexts. Intranasal OT administration has been linked to improved interpretation of social states and emotion recognition in children with and without autism spectrum disorder (Domes et al., 2007; Feeser et al., 2015; Guastella et al., 2010). One study found that compared to placebo-treated controls, adults who were administered intranasal OT reported less jealousy or arousal in response to discussions with a romantic partner regarding instances of infidelity (Zheng et al., 2021). Alternatively, another study showed that adult opponents in a competitive game who were administered intranasal OT displayed increased gloating or envy responses to winning and losing respectively compared to placebo-treated controls (Shamay-Tsoory et al., 2009).

OT is thought to modulate valuations of social input, such as approach-avoidance behaviors, by increasing the motivational salience of stimuli with high personal relevance (Alaerts et al., 2021; Harari-Dahan and Bernstein, 2017). This suggests that OT may be especially influential in the context of close interpersonal relationships. Within child-parent contexts, parents' endogenous OT levels are shown to be positively associated with their pleasurable emotions following affectionate contact with their infant as well as with their reciprocal behavior and responsiveness (Feldman et al., 2007, 2010, 2013). Conversely, maternal approach behavior in response to infant crying vocalizations was found to be negatively correlated with salivary OT levels (Hiraoka et al., 2020). OT also tends to vary in its effects on interpersonal behavior based on degree of social familiarity (Declerck et al., 2010) and the strength of personal attachments (Ebner et al., 2019) between social partners, making it a sensitive biological measure for approximating variations in closeness among children and parents.

Consistent environmental experiences linked to distinct physiological responses (e.g., stress) can produce long-term changes in endocrine activity and behavioral phenotypes through epigenetic regulation of gene expression. The binding of OT to its receptor underlies a portion of its endogenous activity; expression of the oxytocin receptor gene (*OXTR*) is epigenetically regulated (Haas et al., 2016; Hill et al., 2014). DNA methylation of the promoter region of *OXTR* (*OXTR*m) has been associated with reduced *OXTR* expression over a time scale of weeks or months and is considered a proxy for an individual's endogenous oxytocinergic system function (Danoff et al., 2021; Gregory et al., 2009). Natural variability in *OXTR*m has been linked with socioemotional brain function and empathic processes across the human lifespan (Haas et al., 2016; Hill et al., 2014; Krol et al., 2019b; Puglia et al., 2015; Skyberg et al., 2022; Spencer et al., 2022). Higher maternal engagement has also been associated with reduced *OXTR*m in children (Krol et al., 2019a). However, while intranasal OT administration has been shown to enhance INS in adult dyads (Mu et al., 2016), there is little work to date examining links between *OXTR*m and child-caregiver INS (Feldman et al., 2011).

1.3. Interpersonal bonds and acute neural and behavioral activity

Some of the earliest studies leveraging *hyperscanning*, the simultaneous measurement of neural responses across individuals, identified increased INS during infant-caregiver interactions (Feldman et al., 2007; for review, see Marzoratti and Evans, 2022; Turk et al., 2022). For instance, some work suggests that INS reflects cognitive processes underlying the formation of attachment bonds in early life, including reciprocal attention and processing non-verbal social cues (Feldman, 2007, 2012b; Hasson et al., 2012; Markova et al., 2019). Various studies have shown evidence of a relationship between socioemotional skills with lifelong implications and early experiences of heightened INS (i.e., when compared to controls exhibiting lower or no INS). INS measured via electroencephalography (EEG) has been positively associated with the frequency of contingent social responses within child-caregiver interactions during collaborative tasks (Markova et al., 2019; Sinha et al., 2016). More frequent instances of INS during child-caregiver interactions, as measured by functional near infrared spectroscopy (fNIRS), have been linked with children's increased scores on assessments of emotion regulation (Reindl et al., 2018). Additionally, sociodemographic risk was found to be negatively correlated with fNIRS-measured child-parent INS in the prefrontal cortex during experimentally-induced stress, interpreted as reflecting the relational effects of variations in cognitive responses to stress (Hoyniak et al., 2021). Thus, INS is a potential metric for assessing wide-spanning child-parent interaction qualities that moderate children's socioemotional outcomes, although further study is needed to validate this.

1.4. Linking acute behavior and biological measures

Findings are mixed regarding relative differences in the prevalence of INS across cooperative and competitive contexts, despite their inherent behavioral differences (Balconi and Vanutelli, 2017). During a decision-making game, when told they were interacting with a machine as opposed to a human, female dyads demonstrated decreased cooperation and EEG-measured INS within the theta/alpha-band with their human partner (Hu et al., 2018). Dyads have been found to exhibit higher INS as measured via both fNIRS and EEG while playing computerized games cooperatively relative to competitively (Cui et al., 2012; Reindl et al., 2018; Sinha et al., 2016). However, in a study of dyads playing cooperative, competitive, and parallel single-player versions of a card game, both cooperative and competitive conditions resulted in dyads showing increased EEG-measured INS (Hsu et al., 2021). Another study using fNIRS revealed significant correlations in right interfrontal gyrus activation among dyads playing a competitive building game where one player was instructed to hinder their partner (Liu et al., 2015). Comparing child-parent INS across interactional contexts that inherently capture the extremes of behavioral alignment (i.e., cooperation and competition) in this study allows us to comprehensively evaluate the extent to which behavioral and neural markers of interpersonal alignment correspond.

1.5. This study

Dyads of typically developing children and their parents ($n = 27$) performed a joint visuospatial tower-building task cooperatively and competitively. We recorded EEG time series from dyad members using hyperscanning and calculated INS through windowed cross-correlation analysis (Boker et al., 2002; Marzoratti and Evans, 2022). *OXTR*m was measured from saliva obtained from both children and their parents. Videos captured while the dyads completed the tasks were coded post-hoc for child-parent behavioral attunement. We hypothesized that INS would be positively associated with behavioral attunement and that both would be greatest during cooperation. Additionally, we predicted that child and parent *OXTR*m would negatively correlate with both INS and behavioral attunement.

Our research examines links between an individual-level biological correlate associated with social processing traits (i.e., *OXTR*m) and situational, dyad-level markers of interactional closeness (i.e., INS and behavioral attunement) across two distinct interactional contexts. Leveraging metrics of both biological and phenotypic data provided unique insights into the dynamics of child-caregiver relationships in semi-naturalistic environments through multi-measure triangulation.

2. Methods

2.1. Experimental design

Child-caregiver dyads were recruited from the local community in Albemarle County, Virginia as part of a larger study assessing multiple biological measures among children with or without diagnosis of Autism Spectrum Disorder and their caregivers as they completed a series of joint tasks (Fig. A.1; Table B.1). Caregivers responded to flyers posted throughout the community or were contacted using a University of Virginia-managed database of families who had previously expressed interest in research participation. All adult participants were children's biological parents. Upon recruitment, parents completed questionnaires containing family demographic information and their child's medical history. Dyads were included only if the responding parent was over eighteen years of age, their child was aged 6–11 years, and if the parent reported that the child could communicate verbally and had no diagnoses of neurodevelopmental or learning disorders.

At the Sheila Johnson Center for Clinical Services at the University of Virginia, dyads completed two sessions on separate days: one for cognitive assessment and the other to complete a neuroscientific experimental paradigm. At the start of the first session, in accordance with the Declaration of Helsinki, parents provided informed, written consent for their and their child's participation. All children provided verbal assent following developmentally appropriate explanation of the study and their rights, and children aged seven years or older provided written assent. Participants were excluded from analysis post-cognitive assessment if the child's standardized Intelligence Quotient (IQ) was under 85, and excluded post-testing if the child could not complete the experimental tasks (e.g., due to behavioral problems or discomfort with equipment). The final sample (Table B.1; Fig. A.1.) included 27 children (M_{age} = 9.04 years, SD = 1.84 years, 15 males) and their parents (M_{age} = 41.91 years, SD = 5.79 years, 3 males).

