



Brain-to-brain synchrony in parent-child dyads and the relationship with emotion regulation revealed by fNIRS-based hyperscanning

Vanessa Reindl^{a,b,*}, Christian Gerloff^{b,c,d}, Wolfgang Scharke^a, Kerstin Konrad^{a,b,e}

^a Child Neuropsychology Section, Department of Child and Adolescent Psychiatry, Psychosomatics and Psychotherapy, Medical Faculty, RWTH Aachen University, Germany

^b JARA-Brain Institute II, Molecular Neuroscience and Neuroimaging, RWTH Aachen & Research Centre Juelich, Germany

^c Lehrstuhl II für Mathematik, RWTH Aachen University, Germany

^d Department of Management Science, Lancaster University, UK

^e Institute of Neuroscience and Medicine (INM-3), Research Centre Juelich, Germany

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ABSTRACT

Parent-child synchrony, the coupling of behavioral and biological signals during social contact, may fine-tune the child's brain circuitries associated with emotional bond formation and the child's development of emotion regulation. Here, we examined the neurobiological underpinnings of these processes by measuring parent's and child's prefrontal neural activity concurrently with functional near-infrared spectroscopy hyperscanning. Each child played both a cooperative and a competitive game with the parent, mostly the mother, as well as an adult stranger. During cooperation, parent's and child's brain activities synchronized in the dorsolateral prefrontal and frontopolar cortex (FPC), which was predictive for their cooperative performance in subsequent trials. No significant brain-to-brain synchrony was observed in the conditions parent-child competition, stranger-child cooperation and stranger-child competition. Furthermore, parent-child compared to stranger-child brain-to-brain synchrony during cooperation in the FPC mediated the association between the parent's and the child's emotion regulation, as assessed by questionnaires. Thus, we conclude that brain-to-brain synchrony may represent an underlying neural mechanism of the emotional connection between parent and child, which is linked to the child's development of adaptive emotion regulation. Future studies may uncover whether brain-to-brain synchrony can serve as a neurobiological marker of the dyad's socio-emotional interaction, which is sensitive to risk conditions, and can be modified by interventions.

The development of brain structures and functions is shaped by a complex interaction between genetic influences and pre- and postnatal environmental factors continuously affecting the neural architecture throughout lifetime (Fox et al., 2010; Belsky and de Haan, 2011; Kolb et al., 2012). As humans are social creatures by nature, social interactions have been recognized as a crucial factor impacting human brain and cognition, development, and well-being in general (Belsky and de Haan, 2011; Hari et al., 2015). This influence might be particularly strong early in life (Fox et al., 2010).

During social encounters, both conscious and unconscious social cues are received from others, e.g., from their actions, postures, gestures or emotional expressions (Hari et al., 2015). In such situations, people are inclined to automatically synchronize their behaviors, emotions, physiological and neural activities (Semin, 2007; Hasson et al., 2012; Wheatley et al., 2012; Babiloni and Astolfi, 2014; Hari et al., 2015;

Palumbo et al., 2016). Interpersonal synchronization has been postulated as an evolutionary adaptive mechanism of bond formation (Hove and Risen, 2009; Wheatley et al., 2012). By providing both individuals access to another's internal states (Semin, 2007), it may facilitate emotional sharing and social understanding (Wheatley et al., 2012; Koole and Tschacher, 2016). In addition to fostering social cohesion, synchrony may hone the ability to perform cooperative actions (Valdesolo et al., 2010).

Synchrony in biological rhythms and social signals is thought to be first experienced with the parent/caregiver, shaping the developing brain during early sensitive periods, with long-lasting effects on the child's socio-emotional development (e.g., biobehavioral synchrony model of Feldman, 2007, 2015a). Behavioral studies have shown that patterns of parent-child synchrony are individually stable from infancy to adolescence and are longitudinally predictive for the child's development of

* Corresponding author. University Hospital RWTH Aachen, Neuenhofer Weg 21, 52074, Aachen, Germany.

E-mail address: vreindl@ukaachen.de (V. Reindl).

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emotion regulation and adjustment (Feldman, 2010; 2015b). How is this link between parent-child synchrony and child emotion regulation established? This coupling of affective behaviors and biological signals might allow parent and child to co-regulate their affective arousals, which is conceptualized as an important precursor for the child's capacity for regulating own emotional states (Schore, 2005; Feldman, 2007; Koole and Tschacher, 2016). Moreover, the link between synchrony and child emotion regulation may be mediated by attachment security (Feldman, 2007). Over time, parent's and child's behavioral and biological systems may become mutually attuned to the patterns of the attachment partner, supporting the formation of an affectionate bond (Field, 1985; Feldman, 2007), which in turn sets the framework for the child's emotional development (Kobak et al., 1993). Critical for the parent's ability to engage in synchronous interactions and to positively modulate the child's affective arousal, may be the ability to adequately regulate his or her own emotions (Schore, 2005).

While parent-child synchrony as well as its relationship to child's emotion regulation have been demonstrated on a behavioral level (Feldman, 2015b), little is known about the neural underpinnings of these processes. Brain-to-brain synchrony may be a neural marker for social interaction. It may arise through continuous moment-to-moment mutual adaptations between conscious and unconscious behaviors of interacting partners (Konvalinka and Roepstorff, 2012). As proposed by Konvalinka and Roepstorff (2012) these moment-to-moment interactions between brains can be understood as a two-way behavioral stimulus-to-brain coupling, in a way that the behavior of each person is coupled to the brain of the other. Additionally, brain-to-brain synchrony may not directly follow from behavioral coupling but result from inter-individual top-down modulations during the interaction (Konvalinka and Roepstorff, 2012).

To date, little is known about the functional role of these brain-to-brain couplings. It has been suggested that brain-to-brain synchrony may enable humans to assume the mental and bodily perspectives of others and to predict and understand each other's actions (Nummenmaa et al., 2012). Thus, it may potentially not only be anchored in, but, in addition, support interpersonal behavioral synchrony (Novembre et al., 2017). Moreover, being in synchrony with each other, not only on behavioral but also on neural level, may increase affiliation and elicit prosocial behavior (Hove and Risen, 2009; Hu et al., 2017).

Examining brain-to-brain synchrony in parent-child dyads, Levy et al. (2017) showed a coupling of mother's and child's gamma-band power in the superior temporal sulcus while they independently watched video-clips showing episodes of high behavioral synchrony between the two of them, which was not observed during non-synchronous episodes. However, the main limitation of the study is that brain activities were not measured concurrently, which is necessary to capture the dynamic and reciprocal exchange between interacting brains.

