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„Interpersonal neural and physiological synchrony in early development: The role of communicative rhythms and priors"

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List of Scientific Publications for the Cumulative Thesis

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3) Nguyen, T., Schleihauf, H., Kayhan, E., Matthes, D., Vrtička, P., & Hoehl, S. (2020). The effects of interaction quality on neural synchrony during mother-child problem solving. *Cortex, 124,* 235-249. doi.org/10.1016/j.cortex.2019.11.020

4) Nguyen, T., Schleihauf, H., Kungl, M., Kayhan, E., Hoehl, S., & Vrtička, P. (2021). Interpersonal neural synchrony during father-child problem solving: An fNIRS hyperscanning study. *Child Development, 92*(4), e565-e580. doi.org/10.1111/cdev.13510

1. Introduction

Early social interactions are vital for child development as they afford many learning opportunities to infants (Stern et al., 1985; Trevarthen, 1993; Tronick, 1989). Learning about the social world from and with others entails, for instance, making better predictions about others' actions (Hoehl & Bertenthal, 2021). These early interactions help the infant resolve social uncertainties and generate better-adapted models to derive more accurate predictions. Precise predictions are critical to social communication – otherwise, we would not be able to coordinate as quickly and smoothly as already observed in early social interactions.

From early on, social interactions between infants and their caregivers alternate between coordinated states, (repairs of) mis-coordinated states, and moments of heightened affect (Beebe & Lachmann, 2002; Tronick & Cohn, 1989). The coordinated states, summarized under the term interpersonal behavioral synchrony, include face-to-face exchanges, physical proximity, and a turn-taking structure, which depend upon reciprocal behaviors of the dyad (Leclère et al., 2014). Through interpersonal synchronization, infants and children can build interaction patterns with close others. The internalization of these patterns in so-called inner working models is suggested to develop their attachment bond with caregivers (Bretherton, 2005). While much behavioral research has demonstrated the primacy of interpersonal behavioral synchrony in early social exchanges, research on neural and physiological synchronization in early childhood is only emerging.

Recent advancements in neurophysiological methodologies now allow us to simultaneously measure the brain activity of two or more interacting partners, so-called hyperscanning. Once interacting, people show alignment in their brain activity – we are literally in tune (e.g., Babiloni & Astolfi, 2014; Dumas et al., 2011; Hasson et al., 2012; Hoehl et al., 2020; Konvalinka & Roepstorff, 2012). In addition, the simultaneous assessment of cardio-respiratory rhythms in two or more people allows us to assess their potential alignment on the physiological level. The research on neural, behavioral, and physiological synchrony using adult hyperscanning is quickly growing (see Czeszumski et al., 2020 for a review). Yet, the factors and outcomes to neural and physiological synchrony in development are not well understood.

In my dissertation, I present work investigating neural, behavioral, and physiological synchrony in naturalistic caregiver-child interactions utilizing functional near-infrared spectroscopy (fNIRS; see Info Box 1) and electrocardiography (ECG) combined with behavioral coding. First, I will introduce interpersonal synchrony in early development and outline recently proposed mechanisms and functions to interpersonal synchrony, thereby attempting an integration of the theoretical frameworks of Predictive Processing and Attachment Development. Then, I will summarize four empirical studies conducted to test interpersonal neural, behavioral, and physiological synchrony between caregiver-child dyads in various social contexts. The studies examined interpersonal synchrony in dyads of two different age ranges, infancy and preschool, to further understand how synchrony evolves with interactional experience. The studies were additionally modified based on social complexity (according to Predictive Processing) and included different types of caregivers (according to Attachment Theory). Based on the results of these studies, I will discuss how interpersonal synchrony in early social interactions is shaped by the caregiver's communicative rhythms and priors, such as motivations and caregiving beliefs.

Info Box 1 – Functional near-infrared spectroscopy (fNIRS)

With fNIRS, source optodes emit light, which travels through skin, skull, and underlying brain tissue to be absorbed by detector optodes (Elwell, 1995). The light will be attenuated due to absorption and scattering effects. Using the change in near-infrared light, we can measure changes in oxygenated and deoxygenated hemoglobin concentrations in the cortex. Regional changes in blood flow and oxygenation are then related to brain activity (Fox & Raichle, 1986). Still, the relation between neuronal activity and the vascular response is not yet understood (Logothetis et al., 2001). Studies of hemodynamic behavior assume that an increase in blood flow results in higher local oxygenation levels, which should reflect higher neuronal activity.

While electroencephalography (EEG) has been the primary choice to study infants and young children for many years, fNIRS is now well established in studying developing brains (Lloyd-Fox et al., 2010; Minagawa-Kawai et al., 2008). A significant advantage of fNIRS is that it is less susceptible to movement artifacts than EEG, and it provides spatial localization of brain responses in specific cortical regions. fNIRS provides a suitable method to study naturalistic social interactions with infants and young children in ecologically valid settings, allowing participants to speak and move. There are, however, limiting factors to fNIRS, which are a lower temporal resolution than EEG. fNIRS also has a lower spatial resolution than magnetic resonance imaging (MRI), and the depth resolution depends on the infant’s age. Therefore, the optode configuration needs to be adapted to the developmental sample and predetermined to a cortical region of interest when using fNIRS.

2. Interacting brains, bodies, and minds

2.1. Interpersonal synchrony in development

Social interactions are integral to human development. Infants are embodied agents in their interactions with other people (Di Paolo & De Jaegher, 2012; Markova et al., 2019; Raz & Saxe, 2020). By engaging in dynamic mutual exchanges, infants begin to make sense of themselves and others to learn from them (Stern et al., 1985). The Predictive Processing framework suggests that even early learning from and with others entails making better predictions about others' actions (Köster et al., 2020). Predictive Processing offers a valuable model for understanding how the (Bayesian) brain functions (Clark, 2013). According to the framework, our brain actively and continuously makes predictions about upcoming input and events to infer causality. Internal models generate predictions based on priors and update upon integration of prediction and incoming sensory information. Inferences can be made in two ways: perceptual inference and active inference. Perceptual inference implies that the internal model is adjusted to the perception of new sensory information. Active inference implies that by acting on the world, incoming sensory input is adjusted according to internal models. The discrepancy between prediction and observation, so-called prediction error, helps the generative models to adapt to the environment and minimize prediction errors in the future. By weighting priors, e.g., previous experiences, and incoming sensory information, individuals can flexibly adjust their predictions depending on the complexity of the environment to further minimize prediction error (Precision-weighting; Yon & Frith, 2021). While neurobiological evidence on Predictive Coding in development is still sparse, promising findings show that infants as young as six months of age demonstrate heightened activity in the occipital cortex in response to a mismatch between an infant's visual expectation and current sensory input (Emberson et al., 2015).

In early social exchanges, infants' predictions are facilitated by naturally occurring communicative rhythms (Markova et al., 2019). These rhythms can entail "motherese", nursery rhymes, affective touch, interactive play, and daily routines between caregivers and infants. Communicative rhythms allow individuals to predict specific actions more easily and react accordingly, resulting in interpersonal synchronization (Condon & Sander, 1974). Interpersonal synchrony is a dynamic process by which hormonal, physiological, and behavioral cues are exchanged and reciprocally adjusted between two or more persons (Feldman, 2012). Interpersonal synchrony can be distinguished between concurrent synchrony (e.g., joint action, mutual gaze, mirroring, postural sway; Chang et al., 2017; Louwerse et al., 2012) and sequential synchrony (e.g., turn-taking, reciprocity, imitation; Feldman, 2012; Markova et al., 2019). Both ways of achieving synchrony are not mutually exclusive and might work in combination.

Interpersonal synchrony between infants and caregivers plays a vital role in infants' socio-cognitive and attachment development (Atzil & Gendron, 2017; Harrist & Waugh, 2002; Leclère et al., 2014). Attachment can be described as an infant's disposition to identify and interact with a person (primary caregiver) or a small set of persons considered most likely to provide them with care and protection (Ainsworth, 1979; Bowlby, 1969). When infants are in distress, they signal their need to the caregiver by using attachment behaviors, such as crying, calling, and proximity seeking. Consequently, the caregiver will try to soothe the infant and help to re-establish a state of homeostasis through co-regulation (Feldman et al., 2011). As infants and caregivers gain experience by interacting day by day, the structure of those interactions is suggested to become internalized and subsequently represented in both infant's and caregiver's minds (Bretherton, 2005). If available and responsive caregivers meet infants' proximity-seeking attempts, infants start building mental representations of others associated with trust and positive experiences. These characteristics describe a secure attachment (Ainsworth, 1979; Bowlby, 1969). Conversely, if caregivers are constantly unavailable during times of need, infants are more likely to attempt to self-soothe instead of reaching out to their caregiver (insecure-avoidant attachment). If caregivers respond unpredictably to infants' proximity-seeking, children start to develop ambivalent feelings towards the caregiver (insecure-anxious attachment). In attempts to reach their unpredictable caregiver, these infants instead intensify their proximity-seeking attempts. In the long term, the experiences are internalized as part of the so-called internal working models (Sroufe, 1988). The internal working models then in turn can guide future encounters with peers and a variety of others. The internal working models are separately developed for each caregiver infants interact with. Thus, the models can differ between close others. Overall, the internal working models are similar to the internal generative models in the predictive processing framework (Friston, 2010) and might therefore serve as priors to inform predictions about close others.

By preschool age, children's interactions with their caregivers rely on a much more extensive collection of experiences than during the first year of life (Harrist & Waugh, 2002). Priors, such as their attachment relationship with their caregiver, might now play into the level of interpersonal synchrony during social interactions (Leclère et al., 2014). Children, however, start to become more independent from their caregivers at this age. Therefore another important and preschool-age specific prior is children's agency (Harrist & Waugh, 2002). In contrast to infants, preschool-aged children are no longer easily coaxed into interactions with their caregiver but can engage and withdraw their participation at will. Children can display vigor, confidence, and eagerness in their engagement with others. This developing sense of agency is proposed to be an essential prior in active inferences (Friston et al., 2013). Accordingly, the structure of interactions in the preschool period is described by equal initiation of both child and caregiver, as children mature in their communicative and cognitive abilities. Additionally, children can now engage in sophisticated dialogues with their caregivers and more complex forms of coordination, such as joint problem-solving. Another difference between infancy and early childhood interactions is the temporal scale of mutual engagement. While synchronous caregiver-infant interactions have been observed to be more transient (Wass et al., 2020), caregiver-child synchronous interactions are described as highly interconnected over the whole interaction period (Harrist et al., 1994).

Taken together, communicative rhythms in early social interactions are suggested to facilitate mutual prediction, helping caregivers and children to synchronize on the behavioral level and therefore create attachment bonds (Beebe et al., 2010; Markova et al., 2019). These communicative rhythms enable various forms of coordination throughout early childhood. As caregiver-child dyads gain interaction experience, individual and dyadic factors start to play a role in caregiver-child behavioral synchronization. In recent years, interpersonal behavioral synchrony was also observed on neural and physiological levels (see Feldman, 2017, for review). However, the role of communicative rhythms and caregiver-child priors for neural and physiological synchrony needs further investigation.

2.2. Interpersonal neural synchrony

Interpersonal synchronization of brain activities can be measured using simultaneous recordings of brain activations from several persons (*hyperscanning*; Dumas et al., 2011; Hasson et al., 2012). Synchronization of neural signals is assumed to reflect mutual attunement of behavioral and physiological rhythms (Babiloni & Astolfi, 2014; Dumas et al., 2011; Hasson et al., 2012) that are transmitted through the environment. For example, activation of one person's motor system (to generate actions) is coupled to processing incoming sensory information in another person. When two or more neural systems align, the processing of social (interaction) stimuli is optimized, leading to the enhanced mutual prediction of incoming information and thus optimizing behavior during interactions (Hoehl et al., 2020; Kingsbury et al., 2019; Koban et al., 2019; Large & Jones, 1999). Therefore, the communicative rhythms used by caregivers to enhance mutual predictions are suggested to play an essential role in early interpersonal neural synchronization (Markova et al., 2019).

In adults, a growing body of evidence highlights that interpersonal neural synchrony is associated with effective communication and co-regulation (Czeszumski et al., 2020; Goldstein et al., 2018; Jiang et al., 2020). Beyond this correlational evidence, multi-brain stimulation has been used to enhance interpersonal neural synchrony artificially. Stimulating two people's brains during interaction led to increased behavioral coordination and social learning (Novembre et al., 2017; Pan et al., 2021), supporting the notion that neural synchrony functionally promotes social coordination and exchange. Based on existing behavioral evidence from developmental research reviewed above and this recent neuroscience research with adults, interpersonal neural synchronization may play a substantive role in caregiver-child coordination, communication, and child attachment formation (see Atzil et al., 2018; Atzil & Gendron, 2017). Nonetheless, the empirical evidence is still sparse.

Initial fNIRS hyperscanning studies investigated parent-child interactions during a computerized reaction time task and revealed increased neural synchrony in frontal and temporal areas during parent-child cooperation compared to competition and stranger-child interaction (Miller et al., 2019; Reindl et al., 2018). Neural synchrony during cooperation was related to temporally aligned motor reactions of parents and children, underscoring the link between rhythmic, predictive behavior and synchrony (Reindl et al., 2018). However, the broadly assessed behaviors were specific to the task. The question remains on how caregiver and child use naturally occurring communicative rhythms to synchronize on a day-to-day basis. The role of communicative rhythms for interpersonal neural synchrony was only investigated in infant-adult rather than infant-caregiver interactions. For example, Leong and colleagues (2017) found that mutual gaze is associated with enhanced neural synchrony (assessed using EEG hyperscanning) between infants and experimenters. In another fNIRS hyperscanning study, infants' and adults' synchronization was increased during joint attention, infant positive affect, and mutual gaze (Piazza et al., 2020). Whether these findings apply to caregiver-infant dyads has not yet been investigated.

Beyond the preliminary link between neural synchrony and rhythmic behavior, parent-child neural synchronization was related to the emotion regulation of both parent and child and the child's attachment quality (Reindl et al., 2018; Miller et al., 2019). These findings imply that the caregiver and child's individual and dyadic factors to the interaction might affect how well they synchronize with others. Therefore, it is vital to study further factors to understand the facilitative and attenuating components of interpersonal synchrony. Based on these preliminary results and behavioral research (Leclère et al., 2014), caregiving and attachment factors seem promising variables to study in early naturalistic caregiver-child synchrony.

2.3. Interpersonal physiological synchrony

Synchrony on the physiological level describes the interpersonal coordination of arousal (interbeat-intervals) or intra- and interpersonal regulation (respiratory sinus arrhythmia; RSA). The attunement of cardio-respiratory rhythms between mother and child emerges early in life (Feldman, 2007). In prenatal development, the mother's cardiac rhythm is one of the earliest and most significant auditory cues for a fetus. It shapes the infant's familiarity with such rhythms from even before birth (Provasi et al., 2014). Feldman and colleagues (2012) suggest that early physiological attunement scaffold infants' still immature physiological systems and supports the development of infants' self-regulation, thereby strengthening the attachment relationship between infant and caregiver (Atzil & Gendron, 2017; Feldman, 2017).

Generally, interpersonal physiological synchrony of arousal in early parent-child dyads seems to emerge when both interaction partners are mutually engaged in social interaction. For example, in face-to-face interactions at three months of age, infants' heart rhythms (inter-beat intervals) were synchronous with maternal heart rhythms within less than 1 second (Feldman et al., 2011). Especially moments of high physiological synchrony were matched with vocal and affect concordance in the dyad. However, recent evidence suggests that interpersonal physiological synchrony emerges in even more specific social scenarios, such as when co-regulation occurs (Wass et al., 2019). Wass and colleagues (2019) report that mother-infant interpersonal physiological synchrony, measured throughout the day, was only evident during and after instances of infants showing high arousal and negative affect.

When considering intra- and interpersonal regulation processes, RSA is an additional suitable index, as it describes the regulation of the vagal system. Regulation of the vagal system allows us to adapt by reacting and predicting changes in our social environments (see Porges, 2007). Accordingly, RSA can be considered a converging measure of prediction error or social uncertainty, as low levels of RSA are associated with increased sensitivity to unpredictable threats (Gorka et al., 2013). Overall, physiological synchrony in RSA occurs in similar contexts as arousal synchrony, namely during engagement in contrast to disengagement (Skoranski et al., 2017). But beyond general synchronization during social engagements, infants as young as 4-months of age seem to show synchrony in RSA with their caregivers during co-regulation phases of a still-face paradigm (Abney et al., 2021).

Still, physiological synchrony is not uniformly associated with adaptive outcomes (Ham & Tronick, 2009). For instance, physiological synchrony has been related to lower empathy in adolescence (Woody et al., 2016), and suggested links to attachment were not yet evidenced (DePasquale, 2020). Therefore, to understand the occurrence and functions of physiological synchrony, we need to examine further factors and outcomes to interpersonal physiological synchrony in early interactions. Moreover, interpersonal physiological synchrony of RSA might be related to interpersonal neural synchrony due to the suggested link between the prefrontal brain-amygdala circuit and the vagal system (Beauchaine, 2015). Probing the associations between the different levels of synchrony might thus inform when and why we synchronize with others.