2.2. Experimental procedure

2.2.1. Cognitive assessments

On a separate date before or after the experimental session, children completed a variety of cognitive tests with a researcher, including the Differential Ability Scale II (DAS-II) to assess children's IQ. Table A.1 contains a full list of cognitive assessments administered.

2.2.2. Experimental session

Children first completed an adapted version of the Toronto Alexithymia Scale (TAS-C; Table A.1; Rieffe et al., 2006), which assesses a child's perception of their aptitude for emotional communication. This was verbally administered by an experimenter following procedures in Lampi et al. (2021) while parents were in a separate waiting room. Children and parents were then fitted with 20-channel mobile EEG headsets and completed various tasks designed to elicit social interaction.

2.2.3. Tower task conditions

Competitive and cooperative conditions of a visuospatial tower-building task were the focus of this study. These conditions, each lasting approximately three minutes, were performed consecutively during the session with condition order counterbalanced. In both conditions, participants were presented with a pre-constructed Jenga® tower and instructed to remove blocks in turns, one-by-one from the tower and to place each removed block on top (for a demonstration of Jenga® gameplay, see www.hasbro.com/jenga). In the competitive condition, participants were instructed to take turns removing blocks and told they would lose the game if the tower fell down on their turn. In the cooperative condition, participants were instructed to work together to build the tallest tower possible and turn-taking was not mandated. For this condition, the children were told that following task completion, they would receive stickers corresponding to the number of levels in their tower.

2.3. Behavioral scoring

Behavioral attunement during each condition of the tower task was separately scored using an adapted version of the *Positive Synchrony Coding Manual*, a macro-level observational coding scale developed for measuring this construct during dyadic interactions (Criss et al., 2003; Jirout et al., 2022). The original scale calls for evaluating interactions based on criteria reflecting the degree of mutuality, engagement, and responsiveness between dyad members. The original 9-point scale was collapsed to an 8-point scale for this study, as the factors differentiating scores of 7 and 8 were particular social miscues that were less discriminative in the context of parent-child gameplay as opposed to other naturalistic interactions (i.e., minute differences in balance of leading and following). Dyads that exhibited clear imbalance and/or other forms of asynchronous or disjointed interaction were assigned lower scores (i.e., 1–4; Fig. A.2). Higher scores (i.e., 5–8) were assigned to dyads who exhibited a balance in leading and following, shared affect (i.e., smiling and laughing) and eye contact, and mutual responsiveness to verbal and nonverbal behaviors. For example, during the cooperative tower condition, an interaction in which both dyad members were engaged but one consistently directed the other member's actions and disregarded their input was awarded a 4. Conversely, an interaction during the same task in which both members were engaged, discussed strategies equally, and helped each other complete moves was awarded a score of 7 or 8 depending on their consistency of engagement.

For each condition, a video recording was coded for its full length by two trained research assistants, and the average of the two coders' ratings was assigned as a global dyadic score. Task length was approximately 3 min (M: 193 s, range: 160–362 s). The variability in task length occurred because of a subset of dyads (n = 2) in which the child requested additional time to complete the game of Jenga®. Only the first three minutes of the video and EEG-recordings in these cases were analyzed. Inter-rater reliability was measured using intraclass correlations (ICC): 0.93 for the cooperative condition and 0.85 for the competitive condition.

2.4. DNA collection and analysis

Following completion of the EEG paradigm, saliva was collected from child participants with assisted collection CS-2 sponges stored in OG-250 kits from DNA Genotek (2015) (Ottawa, Canada; Fig. A.3). Passive drool was collected from parents in OG-500 collection tubes, and all saliva samples were stored at room temperature. Prior to DNA isolation, samples were incubated for one hour at 50 °C. Child samples were centrifuged for 10 min at 200 rcf/g to extract all liquid from the sponges. Salivary DNA from both parent and child was analyzed using the manual purification protocol from DNA Genotek (2015). Isolated DNA was stored in Hydration Solution from QIAGEN (Hilden, Germany), and DNA concentration was measured via NanoDrop. 200 ng of

DNA underwent bisulfite treatment using MECOV50 Kits from ThermoFisher Scientific (Waltham, MA). Instead of complete randomization on the 96-well plate, child-parent dyad numbers were randomized, and all dyad members (child or parent) were placed adjacent to each other in randomized member order to ensure similar treatment.

After bisulfite conversion, the following protocols were performed in triplicate. 40 ng of bisulfite-converted DNA were amplified via polymerase chain reaction (PCR) using PyroMark PCR Kits from QIAGEN (Hilden, Germany) and 0.2 μM primers [TSL101F, 5′-TTGAGTTTTGGATTTAGATAATTAAGGATT-3′ (forward); TSL101R, 5′-biotin-AATAAAATACCTCCCACTCCTTATTCCTAA-3′ (reverse)]. The following cycling conditions were used for amplification: (i) 95 °C for 15 min for 1 cycle, (ii) 94 °C for 30 s, 56 °C for 30 s, 72 °C for 50 cycles, (iii) 72 °C for 10 min for 1 cycle, (iv) 4 °C hold. This process amplified a 116-base pair region on the coding strand of *OXTR* containing the CpG-934 site (hg19, chr3:8810,729–8810,845). Methylation standards of 0 %, 50 %, and 100 % as well as negative controls for bisulfite conversion and PCR were present on each PCR plate. PCR amplification of the *OXTR* fragment was verified and lack of contamination confirmed using agarose gel electrophoresis. The remaining un-converted (methylated) cytosines were quantified via pyrosequencing (PyroMark Q24, Qiagen). Replicate variability for the CpG-934 site averaged 1.69 %. The reported level for this methylation site is the average of the three replicates.

2.5. *EEG Data*

2.5.1. *EEG data collection*

EEG recordings were obtained using Cognionics dry wireless Quick-20 m EEG headsets (Cognionics, Inc., San Diego), with 19 channels plus a reference and ground electrode (Fig. A.4a-b*;* Cognionics Quick 20 Dry EEG Headset, 2017). The A2 electrode (placed on the right earlobe) served as the reference channel. Data were digitized at 500 Hz at a 24-bit resolution. Electrodes were adjusted until each reached a signal impedance <5 Ω. Caps were fitted with dry pad sensors (Fig. A.4c) for the frontal electrodes that made contact with participants' foreheads and comb-shaped flex sensors (Fig. A.4d) for the rest of the scalp. Electrodes were placed using a standard 10–20 placement pattern.

This EEG headset utilizes a Bluetooth-enabled wireless trigger. While one experimenter communicated with both participants to provide instructions on how and when to complete experimental tasks, a second experimenter controlled a computer to embed trigger codes (i.e., identification numbers) in the signal file corresponding with task start- and end-times.

2.5.2. *EEG data preprocessing*

Preprocessing steps were completed according to the best practices reported in a review of EEG preprocessing methods (Robbins et al., 2020) and several empirical studies which utilized mobile EEG to collect neural data in naturalistic contexts (Bevilacqua et al., 2019; Dikker et al., 2017; Marini et al., 2019). Data from all 20 EEG channels were preprocessed for each participant using EEGLab, a MatLab-based toolbox (Delorme and Makeig, 2004; The MathWorks Inc., Natick, MA, USA). Due to errors in equipment set-up prior to recording, three participants' data which were initially sampled at 1000 Hz were re-sampled to 500 Hz before pre-processing. High and low-pass filters were applied at 1 Hz and 50 Hz respectively.

Using the PREP pipeline, iterative algorithms were used to remove line noise and estimate a robust reference less affected by artifacts (Bigdely-Shamlo et al., 2015). The common median was used as the reference signal for improved signal-to-noise ratio given the small electrode array (Rolston et al., 2009). Noisiness was defined by calculating the ratio of the median absolute deviation of the high frequency over the low frequency for each channel (following initial high- and low-pass filtering steps). A robust, noise-adjusted z-score relative to the average reference was calculated for each channel in non-overlapping 1-s windows. Time series segments with mean z-scores that exceeded five were spherically interpolated in relation to the previously estimated robust reference for each channel identified by this metric (channels per subject: M = 4.05, SD = 0.57; Fig. B.1).