Recent reviews highlight the potential and necessity of concurrent brain recordings, a technique termed “hyperscanning” (Dumas et al., 2011; Hasson et al., 2012; Babiloni and Astolfi, 2014; Hari et al., 2015). These studies have shown a synchronization between brains in a variety of different paradigms, e.g. communication (Jiang et al., 2012), music production (Lindenberger et al., 2009), joint attention (Bilek et al., 2015) and temporal synchronization of simple movements (Funane et al., 2011), however, so far, mostly for interacting adults. One highly standardized experimental design, which could potentially be applied across a wide age range, was introduced by Cui et al. (2012). In a functional near-infrared spectroscopy (fNIRS) hyperscanning study, the authors found an increased brain-to-brain synchrony in the right superior frontal cortex during a cooperative game, which required both subjects to respond simultaneously to a signal. To succeed in the task, a temporal fine-tuning of behavioral responses within the dyad was essential, which is also a prerequisite for more complex forms of behavioral synchrony. Better cooperative task performance was associated with increased brain-to-brain synchrony. Moreover, brain-to-brain synchrony was not observed during a competitive control condition, in which the task was to

respond faster than the partner, ruling out the possibility that simply reacting to the same signal at the same time is sufficient to elicit brain-to-brain synchrony. In lieu thereof, brain-to-brain synchrony in prefrontal brain areas might be a neural mechanism which sub-serves the social interaction (Babiloni and Astolfi, 2014). Using the same cooperative game, Pan et al. (2017) examined the influence of the participants' relationship on brain-to-brain synchrony. Interestingly, they found a better cooperative performance and an increased brain-to-brain synchrony for lover dyads compared to both, friend and stranger dyads. In fact, in the latter two groups no significant brain-to-brain synchrony was observed. Thus, these results indicate that in close relationships people may indeed be more “in tune” with each other.

In the present study, we applied fNIRS hyperscanning to determine whether brain-to-brain synchrony occurs in the prefrontal brain regions of parent-child dyads and whether it is linked to parental and child habitual emotion regulation, measured by questionnaires. fNIRS was chosen as the neuroimaging technique because it can measure local hemodynamic effect with a high temporal resolution in more naturalistic environments than functional magnetic resonance imaging (fMRI) and is less susceptible to motion artifacts than electroencephalography (EEG), making it well-suited for studying young children (Lloyd-Fox et al., 2010). We adapted the hyperscanning paradigm of Cui et al. (2012): each child played both the cooperative and the competitive game with the parent as well as an adult stranger. Thus, the experiment consisted of the following four conditions: parent-child competition (CompP), parent-child cooperation (CoopP), stranger-child competition (CompStr) and stranger-child cooperation (CoopStr). Based on the studies of Cui et al. (2012) and Pan et al. (2017), we expected to find an increased brain-to-brain synchrony for parent-child dyads in the cooperative condition. Moreover, we expected higher parent-child brain-to-brain synchrony during cooperation to be related to better cooperative behavioral performance during the task. Finally, we explored the associations between brain-to-brain synchrony and rating scales of child and parent emotion regulation. Based on the biobehavioral synchrony model (Feldman, 2007; 2015a), higher parent-child brain-to-brain synchrony during cooperation should be associated with better emotion regulation abilities of the child.

Materials and methods

Participants

A total of 33 children, aged between five and nine years ($M = 7.52$ y, $SD = 0.87$ y), participated in the study with their parents. This included 13 mother-daughter dyads, 17 mother-son dyads, one father-daughter dyad, and two father-son dyads. In addition, adult strangers performed identical tasks with the participating children (stranger-child dyads). A total number of 21 adults served as strangers in the study: of these, 15 strangers took part once, two strangers took part twice, three strangers took part three times and one stranger took part four times (for more information see Text A.1). The gender of the stranger was matched to the gender of the parent; however, the parents were significantly older than the strangers (Parents: $M = 41.24$ y, $SD = 4.32$ y, Range: 33–49 y; Strangers: $M = 24.33$ y, $SD = 4.70$ y, Range: 20–45 y; $t(32) = 15.74$, $p < 0.001$). From this sample, fNIRS data for seven experimental tasks were missing due to non-compliance of the child or to technical reasons (4x CompStr, 2x CoopStr, 1x CompP). More specifically, for one child both the CoopStr and CompStr condition was missing.

Parent-child dyads were recruited via previous studies of the University Hospital RWTH Aachen. Strangers were recruited through the social networks of the researchers and participants. Parents, children, and adult strangers were reimbursed for study participation. The study was approved by the Ethics Committee of the Medical Faculty, University Hospital RWTH Aachen (EK 096/14). All parents and adult strangers gave written informed consent. All children were informed about the study and agreed to take part. Children aged 7 years or older gave written informed assent.

Experimental protocol

Computer game tasks. The computer game tasks were developed by Cui et al. (2012) and modified to be suitable for children; each player manipulated the on-screen movement of a dolphin toward a ball using a key press, with the aim to either catch the ball together (cooperation task) or to win the ball for themselves (competition task).

In the cooperation task, participants were instructed to press their keys as simultaneously as possible to “catch the ball together”. If the difference between response times was below a threshold, both dolphins jumped to the ball (feedback screen), caught the ball (result screen), and earned a point. If the difference between the response times was above the threshold, only the faster dolphin jumped to the ball (feedback screen), neither dolphin caught the ball (result screen), and both lost a point. Participants could adjust their response times based on the provided feedback. The threshold was set to $T = 1/8 (RT1 + RT2)$, where $RT1$ and $RT2$ are the response times of the two participants.

In the competition task, participants were instructed to respond faster than the other player to “catch and win the ball”. Only the faster dolphin jumped to the ball (feedback screen) and caught the ball (result screen). In each trial, the faster dolphin earned a point, and the slower dolphin lost a point. If both participants reacted simultaneously with a margin of error of 50 ms, both dolphins won a point.

Procedure. Participants sat side by side while playing the cooperative and competitive computer games. They were instructed to keep their heads still on a chin rest and to refrain from talking to the other player during the fNIRS measurements. To reduce the participants' ability to view each other's motor activities, a towel was placed over their hands. For both the cooperative and the competitive task, five practice trials were completed at the beginning of the experiment. In each trial, two dolphins were shown on the screen. After 2 s, a hollow black circle appeared above the two dolphins (“Ready” signal) and remained on the screen until it was replaced by a colorful ball (“Go” signal) after a random delay of 0.6–1.5 s. Participants were instructed to press their response keys only after the “Go” signal had appeared. After both participants/the faster participant had reacted (cooperation/competition), a feedback screen was shown, followed by a result screen. Both the feedback and result screen were presented for 1 s each during the competition task and for 1.5 s each during the cooperative task. The task flow is shown in Fig. 1.

Design. Each computer game task consisted of two task blocks with 20 trials each and three 30 s rest blocks in the following order: Rest, Task Block 1, Rest, Task Block 2, Rest. The order of the two computer game tasks (cooperation/competition) was balanced across children but kept constant for both dyads each child was part of. Fourteen children first performed both tasks with the parent and after a break with the stranger.

For 19 children, it was the other way around.

Behavioral measures of task performance

The response times of the two participants as well as the differences in their response times were recorded during the cooperative and competitive task. Because outliers (>3 SD) were present in the data, the median response time (median-RT) and median of the difference in response times (median-DRT) were reported for each participant and dyad, respectively (in accordance to Pan et al., 2017). To further quantify the participant's task performance, the percentage of joint wins during cooperation and the percentage of child wins during competition were reported.