2.4. Section Summary

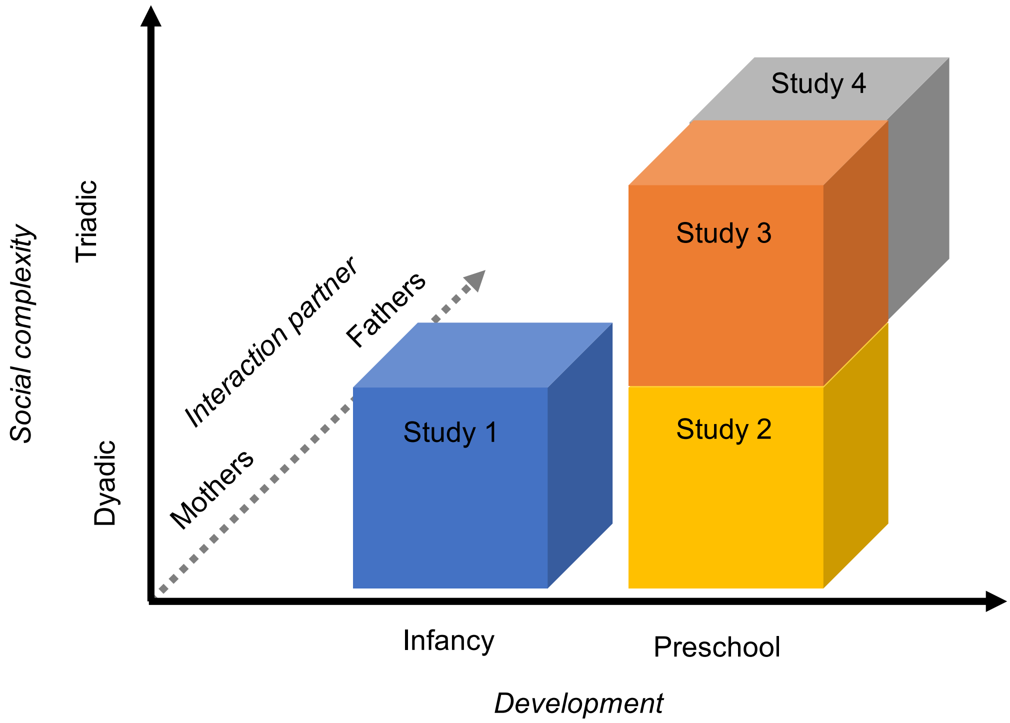
Interpersonal behavioral, neural, and physiological synchrony are suggested to be driven by communicative rhythms facilitating social information processing and predicting future actions (Hoehl & Bertenthal, 2021; Markova, 2018). While the facilitative role of rhythmic communicative behaviors has been evidenced for interpersonal behavioral synchrony (Beebe et al., 2010; Feldman, 2012), evidence for the involvement of communicative rhythms in interpersonal neural and physiological synchrony between caregiver and child is missing. Moreover, the link between (mutual) prediction and interpersonal synchrony in development should be investigated by considering different social contexts entailing various complexities. In addition, few individual and dyadic priors were considered when studying caregiver-child neural synchrony. While first studies indicate the involvement of priors, such as emotion regulation and attachment quality, in neural (and physiological) synchrony between caregiver and child, further factors need to be considered. To extend these preliminary results, priors related to caregiving (including mothers and fathers) and child development (such as the role of agency) should be considered.

3. Interpersonal synchrony in naturalistic caregiver-child interactions

As reviewed in the previous section, the literature on when and why parents and children show neural and physiological synchronization is still sparse and comprises divergent results. In the following four studies, we utilized fNIRS hyperscanning to shed light on interpersonal neural and physiological synchrony in naturalistic caregiver-infant and caregiver-child interactions. In Study 1, fNIRS hyperscanning was combined with electrocardiography (ECG) measurements and behavioral micro-coding to assess the roles of touch and affect as communicative rhythms in association with neural and physiological synchrony in dyadic mother-infant interactions. Studies 2-4 move into preschool age to consider communicative behaviors as well as individual and dyadic priors related to neural and behavioral synchrony in various social contexts and with different caregivers. Study 2 includes a sample of mothers and their children, in which we examined a dyadic social interaction. We tested how verbal communication patterns were related to neural synchrony during a conversation. Study 3 and 4 expanded the social interaction to include an object, a game that parents and children were instructed to play together or alone. Study 3 looked at the same sample of mothers and children and compared neural and non-verbal behavioral synchrony in cooperative to individual problem-solving. Study 4 used the same paradigm as in Study 3 to study fathers and their children. Examining fathers will allow us to gain more knowledge on the role of different caregivers for interpersonal synchrony. Overall, the studies examine communicative rhythms and potential individual and dyadic differences concerning caregiver-child synchrony and how these might depend on children's development, interaction partner, and the social complexity of the interaction (see Figure 1). In Chapter 4, I will discuss the combined findings of these studies concerning the integration of communicative rhythms and priors for interpersonal synchrony.

Figure 1

Overview of Studies 1 to 4



Note. The studies are mapped onto three dimensions: Development (x Axis), Social Complexity (y Axis), and Interaction partner (z Axis). While Study 1 includes a mother-infant sample in a dyadic social context, Study 2 looks at a mother-preschool child during a dyadic conversation. Next, Studies 3 and 4 comprise two samples of mother-child and father-child dyads engaged in a triadic problem-solving task.

3.1. Study 1. Neural and physiological synchrony during mother-infant interaction

At 3-4 months of age, coordinated patterns are traceable in caregiver-child interactions (Beebe et al., 2010). Both caregiver and infant not only reactively adjust their behavior to the other person but start to show clear prediction patterns (i.e., interpersonal synchrony; Feldman, 2012). Whether those early predictive behavioral patterns scaffold neural and physiological synchrony remains to be examined. Importantly, interpersonal behavioral synchrony in those early interactions seems to set infants up for a secure attachment relationship with their caregiver (Beebe et al., 2010; Isabella & Belsky, 1991). Therefore, based on attachment theory, we specifically examined the role of physical proximity and touch in coordinated states in caregiver-infant interactions. While the importance of touch for child development has been implicated in previous work (i.e., Carozza & Leong, 2021; Van Puyvelde et al., 2015; Waters et al., 2017), there is little empirical evidence about their role to convey communicative (rhythmic) signals in interpersonal neural and physiological synchrony.

The present study thus examined the role of proximity and touch on caregiver-infant neural and physiological synchrony during early social interactions. Brain activity (measured via fNIRS) in frontal regions and respiratory sinus arrhythmia (measured via ECG) of 4- to 6-month-old infants and their mothers were simultaneously measured during interactive vs. non-interactive contexts utilizing a multi-level hyperscanning setup. Brain activity was measured in bilateral inferior frontal regions, lateral and medial prefrontal regions. Synchronization in these regions is suggested to mark mutual attention, prediction, and shared affect, which are critical to infants' interactions with their caregivers (Feldman, 2017; Gvirts & Perlmutter, 2020). What is more is that the prefrontal cortex is suggested to be associated with the vagus system, assessed through respiratory sinus arrhythmia (Beauchaine, 2015). By measuring both systems, we also explored how the different levels of synchrony might relate to one another. During the free play condition, mothers' spontaneously occurring touching behavior (i.e., affective touch, stimulation touch) and infants' facial expressions (i.e., positive and negative affect) were assessed using micro-coding.

We expected caregiver-infant dyads to show increased neural and physiological synchrony during phases of high, experimentally manipulated physical proximity between mother and infant. We contrasted the dyads' neural and physiological synchrony during a distal non-interactive condition to a proximal non-interactive condition while caregiver and infant attended to the same video. Subsequently, we assessed whether spontaneous use of maternal touch during a face-to-face interaction was related to differences in interpersonal neural and physiological synchrony. We hypothesized that increased durations of social touch would be associated with increased interpersonal neural and physiological synchrony. Additionally, we studied infant affect in relation to neural and physiological synchrony and examined potential links between neural and physiological synchrony in the mother-infant dyad.

Nguyen, T., Abney, D.H., Salamander, D., Bertenthal, B.I., & Hoehl, S. (2021). Proximity and touch are associated with neural but not physiological synchrony in naturalistic mother-infant interactions. *NeuroImage, 244*, 118599. doi.org/ 10.1016/j.neuroimage.2021.118599

Results of Study 1 showed increased mother-infant neural synchrony, assessed by Wavelet Transform Coherence (see *Info Box 2*), in bilateral lateral and medial prefrontal cortex during proximal vs. distal joint watching and with spontaneously occurring affectionate touch during free play. Interpersonal physiological synchrony (assessed by Percentage Determinism [DET], see *Info Box 2*), on the other hand, was neither related to proximity nor spontaneous touching behavior of the mother during free play. We find that higher physiological synchrony was associated with higher durations of infant negative affect, and lower physiological synchrony was associated with higher durations of infant positive affect in the free play condition.

To conclude, the communicative rhythms and signals (touch and affect) might have enhanced the predictability of the interaction, which was related to increased neural and physiological synchrony, reflecting mutual engagement and co-regulation, respectively (Hoehl et al., 2020; Koban et al., 2019). Both neural and physiological synchrony were higher in interactive conditions than when passively viewing the same visual stimuli. Nonetheless, interpersonal neural and physiological synchrony were not correlated, as indicated by different behavioral correlates between synchrony levels.

Info Box 2 – Synchrony Measures

Wavelet Transform Coherence (WTC)

WTC assesses the relation between two time series over frequency and time (Grinsted et al., 2004) and assumes the alignment between time-series to be non-linear. Accordingly, WTC does not assume the data to be stationary. High coherence would emerge when the two time series are aligned in phase, when the signals are phase-lagged and anti-phase. WTC is invariant to interregional differences in the hemodynamic response function (HRF; Sun et al., 2004), which are also assumed to be different between individuals (especially of different ages).

Cross-Recurrence Quantification Analysis (CRQA)

CRQA assesses shared, non-linear dynamics between two time series (Coco & Dale, 2014). Similar to WTC, CRQA does not assume the data to be stationary. This method provides many measures, here, we would like to highlight Percentage Determinism (DET). DET describes the percentage of recurring points forming diagonal, which reflect sequences of revisitation within a specific duration threshold.

3.2. Study 2. Neural synchrony during mother-child conversation

Infants primarily engage with others through non-verbal behavior (e.g., Gratier et al., 2015; Trevarthen, 1993). However, children's ability to engage in and uphold dyadic social interactions becomes more sophisticated as children acquire language and advance in their social and cognitive competencies (Black & Logan, 1995). By preschool age, they thus gain an additional context of dyadic interaction and can engage in sophisticated, adult-like conversations. Conversations are a particular form of speech exchange as individuals convey information via vocalizations, which decode semantic, conceptual, and syntactic information (Jiang et al., 2020). Information is structured in a turn-taking pattern, which develops over early childhood (Gratier et al., 2015). The coordination needed to engage in and maintain conversational turn-taking is highly complex and presupposes multifaceted cognitive processes, such as mutual prediction of one's own and the other's turn (Friston & Frith, 2015). Creating mutual understanding through turn-based interpersonal communication is suggested to strengthen the caregiver-child relationship (Jiang et al., 2020; Leclère et al., 2014). However, the neural mechanisms supporting such central qualities, namely turn-taking, in parent-child interaction, and especially conversation, have only been sparsely investigated so far.

Accordingly, Study 2 examined a free verbal conversation between mothers and their preschool children to identify conversation patterns associated with neural synchronization. Mothers and 5-6-year-old children engaged in a conversation for four minutes. The individual brain activity of mothers and children was simultaneously measured using fNIRS over frontal and temporo-parietal regions and subsequently assessed for interpersonal neural synchrony using WTC analysis. Chosen regions of interest are involved in social-cognitive processes during live interaction (Redcay & Schilbach, 2019). They have previously displayed increased neural synchronization during a face-to-face conversation in adults (Jiang et al., 2012). Dyads' turn-taking was assessed by coding turns (response offset) between speakers, and the sum of turns was taken as the turn-taking index.

Based on previous work (e.g., Jiang et al., 2012), we hypothesized that turn-taking would be positively associated with neural synchronization during a mother-child verbal conversation. In addition, we were interested in the dynamic time-course of neural synchrony during the mother-child conversation. A finer resolution of the time dynamics of interpersonal neural synchrony during a conversation can add to the understanding of such complex social interactions. We, therefore, hypothesized that neural synchrony would change over time in association with the frequency of turn-taking shown during the mother-child conversation.

Nguyen, T., Schleihauf, H., Kayhan, E., Matthes, D., Vrtička, P., & Hoehl, S. (2021). Neural synchrony in mother-child conversation: Exploring the role of communicative patterns. *Social Cognitive and Affective Neuroscience, 16*, 93-102. doi.org/10.1093/scan/nsaa079

We found that mothers and children showed above chance-level neural synchronization in temporo-parietal and prefrontal areas during the free verbal conversation. As hypothesized, neural synchrony increased over the course of the conversation. It showed a steeper increase in the latter half of their conversation when caregiver and child showed more frequent turn-taking. These results indicate that turn-taking during a conversation might increasingly support the precision of mutual predictions, as indicated by the rise in interpersonal neural synchrony further along with the interaction.

3.3. Study 3. Neural synchrony during mother-child problem-solving

The focal point of synchrony research in early development has been given to dyadic interactions (see Leclère et al., 2014). However, from 3-months on, infants are already sensitive to triadic interactions, including objects and toys (Striano et al., 2006). Triadic interactions afford many learning opportunities to children, allowing them to engage in more complex behaviors with their caregivers, such as joint attention, reciprocity, and cooperation (Harrist & Waugh, 2002). Therefore, mutual prediction is an essential part of triadic interactions as well and whether neural synchrony marks these triadic caregiver-child interactions remains open. Notably, there are large variations in how parents and children interact during dyadic and triadic interactions (Harrist & Waugh, 2002). The levels of coordination are highly varied, and preschool children are more likely to engage and disengage at their own will. These individual and dyadic differences in reciprocity and motivations shape children's coordination with their caregiver and subsequently the development of secure attachment relations and cognitive, emotional, and social competencies (Leclère et al., 2014).

Study 3, therefore, tested whether mothers and their preschool children showed neural synchrony during problem-solving and whether the level of synchronization was related to communicative rhythms (i.e., reciprocity) and priors (children's agency). Mothers and 5-6-year-old children engaged in two repetitions of two minutes of joint problem solving and individual problem solving of a tangram puzzle. The procedure preceded the procedure of Study 2. Mothers' and children's brain activity was simultaneously measured using fNIRS over frontal and temporo-parietal regions and assessed for interpersonal neural synchrony using WTC analysis. In addition, two trained coders rated the dyads' reciprocity and children's agency during joint problem-solving.

As previously shown for dyadic interaction (Study 1 & 2), we expected caregivers and children to show neural synchrony in frontal and temporal brain areas during a triadic interaction, namely joint problem-solving. We predicted higher neural synchronization to be associated with successful joint problem-solving. In addition, we expected behavioral reciprocity (as a salient communicative rhythm) to be related to higher neural synchronization. In addition, we hypothesized that priors pertaining to the children's specific age range, namely children's agency in the interaction, are related to more neural synchronization.

Nguyen, T., Schleihauf, H., Kayhan, E., Matthes, D., Vrtička, P., & Hoehl, S. (2020). The effects of interaction quality on neural synchrony during mother-child problem solving. *Cortex, 124,* 235-249. Doi.org/10.1016/j.cortex.2019.11.020

In line with previous studies using more controlled and artificial tasks (Leong et al., 2017; Reindl et al., 2018), the findings demonstrate that mother-child dyads showed higher neural synchrony in the temporo-parietal and lateral prefrontal areas when jointly solving a tangram puzzle in cooperation, in comparison to when they solved the same task individually. Extending those findings, we found that neural synchronization was accompanied by higher behavioral reciprocity during joint problem-solving in caregiver-child dyads. Strikingly, only neural synchronization but not behavioral reciprocity was associated with the dyad's task performance. Finally, regarding individual factors to neural synchronization, we found that children's agency during joint problem-solving correlated positively with neural synchrony and reciprocity, highlighting the involvement of agency as a prior in early social prediction processes.

3.4. Study 4. Neural synchrony during father-child problem-solving

Studies 2 and 3 had evidenced that mothers and children synchronize in brain and behavior during different contexts and in both studies, more so when caregiver and child showed rhythmic communication (i.e., turn-taking and reciprocity). However, children do not only form an attachment relationship with their primary caregiver, but they can also form several independent attachments to different others. During the last decades, the paternal role in Western Europe and North America has evolved substantially alongside significant societal changes (Lamb, 2010). Fathers, however, seem to show a different interaction pattern with their children in comparison to mothers (Feldman, 2003). Father-child synchrony is marked by high positive arousal that is spontaneous and organized in multiple peaks. Whether the same communicative rhythms might enhance predictability in father-child interactions as in mother-child interactions is unclear. Therefore, studying interpersonal neural synchrony in father-child interactions exclusively could deepen our understanding of the role of other caregivers. What is more is that fathers' involvement in caregiving is still highly varied (Brown et al., 2012). The role of paternal beliefs in their role as caregivers could therefore play a role in how well they can synchronize with their children. Taken together, whether fathers and children show neural synchrony and whether their synchronization is tied to previously evidenced rhythmic communicative behaviors and motivations between mothers and children remain open questions.

Study 4 tested father-child dyads in the same paradigm as in Study 3. Fathers and 5–6-year-old children engaged in a joint vs. an individual problem-solving task (tangram puzzle). The dyads' brain activity was simultaneously measured using fNIRS in frontal and temporal areas. Neural synchrony was assessed using WTC analysis. Two trained coders rated the dyad's reciprocity and child agency. Father's caregiving beliefs were assessed using a self-report questionnaire on the Role of the Father (Palkovitz, 1984).

We hypothesized that fathers and children would show increased neural synchrony during joint compared to individual problem-solving. Like mothers, we expected fathers and children to show increased neural synchrony when they behave more reciprocally and when children showed more agency during joint problem-solving. Moreover, we investigated potential factors specific to father-child dyads either facilitating or attenuating neurobehavioral synchronization, such as the father's caregiving beliefs.