Independent components analysis (ICA) was then used to identify and remove eye blinks and other small movement artifacts (Parent: M = 10.70, SD = 6.75; Child: M = 11.30, SD = 7.34; Fig. B.1; Makeig et al., 1995). Artifacts were rejected automatically using criteria of the multiple artifact rejection algorithm (MARA; Fig. A.5; Winkler et al., 2011). Channels with insufficient clean data for interpolation were removed from analysis (per dyad M = 0.98, SD = 3.32; see Fig. B.1 for cleaning statistics and analysis).

For each participant, we isolated portions of the EEG time series associated with each of the two task conditions by referring to onset and offset trigger codes for each condition. Dyads' data were only included in analyses if both members' data was available. In both cooperative and competitive conditions, there was one dyad for whom the number and identity of channels with sufficiently clean data differed between the child and parent, preventing synchrony analysis within that dyad for that specific task condition. These dyads' EEG data were not included in any cross-task comparisons but were included in the regression analyses evaluating individual tasks for which INS could be calculated.

2.5.3. *Synchrony calculations*

Correlations in neural activity across dyad members were established using windowed cross-lagged correlation analysis, which quantifies the correspondence between two time-varying signals while accounting for potential lag in their association (Boker et al., 2002; Tschacher et al., 2014). This analysis, using peak picking algorithms specified by Boker and colleagues (2002), required calculating the correlations between absolute power (Marriott Haresign et al., 2022; Müller and Lindenberger, 2022) of the time series for the child (C) and the parent (P; Fig. 1). We chose P as the reference to increase the interpretability of our results given the theoretical basis for the child relying upon the parent as a model, especially in unfamiliar contexts (Woszidlo and Kunkel, 2017). However, the same magnitude of correlation would result for these data regardless of the reference time series (i.e., only the sign would differ).

Window size (w_{max}; the length of C and P times-series analyzed at each step) was 1000-ms, the window increment (w_{inc}; the time segment separating changes in the window of P analyzed at each step) was 50-ms, the maximum lag (τ_{max}; the maximum time-window separating the beginning of the segments of C and P whose correlations were calculated) was 1000-ms, and the lag increment (τ_{inc}; the time segment separating the changes in the time-segment of C being evaluated) was 50-ms. Hyperparameters were chosen based on existing EEG-WCC literature, which demonstrates that window lengths as long as 30-s are sufficient to maximize the algorithm's performance with EEG data (Damaraju et al., 2020). Given our 500 Hz sampling rate, these parameters led to 500 observations per 1000-ms window, analyzed in increments of 25 observations (i.e., 50 ms).

Correlations were calculated between 50-ms segments (w_{inc}) of 1000-ms rolling windows (w_{max}) of the C and P time series over their total 180-s length, beginning with zero lag between C and P windows. Correlations across dyads were then calculated across windows with increasing increments of −50-ms and +50-ms lag (τ_{inc}) until a distance of 1000-ms (τ_{max}) was reached between the beginnings of the windows for both C and P. This produced a matrix of correlations across time series. The highest correlation, or the *peak*, was chosen from among these values, with higher scores indicative of greater synchrony. Given the 180-second task-length, 180 *mean peak correlations (MPC)* values per electrode, per dyad resulted (Fig. 1). We calculated the *mean* of the MPC vector per electrode (*MMPC*). We applied a Fisher r to Z transform to these correlations (Fisher, 1915, 1921). We calculated the *mean* and *maximum MMPC* across electrodes, producing two measures of INS per task condition, all of which were evaluated as model predictors (Fig. A.6).

Examining both measures allowed us to account for whole-scalp

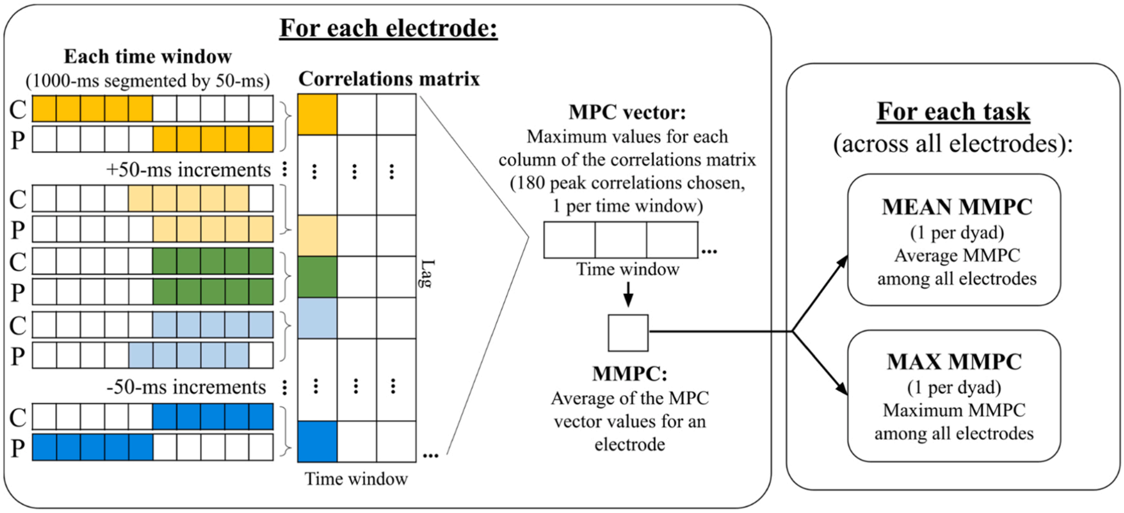

Fig. 1. Graphical overview of the windowed cross-lagged correlation analysis strategy to leveraged to quantify INS. *Note.* The *left box* outlines the procedure used to calculate an average peak correlation across the whole task for each electrode. Per electrode, the 180-s task was partitioned into 1-s (1000-ms long) windows. Each 1000-ms time window of the child (C) and parent (P) time series were compared (green). The beginning of the child time series was then offset from the beginning of the parent time series at 50-ms increments. Correlations between these 1000-ms windows at every lag were calculated to produce a correlations matrix: each row corresponds to a differing amount of lag, and each column corresponds to a different 1000-ms time window. The highest value for each time window (column) of the correlation matrix was chosen to create a vector of 180 entries, representing the greatest correlation between the C and P time series within each 1000-ms window of the task. The vector was averaged to produce one value per electrode (MMPC), the average peak correlation for a given electrode in one condition. The *right box* displays the strategy used to aggregate MMPC across electrodes. The average (Mean MMPC) and maximum (Maximum MMPC) across electrodes were calculated and used as INS variables in our models.

trends as well as electrode-level variations. Leveraging both was relevant for this analysis, as the individual differences in social processing we sought to identify may impact the degree to which a dyad exhibits INS or the channel(s) in which it manifests. Further, in using mobile EEG with only 20 channels, there was a higher probability of one or more individual channels producing data abnormalities that could have occluded relevant effects should electrode-level data be aggregated for analysis. Only INS models with maximum MMPC as the outcome variable yielded significant results. Thus, only results for models including this measure are discussed. Results for analyses of *mean MMPC*, which reflects the highest correlation across the task time series averaged across all electrodes, are shown in Table B.6.

2.6. Analyses

Primary statistical analyses were conducted using IBM SPSS Statistics (version 28.0.1.0). We calculated descriptive statistics for demographic variables and substantive variables of interest, which included four measures of INS per dyad (i.e., *mean MMPC* and *maximum MMPC* for both cooperative and competitive conditions; Fig. A.6), two *OXTR*m values (i.e., child and parent values; Fig. 2), and two behavioral attunement scores (Fig. 3). For these measures, we assessed skewness and kurtosis using the “Explore” subcommand and conducted one-sample Kolmogorov-Smirnov tests for normality prior to running linear regression models. The measures satisfied the necessary assumptions (Kolmogorov-Smirnov, all $p > .05$; Table B.2). We plotted distributions of *OXTR*m values across dyad members (Fig. 2) and behavioral attunement scores across conditions (Fig. 3). We produced a bivariate correlation matrix for included variables (Table B.3).