Emotion regulation measures

Emotion Regulation Checklist. The Emotion Regulation Checklist (ERC) (Shields and Cicchetti, 1997) is a 24-item questionnaire that uses a 4-point Likert scale (1 = *almost always* to 4 = *never*) to measure processes related to the child's affective lability, intensity, valence, flexibility, and situational appropriateness. The questionnaire was filled out by the parent. A composite emotion regulation score was calculated as described by Shields and Cicchetti (1997), with higher scores indicating better emotion regulation skills of the child (Cronbach's alpha in the current sample, $\alpha = 0.74$). Sample items include “Can say when s/he is feeling sad, angry or mad, fearful or afraid.” and “Can recover quickly from episodes of upset or distress.”.

Emotion Regulation Questionnaire. The Emotion Regulation Questionnaire (ERQ) (Gross and John, 2003; Abler and Kessler, 2009) assesses two common emotion regulation strategies: suppression (4 items; $\alpha = 0.78$) and reappraisal (6 items; $\alpha = 0.83$). Parents were asked to indicate how strongly they agreed with each of the 10 items on a 7-point Likert scale (1 = *strongly disagree* to 7 = *strongly agree*). Cognitive reappraisal is defined as “a form of cognitive change that involves construing a potentially emotion-eliciting situation in a way that changes its emotional impact” (Gross and John, 2003) and expressive suppression is defined as “a form of response modulation that involves inhibiting ongoing emotion-expressive behavior” (Gross and John, 2003). Sample items include “I control my emotions by changing the way I think about the situation I'm in.” (reappraisal) and “I control my emotions by not expressing them.” (suppression).

fNIRS data acquisition

We used a single NIRS device (ETG-4000, Hitachi Medical Corporation, Japan) to measure the concentration changes in oxygenated

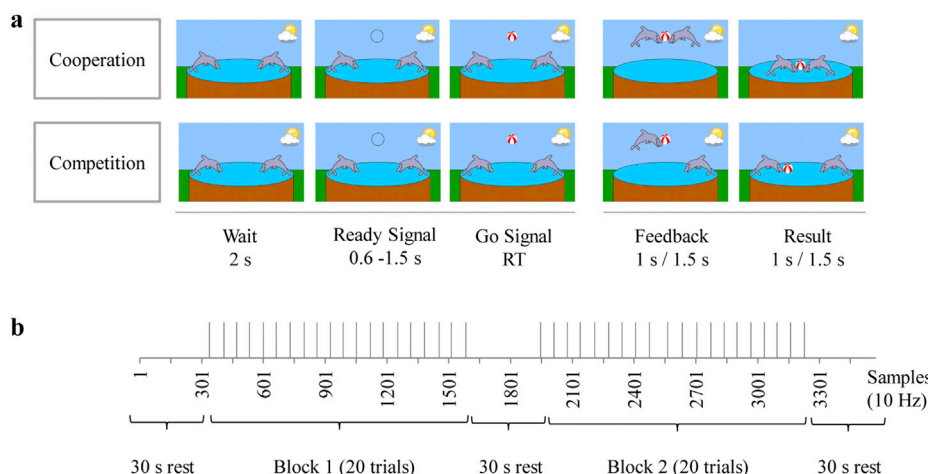


Fig. 1. Illustration of the experimental design. (a) Individual trial organization during the cooperation and competition computer game task. The task was either to respond as simultaneously as possible to a “Go” signal (cooperation) or to respond faster than the partner (competition). Feedback and result screen appeared for 1 s each in the competitive game and for 1.5 s each in the cooperative game. RT: response time of the slower participant (cooperation)/faster participant (competition). (b) Overall organization of the computer game task. Single trials are visualized as vertical lines. Both the cooperative and competitive game consisted of two subsequent task blocks with 20 trials each, which were separated by a 30 s rest period.

hemoglobin (oxy-Hb) and deoxygenated hemoglobin (deoxy-Hb) in both players simultaneously. The sampling frequency was 10 Hz. A “3 × 5” measurement patch was attached to a cap made of robust fabric (EasyCap GmbH, Germany). In each patch, eight emitters and seven detectors were positioned so that they alternated in three rows for a total of 15 probes, resulting in 22 measurement channels (CHs). The source-detector distance was 3 cm. The caps were placed symmetrically over the participants' foreheads as described by Cui et al. (2012) so that the bottom of the cap was touching the tops of the participants' eyebrows and the middle probe column was aligned above the nose.

Estimation of anatomical locations

To estimate the spatial location of the CHs, we used the virtual registration results of stand-alone fNIRS data onto the stereotactic brain coordinate system (Singh et al., 2005; Tsuzuki et al., 2007) and automated Talairach atlas labels (Lancaster et al., 2000). The position of the optodes closely resembled one of the “3 × 5” holder placements for which virtual registration results are provided by the Jichi University: the middle optode of the lowest probe row placed on the frontal pole midline point (Fpz), and the middle probe column aligned along the sagittal reference curve (http://www.jichi.ac.jp/brainlab/virtual_registration/Result3x5_E.html) (Fig. 2). However, it should be noted that the optodes were not placed on the participant's head by measuring the exact location of Fpz according to the 10–20 system.

fNIRS data preprocessing

Preprocessing of fNIRS signals was conducted with the SPM for fNIRS Matlab toolbox (https://www.nitrc.org/projects/spm_fnirs/). The modified Beer–Lambert law was used to calculate changes in oxy-Hb and deoxy-Hb. The differential pathlength factor was calculated with dependence on wavelength and the participants' individual age (Scholkmann and Wolf, 2013). Motion artifacts were reduced by

applying a slightly modified version of the MARA algorithm (Scholkmann et al., 2010), as implemented in the toolbox. Moreover, low frequency confounds were reduced using a high-pass filter based on a discrete cosine transform set (SPM12 version 6906, <http://www.fil.ion.ucl.ac.uk/spm/software/spm12/>). Noisy CHs were identified by visual inspection and excluded from all further analysis (approximately 9% of the CHs).

Brain-to-brain synchrony analysis

Wavelet coherence analysis. In line with previous studies (Cui et al., 2012; Cheng et al., 2015; Baker et al., 2016), wavelet coherence was calculated between the oxy-Hb time series of corresponding CHs as a measure of brain-to-brain synchrony. All wavelet analyses were performed with the ASToolbox (Aguilar-Conraria and Soares, 2014) as described below.

Instead of the most commonly used Morlet wavelet, we chose the generalized Morse wavelet (GMW) with the parameters $\beta = 3$ and $\gamma = 3$. By varying these parameters, the GMW can take on a variety of forms. For $\gamma = 3$, as compared to other integer values of γ , the wavelet is most symmetric, most nearly Gaussian, and most time-frequency concentrated, while remaining exactly analytic (the wavelet is also known as “Airy wavelet”). Thus, for this parametrization, the GMW captures the idea of the Morlet wavelet, but shows improved performance for highly time-localized settings (Lilly and Olhede, 2012).