Nguyen, T., Schleihauf, H., Kungl, M., Kayhan, E., Höhl, S., & Vrtička, P. (2021). Interpersonal neural synchrony during father-child problem solving: An fNIRS hyperscanning study. *Child Development, 92,* e565-e580. doi.org/10.1111/cdev.13510

Overall, father-child dyads showed increased neural synchrony frontal and temporal areas during joint compared to individual problem-solving. The data also tentatively suggest that neural during joint problem-solving in father-child dyads may reflect somewhat different underlying processes than those found in mother-child dyads. For example, findings on neural synchrony in father-child dyads did not relate to dyadic reciprocity and child agency as central behavioral, communicative rhythms, and motivations related to caregiver-child neural synchrony. Interestingly, there was a significant positive association between the father's belief in their role as a warm and supportive caregiver with neural synchrony during father-child joint problem-solving. Fathers' caregiving beliefs might act as a prior to help fathers derive better predictions about their children's actions and intentions.

4. Discussion. Components of interpersonal synchrony

When and why did caregivers and children show interpersonal synchronization in our studies? In this dissertation project, I investigated the role of related communicative rhythms and priors (individual and dyadic factors related to caregiving and attachment) associated with interpersonal neural and physiological synchrony. In infancy and preschool age, communicative rhythms conveyed through affectionate touch, conversational turn-taking, and reciprocal behaviors (i.e., behavioral synchrony) were related to increased interpersonal neural synchrony in frontal and temporal brain areas (Studies 1-3). These areas are associated with the multimodal representation of social signals (Schirmer & Adolphs, 2017), regulatory (Perlman & Pelphrey, 2010), and predictive processes (Friston, 2010; Raz & Saxe, 2020). Indeed, a growing number of developmental hyperscanning studies have evidenced the involvement of the frontal cortex in early neural synchronization (e.g., Azhari et al., 2019; Miller et al., 2019; Piazza et al., 2020; Reindl et al., 2018; Wang et al., 2020). However, the salient modality in communicative rhythms differed between levels of synchrony and interaction partner. While physical proximity and affectionate touch were associated with interpersonal neural synchrony, physiological synchrony was enhanced when infants showed negative affect (Study 1). Next, while behavioral synchrony and verbal turn-taking in mother-child dyads were related to enhanced neural synchrony in dyads (Study 2-3), father-child neural synchrony was not associated with the same communicative rhythms (Study 4). Regarding the role of priors for interpersonal synchrony, we identified child agency as integral to interpersonal neural synchronization between mother-child dyads at preschool age. On the other hand, fathers' beliefs on their role as caregivers were positively related to interpersonal neural synchronization in father-child dyads at preschool age.

Overall, the findings implicate that interpersonal neural, behavioral, and physiological synchrony are associated with transient communicative rhythms. However, specific behavioral modalities might be differently relevant for neural and physiological synchrony. Additionally, at preschool age and potentially even earlier, priors, such as motivations and beliefs of the interactants, play an additional role in interpersonal neural synchronization between caregiver and child.

4.1. Communicative rhythms

The alignment of brain activity, behavior, and physiology are suggested to be computationally efficient and cues infants for social communication (Hoehl et al., 2020; Wass et al., 2020). Thus, caregivers often use rhythmic communicative signals (Markova et al., 2019; Wass et al., 2020), for instance, gaze, singing, and touch, to increase the predictability of early social interactions. While gaze and joint attention were previously related to interpersonal neural synchronization in adult-infant dyads (Leong et al., 2017; Piazza et al., 2020), less is known about the role of other communicative rhythms for interpersonal neural and physiological synchrony, specifically in early caregiver-infant interactions. We thus investigated the role of proximity, touch, and reciprocity in caregiver-child synchrony.

In Study 1, mothers' physical proximity and affectionate touch were related to increased mother-infant neural synchrony. Proximity and touch have been previously indicated as essential tools for caregivers to create a secure base for infants when distressed (E. Waters, 1995). In other words, physical proximity and affectionate touching behaviors, such as stroking and kissing, seemed to enhance the predictability of the interaction with the specific caregiver. Physical proximity has previously been suggested to facilitate the perception of each other's cardio-respiratory rhythms (Van Puyvelde et al., 2015) and the perception of micro-adjustments during bodily contact (Little et al., 2019). Affectionate touch, such as stroking, has been suggested to strengthen socio-affective processing (Tuulari et al., 2019). By utilizing these interpersonal communicative rhythms, mother and infant were able to attune themselves to each other (Provasi et al., 2014). Next, besides conveying rhythms and predictability, proximity and touch are also proposed to be ostensive signals for early social communication (Wass et al., 2020). They are evidenced to elicit infant attention and regulate infant's affect (Della Longa et al., 2019; Stack & Muir, 1992). Proximity and affectionate touch thus might help mother and infant to establish and maintain engagement with one another. Mother and infant might have similarly processed the common sensory input from the video, resulting in interpersonal neural synchronization (e.g., Azhari et al., 2019).

Interestingly, not all forms of rhythmic touch were equally associated with interpersonal synchrony. Stimulating touch was related to decreased interpersonal neural synchrony between mother and infant in Study 1. This finding highlights the potential risk of intrusive caregiving behaviors, especially if the caregiver's behavior is not sensitively matched to the infant's behavior (Isabella & Belsky, 1991). Too much stimulating touch thus might have decreased the infant's engagement and thus interpersonal neural synchrony between mother and infant.

Studies 2 and 3 provide further evidence on the role of communicative rhythms in interpersonal neural synchrony at preschool age. The findings show that verbal and non-verbal behavioral synchrony (i.e., turn-taking and reciprocity) are associated with increased interpersonal neural synchrony during mother-child problem solving and conversation. Corroborating the results, Quiñones-Camacho et al. (2020) examined parents and children during an interactive repair phase (free play with toys) after a stressor. They showed that higher behavioral synchrony was related to enhanced neural synchrony as well. In general, reciprocal interactions, as well as conversational turn-taking, are suggested to generate rhythmicity between the two interactive partners that helps individuals to generate predictions based on the temporal regularity of behaviors and speech, allowing them to make mutual adjustments (Keller et al., 2014; Reddy et al., 2013). The enhanced predictability in such interactions enables caregiver-child interactions to successfully cooperate in the short term and children to develop predictable relationship patterns (attachment) in the long term. Taken together, we propose that interpersonal neural synchrony is a biomarker for mutual prediction processes within caregiver-child interactions and potentially their relationship quality.

While communicative rhythms across modalities seem to be closely linked if not essential to interpersonal neural synchrony, physiological synchrony between caregiver and infants seems to emerge through the processing of communicative rhythms from a specific modality. In Study 1, mothers and infants show higher physiological synchronization when infants showed negative affect and thus might have needed co-regulation. The saliency of affect for physiological synchronization has been initially raised in findings from a study showing that physiological synchrony is associated with positive affect synchrony in mother-infant dyads (Feldman et al., 2011). More recent results show that parents and infants physiologically synchronize during negative affect and high arousal (Wass et al., 2019) and emotion-regulation following a stressor (Abney et al., 2021). Nonetheless, affective information remains integral to physiological responses (see DePasquale, 2020 for a review). In comparison to other modalities, affective information might more likely cue interpersonal physiological synchronization. Accordingly, different behavioral modalities might be salient to different levels of synchrony. This finding underscored that interpersonal neural and physiological synchrony might have different functionalities (Study 1; Reindl et al., 2021), even though both are increased during interactive compared to non-interactive contexts. Still, further research is needed for deciphering the concrete contexts and directions of neural and physiological synchrony.

Additionally, not all caregivers use the same rhythmic communicative signals to enhance structure and predictability in social interactions with their children. Fathers and children in Study 4 showed less frequent and less varied reciprocal behaviors than mothers and children in Study 3. This finding is not uncommon in (German-speaking) father-child dyads, who naturally favor active games with steeper changes in affect compared to when children interact with their mothers (Robinson et al., 2021). Despite the different interaction patterns, father-child dyads still showed neural synchronization in Study 4. The findings thus suggest that caregiver-child synchronization is not only associated with rhythmic communicative signals but can emerge from minimally communicative cues (Hirsch et al., 2017) and similar neural responses to common sensory input. For instance, similar neural responses were evidenced amongst friends compared to strangers (Parkinson et al., 2018) and thus underscored the involvement of individual and dyadic priors pertaining to the individual's relationship in interpersonal synchrony.

4.2. Individual and dyadic priors

Hoehl and colleagues (2020) propose in a recent theoretical account that, next to the role of communicative rhythms, the motivation to engage with the interaction partner can be a crucial factor for interpersonal synchronization. Indeed, Study 3 underscores the role of motivational factors as children's agency in the problem-solving task was associated with higher interpersonal neural synchrony. Once children can determine when to engage and disengage in social interactions during the preschool period, their motivation plays an essential role for the dyad's mutual engagement in the same task (Harris & Waugh, 2002). In Study 3, children, who displayed more confidence and eagerness in the problem-solving task, might have integrated this prior into making better and potentially more active predictions about the caregiver's actions and intentions. At the same time, interpersonal synchrony between caregiver and child can also decrease when they struggle to engage in a situation mutually. For instance, children's temperamental irritability was related to less parent-child neural synchrony (Quiñones-Camacho et al., 2020). More irritable children might have difficulties engaging with their caregivers after a distressing situation (Brotman et al., 2017). Moreover, individual factors concerning the caregivers, such as stress, can also modulate and impede caregivers' engagement with their children. Azhari et al. (2019) report that mothers' stress levels seemed to attenuate mothers' interpersonal neural synchrony with their children when they watched animated videos together. To conclude, parents and children can be differently affected by individual motivational and temperamental factors strengthening or impeding interpersonal synchrony.

Interpersonal neural synchrony is also proposed to be linked to the relationship quality of parents and children (Miller et al., 2019). Infants and children generally show interpersonal neural synchrony with close adults and strangers (Reindl et al., 2018). Yet, the unique bond between caregiver and children might provide them with an advantage at synchronizing with one another. For example, children and parents show higher neural synchronization than children and strangers (Endevelt-Shapira Yaara et al., 2021; Reindl et al., 2018). Beyond these group-level differences, there are indications of dyadic differences in levels of synchronization between caregiver-child dyads. For example, children who were avoidantly attached to their mothers seemed to show decreased neural synchronization during a button-press task, even though the results did not survive correction for multiple comparisons (Miller et al., 2019). Still, the results underscore the potential involvement of the attachment system in interpersonal neural synchrony. In fact, the findings from Study 4 show that differences in parental caregiving beliefs were related to differences in interpersonal neural synchrony between dyads. Fathers' higher identification with the role of a warm, sensitive, and supportive caregiver was related to enhanced neural synchrony during father-child joint vs. individual problem-solving. However, the links between the father's caregiving beliefs and interpersonal neural synchrony were not mediated by the communicative rhythms assessed in the study. Instead, it has been shown that paternal caregiving beliefs were associated with structural changes in the father's brain (Long et al., 2021). These changes, therefore, point towards a neurobiological structural and functional mechanism to how priors are related to interpersonal synchrony.

4.3. Anatomical and functional similarities between caregiver and children

While the results of Studies 1-3 and others (Leong et al., 2017; Piazza et al., 2020) have highlighted the facilitating role of communicative rhythms for interpersonal synchrony, Dumas and colleagues (2012) found that the anatomical and functional similarity of the two interactants' brains partly facilitated interpersonal synchronization as well. Anatomical similarities can be expected to be greater in biological parent-child dyads which might play a role in their propensity to synchronize. Nonetheless, studies with foster parents might be necessary to single out genetic factors.

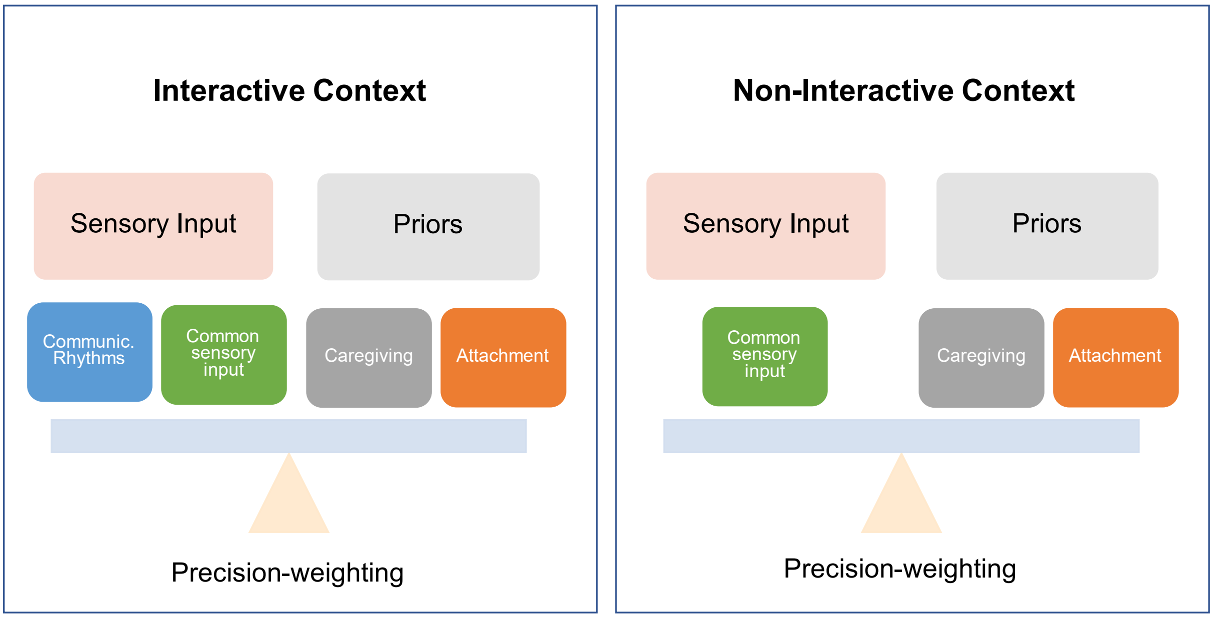
Beyond the role of anatomical similarities, Dumas et al. (2012) show that functional similarities explain more variance in interpersonal synchrony. Indeed, neural responses to audiovisual movie watching are more similar amongst friends, and the similarity decreased with increasing social distance (Parkinson et al., 2018). The participants separately observed the movies and were unable to interact with one another. Further evidence in adults showed increased physiological synchrony between firewalkers and relatives compared to strangers during a firewalking ritual (Konvalinka et al., 2011). Again, physiological synchrony in arousal was not related to concurrently executed behaviors, as the participants either only observed the ritual or actively participated in the ritual. Therefore, interpersonal synchrony also emerges in non-interactive contexts due to common sensory input and when participants are more likely to show functional similarities. But how do these functional similarities emerge?

Repeatedly learning about the world from others, such as caregivers or siblings, has been suggested to likely lead to more overlapping mental models and predictions among these individuals (Friston & Frith, 2015). Therefore, the coupling of mental models during interactive and non-interactive contexts could result in interpersonal neural synchrony between interactants and similar *intrapersonal* brain connectivity across interactants (Shamay-Tsoory, 2021). In non-interactive contexts, such as video watching, individuals' responses are cued to the same (affective) moments, potentially resulting in a similar neural or physiological response between friends and relatives. On the other hand, strangers might have responded differently to the same situation. It has been recently shown that mothers' and infants' functional connectivity become more similar over the first three months of life as they continuously expand their interaction experience (Kim et al., 2021). Accordingly, interpersonal synchrony in parent-child dyads could emerge due to the integration of common sensory input, if available - communicative rhythms, and their (overlapping) mental models and thus functional similarities built from their prior experiences (i.e., caregiving and attachment models).

In consideration of both incoming sensory input and priors to interpersonal synchrony, how both components are integrated is unclear. How much weight is put on the incoming sensory input, and how much weight is put on prior representations? The relative importance of components can be considered in precision-weighting terms (Yon & Frith, 2021). Accordingly, whether interpersonal synchronization in parent-child dyads relies on prior experiences or incoming sensory input is weighted depending on the amount and quality of current communicative rhythms (such as signal to noise ratio in the environment; Yon & Frith, 2021) as well as the amount and quality of prior interaction experiences (Feldman, 2017; Vrtička, 2017), as illustrated in Figure 2.

Figure 2

Schematic outline of the integration of sensory input and priors



Note. During interpersonal synchronization of behavior, brain, and physiology in interactive contexts, communicative rhythms, common sensory input, and priors (e.g., caregiving and attachment) are weighted depending on the reliability of the incoming signal and the priors. In non-interactive contexts, interpersonal synchrony can emerge from common sensory input and priors, despite the lack of communication between individuals.

4.4. Weighing communicative rhythms and priors for interpersonal synchrony

Interactions between caregivers and children are highly varied (Harrist & Waugh, 2002; Leclère et al., 2014). They vary in structures within themselves as only 30 % of interactions are synchronous (Tronick & Gianino, 1986), and they vary between different interaction partners. We rarely have the same interaction twice. Therefore, we must balance the incoming information with our prior beliefs in every social interaction (Yon & Frith, 2021). Precision-weighting is suggested to depend on the reliability of the perceived signals in the environment (Lawson et al., 2021; Yon & Frith, 2021). In reliable environments, we might be advised to rely on the continuously incoming communicative rhythms and common sensory input to synchronize with others. In contrast, unreliable environments might push us to rely on our previous interaction experiences to navigate the current one. Indeed, in studies with adults, neural synchronization was increased with higher predictability of verbal content (Dikker et al., 2014).