2.6.1. Primary analysis

Using stepwise hierarchical linear regression analyses with forward selection, we could specify flexible yet tailored models which best described the relationships between our outcome variables and multiple predictors with unknown associations (Skyberg et al., 2022).This served as a data-driven method for reducing the predictors included in our final models in the absence of a clear basis for prioritizing them given the relatively limited literature on relationships of INS with the factors and context investigated in this study (Denis, 2018; Petrocelli, 2003).

Outcome variables included our INS metrics (i.e., *mean MMPC* and *maximum MMPC*) for each task condition, resulting in four total models specified for our primary analysis of INS (Fig. A.6). Substantive predictors for each model included child and parent *OXTR*m values and behavioral attunement scores for each task condition. Covariates included child sex (female gender coded as "1”) and age, both factors shown to be associated with children’s neural and behavioral markers of social processing (Chaplin and Aldao, 2013; Pavlova, 2017) and their neural activity more broadly (Kaczkurkin et al., 2019; Kurth et al., 2021). To account for the effects on signal quality of errors in data collection related to hardware, noise, or human error, (1) the number of channels for which data was interpolated (M=4.05, SD=0.57) and (2) the number of channels averaged across dyad members excluded due to their having insufficient data for interpolation (M = 0.98, SD = 3.32) were also used as covariates in all analyses. Separate models were estimated with behavioral attunement for each task condition as the outcome variable. Predictors included child and parent *OXTR*m and *maximum MMPC* for that task, and the same covariates specified for our models predicting INS.

Variables were added in a stepwise fashion based on the p value of the F-statistic. Criteria for entry was $p < .98$ and the criteria for stopping was when no further variables had $p < .99$, visualizing all possible predictor influences. We evaluated adjusted R-squared values for models of interest as measures of fit and effect size. Given our multiple hypothesis testing, we adjusted p values to control for false discovery rate via the Benjamini-Hochberg procedure using the p.adjust function in R (version 4.2.2; Benjamini and Hochberg, 1995; Jafari and Ansari-Pour, 2019). We reported q values calculated with a significance threshold of $q < 0.05$ (Somerville, 2004). In addition, 95 % confidence intervals are reported for all coefficients. Cumulative probability plots (P-P plots) and quantile plots (Q-Q plots) were produced per model to evaluate the distribution of residuals.

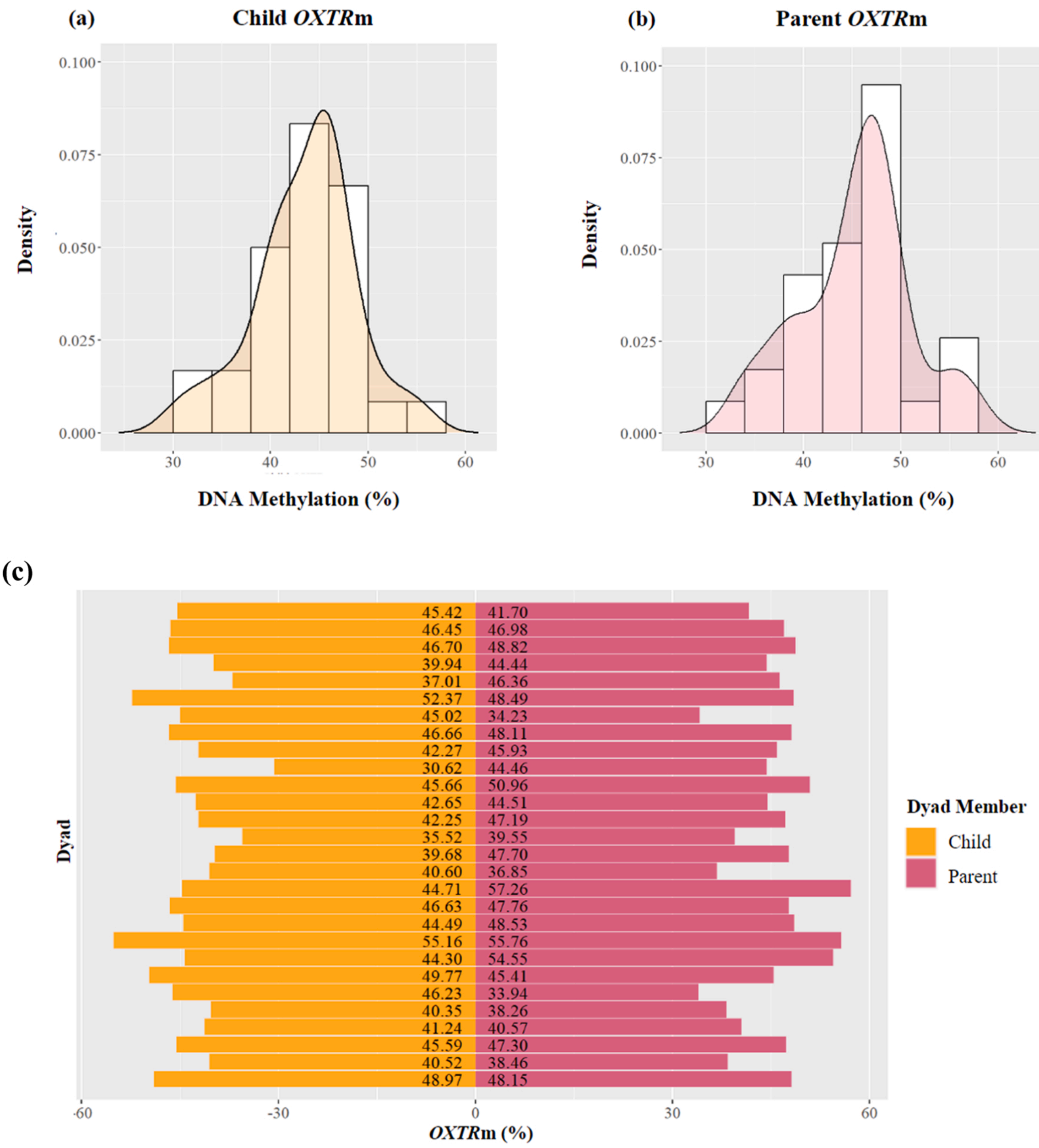

Fig. 2. Distributions for child and parent OXTRm. *Note.* Panels (a) and (b) show the histogram and overlaid density plots for DNA methylation levels at CpG site − 934 on *OXTR* for child and adult participants respectively. Panel (c) displays values for each dyad with child and parent *OXTR*m contrasted.

3. Results

3.1. Descriptive results

Model residuals met all assumptions (Osborne and Waters, 2019). There were strong, positive correlations between task conditions in values for *mean MMPC* ($r(25) = .595$, $p < .001$), *maximum MMPC* ($r(25) = .473$, $p = .015$), and behavioral attunement ($r(25) = .442$, $p = .019$; Table B.3). Child and parent *OXTR*m values (Fig. 2) were significantly positively correlated ($r(25) = .382$, $p = .045$). Descriptive statistics for substantive variables are in Table B.2.

3.2. Relationship between INS during competition and child OXTRm

The only measure of INS significantly related to substantive predictor variables was the *maximum MMPC,* which reflects the highest correlation displayed across the task time series by any one electrode. For the competitive task, the best fitting linear model examining the *maximum MMPC* (F(1,24)= 4.300, $p = .049$, adjusted $R^2 = .117$; Table B.4.a) showed a significant, negative relationship with the child's *OXTR*m ($B = -.390$, $p = .049$, $q = .049$; Fig. 4).