First, the continuous wavelet transform is performed by a convolution of the time series with a scaled and translated version of the mother wavelet function. The continuous wavelet transform returns a complex coefficient matrix W , which provides information about both the signal's amplitude and phase at any point in time and at any scale. Subsequently, the cross-wavelet transform $W_{xy} = W_x W_y^*$ of the two signals x and y is calculated, with “*” indicating the complex conjugate. Finally, the wavelet coherence is computed by

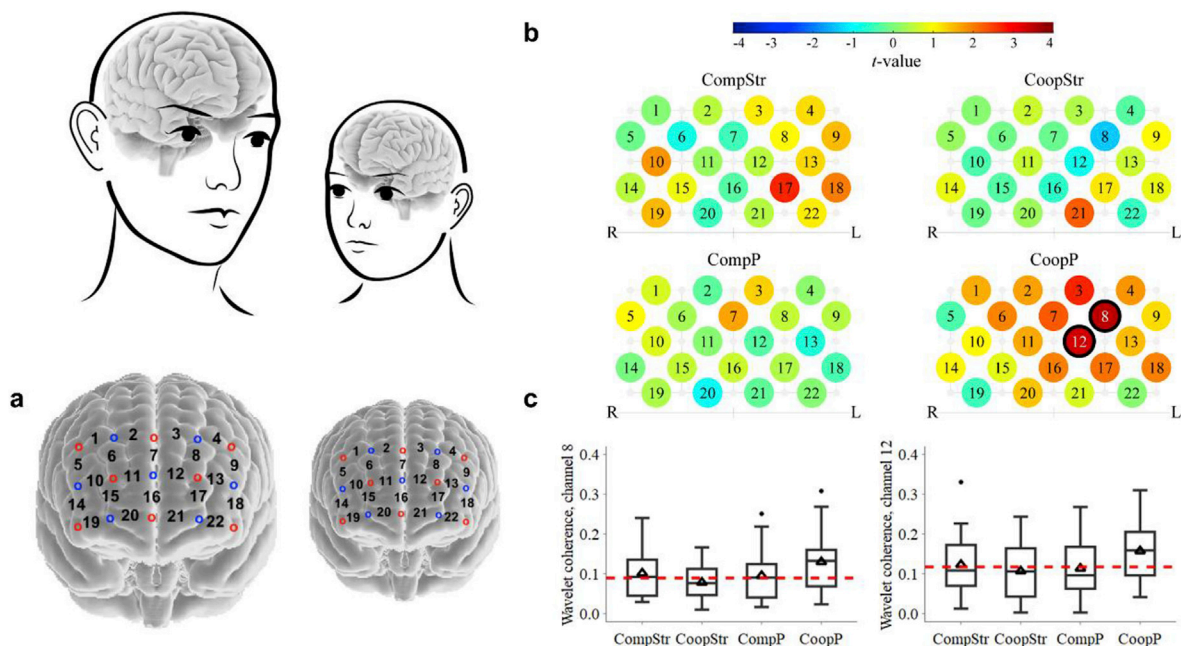


Fig. 2. (a) Cap configuration. Emitters are depicted as red circles, detectors as blue circles. The numbers indicate measurement CHs. (b) Comparison between the coherence of random participant pairs and the task-related coherence of stranger-child competition (CompStr), stranger-child cooperation (CoopStr), parent-child competition (CompP) and parent-child cooperation (CoopP). Color indicates the t -value, whereby more positive t -values (red) indicate greater coherence. The numbers depict the measurement CHs. Only coherence of CoopP in CHs 8 and 12 was significantly higher than coherence of random pairs (indicated by the black circles), which most likely correspond to the DLPFC and FPC. (c) Boxplots of the wavelet coherence in CHs 8 and 12 in the four conditions. The mean coherence is represented by the triangle within the box. The red dashed line represents the coherence of random adult-child pairs in the respective CH. For both CHs 8 and 12, a significant interaction of task and partner was observed, indicating a higher coherence in the CoopP condition.

$$R_{x,y} = \frac{|S(W_{x,y})|}{\sqrt{S(|W_x|^2) S(|W_y|^2)}},$$

where ‘S’ denotes a smoothing operator (Aguilar-Conraria and Soares, 2014). Smoothing is obtained by convolution with Hanning window functions in both time and scale. In accordance with the sampling theorem, wavelet coherence was calculated for frequencies between 0.016 Hz and 5 Hz (period length: 64 s - 0.2 s). The values of $R_{x,y}$ are bound by zero and one, with the value of one indicating a perfect linear relationship between two signals at a particular time and scale if noise is absent (Aguilar-Conraria and Soares, 2014). For each CH from each dyad and in each condition, we obtained a two-dimensional matrix of wavelet coherence values, which is visualized in Fig. A1 with time on the x-axis and period length on the y-axis.

Significant coherence. To estimate the statistical significance of each wavelet coherence value in the two-dimensional matrix, an AR (1) model was fitted to the oxy-Hb signal, and 300 surrogate signals were constructed using a bootstrapping technique (Aguilar-Conraria and Soares, 2014). If the observed coherence value at a specific time and scale was higher than 99% of the coherence values obtained for surrogate signals at the same time and scale, it was regarded as significant. Because this procedure was very time consuming, it was performed for 15 children and all available conditions as well as CH pairs. Based on these analyses, a cut-off value of 0.65 was attained, above which coherence values reached statistical significance on average (Fig. A1).

Task-related frequency band. We then identified a frequency band in which the task-related coherence was expected to occur, which was between 0.08 Hz and 0.5 Hz (period length: 12.80 s - 2.02 s). This frequency band was chosen based on the trial duration, previous studies, and visual inspection of the data.

Outcome measures. While previous studies calculated the mean wavelet coherence value (Cui et al., 2012; Cheng et al., 2015; Baker et al., 2016; Pan et al., 2017), we reported the number of wavelet coherence values higher than the cut-off value in the task-related frequency band, relative to the total number of wavelet coherence values in this frequency band. This ratio was computed separately for wavelet coherence in block 1 and in block 2. Subsequently, both values were averaged to yield one coherence value for the cooperative game and one for the competitive game. This ratio was used as our primary outcome variable of brain-to-brain synchrony and is denoted by ‘coherence’ in the following.

Moreover, in contrast to previous studies (Cui et al., 2012; Cheng et al., 2015; Baker et al., 2016; Pan et al., 2017), we did not report coherence increase, defined as the mean coherence in the task block minus the mean coherence in the rest block, as our outcome measure. Instead, we directly compared coherence of the four conditions (CoopP, CompP, CoopStr and CompStr). Additionally, we calculated individual contrast scores for the coherence of parent-child cooperation vs. parent-child competition (CoopP-CompP) and the coherence of parent-child cooperation vs. stranger-child cooperation (CoopP-CompStr) by subtracting the respective coherence values from each other. Our reasons for choosing these more direct comparisons are based on results of neuroimaging studies showing that appropriate task conditions often provide a better baseline than rest conditions (Stark and Squire, 2001).