Consequently, if the communicative rhythms in early caregiver-child interactions are prominent, easily, and accurately perceived, it is more likely for the caregiver and child to show neural synchronization. In Study 1 and 2, the dyadic interactions (especially in a lab setting) offer a social context with relatively little noise in the environment. Communicative rhythms such as those observed through affectionate touch, turn-taking, and reciprocity allow mother and child to attune to one another easily. Common sensory input conveyed through video, especially when comprising affective cues, can relate to interpersonal synchronization between parent and child as well (Study 1, Azhari et al., 2019; Levy et al., 2017), but communicative rhythms in live social interactions seem to allow the dyads to synchronize more strongly with one another (Study 1; Fishburn et al., 2018). Compared to dyadic interactions, triadic interactions are marked by a rise in complexity and thus lower social predictability. Mother-child dyads in our sample for Study 3 still showed rhythmically structured behaviors (i.e., reciprocity) for the dyads to mutually attune their brain activity. Still, children's motivational priors also mattered, and thus weighting seemed to have shifted from a major focus on communicative rhythms. Father-child dyads, on the other hand, might not be used to such an interaction pattern (see Lamb, 2010), and thus, the reliability of the communicative rhythms might have been decreased. Attuning to transient communicative rhythms was generally difficult as the dyads also showed few reciprocal behaviors. Thus, father-child neural synchronization could have been more strongly related to their functional similarity in response to the task, as suggested by the change in the paternal brain in relation to fathers' caregiving beliefs (Long et al., 2021).

As aforementioned, precision weighing depends on the reliability of the transient social signals in the environment (Yon & Frith, 2021). In early interactions, the child's environment includes the reliability of their caregiver. In attachment research, the reliability of caregivers is internalized in working models, which describe infants' attachment relationships with their caregivers (Sroufe, 1988). Interestingly, behavioral research shows that caregivers do not need to constantly provide infants and children with cues and rhythms to synchronize to. Instead, an optimum mid-range model should be assumed (Beebe et al., 2010), in which variability in caregiver's behaviors scaffolds children's perception of fixed patterns and invariants (Gómez, 2002). Mid-range variability in caregivers' behaviors can thus increase flexibility within infants and in engagement with others, which is associated with a secure attachment style (Beebe et al., 2010). Miscoordination could prepare the infants for future instances of non-contingency in their environment, trading short-term "unreliability" for long-term reliability. Beyond the regulatory function of variability in caregivers' behavior, variability can even be engaging, such as with syncopation in music perception (Witek et al., 2014), and in the long-term offer learning opportunities to the infant (Chapman, 1991; Wass et al., 2020). Therefore, caregivers can place "noisy" or unexpected instances to increase the intelligibility of specific contents they want to communicate (Doelling et al., 2014). These caregiving behaviors might be observed during game routines (Markova, 2018).

Near perfectly contingent interactions can indicate anxious mothers and, more generally, anxious attachment relationships related to increased physiological and behavioral synchrony (e.g., Smith et al., 2021, Beebe et al., 2010) and decreased neural synchrony

(Azhari et al., 2020). Low variability in the infant's environment could thus be associated with over-weighting the reliability of the social partner, resulting in rigid behaviors and belief patterns, as seen in anxiously attached individuals (Vrtička, 2017). Conversely, very high variability in an infant's environment, including unavailable caregivers, could lead to over-weighting the communicative signals. It might be more difficult for such individuals to uphold social interactions despite the naturally occurring miscoordination, resulting in less neural, physiological, and behavioral synchrony (e.g., Miller et al., 2019).

5. Conclusion

In this dissertation, I discussed the emergence of interpersonal neural and physiological synchrony through incoming sensory input, which can be communicative rhythms and common sensory input. However, evidence from our studies and others highlights the integration of priors in the alignment of brain, body, and behavior. In caregiver-child dyads, the weighting of the reliability of the sensory input and priors related to caregiving and attachment might give rise to interpersonal synchrony in various contexts, modalities, and with multiple interaction partners.

While some but not all communicative rhythms in caregiver-child interactions were examined in previous and presented studies, identifying further naturally occurring communicative signals, such as body odor (Endevelt-Shapira et al., 2021) or singing (Nguyen et al., in preparation) as well as the variability of those can inform our research on early development. Further study of the caregivers', children's, and dyadic behaviors can offer interesting insights into optimal environments for social learning (e.g., Ward & Hunnius, 2020) and attachment development (e.g., Isabella & Belsky, 1991) in relation to neural and physiological synchrony.

Notably, the role of priors in interpersonal synchrony has only recently received attention and needs further consideration. While I focus on motivation, caregiving, and attachment in the dissertation, additional priors can be considered, such as those brought by different caregivers, peers, and strangers. Generally, the development of priors and precision-weighting can provide deeper insight into the early forms of interpersonal synchrony. Moreover, priors might work through functional and structural similarities between caregiver and child. Future research could investigate changes in intraindividual functional connectivity and structural changes as well as the (developing) brain-body connection, such as a potential link between the prefrontal cortex and RSA activity (Nguyen et al., 2022). Understanding intra-individual connections will help us understand inter-individual connections across levels (neural, physiological, and behavioral).

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7. Annex

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7.3. English Abstract

Early social interactions are vital for children's socio-cognitive and affective development. In these early interactions, caregivers use communicative rhythms to facilitate the mutual prediction of actions and intentions, resulting in interpersonal synchrony. This interaction pattern is suggested to become internalized in individual generative models, facilitating the attachment between child and caregiver. Beyond interpersonal synchrony on the behavioral level, neural and physiological synchrony have been shown to emerge in live and dynamic social interactions. However, less researched is whether enhanced mutual prediction through communicative rhythms is linked to caregiver-child neural and physiological synchrony. In addition, the role of individual and dyadic priors to interpersonal synchrony remains uninvestigated.

The thesis thus investigates interpersonal neural, behavioral, and physiological synchrony in naturalistic parent-child interactions while considering the role of communicative rhythms, motivations, and beliefs. The first study highlights social touch and proximity as communicative rhythms related to enhanced neural synchrony in mother-infant dyads. In contrast, physiological synchrony is related to infant negative affect. The second and third studies underscore the importance of verbal turn-taking and behavioral reciprocity for interpersonal neural synchrony in mother-preschool-child interaction. The third study further finds that children with higher agency also achieved higher synchronization with their mothers. The fourth study examines father-child interactions in which the dyads show neural synchronization, unrelated to the recorded communicative rhythms. Instead, fathers' belief in their role as warm and supportive caregivers is associated with enhanced neural synchrony.

Overall, the four studies show that children and caregivers integrate incoming transient communicative rhythms, common sensory input, and priors, such as motivations and caregiving beliefs, to synchronize. I propose that precision-weighting of communicative rhythms and priors are integral to interpersonal synchrony and can have important implications for caregiving and attachment.

7.4. Deutsche Zusammenfassung

Frühe soziale Interaktionen sind für die sozio-kognitive und affektive Entwicklung von Kindern entscheidend. In diesen frühen Interaktionen nutzen die Betreuungspersonen kommunikative Rhythmen, um die gegenseitige Vorhersage von Handlungen und Intentionen zu erleichtern, was zu interpersonal Synchronität führt. Dieses Interaktionsmuster wird dann in generativen Modellen von Bezugsperson und Kind verinnerlicht, wodurch sich ihre Bindungsbeziehung entwickelt. Es wird angenommen, dass neben der Verhaltenssynchronität auch die neuronale und physiologische Synchronität in live und dynamischen sozialen Interaktionen die gegenseitige Vorhersage kennzeichnen und die Bindungsbeziehungen fördern. Allerdings fehlt es an empirischen Belegen für die Rolle kommunikativer Rhythmen und anderer individueller und dyadischer Faktoren (*Priors*) für die neuronale und physiologische Synchronie zwischen Bezugsperson und Kind.

In dieser Arbeit wird daher die interpersonale neuronale, verhaltensbezogene und physiologische Synchronie in naturalistischen Eltern-Kind-Interaktionen untersucht, wobei die Rolle von kommunikativen Rhythmen, Motivationen und Überzeugungen berücksichtigt wird. Die erste Studie hebt soziale Berührung und Nähe als kommunikative Rhythmen hervor, die mit erhöhter neuronaler Synchronie in Mutter-Kind-Dyaden zusammenhängen, während physiologische Synchronie mit negativem Affekt des Säuglings in Verbindung gebracht wurde. Die zweite und die dritte Studie unterstreichen die Bedeutung der verbalen Abwechslung und des reziproken Verhaltens für die interpersonale neuronale Synchronie in der Interaktion zwischen Mutter und Vorschulkind. Die dritte Studie belegt außerdem, dass Kinder mit höherer Handlungskompetenz auch eine höhere Synchronisation mit ihren Müttern erreichen. Die vierte Studie untersucht Vater-Kind-Interaktionen, bei denen die Dyaden neuronale Synchronisation zeigen, die nicht mit den erfassten kommunikativen Rhythmen zusammenhängt. Stattdessen wird die Überzeugung der Väter an ihre Rolle als warme und unterstützende Bezugsperson mit einer erhöhten neuronalen Synchronisation in Verbindung gebracht.

Insgesamt zeigen die vier Studien, dass Kinder und Betreuungspersonen zur Synchronisierung sowohl eingehende kommunikative Rhythmen, gemeinsame sensorische Informationen als auch Vorannahmen wie Motivationen und Betreuungsüberzeugungen integrieren. Ich argumentiere, dass die präzise Gewichtung von kommunikativen Rhythmen und Priors ein wesentlicher Bestandteil der interpersonalen Synchronie ist und wichtige Auswirkungen für Fürsorge und Bindung haben kann.

7.5. Scientific Publications for the Cumulative Thesis

Accepted for publishing in a journal / book / anthology.

1) Nguyen, T., Abney, D. H., Salamander, D., Bertenthal, B. I., & Hoehl, S. (2021). Proximity and touch are associated with neural but not physiological synchrony in naturalistic mother-infant interactions. *NeuroImage, 244*, 118599. https://doi.org/10.1016/j.neuroimage.2021.118599

2) Nguyen, T., Schleihauf, H., Kayhan, E., Matthes, D., Vrtička, P., & Hoehl, S. (2021). Neural synchrony in mother-child conversation: Exploring the role of communicative patterns. *Social Cognitive and Affective Neuroscience, 16*(1-2)*,* 93-102. doi.org/10.1093/scan/nsaa079

3) Nguyen, T., Schleihauf, H., Kayhan, E., Matthes, D., Vrtička, P., & Hoehl, S. (2020). The effects of interaction quality on neural synchrony during mother-child problem solving. *Cortex, 124,* 235-249. doi.org/10.1016/j.cortex.2019.11.020

4) Nguyen, T., Schleihauf, H., Kungl, M., Kayhan, E., Hoehl, S., & Vrtička, P. (2021). Interpersonal neural synchrony during father-child problem solving: An fNIRS hyperscanning study. *Child Development, 92*(4), e565-e580. doi.org/10.1111/cdev.13510

1) Manuscript

Nguyen, T., Abney, D. H., Salamander, D., Bertenthal, B. I., & Hoehl, S. (2021). Proximity and touch are associated with neural but not physiological synchrony in naturalistic mother-infant interactions. *NeuroImage, 244*, 118599. https://doi.org/10.1016/j.neuroimage.2021.118599

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Proximity and touch are associated with neural but not physiological synchrony in naturalistic mother-infant interactions

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ABSTRACT

Caregiver touch plays a vital role in infants' growth and development, but its role as a communicative signal in human parent-infant interactions is surprisingly poorly understood. Here, we assessed whether touch and proximity in caregiver-infant dyads are related to neural and physiological synchrony. We simultaneously measured brain activity and respiratory sinus arrhythmia of 4–6-month-old infants and their mothers (N=69 dyads) in distal and proximal joint watching conditions as well as in an interactive face-to-face condition. Neural synchrony was higher during the proximal than during the distal joint watching conditions, and even higher during the face-to-face interaction. Physiological synchrony was highest during the face-to-face interaction and lower in both joint watching conditions, irrespective of proximity. Maternal affectionate touch during the face-to-face interaction was positively related to neural but not physiological synchrony. This is the first evidence that touch mediates mutual attunement of brain activities, but not cardio-respiratory rhythms in caregiver-infant dyads during naturalistic interactions. Our results also suggest that neural synchrony serves as a biological pathway of how social touch plays into infant development and how this pathway could be utilized to support infant learning and social bonding.

1. Introduction

Human development is driven by social interactions. From early on, infants begin to actively seek information as embodied agents in their social interactions (De Jaegher et al., 2016; Raz and Saxe, 2020). These exchanges are essential for infants' developing understanding of self and others. In these interactions infant and caregiver typically fluctuate between aligned and misaligned states (Montirosso and McGlone, 2020). Communicative signals allow the dyad to "repair" such misaligned states (Tronick and Gianino, 1986). This kind of coordination is referred to as interpersonal synchrony (Feldman, 2012) or mutual attunement (Stern et al., 1985), a dynamic process by which behavior and neurophysiological processes are reciprocally adjusted between two or more persons. Temporally aligning with another person facilitates mutual prediction and allostasis, i.e., the ongoing interpersonal physiological regulation required to meet the changing demands of the environment (Atzil et al., 2018). The occurrence of early interpersonal synchrony in various modalities is evidenced at 3-4 months of age, when the social capacities of infants begin to emerge (Beebe et al., 2010; Feldman, 2012). Infants begin to perceive contingent relations, discriminate the strength of these relations, and generate predictions based on these contingencies (e.g., Beebe et al. 2016, Harrist and Waugh 2002). By this age, caregiver and infant have had a sufficient amount of interaction history, so the infant's predictions of the interactive time course with their caregiver become more precise, highlighting the infant's communicative capacity (Tronick, 1989). Interpersonal synchrony occurs on the behavioral, neural and physiological level, yet we know little about their relational and developmental dynamics (Beauchaine, 2015; Feldman, 2017). Here, we simultaneously measured the brain activity and physiology of 4–6-month-old infants and their mothers during non-interactive and interactive contexts utilizing a multi-method "hyperscanning" setup to investigate the role of social touch, as a communicative signal, on caregiver-infant neural and physiological synchrony.

Recent research with adults using simultaneous recordings of brain activities from several persons (hyperscanning) demonstrates that interactive synchrony also manifests as interpersonal synchronization of brain activities (Dumas et al., 2011; Hasson et al., 2012). This interpersonal neural synchrony (INS) is thought to facilitate turn-taking interactions (Wilson and Wilson, 2005) and interpersonal transmission of in-

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formation through verbal and non-verbal communication (Dumas et al., 2011; Hasson et al., 2012). A facilitative function of touch for INS was highlighted by a recent study showing that handholding in adults increases INS (Goldstein et al., 2018). INS has been mainly identified in brain regions associated with socio-cognitive processes (Gvirts and Perlmutter, 2020; Hoehl et al., 2020; Koban et al., 2019; Redcay and Schilbach, 2019), including mutual attention, prediction (prefrontal cortex), affect sharing (inferior frontal gyrus), mentalizing and shared intentions (temporo-parietal junction).

By contrast, the neural mechanisms of social exchanges in early child development are still poorly understood as few developmental hyperscanning studies exist to date. The emerging evidence demonstrates that adults and children synchronize their brain activities to a greater degree in interactive contexts that require mutual engagement than when solving the same tasks individually or when interacting with a third person (Nguyen et al., 2020, 2021; Piazza et al., 2020). Importantly, behavioral indicators of high mutual attunement, such as reciprocity and eye contact were linked with heightened levels of INS. These studies suggest that INS could be a sensitive biomarker for successful attunement between caregivers and their infants. However, social touch has not yet been considered in caregiver-infant neural synchronization.

Synchronous interactions on the behavioral level have also been linked to physiological synchronization (IPS). Respiratory sinus arrhythmia (RSA) is an index of the functioning of the vagal system. The regulation of the vagal system allows us to adapt to our ever-changing social environments (Porges, 2007). The attunement of cardio-respiratory rhythms between mother and child emerges very early in life and is suggested to function as a scaffold for infants' still immature physiological systems (Abney et al., 2021a; Feldman et al., 2011). The coupling of physiological states thereby supports the development of infants' self-regulation and various other neurobehavioral and physiological functions (Atzil et al., 2018). Overall, the importance of infant-parent RSA co-regulation for properties and outcomes of social interaction like emotion regulation and distress provides the basis for why we focus on the physiological measure in the current study.

Research on early IPS underscores that physiological alignment occurs under conditions of mutual engagement and decreases when interacting partners disengage (Feldman et al., 2011). More specifically, IPS seems to emerge after instances of infants showing high arousal and negative affect in daily life (Wass et al., 2019). After a negative affect manipulation, 12–14 month-old infants displayed IPS with their mothers when the infant was seated on the mother's lap in comparison to a no-touch condition (Waters et al., 2017). Though preliminary, findings speak to a potential role of touch in affect contagion through physiology. Across development, there is growing evidence pointing towards the role of touch in IPS (Goldstein et al., 2017; Van Puyvelde et al., 2015). Yet, a systematic investigation of the role of spontaneous maternal touch on IPS during a naturalistic interaction with the infant is still lacking.

This study integrates the concurrent assessment of INS and IPS in a multi-level hyperscanning paradigm with mother-infant dyads naturally interacting with each other. We tested whether attunement through proximity and touch between the dyad is associated with INS and IPS. INS was assessed in 4- to 6-month-old infants and their primary caregivers by using dual-functional near-infrared spectroscopy (dual-fNIRS). As aforementioned, social interactions at this age provide a unique opportunity to study infants' social capacities to synchronize with their caregivers (Beebe et al., 2010). Importantly, we limited the age range to 6 months of age, as by then the primacy of face-to-face exchanges tends to decrease as infants begin to increasingly explore physical objects (Jaffe et al., 2001). We focused on prefrontal and inferior frontal regions. Synchronization in these regions is suggested to mark mutual attention and shared affect, which are critical processes to infants' interactions with their caregivers (Feldman, 2017). We further assessed IPS through electrocardiography (ECG) and coded the dyad's behavior from video recordings.

According to our pre-registered hypotheses, we expected caregiver-infant dyads to show increased INS and IPS during phases of high, experimentally manipulated physical proximity between mother and infant. We contrasted the dyads' INS and IPS during a distal joint watching condition to a proximal joint watching condition while caregiver and infant were attending to the same video. Subsequently, we assessed whether spontaneous use of maternal touch during a face-to-face interaction was related to differences in INS and IPS. We hypothesized that increased durations of social touch would be associated with increased INS and IPS. Additionally, we studied infants' affect in relation to INS and IPS and examined potential links between INS and IPS in the mother-infant dyad.