3.3. Relationships between observed behavioral attunement across task conditions and parent OXTRm

The best-fitting model predicting behavioral attunement scores in the competitive condition (F(1,24) = 6.131, $p = .021$, $R^2 = .170$; Table B.4.b) demonstrated positive associations between behavioral attunement and parent *OXTR*m during that task ($\beta = .451$, $p = .021$, $q = .021$; Fig. 5). The best-fitting model predicting behavioral attunement scores in the cooperative condition (F(1,26) = 4.801, $p = 0.038$, adjusted $R^2 = .123$; Table B.4.c) also demonstrated positive associations between behavioral attunement and adult *OXTR*m for that condition ($\beta = .395$, $p = 0.038$, $q = .038$; Fig. 5). No significant relationships

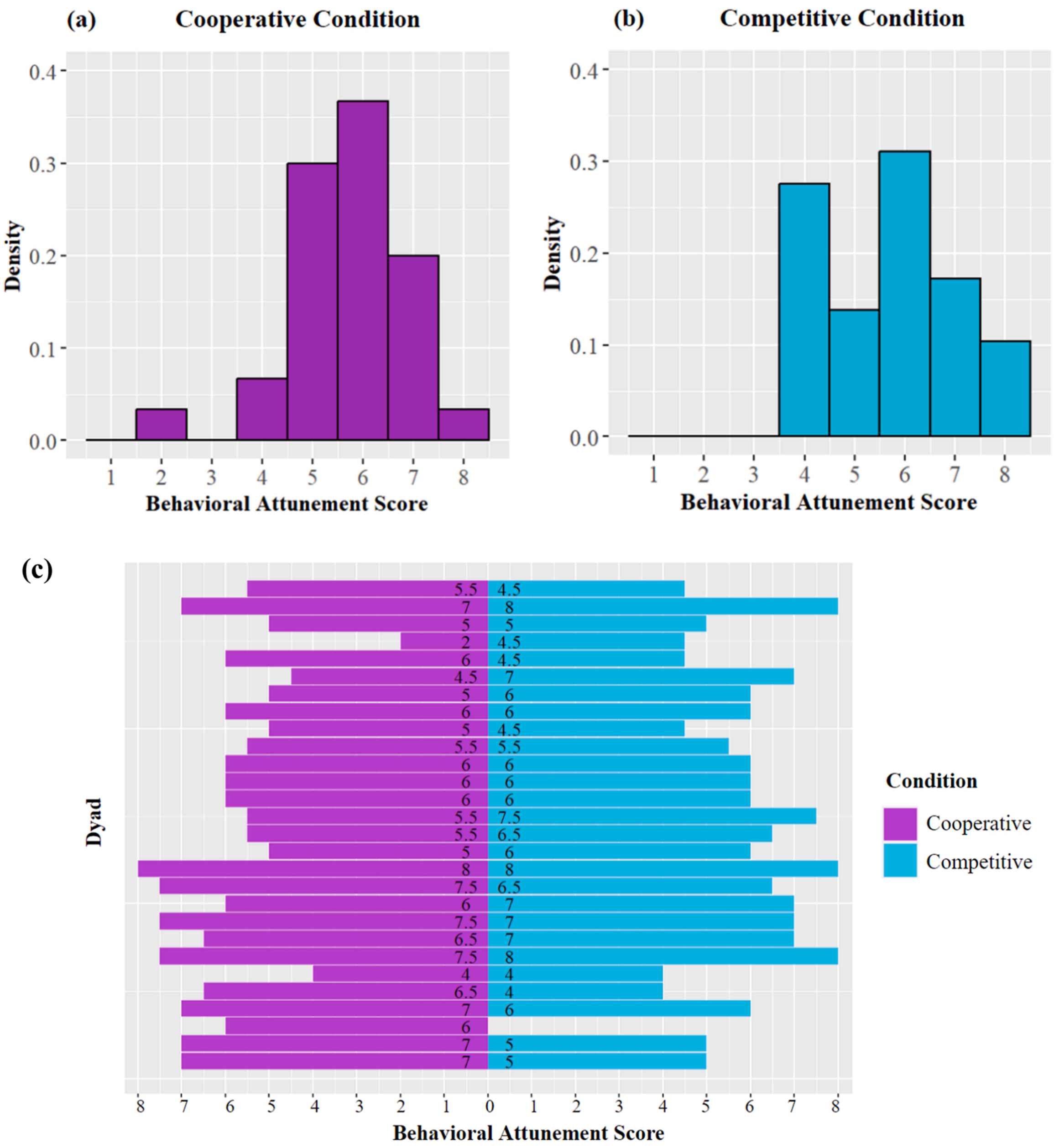

Fig. 3. Distributions for behavioral attunement scores. *Note.* Behavioral attunement score distributions for (a) cooperative and (b) competitive task conditions and (c) those scores contrasted per dyad. One dyad did not complete the competitive task condition and thus no score is listed in (c).

emerged between observed behavioral attunement and INS.

3.4. Post-Hoc analyses

3.4.1. Evaluating child-reported alexithymia as a mechanism for relationships between observational and biological measures of socioemotional function

We sought to further interrogate the mechanism for the relationships between long-term socioemotional capacities correlated with methylation of *OXTR* and acute social dynamics reflected by INS and behavioral attunement scores. We evaluated the relationship between these variables and children's self-reported *alexithymia* (i.e., difficulty with emotional reflection and communication measured via TAS-C score; Lampi et al., 2021). TAS-C scores directly reflected the child's perceptions of their own socioemotional capacity and allowed us to evaluate its independent relationships with dyadic relational dynamics (i.e., behavioral attunement and INS measures), and with biological measures which indirectly reflect socioemotional capacity (i.e., child *OXTR*m). We specified a linear regression model with children's scores on the TAS-C as the outcome variable using similar parameters to those used for primary analyses. Two dyads for whom TAS-C scores were not collected were removed. Predictors included child and parent *OXTR*m values, *maximum MMPC* and behavioral attunement scores for both task conditions, and covariates (i.e., child's sex, age, number of interpolated EEG channels, and number of missing channels).

In the model explaining the greatest variability in child-reported emotional communication difficulty (i.e., TAS-C scores; F(7, 16) = 9.623, $p < .001$, $R^2 = 0.724$; Table B.5), scores were found to be significantly, positively associated with child *OXTR*m ($\beta = 0.654$, $p < .001$, $q = .004$; Fig. 6), female gender identity ($\beta = 0.310$, $p = 0.043$, $q = .043$), and cooperative task INS ($\beta = .381$, $p = .021$, $q = .025$). TAS-C scores were also significantly negatively associated with parent *OXTR*m ($\beta = -0.621$, $p < .001$, $q = .004$; Fig. 6), and competitive task INS ($\beta = -0.399$, $p = 0.008$, $q = .019$).