Validation by random pair analysis

FNIRS signals of independent participants might show genuine similarities due to the same experimental condition (examination of EEG synchronization of pseudo-pairs: Burgess, 2013) and common slow physiological oscillations, such as respiration and pulsation. For this reason, we implemented a validation strategy that aims to reveal such synchrony that is not related to the experimental interaction. In the validation by random pair analysis, we calculated the wavelet coherence

of random adult-child pairings who did not play together but performed the same experimental task, termed random pairs, and compared them with the wavelet coherence of actual interacting pairs in the corresponding CH. A series of *t*-tests, described in the section “statistical analysis”, was applied to indicate whether the coherence was significantly higher in actual pairs compared to random pairs for each CH and condition. Although this validation procedure by random pair analyses can already provide a first indication regarding potential differences between experimental conditions, it cannot replace direct statistical comparisons. For this subsequent analysis, only CHs were considered in which the coherence was significantly higher than the coherence of random pairs in at least one experimental condition. By excluding those CHs which did not show a valid coherence, which was related to the interaction above chance level, we reduced the risk of spurious findings and thereby increased the robustness of the results.

For the validation analyses, wavelet coherence was calculated for 1200 random pairs (300 random pairs for each of the four conditions). As noisy CHs were excluded from the analysis, the number of random pair coherence values varied between CHs. It should be noted that even though both participants performed the same experimental task, the timing and length of the blocks was not identical due to differences in response times and the variable inter-trial interval. As coherence analysis requires both time series to be equal in duration, the longer block was cut at the end so that it was the same length as the shorter block for each random pair. This procedure was repeated for all blocks separately. Afterward, they were reconnected and wavelet coherence was calculated for the entire Oxy-Hb time series.

Statistical analysis

Statistical analyses were carried out with IBM SPSS Statistics 22 and R version 3.4.1 (R Core Team, 2017). All statistical tests were two-tailed and 95% confidence intervals were derived by bootstrapping ($n = 5000$ runs). To examine whether the dyad's coherence values were significantly higher than coherence values of random adult-child pairs, independent-samples *t*-tests and Welch's *t*-tests for unequal variances were conducted. All subsequent analyses were performed only for the CHs which showed a significantly higher coherence than the coherence of random pairs, as described above (“Validation by random pair analysis”).

To directly examine differences between conditions in brain-to-brain coherence, we applied linear mixed models (LMMs) with coherence in the respective CH as the dependent variable. The full model included the fixed effects of task, partner and the task \times partner interaction as well as the random intercept of subject. To test for influential factors, child's age (in months), child's gender as well as condition order were added separately to the LMM. Again, the full model included all main and interactive effects of task, partner as well as child's age or child's gender or condition order as fixed effects and the random intercept of subject. LMMs were performed with the R package lme4 (Bates et al., 2015). For statistical inference, models were fitted using REML and *p*-values were derived by the summary/anova function of the lmerTest package (Kuznetsova et al., 2016) using the Satterthwaite approximation for the degrees of freedom, following the recommendations of Luke (2017).

Differences between conditions in behavioral measures were examined by paired-samples *t*-tests. The relationship between behavioral measures and coherence was examined by partial Pearson correlations controlling for the child's gender as well as by hierarchical multiple regressions.

Associations between emotion regulation as well as coherence measures were first examined by partial Pearson correlations controlling for the child's gender. Afterwards, a mediation analysis was performed with the PROCESS macro for SPSS (Hayes, 2013). The indirect effect was tested by bias-corrected bootstrapping of the 95% confidence interval ($n = 5000$ runs).

Due to multiple testing, we adjusted the *p*-value using the False

Table 1

Results of the LMM analyses of wavelet coherence in CHs 8 and 12.

	CH 8				CH 12			
	FE (SE)	t	df	p	FE (SE)	t	df	p
Intercept	0.101 (0.012)	8.61	104.00	<0.001	0.121 (0.014)	8.48	105.37	<0.001
Partner	−0.006 (0.016)	−0.39	104.00	0.70	−0.009 (0.018)	−0.48	83.86	0.64
Task	−0.023 (0.017)	−1.39	104.00	0.17	−0.016 (0.018)	−0.86	82.64	0.39
Partner x Task	0.058 (0.023)	2.51	104.00	0.014 ^a	0.059 (0.025)	2.35	81.76	0.021 ^a

Note. $N = 33$ (108 observations in CH 8 and 113 observations in CH 12). FE (SE) = Fixed Effect Estimate (Standard Error). $t = t$ -tests use Satterthwaite approximation for degrees of freedom. The intercept refers to coherence in the stranger-child competition condition.

^a Marks significance according to FDR-adjusted alpha level (threshold: $p \leq 0.021$).

Discovery Rate (FDR) procedure (Benjamini and Hochberg, 1995; Yekutieli and Benjamini, 1999). For the comparison to random pairs, the number of t -tests corrected for was 88 (corresponding to 22 CHs in four conditions). The p -values of the LMMs were adjusted for two tests, as the LMMs were conducted for two CHs. Two-way interactions were broken down by examining four simple effects, thus, the p -values were adjusted for four tests. For the relationship between coherence and behavioral measures of task performance the number of tests corrected for was four (four correlations and four regressions) and for the correlations between coherence and emotion regulation measures it was 18.

Results

Increased coherence during parent-child cooperation

Comparison to random pairs. To first identify CHs in which there was an increased coherence, we compared the dyad's coherence to the coherence of random adult-child pairs, who did not play together. Our results showed that the coherence of parent-child dyads during cooperation (CoopP) was significantly higher than the coherence of random adult-child pairs in CH 8 ($t(946) = 3.48$, $p < 0.001$, $p_{adj.} = 0.038$, $d_{Cohen} = 0.67$) and in CH 12 ($t(1017) = 3.34$, $p < 0.001$, $p_{adj.} = 0.038$, $d_{Cohen} = 0.63$), which most likely correspond to the dorsolateral prefrontal cortex (DLPFC; Brodmann area, BA 9) and the frontopolar cortex (FPC; BA 10), respectively. None of the CH pairs showed significant coherence in any other condition (CompP, CompStr or CoopStr) after FDR adjustment (Fig. 2).

Comparison between conditions. To directly compare conditions, we examined the main and interaction effects of task (0 = competition; 1 = cooperation) and partner (0 = stranger, 1 = parent) on coherence in CHs 8 and 12 with LMMs. For both CHs, there was no effect of task or partner; however, a significant interaction of task and partner was observed (results of the LMMs are shown in Table 1, boxplots in Fig. 2). Namely, as indicated by the fixed effects estimates, coherence was increased for the CoopP condition. These results were further confirmed by simple effects analyses revealing a significant effect of task for parent-child dyads only, with higher coherence during cooperation (CH 8: $t(27.48) = 2.11$, $p = 0.044$, $p_{adj.} = 0.088$; CH 12: $t(27.29) = 3.06$, $p = 0.005$, $p_{adj.} = 0.020$). However, after FDR adjustment, this effect was only significant for CH 12 and was marginally significant for CH 8. Correspondingly, we observed a significant effect of partner for the cooperative task only, with higher coherence for parent-child dyads in both CHs (CH 8: $t(51) = 3.21$, $p = 0.002$, $p_{adj.} = 0.009$; CH 12: $t(56) = 2.53$, $p = 0.014$, $p_{adj.} = 0.029$).