2. Material and methods

2.1. Participants

Overall, 81 mother-infant dyads participated in the present study and were recruited from a database of volunteers. Out of those dyads, 72 completed the experiment, while the procedure was incomplete for 9 dyads due to fussiness (infants started to cry during the preparation phase or before the end of the experiment), and sleepiness. Due to the novel paradigm and lack of effect sizes, we aimed for a final sample size of 50 infants and oversampled for expected attrition rates (~30%). Infants' age ranged from 4–6-months-old (*M*=4.7 months; *SD*=16 days; 33 girls). Infants were born healthy and at term, with a gestation period of at least 36 weeks. Mothers' age averaged 33.97 years (*SD*=4.94) and 57% of mothers had a university degree. All dyads were of White European origin and came from middle to upper-class families based on parental education. All infants and mothers had no neurological problems as assessed by maternal reports. The study was approved by the local ethics committee. Parents provided written informed consent on behalf of their infants and themselves. Participation was remunerated.

2.2. Experimental procedure

During the experiment, caregiver and infant were either seated next to one another or the infant sat on the caregiver's lap while watching a calm aquarium video on a tablet (distal watching and proximal watching conditions; see Fig. 1). The videos lasted 90 sec. and depicted fish swimming in a tank. The order of the watching conditions was counterbalanced. Next, mother and infant engaged for 5 min. in free play without toys and song while both were seated face-to-face (interactive free play condition). Neural activity in the mother-infant dyad was simultaneously measured with fNIRS. We assessed RSA through ECG and each dyad was filmed by three cameras (angled towards the dyad, the infant, and the mother) throughout the experiment.

2.3. Data acquisition and processing

2.3.1. fNIRS recordings

We used two NIRSport 8-8 (NIRx Medizintechnik GmbH, Germany) devices to simultaneously record oxy-hemoglobin (HbO) and deoxy-hemoglobin (HbR) concentration changes in mother and infant. The 8 × 2 probe sets were attached to an EEG cap with a 10-20 configuration (Fig. S1). The probe sets over the left and right inferior frontal gyrus (IFG) surrounded F7 and F8, whereas the probes on the medial prefrontal area (mPFC) surrounded FP1 and FP2. These regions of interest were based on previous work involving adult-child interactions (Nguyen et al., 2020; Piazza et al., 2020; Redcay and Schilbach, 2019). In each probe set, 8 sources and 8 detectors were positioned, which resulted in 22 measurement channels with equal distances of ~2.3 cm between the infants' optodes and 3 cm between the mothers' optodes. The absorption of near-infrared light was measured at the wavelengths of 760 and 850 mm and the sampling frequency was 7.81 Hz. fNIRS measurements were processed using MATLAB-based functions derived

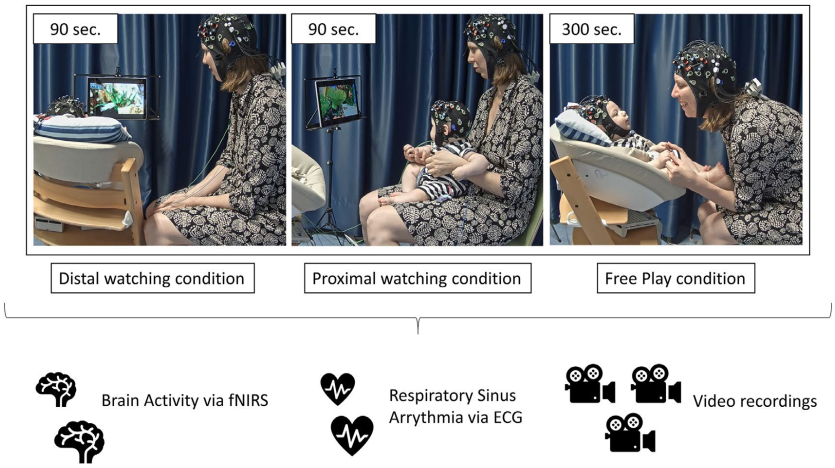

Fig. 1. An exemplary mother-infant dyad during the joint watching conditions with and without physical contact (90 s) and the free play interaction condition (300 s) (from left to right). Throughout the experiment, we simultaneously measured brain activity via functional near-infrared spectroscopy (fNIRS), respiratory sinus arrhythmia (RSA) via electrocardiography (ECG) and subsequently coded the dyads behavior through video recordings. The three cameras were facing the infant, the mother, and the dyad, respectively.

from Homer 2 (Huppert et al., 2009). Raw data was converted into optical density. Next, optical density data were motion-corrected with a wavelet-based algorithm with an interquartile range of 0.5. Motion-corrected time series were further visually inspected during a quality check procedure. Before continuing, 22.87% of the channels from both mother and child were removed from further analyses due to bad signal-to-noise ratio and motion artifacts. Then slow drifts and physiological noise were removed from the signals using a band-pass second-order Butterworth filter with cutoffs of 0.01 and 0.5 Hz. The filtered data were converted to changes (μMol) in oxygenated (HbO) and deoxygenated hemoglobin (HbR) based on the modified Beer-Lambert Law. For later analyses, both HbO and HbR synchrony are reported.

2.3.2. *Electrocardiography (ECG) recordings*

We made use of a Brain-Amp system (Brain Products GmbH, Germany) with two amplifiers to measure two standard single-channel ECG registrations (lead II derivation). One electrode was placed on the upper right chest, one on the left side of the abdomen, and the grounding electrode was placed on the right side of the abdomen on both infant and mother. The ECG signal was recorded with a 500 Hz sampling frequency.

Interbeat-intervals (IBIs) were extracted offline using ARTiiFACT (Kaufmann et al., 2011). The ECG data were visually inspected for (in)correct detections and artifacts by trained research assistants. When ectopic beats or erroneous detections were found, the data were manually corrected (removal of erroneous detection/artifact followed by a cubic spline interpolation; corrections < 1%). Next, IBIs were downsampled to 5 Hz and a 51-point band-pass local cubic filter was used to estimate and remove the slow periodic and aperiodic components of the time-series. A FIRtype bandpass filter was applied to further isolate the variance in the IBI series to only the frequency range of spontaneous breathing for infants (0.3-1.3 Hz) and adults (0.12–1.0 Hz). The range for mothers' respiration was expanded from its typical value of 0.4 to 1.0 to account for the infrequent occurrence of faster breathing during talking or playing segments so that the same filter could be used for all mothers in all conditions. The Porges and Bohrer (1990) technique for RSA magnitude estimation includes parsing this component signal into discrete epochs (lasting 10 to 120 sec), then calculating the natural log of the variance in each epoch. RSA is reported in units of $\ln(ms)^2$. In order to collect a more continuous measure of RSA, a sliding window of 15 s was used to extract a continuous (updated every 200 ms) estimate of cardiac vagal tone for both participants. The estimated RSA value corresponded to the first value of the sliding window (see Abney et al., 2021b for detailed information).

2.3.3. *Synchrony estimation*

We used Wavelet Transform Coherence (WTC) and Cross-Recurrence Quantification Analyses (CRQA) to estimate INS and IPS, respectively. WTC and CRQA are non-linear approaches to estimate synchrony in two non-stationary time-series, as we cannot assume stationarity for HbO, HbR and RSA time-series. Both methods allow the quantification of dynamical systems and their trajectories. Utilizing these methods, we are able to capture many properties of the neural and physiological dynamics that would otherwise be lost due to averaging with more traditional correlation analysis.

We assessed the relation between the fNIRS time series in each caregiver and infant using Morlet WTC as a function of frequency and time (Grinsted et al., 2004). WTC is more suitable in comparison to correlational approaches, as it is invariant to interregional differences in the hemodynamic response function (HRF) (Sun et al., 2004). Correlations, on the other hand, are sensitive to the shape of the HRF, which is assumed to be different between individuals (especially of different ages) as well as different brain areas. Moreover, a high correlation may be observed among regions that have no blood flow fluctuations. In previous hyperscanning research in both adults and children, the analyses have shown that synchronization occurs in different frequency bands (Cui et al., 2012; Jiang et al., 2012; Zhao et al., 2021). For the current study, we knew little about the relevant frequency bands (especially in parent-infant interactions), and thus we determined the frequency band after we estimated the coherence between mother and infant. Accordingly, based on previous studies (Nguyen et al., 2020, 2021), visual inspection, and spectral analyses, the frequency band of 0.012 Hz – 0.312 Hz (corresponding to 8–32 s) was identified as the frequency-band of interest. Average coherence (INS) was then calculated for the distal watching condition, the joint watching condition, and the interactive free play condition in each channel, which resulted in 3 (conditions) x

22 (channels) coherence values for each dyad. To ensure that the different durations between the first two and last conditions did not confound coherence values, we also estimated WTC in 90 s epochs in the free play condition, and subsequently compared the values to the joint watching conditions while controlling for duration. The results are described in the Supplement S1.

To examine IPS, we used cross-recurrence quantification analysis (CRQA) (Coco and Dale, 2014) to identify coupling between mothers' and infants' RSA time-series. CRQA is a nonlinear method for analyzing shared dynamics between two different data series and has been applied successfully to investigate cardio-respiratory dynamics (Konvalinka et al., 2011). The method is especially suitable for RSA synchrony estimations, as RSA is an estimate derived from a specific frequency band in IBIs, this renders RSA synchrony calculations unsuitable for measures of coherence. The metric we used to evaluate the RSA time-series is %DETerminism (%DET). %DET quantifies the predictability of the time-series and is calculated as the percentage of recurrent points that form diagonal lines in a recurrence plot (i.e., which are parallel to the central diagonal). Higher determinism with the same amount of recurrence implies stronger coupling. For this analysis, the recurrence rate was fixed at 2% to be able to compare CRQA estimates across conditions. We used the function optimizeParam to estimate the parameters for radius, embedding dimension(s) and delay, which resulted in radius=0.02, emb=1 and delay=16.

We also estimated the lag-0 cross-correlation between mothers' and infants' fNIRS as well as detrended RSA time series. Results for cross-correlation of HbO, HbR and RSA time-series are detailed in the supplements.

2.4. Behavioral coding

To assess maternal touch, infants' affect, and infants' gaze during the watching conditions (adapted from Feldman et al. 2011), trained graduate students coded video recordings of the free-play sessions using Mangold INTERACT. The experimental sessions were filmed at 25 frames per second. Maternal touching behavior, infants' facial affect, and gaze were micro-analyzed frame-by-frame for duration and frequency. For social touch coding, we differentiated between periods of touch and no-touch (i.e., no physical contact). Within periods of touch, segments were coded for active, passive, or functional maternal touch. Segments of active touch were subsequently divided into the two categories of affectionate and stimulating touch. For infants' facial affect, we distinguished between positive, negative, and neutral facial expressions. For infants' gaze during watching conditions, gaze directions were differentiated between gaze to screen, gaze to mother, gaze away (refer to Table S1 for a full description of coding categories and S3 for gaze analysis). To establish inter-rater reliability, 25% of randomly chosen videos were coded by two trained coders. Inter-rater reliability was high to excellent, namely kappa=.79 for social touch, kappa=.81 for facial affect and kappa=.92 for infants' gaze in watching conditions.

2.5. Statistical analysis

All statistical analyses were calculated in RStudio (RStudio Team, 2020). We used the function glmmTMB from the R package glmmTMB (Brooks et al., 2017). WTC values were entered as the dependent variable of the first Generalized Linear Mixed Model (GLMM) with condition (distal watching vs. proximate watching vs. free play) and ROI (IFG vs. lPFC vs. mPFC) as fixed factors with random slopes for each ROI and condition and random intercepts of dyads. %DET was entered into a second model with condition as a fixed factor and random slope as well as random intercepts for dyads. As both WTC and %DET values are bound by 0 and 1, we assumed a beta distribution in each model. To further examine significant effects, contrasts of factors were conducted by using post-hoc analyses (emmeans) with Tukey's Honest Significant Difference to correct for multiple

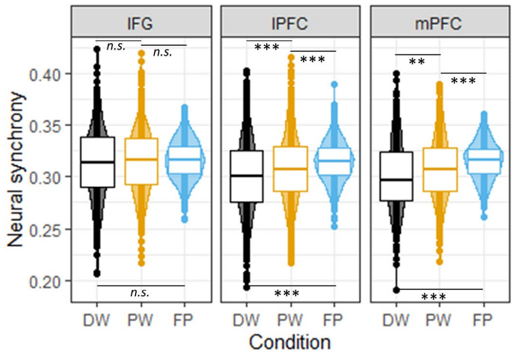

Fig. 2. Plot of the interaction effect of condition (x-Axis) and region (facets) for INS. Neural synchrony (y-Axis) during free play (FP) was significantly higher than during distal (DW) and proximal joint watching (PW) phases in lateral (lPFC) and medial prefrontal areas (mPFC), but not in the inferior frontal gyrus (IFG). Neural synchrony during proximate joint watching was higher than during distant joint watching. n.s.= non-significant, **= p<.010, ***= p<.001.

comparisons. All continuous predictor variables were z-standardized, and distributions of residuals were visually inspected for each model. Models were estimated using Maximum Likelihood. Model fit was compared using a Chi-Square Test (likelihood ratio test; Dobson, 2002).

To test for spurious correlations in both neural and physiological synchrony, we conducted bootstrapped random pair analyses (Nguyen et al., 2020; Piazza et al., 2020). Mother's original data was randomly paired with infant data out of the sample for 1,000 permutations. WTC and %DET were calculated for each random pair. Subsequently, the average of coherence or correlation between random pairs was computed and compared against original pairs using GLMM and post-hoc contrasts (see S1, S2 for details).

Next, we used two different statistical approaches to assess the association between touch and INS and IPS. INS necessitated GLMM to account for the repeated measures (channels/regions) which are nested in each dyad. IPS in the free play condition, on the other hand, was one measure per dyad, therefore we used a linear regression to test the relation of IPS and touch.

3. Results

3.1. Interpersonal neural synchrony

First, we tested INS (estimated with WTC) in HbO concentration changes in the three experimental conditions: the distal joint watching condition vs. the proximal joint watching condition and the interactive free play condition. WTC was entered as the response variable in the GLMM, while condition and region of interest were entered as fixed and interaction effects. We assumed a random slope for all fixed and interaction effects with random intercepts for each dyad (N=69). Three dyads had no fNIRS recordings due to technical problems with the devices. The results revealed that the fixed effects for condition, $\chi^2(2)=39.91$, $p<.001$, and region, $\chi^2(4)=33.32$, $p<.001$, as well as their interaction were significant, $\chi^2(8)=25.15$, $p=.001$. Comparisons (using emmeans) across conditions revealed increased INS during free play and proximal watching in comparison to distal watching that were detected in bilateral lPFC and mPFC, $t>3.10$, $p<.005$. The free play condition and proximal watching condition differed in synchronization in the right lPFC and mPFC with higher INS during free play, $t>3.06$, $p<.006$. None of the conditions differed in INS in bilateral inferior frontal gyri, $p>.071$. The results are depicted in Fig. 2. We were able to replicate the main

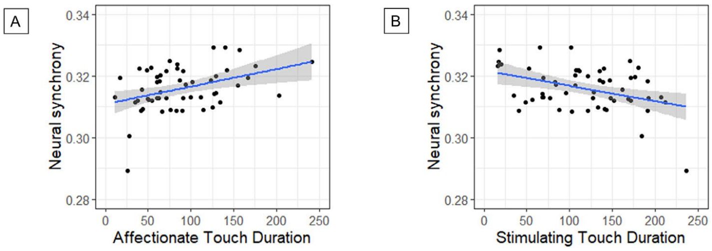

Fig. 3. Graphs depict (A) the positive correlation between durations of affectionate touch (x-Axis) and (B) the negative correlation between durations of stimulating touch (x-Axis) and neural synchrony (y-Axis) during the free play condition. Each dot represents a dyad.

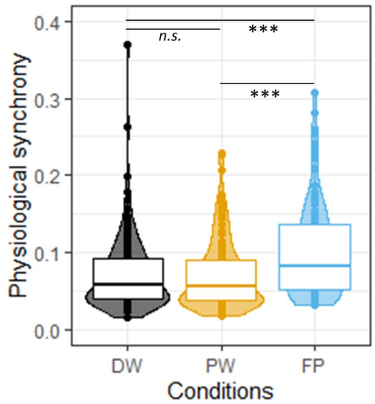

Fig. 4. Physiological synchrony (y-Axis) during free play (FP) was significantly higher than during distal (DW) and proximal joint watching (PW) phases (x-Axis). n.s.= non-significant, ***= *p*<.001.

results we found for INS in HbO with HbR and also when including equivalent epochs (90 s) in all three experimental conditions (see S1).

Next, we tested whether variation in social touch relates to variation in INS with a GLMM. WTC values from the free play condition were tested as the response variable. Affectionate touch, stimulating touch, passive touch, and functional touch durations were included as fixed effect variables. The results revealed a significant effect of affectionate touch, $\chi^2(1)=4.13$, *p*=.042 (Fig. 3A), and stimulating touch durations, $\chi^2(1)=6.24$, p=.012 (Fig. 3B). The model estimates show that longer durations of affectionate touch were related to higher INS, estimate=-0.079, SE=0.031, 95% CI=[0.002 0.107], whereas longer durations of stimulating touches were related to lower INS, estimate=0.055, SE=0.026, 95% CI=[-0.140 -0.018]. Fixed effects for passive touch and functional touch durations were non-significant, *p*>.122.