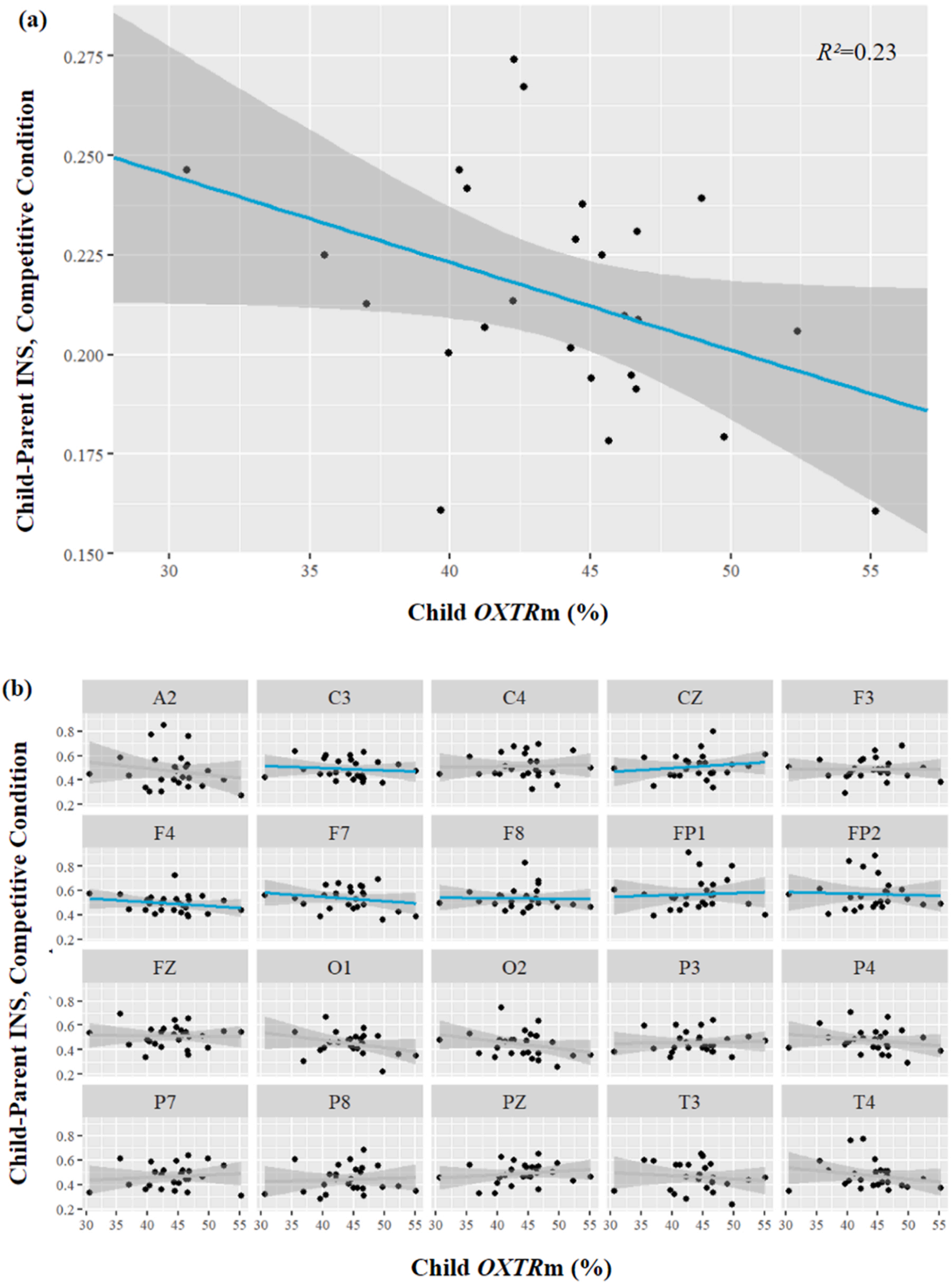

Fig. 4. Associations between INS in the competitive task condition and child *OXTR*m. *Note*. The association between child *OXTR*m and INS in the competitive task condition (a) averaged across all electrodes and (b) separate for each electrode. Blue lines in the lower figure correspond with electrodes from which *maximum MMPC* values were derived for a particular dyad.

3.4.2. Evaluating the influence of across-condition movement differences on EEG results

Participants' patterns of movement could have systematically varied across conditions, despite performing the same tower-building task, based on differences in their goals (i.e., competitive or cooperative) or in their instruction (e.g., turn-taking was mandated only for the competitive task condition). This variation could have affected the quality of EEG signals recorded and/or the degree of INS detected between them.

To evaluate this notion, we quantified movement among dyad members using Motion Energy Analysis (MEA) and compared these

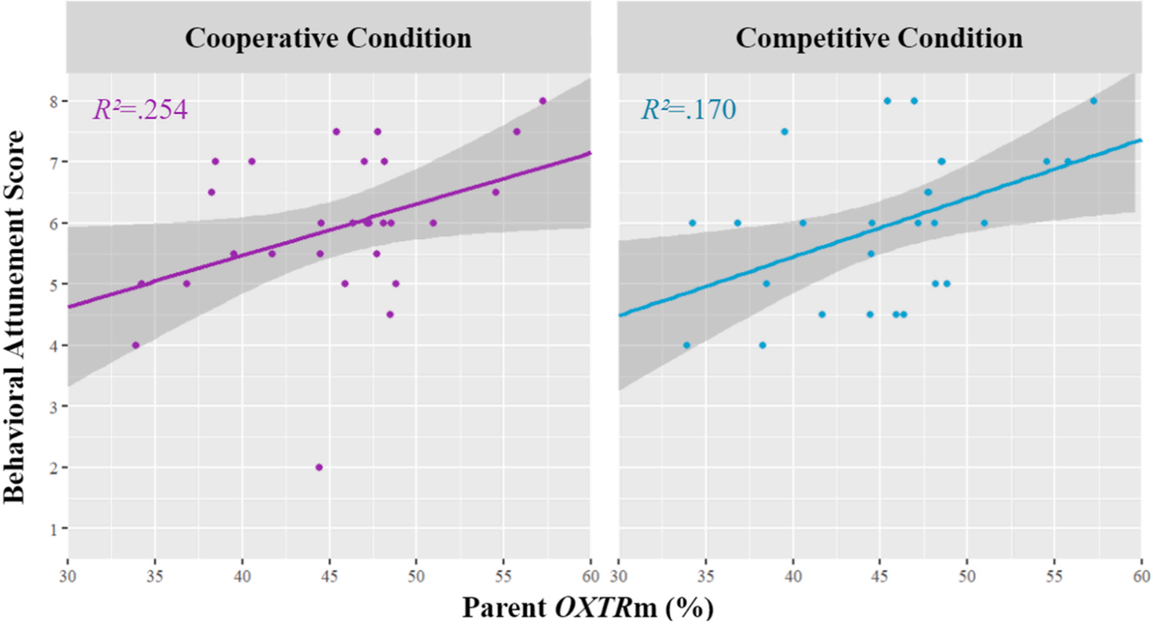

Fig. 5. Positive association between parent OXTRm and dyadic behavioral attunement in both task conditions.

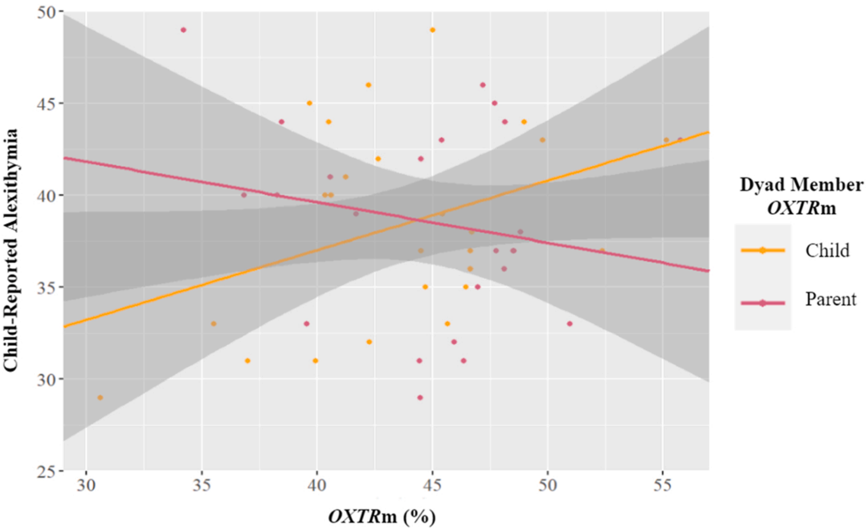

Fig. 6. Differential relationship between child and parent *OXTR*m levels and child alexithymia. *Note.* Child self-reported emotional communication difficulty was measured by the TAS-C assessment, where higher scores indicate greater difficulty (i.e. greater alexithymia).

values across task conditions. MEA is an automated algorithm that quantifies frame-by-frame pixel variation in user-designated regions of interest (ROIs) of a video recording, producing an objective metric for movement (Fig A.7; Grammer et al., 1999; Hamel et al., 2022; Ramseyer, 2020; Ramseyer and Tschacher, 2011). See Table B.7 for detailed methods and results. There were no significant differences across conditions in child or parent movement, or in child-parent movement differences. This suggests similar degrees of overall physical mobility per participant as well as similar levels of relative movement across dyad members (e.g., turn-taking), meaning that large motor differences between conditions are most likely not a factor in the previously reported EEG results.