Influential Factors. To identify factors which influence the increased coherence in the CoopP condition and need to be accounted for in the subsequent analyses, we examined the effects of child's age and gender as well as condition order on coherence in CHs 8 and 12. The child's age and the condition order did not significantly affect the task \times partner interaction (no significant three-way interactions, $p > 0.48$, Text A.2). However, results revealed that increased coherence in the CoopP condition was primarily driven by female children, who mostly participated with their mothers: a significant three-way interaction between task, partner

and child's gender was observed (CH 8: $t(100) = -2.04$, $p = 0.044$; CH 12: $t(78.8) = -2.13$, $p = 0.037$; Table A1).

Taken together, these results indicate that brain-to-brain synchrony was increased only during parent-child cooperation (task \times partner interaction) in the FPC and the DLPFC. Subsequent analyses need to account for gender differences, while child's age and condition order did not systematically affect the task \times partner interaction.

Increased coherence during parent-child cooperation cannot be attributed to differences in task behavior

To test whether increased coherence in the CoopP condition can be attributed to differences in participants' behavior, behavioral similarity and task performance were compared between conditions. Behavioral similarity was measured by the median of the dyad's differences in response times (median-DRT). This index was significantly smaller during competition compared to cooperation, indicating a higher behavioral similarity during competition for both parent-child dyads ($t(30) = 6.21$, $p < 0.001$, $d_{Cohen} = 1.25$) and stranger-child dyads ($t(27) = 4.24$, $p < 0.001$, $d_{Cohen} = 1.07$; see Table A2 for descriptive results). No significant group differences in median-DRT were observed between parent-child and stranger-child dyads during cooperation ($t(29) = 1.47$, $p = 0.15$) or during competition ($t(26) = 0.70$, $p = 0.49$).

Task performance was measured by the relative number of joint wins during cooperation (cooperation rate) and the relative number of child wins during competition. The cooperation rate did not significantly differ between parent-child and stranger-child dyads ($t(29) = -0.69$, $p = 0.49$). However, during competition, the child won more often against the parent than against the stranger ($t(26) = 5.55$, $p < 0.001$, $d_{Cohen} = 1.08$). Taken together, these results indicate that the observed increased parent-child brain-to-brain synchrony during cooperation was not driven by differences in the observed behavior.

Table 2

Results of the hierarchical multiple regression analyses predicting parent-child cooperation rate in block 2.

Predictor	CH 8			CH 12		
	ΔR^2	β	95% CI	ΔR^2	β	95% CI
Step 1	0.26*			0.22*		
Child gender		−0.05	[−0.40, 0.35]		0.01	[−0.32, 0.39]
Cooperation rate 1		0.49*	[0.14, 0.86]		0.47*	[0.13, 0.86]
Step 2	0.16*			0.13*		
Child gender		0.02	[−0.31, 0.39]		0.05	[−0.29, 0.41]
Cooperation rate 1		0.34	[−0.01, 0.69]		0.44*	[0.08, 0.80]
Coherence 1		0.45*	[0.22, 0.81]		0.37*	[0.06, 0.62]
Total R^2	0.43**			0.35*		
N	27			29		

Note. * $p < 0.05$; ** $p < 0.01$ (p -values not FDR-adjusted).

Increased coherence during parent-child cooperation predicts better cooperative performance

Next, we examined whether coherence in the CoopP condition in CHs 8 and 12 was related to cooperative performance. While in the previous analyses we examined the dyads' coherence averaged across the two cooperative blocks as our outcome measure, we now investigated coherence in each of the two blocks separately. First, we analyzed the associations between coherence in the CoopP condition and cooperation rate within each of the blocks. Results showed that coherence was not significantly correlated with the dyad's cooperation rate controlling for the child's gender, neither in block 1 (CH 8: $pr = 0.32$, $p = 0.11$; CH 12: $pr = 0.10$, $p = 0.61$) nor in block 2 (CH 8: $pr = -0.13$, $p = 0.54$; CH 12: $pr = -0.10$, $p = 0.60$).

Second, we applied hierarchical multiple regressions to examine whether coherence in the CoopP condition predicted cooperative performance across the two blocks or vice versa. Results showed that CoopP coherence in block 1, both in CHs 8 and 12, significantly predicted CoopP cooperation rate in block 2, controlling for the child's gender and the dyad's cooperation rate in block 1 (CH 8: $F(3, 23) = 5.66$, $p = 0.005$, $p_{adj.} = 0.019$; CH 12: $F(3, 25) = 4.56$, $p = 0.011$, $p_{adj.} = 0.022$; Table 2). On the contrary, CoopP cooperation rate in block 1 did not significantly predict CoopP coherence in block 2 (Table A.3). Hence, increased parent-child brain-to-brain synchrony in the FPC and DLPFC seemed to yield better cooperative performance, while cooperative performance did not affect brain-to-brain synchrony.

Increased coherence during parent-child cooperation relates to parent and child emotion regulation

Emotion regulation of parent and child. The child's emotion regulation, measured by the ERC composite score, was significantly related to parental reappraisal, measured by the ERQ ($pr = 0.42$, $p = 0.017$, 95% CI = [0.13, 0.68]; Fig. A2a). The more parents used reappraisal as a strategy to regulate their emotions, the better the emotion regulation abilities of the child. No significant correlation was observed for parental suppression and child emotion regulation ($pr = 0.04$, $p = 0.82$). Moreover, the child's emotion regulation was not significantly influenced by the child's age ($r = 0.03$, $p = 0.88$) and child's gender ($t(30) = 0.64$, $p = 0.53$).

Correlations between emotion regulation measures and coherence. Next, we examined associations between coherence in the CoopP condition and in the contrasts CoopP vs. CompP and CoopP vs. CoopStr in CHs 8 and 12 as well as parent and child emotion regulation. In CH 12, coherence in the CoopP-CoopStr contrast was significantly related to both, the child's emotion regulation ($pr = 0.56$, $p = 0.004$, $p_{adj.} = 0.038$, 95% CI = [0.28, 0.79]; Fig. A2b) and parental reappraisal ($pr = 0.57$, $p = 0.004$, $p_{adj.} = 0.038$, 95% CI = [0.24, 0.79]; Fig. A2c), controlling for the child's gender. Thus, higher brain-to-brain synchrony with the parent compared

to an adult stranger in the FPC during cooperation was associated with better emotion regulation of both parent and child. None of the other correlations between coherence and emotion regulation measures reached significance (Table A.4).

Mediation Analysis. Given these pairwise relationships between coherence in CH 12 in the CoopP-CoopStr contrast, child emotion regulation and parental reappraisal, we conducted a mediation analysis to examine whether coherence mediated the relationship between parental reappraisal and child emotion regulation (Fig. 3). Child gender was included as a covariate in the model of the mediator and the dependent variable. Our results showed that the direct effect of parental reappraisal on child emotion regulation was not statistically significant when the mechanism through the mediator, namely, coherence in CH 12 in the CoopP-CoopStr contrast, was accounted for ($B = 0.037$, $SE = 0.043$, $p = 0.39$, 95% CI [-0.051, 0.126]). The indirect effect of parental reappraisal on child emotion regulation via the mediator was statistically significant, as revealed by the bias-corrected bootstrap confidence interval which did not include zero ($B = 0.051$, $SE = 0.026$, 95% CI [0.011, 0.115]). Thus, in the mathematical model, the parental use of reappraisal predicted higher brain-to-brain synchrony in the FPC of parent-child compared to stranger-child cooperation, which, in turn, positively affected the child's emotion regulation.