3.2. Interpersonal physiological synchrony

IPS between mother and infant were compared in the three experimental conditions with %DET of detrended RSA values as the response variable. Condition was entered as a fixed effect, and random intercepts for dyads were included (N=67). Five dyads were excluded due to technical problems or noisy data for which R-peaks could not be detected. The findings revealed a significant fixed effect of condition, $\chi^2(2)=34.62$, *p*<.001 (Fig. 4). Post-hoc contrasts between the conditions revealed that IPS in the free play condition was significantly higher than in the distal watching condition, *t*=5.23, *p*<.001, and the proximal watching condition, *t*=4.99, *p*<.001. IPS in the joint watching conditions did not differ from one another, *p*=.978.

Next, we tested the association between social touch and IPS with a linear regression analysis; %DET (Fisher Z-transformed) was the outcome variable. Affectionate touch, stimulating touch, passive touch and functional touch durations were included as predictor variables. While affectionate, stimulating and passive touch durations were not related to IPS, *p*>.520, functional touch durations were marginally positively associated with IPS, *β*=0.571, *SE*=0.237, *95% CI*=[0.091 1.051], *t*=2.48, *p*=.084.

3.3. Relation between INS and IPS

We assessed a potential relation between INS and IPS (both scores were averaged over each condition). HbO WTC values were entered as the response variable into the GLMM. Condition, %DET and region of interest were entered as fixed and interaction effects. We assumed a random slope for all fixed and interaction effects with random intercepts for each dyad. The results revealed no significant effect of IPS nor its interaction with conditions and/or region of interest in the brain on INS in HbO, *p*>.136.

3.4. Supplementary analyses

Supplementary analyses of the results showed no difference in infants' gaze duration towards the screen between the two joint watching conditions. We also examined the role of infants' affect to shed light on the affective context of the interaction. Overall, we find higher IPS in mother-infant dyads, but not INS, to be associated with higher infant negative affect and lower infant positive affect durations. These results are fully reported in the supplement.

4. Discussion

We tested the relation between mother-infant proximity and social touch and INS and IPS in three naturalistic experimental conditions with varying physical proximity and mutual engagement. Dyads displayed increased INS in bilateral lPFC and mPFC during proximity with spontaneously occurring affectionate touch. While attending to one another mother and infant showed alignment in their prefrontal brain activations, most prominently in the face-to-face interaction. Activation in the PFC is associated with the detection of communicative signals directed toward the self, mentalizing, and reward, all processes which are implicated in mutually engaged interactions (Redcay and Schilbach, 2019). Interestingly, INS in bilateral IFG did not differ between conditions and was not related to assessed behavioral correlates. IPS, on the other hand, was neither related to proximity nor spontaneous touching behavior of the mother during free play. Our findings indicate that INS in the prefrontal cortex and IPS arise in similar contexts, i.e., during mutual engagement of the mother-infant dyad, but diverge in their functionality, as they seem to be driven by different processes.

We directly contrasted the same joint watching conditions, while the proximity of mother and infant was experimentally manipulated. Joint watching of a calm video was associated with higher INS when the infant was seated on the mother's lap instead of next to her. Physical contact allows for multi-modal stimulation and enhances caregiver responsiveness to infants (Fairhurst et al., 2014). The micro-adjustments of bodily contact and the perception of heart rhythms and respiration may have been reciprocally related to neural synchronization during this condition. Holding the infant could additionally be related to the activation of specific sensory nerve fibers through pleasant deep pressure (Case et al., 2020). We controlled for infant's attention towards the visual stimuli (see S3), which was not different between both watching conditions. Our finding implies that proximity allows the caregiver to co-regulate their infant even when their attention is directed away from the infant, potentially preparing them for exploration or learning opportunities (Fairhurst et al., 2014).

In the free play condition, communicative signals are visibly exchanged between caregiver and child (Wass et al., 2020). Here, we identified social touch as one of the communicative signals related to INS. Specifically, affectionate touch was related to higher INS in mother-infant dyads and could serve as a parental ostensive cue (next to gaze and infant-directed speech) that entrains the infant to the ongoing pattern of early social communication (Wass et al., 2020). By eliciting infant attention, affectionate touch might help mother and infant to establish and maintain engagement with one another (Della Longa et al., 2019; Stack and Muir, 1992). The newly revealed link between affectionate touch and INS thus supports the notion that INS might be a biomarker for interaction quality. Interestingly, we find a negative association between stimulating touch and INS. These results tie in with research underlining diverging functions to different touch qualities (Mantis et al., 2019; Moreno et al., 2006). They indicate that stimulating touch, as a feature of intrusive maternal behavior, might actually be disruptive to the interaction and thus be related to lower INS (Field, 2010). Overall, the involvement of social touch in INS highlights the importance of affectionate touch in early interactions, but also the need to investigate the different qualities of touch for child development outcomes.

In addition, we simultaneously examined IPS in mother-infant dyads. IPS was, however, not related to proximity during joint watching in the current study. Previous studies also showed that mother and infant show attenuated IPS in close contact later than 3 months of age due to the widening of infants' social orientation beyond the primary caregiver and increasing self-regulatory abilities (Van Puyvelde et al., 2015). When further probing IPS for behavioral correlates, maternal touch did not correlate with IPS between mother and infant. Instead, we find that higher IPS was associated with higher durations of infant negative affect and lower IPS was associated with higher durations of infant positive affect in the free play condition. As such, our results concur with the co-regulatory account of caregiver-infant IPS, namely its potential function to maintain allostasis (Atzil et al., 2018). The mother-infant dyads show greater physiological synchrony when co-regulation is needed, such as during infant distress marked by negative affect (Abney et al., 2021a; Wass et al., 2019). Longer durations of infants' positive affect could have indicated that the infant was well regulated by herself. Still, more research is needed on the exact behavioral correlates of IPS to understand its functionality. For instance, considering leader-follower relations might provide further insights into IPS.

Probing the relation between INS and IPS in interactions between infants and their primary caregiver, we find both commonality and discrepancy. Passively viewing the same visual stimulation was related to lower levels of INS and IPS in comparison to a face-to-face interaction. Instead of merely reflecting common neural and physiological reactions towards the same perceptual stimulation, INS and IPS depend on the transmission of interactional signals through the environment, reflecting mutual engagement and quality of interaction (Koban et al., 2019). Though both INS and IPS were higher in the interactive than in the joint watching conditions, condition means of INS and IPS were not correlated. While INS was related to the communicative signals exchanged through touch, IPS was related to co-regulatory affective signals. This dissociation could stem from (1) the different approaches to calculate synchrony, but also suggests (2) the discrepant role of social touch for early social communication, as well as (3) a potential functional dissociation of INS and IPS. Future studies should therefore continue to combine neural and physiological assessments to dissociate the functionality of INS and IPS. Importantly, we know little about the *intraindividual* developmental trajectory of brain activation and RSA coupling (Beauchaine, 2015), which could inform *interindividual* coupling.

5. Conclusions and future directions

The present research is the first multi-level hyperscanning study on naturalistic mother-infant interactions with infants as young as 4 months of age. Caregiver-infant interactions between 4-6 months allow us a unique opportunity to examine infants' developing social capacities (Feldman et al., 1996; Stern, 1985; Tronick, 1989). Importantly, these interactions robustly predict later social and cognitive development (e.g., Beebe et al. 2010, Field 1995, Isabella and Belsky 1991). Our approach affords a holistic perspective on when and how mother and infant coordinate their neural, physiological, and behavioral responses. The results revealed that 4–6 month-old infants and their caregivers show INS associated with proximity and social touch. The link between touch and INS provides crucial new insights on the aspects of interaction quality that support caregiver-infant neural alignment. These findings pave the way for further research into the role of INS in facilitating the social bond between caregiver and child as well as the promotion of children's social learning (Atzil et al., 2018; Feldman, 2017). The relation between touch and INS has implications for clinical interventions comprising social touch, such as kangaroo care, and could shed light onto a potential neural mechanism for why close contact is beneficial for infant development (Hardin et al., 2020). Synchronization in close physical contact could also promote children's social learning just as it is suggested during social interactions (Piazza et al., 2021; Wass et al., 2020). It would be important to examine further outcome variables of learning during close contact and whether this relation is mediated by INS. IPS, on the other hand, was related to dyads' co-regulation when infants expressed negative affect. These first results on the different levels of synchrony pave the way toward the future examination of the coupling of brain activation and RSA, especially in infancy, to provide a deeper understanding of the link between body and brain (Beauchaine, 2015). Taken together, the present study highlights the exciting opportunities of multi-level hyperscanning to uncover neurobiological pathways of early social communication and to provide a deeper understanding of the link between body and brain in human development.

Data and code availability statement

MATLAB processing and RStudio analysis code are made publicly accessible on OSF: https://osf.io/59kds/. The conditions of our ethics approval do not permit public archiving of participant data. Readers seeking access to the data should contact the lead author Trinh Nguyen. Access will be granted to named individuals in accordance with ethical procedures governing the reuse of sensitive data. Specifically, requestors must meet the following conditions to obtain the data: completion of a formal data sharing agreement.

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Open practices

The study was formally preregistered on https://aspredicted.org/kw2wf.pdf. The preprint was made available at biorxiv (10.1101/2021.01.21.427664) under a CC-BY 4.0 International license.

Declaration of Competing Interest

The authors declare that there is no conflict of interest. The funders had no role in the conceptualization, design, data collection, analysis, decision to publish, or preparation of the manuscript.

Credit authorship contribution statement

Trinh Nguyen: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Project administration, Writing – original draft, Visualization. **Drew H. Abney:** Methodology, Software, Writing – review & editing. **Dina Salamander:** Investigation, Data curation, Project administration. **Bennett I. Bertenthal:** Methodology, Writing – review & editing. **Stefanie Hoehl:** Conceptualization, Methodology, Resources, Writing – original draft, Supervision, Funding acquisition.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2021.118599.

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Interpersonal Synchrony Special Issue

Neural synchrony in mother–child conversation: Exploring the role of conversation patterns

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Abstract

Conversations are an essential form of communication in daily family life. Specific patterns of caregiver–child conversations have been linked to children's socio-cognitive development and child-relationship quality beyond the immediate family environment. Recently, interpersonal neural synchronization has been proposed as a neural mechanism supporting conversation. Here, we present a functional near-infrared spectroscopy (fNIRS) hyperscanning study looking at the temporal dynamics of neural synchrony during mother–child conversation. Preschoolers (20 boys and 20 girls, *M* age 5;07 years) and their mothers (*M* age 36.37 years) were tested simultaneously with fNIRS hyperscanning while engaging in a free verbal conversation lasting for 4 min. Neural synchrony (using wavelet transform coherence analysis) was assessed over time. Furthermore, each conversational turn was coded for conversation patterns comprising turn-taking, relevance, contingency and intrusiveness. Results from linear mixed-effects modeling revealed that turn-taking, but not relevance, contingency or intrusiveness predicted neural synchronization during the conversation over time. Results are discussed to point out possible variables affecting parent–child conversation quality and the potential functional role of interpersonal neural synchronization for parent–child conversation.

Key words: turn-taking; mother–child interaction; functional near-infrared spectroscopy; neural synchrony; conversation; hyperscanning

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Introduction

Preschool age is a critical time for children as they start to expand their daily interactions with family members and establish peer relationships outside the immediate family context (Harrist and Waugh, 2002). In this transitional phase, communicative abilities play a crucial role. Although interpersonal synchronization processes have recently been functionally implicated in successful communication and information transfer between adults (e.g. Schippers *et al.*, 2010; Hasson *et al.*, 2012), we currently know little about their role in child development. Here, we explore whether variables related to conversation patterns are associated with interpersonal neural and behavioral synchronization between mothers and their preschool-age children.

The ability to engage in and uphold verbal conversations becomes more sophisticated as children acquire language and advance in their social and cognitive competencies during preschool years (Black and Logan, 1995). Conversations are a special form of speech exchange as they are 'managed by the participants, turn by turn, in terms of who speaks when, for how long and about what' (Wilson and Wilson, 2005). The coordination needed to engage in and maintain a conversation is highly complex and presupposes multifaceted social processes, such as joint social attention and temporal contiguity (Romeo *et al.*, 2018). Previous studies reported that if such communicative patterns are lacking during parent–child dyadic conversations—i.e. the dyad is unable to coordinate and does not exhibit verbal turn-taking—atypical language development and the risk for developmental disorders more generally may arise in children (Moseley, 1990; Malin *et al.*, 2011). Furthermore, intervention studies indicate that the promotion of turn-taking leads to higher quality social interactions (Stanton-Chapman and Snell, 2011). The neural mechanisms supporting such central qualities in parent–child interaction and especially conversation, however, have only been sparsely investigated so far (Nguyen *et al.*, 2020). We propose neural synchronization as a neurobiological underpinning to successful communication and particularly turn-taking during parent–child conversations.

Interpersonal neural synchrony

Communication between individuals, and more specifically turn-taking, has recently been linked to interpersonal neural synchronization (Stephens *et al.*, 2010; Hasson *et al.*, 2012). Interpersonal neural synchronization generally refers to the mutual temporal alignment of behavioral, neural and physiological activity (i.e. bio-behavioral synchrony) between two or more individuals (Hoehl, Fairhurst & Schirmer, in press). The neural aspect of interpersonal synchronization, in turn, is defined as the temporal coordination of concurrent rhythmic brain activities between individuals (Uhlhaas *et al.*, 2009). Finally, turn-taking involves a highly organized behavioral structure and timing that allows the speaker and listener to perceive and act upon cues provided during communication. For both conversation partners to adopt this kind of precision in mutual timing, Wilson and Wilson (2005) suggest that endogenous oscillators in the brain are involved. These neural oscillators are made of groups of neurons that collectively show periodic activity and are implicated in timing-related cognitive processes. During verbal communication, neural oscillators in one conversation partner both influence and adapt to the oscillators of the other partner(s) so that a dyad (or a larger group) can become mutually entrained based on each person's speech production (e.g. temporal regularities in syllabic and word boundaries). Entrainment of such cyclic behavior has also been shown in breathing patterns of conversation partners (McFarland, 2001). With the advancement of 'hyperscanning,' that is simultaneously measuring brain activity of two (or more) participants, neural synchrony has been proposed as evidence for the mutual alignment of endogenous neural oscillators during interpersonal communication (for reviews see Dumas *et al.*, 2011; Hasson *et al.*, 2012).

In adults, hyperscanning has been applied in dyadic and group conversation contexts (e.g. Jiang *et al.*, 2012, 2015, 2016; Spiegelhalder *et al.*, 2014; Nozawa *et al.*, 2016; Pérez *et al.*, 2019). In the study by Jiang *et al.* (2012), face-to-face dialogs were contrasted with face-to-face monologs and back-to-back dialogs and monologs. Their findings showed neural synchronization in the left inferior frontal cortex exclusively during face-to-face dialogs between dyads in comparison to all other conditions. These results first highlighted the importance of multi-sensory input during live social interactions for neural synchronization. Additional studies went on to identify factors facilitating neural synchronization during verbal communication, such as leader emergence (Jiang *et al.*, 2015), eye contact (Jiang *et al.*, 2016) and attention towards a speaker (Dai *et al.*, 2018). Whereas some researchers highlighted the role of turn-taking for information exchange and neural synchronization (Pérez *et al.*, 2019), others suggested that synchronized oscillatory patterns would underlie successful turn-taking (Wilson and Wilson, 2005). Although the above studies point towards a relationship between neural synchrony and turn-taking, the exact nature of the interaction between turn-taking and interpersonal neural synchrony is largely unknown.

A growing body of hyperscanning studies examining adult–child dyads focused on either task-based interaction (Reindl *et al.*, 2018; Miller *et al.*, 2019; Nguyen *et al.*, 2020) or free-play interactions with non-verbal infants (Piazza *et al.*, 2020). Due to the context provided by the tasks or the age of assessed children, mostly non-verbal factors associated with neural synchronization have been explored thus far. In two of the available studies, a more naturalistic interaction allowed the additional examination of interaction quality in association with neural synchrony (Quiñones-Camacho *et al.*, 2019; Nguyen *et al.*, 2020). The findings showed that in preschool child–parent dyads, behavioral reciprocity during joint problem solving was correlated with higher neural synchronization. Behavioral reciprocity may thus also play a role for interpersonal neural synchronization in parent–child verbal conversations. Yet, little is known about which verbal communicative patterns influence neural synchronization in parent–child conversations specifically.

Conversation patterns conducive to information exchange

Behavioral research suggests that interactions featuring contingent turn-taking and responsiveness are more effective for social learning (see, for example, Begus and Southgate, 2018). From infancy on, turn-taking in mother–infant 'proto-conversations' has been implicated in language processing and acquisition (Levinson, 2016). Turn-taking also gives way to coordination in behavior, particularly reciprocity (Leonardi *et al.*, 2016). As the child's sensitivity to vocal behavior grows, overlap of speech in dialog has been reported to be rather low and to even decrease over time. To uphold the chain of turns, both the quantity of contingent responses (Jaffe *et al.*, 2001) and the quality in terms of how a child is responded to appear to matter (Murray *et al.*, 2016). Furthermore, school-aged children not only talk in alternating turns but also participate in relevant and contingent discourses with their parents (Black and Logan, 1995). Interestingly, higher occurrences of these conversation patterns were linked to child likability among peers. This comes to show that parent–child communication patterns at preschool age may affect children's social competence beyond language learning (Levinson, 2016).