4. Discussion

Our study evaluates associations between biological measures reflective of interactional closeness (i.e., EEG-measured INS) and a biological metric linked with trait-level variability in social processing (i.e., child and parent *OXTR*m). This study is among the first to specifically evaluate relationships between the degree of INS within child-parent interactions and the gene-environment interplay reflected by *OXTR*m (Levy et al., 2016a, 2016b; Mu et al., 2016).

In addition, while this study took place in a clinical research setting, the visuospatial task was designed to have few behavioral restrictions. In forgoing a traditional lab-based paradigm and the use of wired EEG headsets, we were uniquely able to capture behaviors that may characterize child-parent interactions in more naturalistic contexts and better reflect their typical daily experiences. This research design has the potential to capture ecologically valid social dynamics which may prove more generalizable across environmental contexts (i.e., school, home) and interpersonal relationships (i.e., with caretakers, teachers, or peers) that have a strong influence over a child’s early development (Bevilacqua et al., 2019; Catalano et al., 2004; Dikker et al., 2017; Taylor et al., 2004; Umberson and Montez, 2010).

4.1. *Parent and child OXTRm are positively correlated in 6- to 11-year old children*

*OXTR*m is a marker of activity within an individual's endogenous OT system. When parents show lower levels of *OXTR*m, and thus greater expression of the OT receptor, this may enable OT to function more widely throughout the body, promoting its associated effects on social, emotional, and cognitive brain function (Krol et al., 2019b; Puglia et al., 2015; Skyberg et al., 2022). While *OXTR*m has been shown to vary with age and is implicated in child-parent relationships, previous work in this realm has primarily focused on the relationship between mother and infant *OXTR*m levels (Krol et al., 2019a; Krol et al., 2019b). This study is among the first to demonstrate a significant positive relationship in OXTRm between parents and their children aged 6–11 years old (Fig. 7*;* Krol et al., 2019a).

*OXTR*m may influence adults' affinity for caregiving behaviors. For example, women with lower *OXTR*m have been found to display greater empathic responses towards images of children (Spencer et al., 2022). Thus, the levels of *OXTR*m that adults develop over time may influence the degree to which they engage with their child, which in turn may influence their child's *OXTR*m values. For example, infants that receive higher levels of maternal engagement exhibit lower *OXTR*m levels (Krol et al., 2019a). This suggests that children whose parents show low *OXTR*m and thus are more likely to demonstrate prosocial, bonding behaviors may also exhibit lower levels of *OXTR*m themselves. Conversely, parents that have developed higher levels of *OXTR*m may be less likely to engage with their children, which limits the potential *OXTR*m-buffering effects of this engagement. Thus, it is reasonable to assume that parent and child *OXTR*m levels may be positively correlated as was observed in this study.

4.2. *Child OXTRm is associated with INS during competitive behavioral contexts*

Quantifying *OXTR*m, a measure associated with an individual's social processing, enabled us to disentangle the differing influences of child and parent socioemotional capacities on interactional closeness at the dyad level (i.e., INS). As hypothesized, our results demonstrate that *OXTR*m negatively predicts INS, a metric thought to reflect interpersonal closeness and positive interaction quality within dyads (Lu and Hao, 2019). In line with our results, OT administration has been linked to acute changes in neural markers of interactional closeness. For example, administering intranasal OT to adults during social tasks has been shown to increase their interbrain phase synchrony (i.e., degree of phase overlap across individuals' neural oscillations) in EEG alpha band activity (Mu et al., 2016). It is also shown to reduce changes in activity within neural circuitry subserving emotion following breaches in trust (Levy et al., 2016b). However, contrary to our hypotheses, this association only emerged as significant in relation to INS during competition and was specific to the child's *OXTR*m (Fig. 4*,* Table B.4.a).

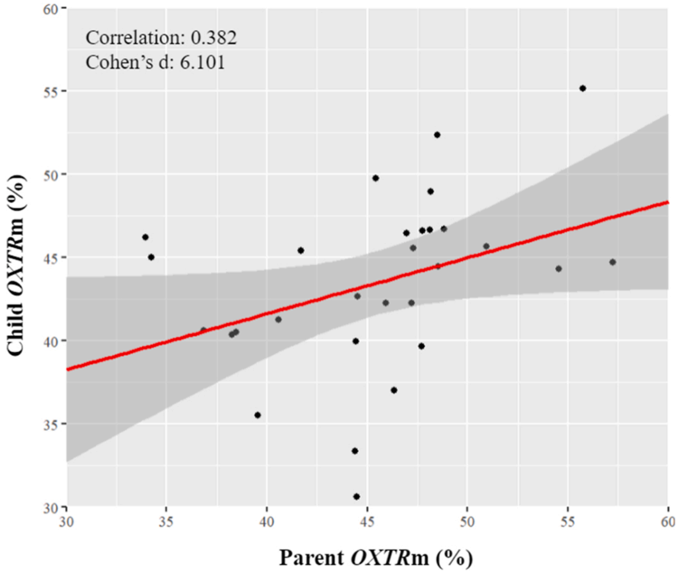

Fig. 7. Positive correlation between OXTR methylation levels of children and their parents.

4.2.1. *OXTRm is associated with child-parent INS during competition*

Cooperative and competitive social contexts inherently elicit different degrees of contingent behavior and place differential demands on social processing of participants (Stapel and Koomen, 2005). Based on the behavioral implications of INS in prior research, we expected that in a cooperative context in which social partners shared a goal, greater alignment of behavioral and neural activity would occur. However, our results revealed a relationship between children's *OXTR*m and child-parent INS only during competition. This suggests that the social processing capacities marked by *OXTR*m may be more predictive of interactional closeness (i.e., INS) in contexts where social partners are behaviorally asynchronous. In other words, when dyad members' goals are not aligned (as is the case during competition), social processing capacity may play a more significant role over the reciprocal, balanced nature of the interaction. Alternatively, with an explicitly cooperative goal, social processing skills may not be "necessary" to scaffold interactions with inherently more consistent alignment between child-parent behaviors.

This explanation is supported by the social-cognitive model of joint attention, which characterizes shared intentionality between social actors as a scaffold for ongoing social behavior (Mundy and Newell, 2007). INS often manifests during instances of joint attention (Babiloni and Astolfi, 2014). The association between children's *OXTR*m and INS specifically during competition thus suggests that both biological measures may reflect increased likelihood or greater prevalence of cognitive processes which scaffold social behaviors (e.g., joint attention) and play a greater role within contexts in which individuals' behaviors may otherwise misalign.

4.2.2. *Child, but not parent, OXTRm is associated with child-parent INS*

While we anticipated the negative direction of the relationship between *OXTR*m level and INS, we did not predict that this effect would be exclusive to the child's *OXTR*m (Fig. 4). This finding suggests that children's social processing may be a more influential factor than their parent's in affecting child-parent interactional quality. Under the assumption that INS requires a leader-follower relational dynamic, if the parent is indeed the "leader" in this context, then the child's social processing skill as the "follower" would be the limiting factor on the extent to which interactions are reciprocal and neural activity aligns. Accordingly, there is evidence that INS predicts infants' social learning, which necessarily includes at least two actors, one of whom *follows* the behaviors of another (Leong et al., 2017; Wass et al., 2018).

Our results suggest that the degree of neural and behavioral alignment may depend more on a child's capacity to adapt their social processes to their parents. Thus, children with higher *OXTR*m and potential reductions in this social flexibility may in turn show reduced INS with their parents. The fact that this effect emerged only in the competitive condition may be attributed to its inherently low degree of behavioral cooperation. Neural alignment associated with interpersonal attunement may show greater variability based on socioemotional competency as measured by *OXTR*m in a context in which cooperative behaviors that produce such alignment are not explicitly required or enforced.