Discussion

Being attuned to the emotions of the other, parent and child synchronize and thereby co-regulate their affective states during the social interaction, which provides the foundation for children to successfully master emotion regulation (Schore, 2005; Feldman, 2007; Koole and Tschacher, 2016). The neurobiological underpinnings of parent-child behavioral synchrony, however, remain poorly understood. Based on our results, we conclude that brain-to-brain synchrony within the dyad might reflect the connection between parents and children during the social interaction at the neural level. Specifically, we found that parent-child dyads had an increased brain-to-brain synchrony in prefrontal brain areas, the DLPFC and FPC, during cooperation. This synchronization was not observed during a competitive control condition and was not observed during the same tasks when played with an adult stranger. Examining the relation between cooperative performance and brain-to-brain synchrony, we did not confirm an association of both measures within the same task block. Instead, we showed that brain-to-brain synchrony during the first task block predicted cooperative performance in the second task block (DLPFC & FPC). Furthermore, when cooperating with the parent compared to an adult stranger, brain-to-brain synchrony in the FPC mediated the association between the parent's and the child's emotion regulation abilities, in our statistical model.

The cooperative and partly also the competitive computer game task of Cui et al. (2012) has been employed by several previous studies, which

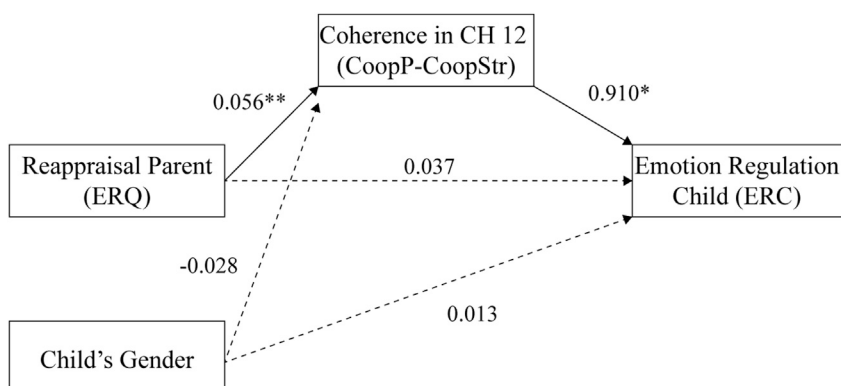


Fig. 3. The link between parental reappraisal and child emotion regulation was mediated by coherence in the frontotopical cortex in the contrast parent-child cooperation vs. stranger-child cooperation (CoopP-CoopStr) ($N = 25$). The indirect effect of parental reappraisal on child emotion regulation via the mediator was tested using 95% confidence intervals derived by bias-corrected bootstrapping technique. Unstandardized coefficients are depicted. The solid and dashed lines represent significant and non-significant effects, respectively. * $p < 0.05$; ** $p < 0.01$. ERC: Emotion Regulation Checklist; ERQ: Emotion Regulation Questionnaire.

examined brain-to-brain synchrony in interacting adults, targeting either the prefrontal cortex (PFC), right frontotemporal or frontoparietal brain regions (Cheng et al., 2015; Baker et al., 2016; Pan et al., 2017). In line with our findings, they observed a significant brain-to-brain synchrony only during cooperation, but not during competition. This significant synchronization was mainly reported in prefrontal brain regions, although the more precise location and the observed effects varied to some extent. Specifically, previous studies found an increased brain-to-brain synchrony during cooperation i) within the right superior frontal cortex across all adult-adult dyads (most of them previously acquainted) (Cui et al., 2012) or ii) only for lover dyads (Pan et al., 2017), iii) within the right temporal cortex for female/female dyads and right inferior PFC for male/male dyads (strangers) (Baker et al., 2016) as well as iv) within the FPC, left DLPFC, and orbitofrontal cortex only for female/male dyads (strangers) (Cheng et al., 2015). Thus, the significant brain-to-brain synchrony during parent-child cooperation in the left DLPFC and FPC in the present study, which was not observed during parent-child competition, is principally in keeping with what has been reported for interacting adults.

Additionally, above mentioned studies (Cheng et al., 2015; Baker et al., 2016; Pan et al., 2017) as well as our own results indicate that the participant's gender significantly affects brain-to-brain synchrony. However, larger samples of mother-daughter, mother-son, father-daughter and father-son dyads are needed to clarify the effects of the parent's gender, child's gender as well as the effects of same-gender vs. mixed-gender dyads on brain-to-brain synchrony.

To successfully cooperate, adult and child need to be attentive to each other's actions and to continuously adapt their own response time in relation to the anticipated response time of the other (see also Keller et al., 2014). In contrast, the competitive task should be completed independently and does not require understanding of the other's actions/mind (Liu and Pelowski, 2014). Our results indicate that parents and strangers behaved differently during competition: parents reacted slower and won in less trials than strangers. It is reasonable to assume that parents let the child win on purpose in some of the trials. This heightened attention to the child's behavior and emotional state, however, does not transfer to an increased brain-to-brain synchrony in the CompP as compared to the CompStr condition. This further supports that brain-to-brain synchrony in this experimental design emerges from the mutual interaction, which is characterized by a common goal and shared attention and adaptation processes. During parent-child competition, these processes are unidirectional rather than bidirectional: while the parent pays attention to the child, the child tries to win as many trials as possible.

Expanding on previous studies which showed that a coupling between brains occurs in attachment relationships, e.g., mother-father (Atzil et al., 2012) and mother-child dyads (Levy et al., 2017) (both studies did not employ concurrent brain recordings) and in response to bonding-related behavior, e.g., romantic kissing (Müller and Lindenberger, 2014), we found, on average, a higher brain-to-brain synchrony for parent-child cooperation compared to stranger-child cooperation. However, it should be noted that for some dyads it was the other way around. Future research may examine whether differences in brain-to-brain synchrony between parent-child dyads in relation to stranger-child dyads can be partly attributed to their affectionate bond.

Based on the study of Pan et al. (2017), we assume that genetic similarity is unlikely to explain these differences between parent-child and stranger-child dyads, alone. Similarly, the authors observed a significant brain-to-brain synchrony only for lover dyads and not for friend and stranger dyads. However, lover dyads also showed a better cooperative performance compared to both friend and stranger dyads raising the critical question of causality: on the one hand, increased brain-to-brain synchrony of lover dyads might lead to a better cooperative behavior; on the other hand, increased brain-to-brain synchrony might be an epiphenomenon of interpersonally coordinated actions.