Temporal dynamics of interpersonal coordination

In general, there are many fluctuations throughout parent–child interactions as the dyad may not always interact in a coordinated manner (Tronick and Cohn, 1989). Research in healthy samples showed that mother–infant and mother–toddler interactions are composed of periods involving high occurrence of reciprocity, mutual gaze and/or affect mirroring, characteristic for high-interaction quality. Such periods were found to be interspersed with brief ruptures of miscoordination that were successfully repaired so that the dyad could return to a coordinative state. Critically, higher fluctuations in behavioral and physiological coordination have been associated with families at risk for child maltreatment (Skowron and Reinemann, 2005; Giuliano et al., 2015). Much less is known, however, regarding the exact temporal dynamics of interpersonal synchrony on a neural level in parent–child interactions, because most of the extant research has focused on averaged synchrony values over the whole length of given experimental conditions (e.g. Reindl et al., 2018). There is some available data from adult dyads by Mayseless et al. (2019), who examined the temporal dynamics of neural synchrony during a creative problem-solving task. They showed that neural synchrony decreased throughout the task and that such decrease in neural synchrony was linked to an increase in behavioral cooperation. These data show that neural synchrony may change over the course of a longer task and that such variation may associate with behavioral and/or communicative patterns—also during mother–child conversation. We thus argue that investigating dynamic changes of interpersonal neural synchrony in parent–child conversations will provide additional information towards generating a neurobiological model of parent–child interactions, as variations reflecting factors that affect neural synchrony might otherwise not be captured.

Current study

In the present study, we examined a free verbal conversation between mothers and their preschool children to identify conversation patterns associated with neural synchronization. We expected the naturalistic face-to-face situation to allow for dyadic differences in conversation patterns between mother and child dyads to emerge. Individual brain activity of mothers and children was simultaneously measured using functional near-infrared spectroscopy (fNIRS) by focusing on frontal and temporo-parietal regions and subsequently assessed for interpersonal temporal alignment (i.e. interpersonal neural synchrony) by means of wavelet transform coherence (WTC) analysis. Chosen regions of interest (ROIs) are known to be involved in social-cognitive processes during live interaction (Redcay and Schilbach, 2019) and have previously been shown to display increased neural synchronization during face-to-face conversation (Jiang et al., 2012).

We aimed to identify relevant conversation patterns, such as turn-taking, and to investigate their associations with interpersonal neural synchrony. Based on previous work (e.g. Jiang et al., 2012), we hypothesized that turn-taking would be positively associated with neural synchronization during mother–child verbal conversation. In addition, we were interested in the dynamic time-course of neural synchrony during the mother–child conversation. A finer resolution of the time dynamics of interpersonal neural synchrony during a conversation can add to the understanding of such complex social interactions. We, therefore, hypothesized that neural synchrony would change over time in association with the frequency of turn-taking shown during the mother–child conversation. When considering turn-taking features during verbal exchanges where intervals between turns mostly range from 200 to 700 ms (Gratier et al., 2015), it is reasonable to assume that intrusive and non-responsive behavior would relate to attenuated neural synchrony. Next to the hypothesized role of turn-taking for neural synchronization, we were probing the relation between conversational relevance as well as contingency and interpersonal neural synchronization, as these variables were shown to be related to turn-taking patterns (Fine, 1978).

Material and methods

Participants

Forty mothers (mean age 36.37 years; s.d. = 4.51 years; range = 28–47 years) and their preschool children (20 boys and 20 girls; mean age 5;07 years; s.d. = 0;04 years; range = 4;11–6;01) were included in the present study. Out of initially, 46 recruited mother–child pairs, six were excluded due to technical problems or self-reported tiredness/fussiness. All included dyads took part in the condition for the whole of the 4 min. Fifty-eight percent of mothers graduated with a university degree, while the remaining mothers graduated from vocational school. Each mother–child pair was biologically related. Participants were recruited from a pre-existing database of volunteers and mothers gave written informed consent for both themselves and their children before participating in the study. We screened for psychiatric/neurological disorders of mothers and children for developmental delay according to mother's self- and parent-report as part of their application to be included in the database. The study procedure was paused as soon as the child or the parent showed any sign of discomfort. Procedures were approved by the local ethics committee and participation was remunerated.

Experimental procedure

During the experiment, mothers and their children sat face-to-face (see Figure 1A), separated by a table. After performing two cooperative and two individual problem-solving task conditions in a naturalistic setting with a tangram puzzle (~12 min) that were unrelated to the present investigation (reported in Nguyen et al., 2020), mothers and children were instructed to engage in a free verbal conversation for 4 min. The instruction is detailed in the Supplementary Section S1. The complete procedure was video recorded from three different angles.

fNIRS data acquisition

We used a NIRScout 8-16 (NIRx Medizintechnik GmbH, Germany) Optical Topography system to record oxy-hemoglobin (HbO) and deoxy-hemoglobin (HbR) concentration changes for each participant. The four 2 x 2 probe sets were attached to an EEG cap with 10–20 configurations. The standard electrode locations allowed us to place the probes more precisely, as the probes over the left and right dorsolateral prefrontal cortex (dlPFC) surrounded AF3

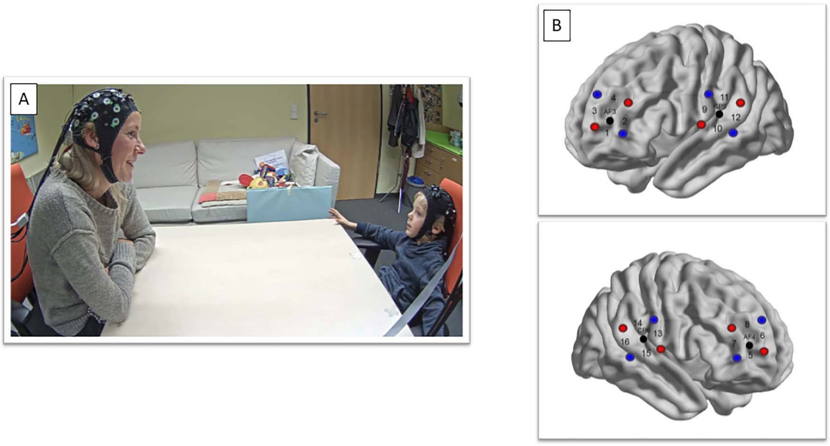

Fig. 1. (A) Study set-up during the free verbal conversation task. (B) Cap configuration. Red circles mark sources and blue circles mark detectors. Numbers (1–16) mark measurement channels between sources and detectors and black circles mark EEG 10–20 channel positions for orientation. The top graphic shows the left hemisphere and the bottom graphic shows the right hemisphere.

and AF4 and the probes on the left and right temporo-parietal junction (TPJ) surrounded CP5 and CP6 (see Figure 1). ROIs were based on previous fNIRS hyperscanning work involving verbal communication (Jiang *et al.*, 2012, 2015). In each probe set, eight sources and eight detectors were positioned, which resulted in 16 measurement channels with equal distances of 3 cm between the optodes per participant. The absorption of near-infrared light was measured at the wavelengths of 760 and 850 mm and the sampling frequency was 7.81 Hz.

fNIRS data analysis

Data were pre-processed using MATLAB-based functions derived from Homer2 (Huppert *et al.*, 2009). Raw optical density data were motion-corrected with a wavelet-based algorithm (Molavi and Dumont, 2012). Corrected data were then visually inspected during an initial quality check procedure. All channels that did not show a clear heart band were removed, which resulted in 93.4% of the channels to be included in further analyses. Data were then band-pass filtered with low- and high-pass parameters of 0.5 and 0.01 using a second-order Butterworth filter with a slope of 12 dB per octave (Baker *et al.*, 2016). Next, the filtered data were converted to HbO and HbR values based on modified Beer-Lambert Law with differential path length factors of 6 for adults and 5.5 for children. Based on previous hyperscanning studies, statistical analyses were focused on HbO values, which were reported to be more sensitive to changes in the regional cerebral blood flow (Hoshi, 2007). However, all analyses were repeated for HbR values (reported in Supplementary Section S4).

Subsequently, neural synchrony was calculated with WTC analysis using the cross wavelet and wavelet coherence toolbox (for more information, see Grinsted *et al.*, 2004; Chang and Glover, 2010). WTC was used to assess the relation between the individual fNIRS time series in each dyad and each channel as a function of frequency and time. Based on earlier literature (e.g. Jiang *et al.*, 2015), visual inspection and spectral analyses

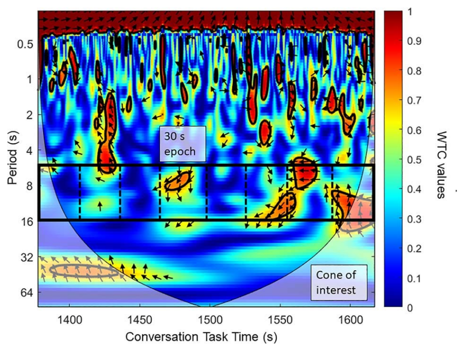

Fig. 2. WTC values were calculated by averaging over the frequency range of interest (6–16 period seconds—~0.06 Hz—0.15 Hz—on the y-axis) for the entire experimental procedure and epochs of 30 s over the 4 min of the conversation condition (indicated by one square along the x-axis [time in seconds]). Coherence values ranged from 0 to 1 (as indicated by the color bar) and all coherence values outside the cone of interest demarcation were excluded from analyses.

identified the frequency band of 0.06–0.15 Hz (corresponding to ~6–16 s) as related to the free verbal conversation. This frequency band did not comprise high- and low-frequency noise—such as respiration (~0.2–0.3 Hz) and cardiac pulsation (~1 Hz). Furthermore, coherence values outside the cone of influence were excluded in the WTC analysis. Average neural coherence (i.e. neural synchrony) was then calculated for 30-s epochs in each channel, which resulted in 8 (epochs) × 16 (channels) coherence values for each dyad (see Figure 2). Epoch length was defined by the minimal time needed to estimate an appropriate coherence value for the indicated frequency range.

Table 1. Conversation patterns divided into categories, sub-categories, examples and inter-rater reliability

Category	Sub-category	Example	ICC
Turn-taking	Alternating turns: An utterance follows a turn by the other speaker	Child: 'It was such a fun game' Mother: 'Yes, what shape did you like building the most?'	0.90
	Long turns: One speaker follows up with another utterance after an utterance	Child: 'It was such a fun game. There were all these shapes and colors and I couldn't decide what to begin with.'	0.70
Relevance	Relevant turns: The utterance shares the thematic content with the preceding initiation or response	Child: 'I liked the rocket the most' Mother: 'Me, too. The rocket had an interesting shape'	0.92
	Irrelevant turns: The utterance lacks shared thematic content with the preceding utterance	Child: 'I liked the rocket the most'; Mother: 'The world map is so colorful'	0.81
Contingency	Contingent utterances: A turn provides the requested information to the previous utterance or the conversation partner performs requested activity	Mother: 'Do you want to start with the puzzle?' Child: 'Ok' and both start to play	0.99
	Noncontingent utterances: A speaker fails to respond to the previous request or question	Mother: 'Do you want to start with the puzzle?' Child: 'I don't know where this shape has to go.'	0.81
Intrusiveness	Turns that fail to leave time for a response: A speaker makes a request and fails to leave time for the other person to respond	Mother: 'Do you want to play with the puzzle? Oh, are you looking forward to this weekend?'	0.79
	Turns that interrupt: A speaker begins a turn before the other person has finished his or her turn	Mother: 'We can start with -?'; Child: 'I really like this shape'	0.96
	Simultaneous turns: Two speakers attempt to speak at the same time	-	0.72

Communication pattern coding

Communication codes were adapted from Black and Logan (1995). This involved coding of communicative reciprocity of mother–child dyads (operationalized through turn-taking), the thematic fit of the utterance (relevance), responding to questions or requests (contingency), and interruptions, overlaps, as well as intrusiveness (as further described in Table 1). Utterances were coded in Mangold INTERACT by trained graduate students. Utterances were chunked into turns that were defined as 'one person's speech bounded by pauses or by the speech of another person' (Garvey and Kramer, 1989) and transition between turns marked by minimal gaps (ranging from a few milliseconds to 3000 ms) and minimal overlap (Gratier *et al.*, 2015). Twenty percent of conversations were double coded by two graduate students and inter-rater reliability was calculated by intraclass correlations (ICC) for each communication code. ICC ranged between 0.70 and 0.99 and averaged at 0.84, therefore showing high reliability between coders. A score for each category was then calculated by building a composite score of relevant subcategories, which were all equally weighted. This approach in data reduction resulted in one value each for turn-taking, relevance, contingency and intrusiveness per dyad.

Turn and overlap duration coding

Next to the coding of communication features, we assessed turn and overlap duration between utterances. Turn duration was assessed by pauses indicating switches between speakers that ranged from <50 ms to a maximum duration of 3000 ms. Whenever one interaction partner vocalized over the other partner, an overlap for the duration was coded. Twenty percent of conversations were double coded by two graduate students and inter-rater reliability was calculated with weighted kappa. Kappa for turn and overlap duration ranged between 0.81 and 0.97 and averaged at 0.91, therefore showing very high reliability between coders.

Statistical analysis

Generalized linear mixed models (GLMMs) were fitted with the package 'glmmTMB' (Magnusson *et al.*, 2017) extended by custom functions (personal communication with Mundry, 2018) in R Studio (RStudio Team, 2015). For neural synchrony analyses, WTC values were entered as the response variable assuming a beta distribution (because all values of a beta distribution are bound between 0 and 1, such as the values of the WTC). All continuous predictor variables were z-standardized, and distribution of residuals was visually inspected for each model. Models were estimated using maximum likelihood. Model fit was compared using a likelihood ratio test (Dobson, 2002). To further test significant interaction effects, the function 'emtrends' from the package 'emmeans' (Lenth, 2019) was used.

Instead of including ROIs as a fixed effect predictor in the above-mentioned GLMMs, separate models for each region of interest were conducted, which are reported in the Supplementary Section S3. This approach was chosen because optical properties in different regions are suggested to vary systematically and therefore introduce a bias in the analysis. A full random effects structure for all models was assumed and thus random intercepts for dyad, and a random slope for each added fixed and interaction effect were included. The correlation of the random slopes with the random intercept for dyads was removed (as indicated by || in the model formulae in Supplementary Table S2) to help with convergence issues. The resulting random effects structure is shown in the model formulae. All model outcomes for models 1–7 can be found in Supplementary Table S2.

To rule out effects due to spurious correlation, we conducted a random pair analysis (Leong *et al.*, 2017; Piazza *et al.*, 2020). For each original mother–child pair, fNIRS time-courses of children were paired with time-courses of 1000 random mothers. Again, the WTC means were obtained across eight 30 s epochs and the frequency band of interest for each channel (8 epochs × 16 coherence values × 1000 random pairs). Coherence values of original dyads were then tested against the average of randomized pair coherences (considered a threshold for significant synchronization) in each ROI and over time by comparing coherence values using GLMM (see Supplementary Section S3 for separate GLMM in each ROI). This control procedure was repeated using phase randomization as a stricter control analysis (see Supplementary Section S2).

Results

In the present study, we investigated whether mother–child dyads show neural synchronization in temporo-parietal and dorsolateral areas when the dyads engage in a free verbal conversation. Furthermore, we explored the temporal dynamics of neural synchronization throughout the observation and particularly whether certain conversation patterns are associated with increases or decreases in neural synchronization. Specifically, we probed the role of turn-taking, relevance, and intrusiveness for interpersonal neural synchrony in mother–child conversations.

Neural synchrony during conversation

First, we conducted control analyses to determine whether mothers and their children showed higher neural synchronization during the conversation in comparison to randomly paired surrogate dyads (random-pair analysis). WTC was entered as the response variable and the random intercept of each child (indicated by the variable ID) was included in the null model. We assumed dependency between original and random pairs of children and mothers, even though it is important to note, that original and random pairs are neither fully dependent nor independent. In line with previous results in adult–child dyads (Leong *et al.*, 2017), original mother–child dyads showed increased neural synchronization, M(s.d.) = 0.322(0.002), in comparison to neural synchrony values of randomly paired dyads, M(s.d.) = 0.315(0.002), as adding the fixed effect and random slope of pairing resulted in a significant improvement of model fit, $\chi^2(3) = 19.71$, $P < 0.001$. Next, we assessed how neural synchrony of original and random dyads behaved over time. When adding the fixed effect and random slope of time in each dyad, the model fit improved significantly, $\chi^2(3) = 23.56$, $P < 0.001$. Neural synchrony changed in both original and random pairings over time. The next model further included the interaction effect between pairing and time, as well as the random slope of the interaction and shows that the dynamic changes of neural synchrony over time differ in original and random pairings, $\chi^2(3) = 16.12$, $P < 0.001$. Comparing the trend in the change of the original coherence (trend = 0.006, SE = 0.003, 95% CI = [−0.004 0.017]) over time to the change in the random coherence (trend = −0.007, SE = 0.003, 95% CI = [−0.010–0.002]), showed that while original neural synchrony increased over time, random neural synchrony decreased over time. To conclude, original pairs not only showed significantly higher neural synchrony than random pairs, but also showed a positive, instead of a negative trajectory over the course of the conversation.

Next, we examined the role of turn-taking in neural synchronization over the 4 min of free verbal conversation. The null model comprised WTC as the dependent variable and a random intercept for each dyad. To test for the main effect of turn-taking, we first entered verbal turn-taking as a fixed-effect predictor and a random slope (Model 1). Model 1 showed improved model fit in comparison to the null model und thus depicts that turn-taking patterns were significantly related to interpersonal neural synchrony during the conversation, $\chi^2(2) = 6.83$, $P = 0.033$. Higher amounts of turn-taking were associated with higher neural synchronization between mother and child. When the fixed effect and random slope of time was added to the model (Model 2), the model fit improved significantly, $\chi^2(2) = 12.45$, $P = 0.006$. The estimates showed that the dyads seem to show increases in neural synchrony over time. Subsequently, we added the interaction effect as well as the random slope of the interaction between turn-taking and time (Model 3). The model fit improved significantly in comparison to Model 2, $\chi^2(2) = 19.54$, $P < 0.001$ (Figure 3). To further investigate the interaction effect between turn-taking and time, we went on to dichotomize our variable time into early epochs (1–4) and late epochs (5–8). Follow-up contrasts showed that the trend for turn-taking in later epochs, trend = 0.009, s.d. = 0.004, 95% CI = [0.008 0.069], was marginally higher than in earlier epochs, trend = 0.001, s.d. = 0.004, 95% CI = [−0.029 0.039]. Hence, there was an indication for higher turn-taking to relate to higher neural synchrony in later epochs. We then also split turn-taking into two groups (split by the median) to further contrast the high and low turn-taking groups in earlier and later epochs, respectively. Using emmeans and pairwise contrasts, we find that the group with higher amounts of turn-taking showed an increase in neural synchrony in later in comparison to earlier epochs, estimate = −0.017, s.d. = 0.006, 95% CI = [−0.031–0.002] (see Supplementary Figure S1). The group with lower amounts of turn-taking, however, showed no differences in neural synchrony between earlier and later epochs, estimate = −0.003, s.d. = 0.005, 95% CI = [−0.017 0.010]. The results thus underscore the association between high amounts of turn-taking and increases in neural synchrony over the course of the conversation, while less turn-taking was associated with no significant changes in levels of neural synchrony over time.