This interpretation is supported by the primarily fronto-central localization of the electrodes from which maximum INS values in this sample originated (Fig. B.2). Various studies have revealed associations between cognitive processes implicated in cooperative behavior and INS localized to frontal regions of the brain, including frontal gyri and prefrontal cortices (Cui et al., 2012; Fairhurst et al., 2013; Liu et al., 2015). Some cooperative cognitive processes linked to INS are perceptual in nature; for example, musicians playing duets show increased frontal INS while adapting their physical movements and auditory output based on the behaviors of their partner (Fairhurst et al., 2013; Müller and Lindenberger, 2022). However, other studies show links between frontal INS and emotional cognitive processes relevant to cooperation, such as perspective-taking (Markova et al., 2019; Valdesolo and DeSteno, 2011) and emotion regulation (Reindl et al., 2018). Variability in INS localized to frontal regions could thus be attributed to the variability in socio-emotional processing capacity reflected by *OXTR*m, in this case specifically that of the child's capacity. Future studies of INS and *OXTR*m with improved spatial resolution could allow researchers to draw more definitive conclusions based on this line of evidence, more explicitly differentiating between emotional and perceptual mechanisms for the relationship between INS and cooperative behavior.

Our study is among the first to examine associations between INS and OT function in the context of children's social interactions (Atzil et al., 2012; Feldman et al., 2011). As *OXTR*m is a well-characterized measure reflecting moderation in emotion processing (Jack et al., 2012; Puglia et al., 2015), its association with INS elucidates some of its potential impacts on social behavior. Furthermore, this association serves as evidence for the potential viability of INS as an additional neurobiological measure of social function.

4.3. Parent OXTRm is associated with child-parent behavioral attunement

We found that parent *OXTR*m positively predicted child-parent behavioral attunement, but child *OXTR*m did not. While this finding does not align with our initial hypotheses, it coincides with the child-parent INS results. Parents that exhibit higher *OXTR*m levels show fewer caregiving behaviors (Feldman et al., 2011; Kenkel et al., 2019) and are potentially less sensitive to their children's needs. In turn, the onus may be on their children to align their behaviors in the absence of their parents' efforts to do the same. Thus, in our experimental tasks, children whose parents had higher *OXTR*m may have been more accustomed to flexibly aligning their behaviors, resulting in higher scores in behavioral attunement among those dyads.

Accordingly, previous research has linked children's *OXTR*m and attachment security (Ebner et al., 2019; Fujisawa et al., 2019). Children's attachment bonds have also been related to changes in self-regulation and sensitivity (Blair, 2010) which may manifest in the form of increased responsiveness to social cues. In the same way that children's social processing capacity (i.e., child *OXTR*m) in our study was only associated with a measure of dyadic interactional closeness (i.e., INS) during competition, in child-parent relational contexts in which parents contribute less to maintaining relational balance, the child may develop greater behavioral flexibility and social awareness as a compensatory mechanism.

4.4. Child and parent OXTRm differentially relate to child-reported alexithymia

To further interrogate differing implications of child and parent *OXTR*m, we performed post hoc analyses to evaluate the relationship between *OXTR*m, INS, and children's self-reports of their alexithymia (i.e., difficulty identifying and expressing emotions). Higher alexithymia scores reflect lower emotional communication skills and should theoretically correspond with lower INS and behavioral attunement, and higher *OXTR*m. Alexithymia scores were significantly positively associated with child *OXTR*m (Fig. 6) but negatively associated with both parent *OXTR*m and child-parent INS (Fig. 6*;* Table B.5). Based on these trends, children who reported fewer emotional communication difficulties were those that showed higher social processing capacity (i.e., lower *OXTR*m), had parents with lower capacity in this domain (i.e., higher *OXTR*m), and exhibited higher INS.

In the context of our other results, these findings support the notion of children compensating for their parent's decreased social awareness. In cases where a parent is less sensitive to their child's behaviors, their child may become more emotionally aware over time such that they perceive less difficulty with expressing their emotion. Alternatively, children who grow up with less socially attuned parents may be less likely to note their own communication difficulties due to their lack of exposure to positive communicative behaviors. However, the finding that children with higher *OXTR*m levels report higher alexithymia, an association aligning with our predictions, points to a genuine difference in these children's emotional communication skills rather than inaccurate self-evaluations. The negative association between child alexithymia and INS during competition supports the outsized influence of the child on child-parent relational processes, particularly in contexts in which cooperation is not scaffolded behaviorally. As INS during competition was predicted by child *OXTR*m, our study provides evidence for significant associations between dyadic interactional quality (i.e., INS) and children's social processing capacity quantified via both biological correlates (i.e., *OXTR*m) and child self-report.

4.5. Limitations

The sample in this study ($n = 54$, $n_{\text{dyads}} = 27$) is smaller relative to other studies of dyadic EEG measures or DNA methylation, which often have an $n \geq 60$, $n_{\text{dyads}} \geq 30$ (Golds et al., 2022). A larger sample could reveal other patterns relevant to characterizing the relationships amongst any of our measures and produce more generalizable results. Additionally, mobile EEG headsets can lead to greater data loss and lower data quality compared with lab-based EEG systems, especially in a naturalistic setting and with a twenty-channel array (Banville et al., 2022; Marini et al., 2019). However, multiple steps were employed during EEG data-cleaning to reduce potential sources of signal interference. In addition, we included the number of missing and interpolated channels per dyad as covariates in all models to further bolster the robustness of our results.

Our post-hoc MEA analysis results (Table B.7) suggest that differences in gross physical movement do not underlie our EEG findings. While our video resolution meant we could not capture more fine-grained motion such as eye movement, the similar numbers of ICA components across task conditions (Competitive: M = 10.70, SD = 7.26; Cooperative: M = 11.00, SD = 7.06) suggest that cross-condition differences in small movement also did not significantly influence our results. Regardless, some work shows that ICA-based cleaning may rescue but not remove eye movement artifacts, especially in pediatric EEG data (Marriott Haresign et al., 2022; Plöchl et al., 2012). To more fully account for eye movement, future dyadic EEG studies may thus include eye-tracking data as a covariate. Further, although multiple publicly available pipelines for cleaning pediatric EEG data leverage ICA (Debnath et al., 2020; Leach et al., 2020; Levin et al., 2018), other artifact reduction strategies specifically designed for pediatric EEG could provide unique benefits that further enhance data quality in future work.

Finally, the WCC algorithm used to calculate INS evaluated electrode-to-electrode correspondence in absolute power across child and parent, potentially missing relationships between non-corresponding electrodes or within particular EEG frequencies. Given that the arrays in this study contained only 20 spatially distinct channels, we determined that correlations across different channels may not necessarily be meaningful. However, future studies could evaluate relationships between child-parent attunement and/or *OXTR*m with INS across spatially distinct channels (Fig. B.2), especially given the distinct fronto-central localization of our significant INS results (see Section 4.2.2). We conducted supplemental analyses probing relationships between child-parent continuous power spectral density estimates across EEG frequency bands (Table B.8; Kinreich et al., 2017); other analyses which differentiate INS across frequency bands could produce further insights beyond the scope of this article (Dikker et al., 2017; Hu et al., 2017). Additionally, given our surrogate data analysis results (Fig. B.3), an alternative metric for quantifying brain-to-brain synchrony could be better-suited to capture the effects of qualities of the social interaction unique to the dyad (e.g., interpersonal closeness, leader-follower relationships).

5. Conclusions

This study advances neurobiological and developmental cognitive literature in the social domain by cross-validating multiple biological measures reflecting human social capacities across different time scales and degrees of permanence. Results suggest that INS and *OXTR*m, two biological markers implicated in social processing, show similar child-driven moderation effects on child-parent relational dynamics regardless of the dyad's observable interactive behaviors. Additionally, our findings support complex and disparate associations between short-term parent and child social behaviors and children's long-term social outcomes. This work highlights the potential value of employing biologically-based methods in future research on interpersonal dynamics to gain a more nuanced understanding of their underlying mechanisms, particularly in cases where behavioral observations have typically been challenging.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dcn.2023.101302.

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