In the current study, we argue that the observed brain-to-brain

synchrony during the CoopP condition did not originate from synchronous motor behavior because i) dyads reacted more synchronously during competition than during cooperation, ii) parent-child and stranger-child dyads did not differ in their cooperative performance and iii) brain-to-brain synchrony was not significantly correlated with the dyad's percentage of joint wins in the same task block. Instead, CoopP brain-to-brain synchrony in the first task block predicted the cooperation rate in the second task block. In comparison, previous studies using similar experimental tasks in adult dyads reported positive associations between brain-to-brain synchrony and cooperative performance, however, they did not examine the predictive relations of the two measures (Cui et al., 2012; Cheng et al., 2015; Baker et al., 2016; Pan et al., 2017). On a behavioral level, it has been shown that rocking in synchrony enhanced the perceptual sensitivity to the motion of other entities and thereby increased success in a subsequent joint action task (Valdesolo et al., 2010). Whether brain-to-brain synchrony could also hone the ability to predict each other's actions and thereby facilitate the establishment of synchronous actions, is a direction for future research (see also Novembre et al., 2017).

This having said, we cannot rule out the possibility that dyads differed in other forms of behavior, such as the level of attention, which might account for differences in brain-to-brain synchrony. However, the highly standardized task and the experimental setup, i.e. participants did not have any eye contact and were instructed to keep their heads still on a chin rest and to refrain from talking to each other, make differences in behavior, besides the button press response, less likely.

The brain-to-brain synchrony detected in the current study was approximately located in dorsolateral and frontopolar prefrontal brain regions (BAs 9 and 10). Brain lesion and functional neuroimaging studies have linked these regions to various complex cognitive processes (Christoff and Gabrieli, 2000). As part of a wide network, they have been activated in the cognitive control of emotions. For instance, Goldin et al. (2008) showed that reappraisal resulted in early PFC responses (including the medial, dorsolateral, ventrolateral PFC, and lateral orbitofrontal cortex) and suppression produced late PFC responses (including the ventrolateral, dorsomedial and dorsolateral PFC). Moreover, the medial prefrontal cortex, which comprises, i.a., BAs 9 and 10 (medial regions), has been hypothesized to play a critical role for theory of mind (ToM)/mentalizing, i.e., the ability to represent another person's psychological perspective, and thus to predict behavior (Amodio and Frith, 2006). Medial prefrontal cortex activations have been consistently reported for adults, and also for children in ToM tasks (McCabe et al., 2001; Ohnishi et al., 2004; Amodio and Frith, 2006). During the cooperative game, these brain networks may be recruited to model and predict the behavior of the partner.

Moreover, cooperation likely involves shared emotional experiences, while during competition, emotions are more often mutually exclusive (Lanzetta and Englis, 1989). Shared emotional experiences might also be accompanied by an increased brain-to-brain synchronization (Nummenmaa et al., 2012, 2014). Supporting this notion, Nummenmaa et al. (2014) showed, i.a., that when participants listened to narratives of neutral, unpleasant and pleasant events, intersubject phase synchronization increased in dorsolateral and medial prefrontal cortices as valence increased from negative to positive. Thus, future studies may examine whether shared positive emotions during cooperation might contribute to the observed enhanced interpersonal brain synchronization in BAs 9 and 10.

In the current study, parental and child habitual emotion regulation were both positively related to brain-to-brain synchrony of parent-child cooperation compared to stranger-child cooperation in the FPC. Similarly, Lee et al. (2017) found in parent and adolescent child dyads who are more 'neurally attuned' to each other, a higher day-to-day emotional synchrony within the dyad and a higher emotional competence of the youth. In the study of Lee et al. (2017) 'being neurally attuned' was measured by the similarity in fMRI resting state network connectome, which is likely shaped by the accumulating socio-emotional experiences

of the individual (Gabard-Durnam et al., 2016). Thus, shared experiences might fine-tune the brain networks to the dyad, which potentially leads to a higher synchrony in behavior and neural rhythms. Our study expands on the findings of Lee et al. (2017) by showing that during the ongoing parent-child interaction this mental connection might manifest itself in an increased brain-to-brain synchrony.

In addition, being in synchrony with each other might have adaptive benefits: inter-personal couplings across modalities, e.g. behavioral signals, physiological and neural rhythms, have been proposed to facilitate bond formation (Wheatley et al., 2012). On a behavioral level, it has been shown that, indeed, the degree of synchrony predicted subsequent affiliation ratings (Hove and Risen, 2009). In line with our hypothesis, Hu et al. (2017) found in a recent fNIRS-based hyperscanning study that interbrain synchronization during a coordination task was correlated with subsequent mutual prosocial inclination ratings of previously unacquainted adults. Thus, an increased brain-to-brain synchrony in parent-child dyads as compared to stranger-child dyads might not only reflect their connection and the sharing of more similar brain networks (Lee et al., 2017), but it might also be a mechanism supporting bond formation and as such affect the child's socio-emotional development.

Moreover, our findings highlight the role of the parent's ability to adequately regulate his or her own emotions. Synchrony might potentially be one mechanism through which the parent's emotion regulation influences the child's emotional development, along with genetic influences (Hariri and Holmes, 2006) as well as different influences of the rearing environment, such as learning through observation, parenting practices and the emotional climate in the family (tripartite model, Morris et al., 2007; for an overview see Rutherford et al., 2015).

There are several limitations to the study. First, although our results are in line with the biobehavioral synchrony model of Feldman (2007, 2015a), it should be noted that we cannot draw conclusions about the causal relationship between brain-to-brain synchrony and emotion regulation. Longitudinal studies examining parent-child brain-to-brain synchrony, possibly during an early sensitive period in infancy (Feldman, 2007; 2015a), might provide further and valuable insights. Second, in future studies, parent-report questionnaires of habitual emotion regulation may be complemented by measures of emotional experience and emotion regulation during the experimental task. These might include self-report/parent-report questionnaires, physiological indexes associated with regulation and the classification of facial expressions. Third, while the highly standardized games of Cui et al. (2012) have several advantages, the current findings need to be replicated in a more naturalistic task with a greater ecological validity for the parent-child interaction. For instance, there is evidence to suggest that eye-to-eye contact, in particular, is a socially salient stimulus, which might be linked to an increased brain-to-brain synchrony (Hirsch et al., 2017). Fourth, the exact anatomical locations of the channels should be interpreted with caution.

In conclusion, these results indicate that brain-to-brain synchrony may be an underlying neural mechanism, which supports the coupling of social behaviors and affective states during the interaction with the parent, and thereby supports the child's development of adaptive emotion regulation. Future research may examine whether parent-child brain-to-brain synchrony may serve as a neurobiological marker of the dyad's socio-emotional interaction, which is sensitive to risk conditions stemming from either the parent or the child, such as postpartum depression or autism spectrum disorders. For instance, for adults with autism spectrum disorders and typically developed adults, a diminished brain-to-brain synchrony has been reported during eye contact (Tanabe et al., 2012). As such brain-to-brain synchrony may be useful in identifying at-risk dyads and evaluating treatments.

Conflicts of interest

The authors declare no competing financial interests.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.neuroimage.2018.05.060>.

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