Next to turn-taking, we probed the association of neural synchrony and further conversation patterns. Hence, we added turn duration as a fixed effect and a random slope (Model 4) to previous fixed and random effects in Model 3, which did not improve the model fit, $P = 0.301$. Subsequently, relevance (Model 5), intrusiveness (Model 6) or contingency (Model 7) were all added as fixed effects and random slopes to Model 3, but did not significantly improve the model fit, $P = 0.417$, $P = 0.832$ and $P = 0.648$, respectively. Further information on linear mixed effect parameters is included in the supplements.

Discussion

Learning how to communicate is key to exchange information with other people and connect with them (Papousek and Papousek, 1992; McComb and Semple, 2005). In adults, successful communication is known to be related to interpersonal synchronization in brain activation (Stephens *et al.*, 2010). Here, we investigated how affiliated dyads—mothers and their children—communicate with each other and how their communicative patterns relate to synchronous brain activation patterns.

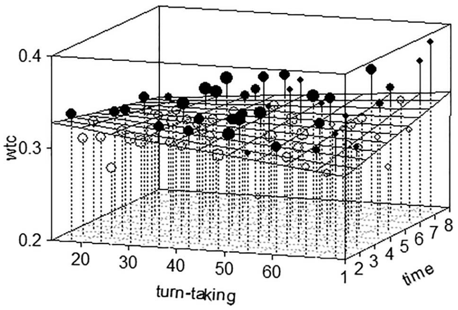

Fig. 3. 3D-plot depicting the interaction between the number of turns taken (*x*-axis) and time in epochs of 30 s (*z*-axis) on neural synchrony (WTC; *y*-axis). The horizontal plane depicts estimates of neural synchrony extracted from the linear mixed-effects modeling. Black and white dots show the observed value of each dyad in each channel either above their model estimate (black) or below their model estimate (white). Larger dots indicate that a higher number of observations were summarized within the dot, while smaller dots indicate fewer observations. Overall, the plot depicts that more turn-taking was linked to higher neural synchronization towards the end of the conversation.

We particularly focused on verbal turn-taking and showed that during this specific process of interpersonal coordination, a higher number of turns between mothers and children was related to higher neural synchrony in frontal and temporo-parietal areas (Meltzoff and Decety, 2003; Redcay and Schilbach, 2019), which increased over the course of the conversation. These results represent an essential step in understanding the temporal dynamics of neurobehavioral synchrony in caregiver–child conversations with natural variability.

We found that mothers and children showed above chance-level neural synchronization in HbO in temporo-parietal (temporo-parietal junction—TPJ) and prefrontal (dorsolateral prefrontal cortex—DLPFC) areas during a free verbal conversation. Activation in temporo-parietal areas and particularly the TPJ is associated with the mentalizing system, which is implicated in both children and adults when trying to understand others' mental states (Frith and Frith, 2006; Koster-Hale and Saxe, 2013). A recently presented framework on interactional synchrony by Hoehl *et al.* (2020) posits that the human brain constantly tracks temporal regularities in sensory input (e.g. auditory rhythms) employing striato-cortical loops. However, alignment to these rhythms depends on a range of stimulus properties and their socio-emotional meaning, which is computed in temporoparietal regions, including TPJ. The dorsolateral prefrontal cortex, on the other hand, is functionally related to the cognitive control system and recruited during tasks that involve top–down control over cognitive and emotional processes in social contexts (Grossmann, 2013; Balconi and Pagani, 2015). Both the mentalizing and cognitive control systems have been implicated in neural synchronization processes in various contexts of interactions, such as conversation, cooperative problem-solving and joint action in adult dyads (Jiang *et al.*, 2016; Liu *et al.*, 2016). However, the present study is the first to date to find these regions associated with neural synchronization during a mother–child verbal conversation. Still, the basic function of neural synchrony in areas involving the mentalizing and cognitive control system during conversation needs to be clarified in further studies. One interesting path for future research in adult dyads would be to experimentally manipulate interpersonal neural synchrony in these brain regions and assess the effects on social cognition (see Novembre *et al.*, 2017).

Next, we were interested in probing time-dependent changes of neural synchrony in relation to conversation patterns. Accordingly, we examined the temporal dynamics of neural synchrony during eight 30 s intervals of the 4-min-long conversation. In contrast to findings obtained in adult dyads (Mayseless *et al.*, 2019), we found that neural synchrony in temporo-parietal and lateral prefrontal regions increased throughout the conversation on average. This discrepancy could be a result of variation in interaction type-related factors as well as individual differences of participants. Firstly, while the interaction assessed during the adult study was a creative problem-solving task, participants in the present study engaged in a free verbal conversation. Second, temporal changes in neural synchrony could be affected by the type of interaction with free conversations constantly involving re-synchronization processes due to their high complexity (Richardson *et al.*, 2008). Third, the amount and effort of coordination could also differ as a function of the relationship quality between the two interaction partners, which could result in different temporal dynamics. Two previous studies employing a cooperative interaction task observed higher synchronization between affiliated dyads compared to non-affiliated stranger dyads (Pan *et al.*, 2017; Reindl *et al.*, 2018). Here, we tested mother–child dyads, who are closer and more accustomed to one another than strangers, and thus, may be faster to find their own mutual rhythm (Markova *et al.*, 2019). In future studies, it will be important to investigate interindividual differences of the interacting dyads' relationship, ideally including a range of variables also comprising parent–child attachment (see Leclère *et al.*, 2014; Long *et al.*, 2020).

Critically, when we considered how often mothers and children took turns, higher neural synchrony was associated with higher turn-taking in later epochs of the conversation. Evidence from studying an individual's entrainment to rhythmic auditory stimuli shows that neural signal alignment is a gradual process and sustains temporarily even after the stimulus is no longer present (Trapp *et al.*, 2018). We therefore suggest that interpersonal alignment of brain activity might assume a similar pattern in that the regularity of turn-taking in parent–child interactions could take effect further along the conversation instead of resulting in immediate alignment. Overall, increased interpersonal neural synchrony during parent–child conversation could reflect higher turn-taking quality, implying a high level of mutual attention and gradually increasing mutual adaptation.

Turn-taking and language development are tightly intertwined, as studies show that conversation patterns, such as turn-taking duration, indicate how fast children can understand a question while planning and initiating their response at the same time (Casillas *et al.*, 2016). Especially contingent speech by parents, as in attuned turn-taking, helps infants to simplify the structure of speech and language and thus catalyze their language production (Goldstein *et al.*, 2003; Elmlinger *et al.*, 2019). What is more, turn-taking was shown to be implicated in heightened neural language processing (Romeo *et al.*, 2018): 4- to 6-year-old children who experience more conversational turns with adults showed greater left inferior frontal (Broca's area) activation in individual neural measurements. Furthermore, the neural activation mediated the relation between children's contingent language exposure and verbal skills. This finding highlights a potential future avenue of investigation into the role of neural synchrony for language development.

Other conversation patterns, such as cohesiveness of conversation indicated by relevance and contingency, were not associated with neural synchronization in the current study. The same was true for communicative intrusiveness. Although previous studies showed that both turn-taking and cohesiveness during parent–child conversations were critical and predictive for later language abilities (Roseberry *et al.*, 2014; Hirsh-Pasek *et al.*, 2015), we only found a link between turn-taking and neural synchrony during a free verbal conversation. Our predefined ROIs where we measured neural synchronization may not have captured such link to cohesiveness, as an influence of cohesiveness was previously observed, for example, in language-related areas such as the left inferior frontal regions (Romeo *et al.*, 2018). Future studies should explore whether neural synchrony in different regions could map onto different conversation patterns.

When we went on to explore the associations between communication patterns and interpersonal neural synchrony in HbR, we were not able to replicate our findings as for HbO synchrony, in contrast to an adult hyperscanning study (Pan *et al.*, 2017). The difference in results could be due to physiological differences between children and adults (Perlman *et al.*, 2014). The blood flow and oxygen metabolism coupling in children is suggested to differ from adults with concurrent increases in HbO and HbR found at times. Hence, further studies exploring both HbO and HbR neural synchrony in parent–child interactions are needed to decipher synchronization processes during early childhood across different age groups.

Our study had several limitations. First, fNIRS data were not measured during a control condition such as a resting period. We would argue, though, that resting phases are not an ideal control condition because changes in synchrony might rather be due to task-evoked changes in the autonomic nervous system (ANS) instead of in neural activity (Tachtsidis and Scholkmann, 2016). We therefore opted for a random pair analysis to control for changes in the ANS as well as other spurious correlations in the signal. In future studies, concurrent measurements of short channel regressors could further improve the signal. Next, due to the limited number of available optodes, we focused on cortical regions that appeared most relevant to social processes and were previously shown to be involved in neural synchronization during similar tasks. In further investigations as well as with the development of devices comprising more measurement channels, neural synchrony in language-related cortical areas could be examined (Zhao *et al.*, 2019).

Conclusion

Our study shows that children and mothers synchronize their brain activity during natural verbal conversation and that neural synchronization increases over time when mother and child engage in more verbal turn-taking. This observed link between conversational turn-taking and neural synchronization opens up new possibilities to understand the potential functional role of neural synchronization during verbal exchanges. Future studies could explore the role of neural synchrony in language acquisition. Overall, our findings point towards neural synchrony as a potential neurobiological marker of successful coordination in mother–child conversation.

Supplementary data

Supplementary data are available at SCAN online.

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Conflict of interest

None declared

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Special Issue "Understanding Others": Research Report

The effects of interaction quality on neural synchrony during mother-child problem solving

1. Introduction

Mutual attunement of behavior and physiology between children and caregivers is thought to play a vital role for both attachment and the development of social and emotional competences (Atzil & Gendron, 2017; Stern, 1985). This relation appears particularly relevant when the child is distressed and thus in a state of allostasis deviation, with allostasis generally referring to the process of maintaining biobehavioral balance through adaptation (McEwen & Wingfield, 2003; Sterling, 2012). The caregiver's actions of soothing the child thus help to reestablish a state of allostasis (Atzil & Gendron, 2017; Feldman, Magori-Cohen, Galili, Singer, & Louzoun, 2011). Both temporal structure and rewarding nature of these synchronous interactions provide children with information to map certain bodily states to underlying mental experiences (Meltzoff & Decety, 2003). Accordingly, by being understood and cared for, children learn how to understand and care for others (Atzil & Gendron, 2017).

Despite available investigations into behavioral and physiological synchrony, we still know little about the potential role of neural synchrony in caregiver-child exchanges. Early findings from social neuroscience research suggest that neural synchrony facilitates the coordination of behavior and predicts cooperative task performance in adult-infant and parent-child interactions (Leong et al., 2017; Miller et al., 2019; Reindl, Gerloff, Scharke, & Konrad, 2018), corroborating findings from previous research in adults (Baker et al., 2016; Liu et al., 2016). Social interactions in these studies were, however, highly controlled due to the use of simplified and artificial tasks and thus did not require elaborate perspective-taking or communication. Although these studies provided important initial evidence for the role of neural synchrony in early behavioral coordination, these interactions did not reflect complex coordinated exchanges that mothers and children engage in everyday life. Hence, these findings lacked the integration of neural data with more complex and naturalistic measures of social behavior (McDonald & Perdue, 2018). In addition, few studies have examined caregiver-child interactions at preschool age when the child moves beyond the dependency experienced during infancy and toddlerhood towards greater agency (Harrist & Waugh, 2002).

Here, we observed mothers and preschool children in a naturalistic problem-solving interaction, which allowed us to examine individual differences facilitating or attenuating mother-child neural synchrony. Based on attachment theory, we predicted that behavioral reciprocity and maternal sensitivity support neural synchronization processes (Vrticka, 2017). We used dual functional near-infrared spectroscopy (fNIRS) to simultaneously measure brain activity in mothers and children during a video-recorded live interaction, thus, probing the supposed links between interaction quality, collaborative success, and neural synchronization.

In recent years, the investigation of neural synchrony has been considerably facilitated through advancements in simultaneous neuroimaging of multiple brains – known as "hyperscanning" (Babiloni & Astolfi, 2014). A growing number of hyperscanning studies looked at neural synchrony in adult dyads during imitation, free verbal conversation, and cooperative versus competitive interaction (for reviews see Dumas, Lachat, Martinerie, Nadel, & George, 2011; Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012; Liu & Pelowski, 2014). Conversely, adult-child and more specifically parent-child neural synchronization has only recently come into the focus of developmental research (Leong et al., 2017; Miller et al., 2019; Reindl et al., 2018). Synchronization of neural oscillations is assumed to reflect mutual attunement of behavioral and physiological rhythms (Hasson et al., 2012) that are transmitted interpersonally through the environment by coupling of the sensory system of one person to the motor system of another person. According to the phase reset model, such coupling occurs because ongoing oscillations in the receiver reset their phases to the incoming oscillations from the sender (Brandt, 1997). In doing so, both the sender's and receiver's brains entrain to the rhythm of the transmitted signal, providing a neural underpinning for interpersonal exchanges and behavioral synchronization in the form of turn taking (Wilson & Wilson, 2005). More specifically, neural synchrony is suggested to facilitate internal predictions about the self and others and thus optimize behavior during interactions (Dai et al., 2018). Beyond enabling complex coordinated behaviors, such as joint action and joint decision making (Novembre, Knoblich, Dunne, & Keller, 2017), neurobehavioral synchrony is further posited to create an optimal learning environment for the child through the regulation of the infants' needs (Atzil & Gendron, 2017). Consequently, the coupling of rhythmic brain activity can emerge dyadically through language or motion, but can be also externally triggered through joint attention or music (Cirelli, Trehub, & Trainor, 2018; Leong et al., 2017; Nummenmaa, Lahnakoski, & Glerean, 2018).

To date, only three studies that investigated adult-child and parent-child neural synchrony have been published. In a dual-electroencephalography (EEG) study by Leong et al. (2017), a female presenter sang either live or prerecorded nursery rhymes to an infant in a direct gaze and an averted gaze condition. Neural synchrony between adults and infants was increased during the live interaction compared to televised singing. In addition, higher neural synchronization was observed during direct as compared to indirect gaze, revealing mutual gaze as a modulator of neural synchrony. Using dual-fNIRS, two recently published studies investigated parent-child interactions, focusing on cooperation (Miller et al., 2019; Reindl et al., 2018). Both studies examined the interaction of school-aged children with their parents during a computerized reaction time task (Cui, Bryant, & Reiss, 2012). Findings revealed increased neural synchrony in frontal and temporal areas during parent-child cooperation in comparison to individual task engagement, competition, and stranger–child interaction. Moreover, neural synchrony predicted dyadic task performance corroborating findings from previous research on the consequences of neurobehavioral synchrony in adults (Baker et al., 2016; Liu et al., 2016). These studies further indicate that neural synchrony with the caregiver is positively related to children's emotion regulation skills (Reindl et al., 2018) and differs depending on the biological sex of the child (Miller et al., 2019). Miller et al. (2019) were also the first to take individual differences into account. They found a negative association between avoidant child-mother attachment and neural synchrony in the right prefrontal cortex during cooperation. However, this association did not survive a more stringent correction for multiple comparisons and therefore remains preliminary.

Given this preliminary evidence of neural synchronization in adult-child and parent-child interactions (Leong et al., 2017; Miller et al., 2019; Reindl et al., 2018), it appears vital to more precisely identify personality, relationship, and interactional factors modulating neural synchrony and its consequences in early social interactions. In particular, attachment theory can provide valuable insights into possible factors reflecting individual differences in interaction quality for neural synchronization (Vrticka, 2017; Vrticka & Vuilleumier, 2012). Behavioral reciprocity is generally thought to be an important aspect of interaction quality in parent-child interactions, fundamental to the development of secure attachment, and associated with cognitive, emotional, and social competences (Leclère et al., 2014). Behavioral reciprocity refers to a "dynamic and reciprocal adaptation of the temporal structure of behaviors and shared affect between interactive partners" (Harrist & Waugh, 2002). It seems as if caregivers and children perform an intricate dance, built on the familiarity of each other's behaviors (Leclère et al., 2014). More specifically, reciprocal interactions generate a rhythmicity between the two interactive partners that helps individuals to form anticipations based on the temporal regularity of behaviors, allowing them to make mutual adjustments (Keller, Novembre, & Hove, 2014; Reddy, Markova, & Wallot, 2013). On this account, it has been shown that contingent interactions between robots and preschool children can foster second language learning (Vogt, de Haas, de Jong, Baxter, & Krahmer, 2017). In addition, temporally and semantically contingent responses from mothers were related to toddlers' expressive vocabulary (McGillion et al., 2013). However, in preschool age research regarding the direct outcomes of synchronization is still lacking (Harrist & Waugh, 2002; Leclère et al., 2014).

Behavioral coordination is assumed to be influenced by both state-like and trait-like characteristics that individuals and dyads bring to the interaction (Leclère et al., 2014). For example, maternal sensitivity has been shown to affect synchrony (Thompson & Trevathan, 2009), which is also maintained to be essential to infants' attachment (Ainsworth & Bell, 1970; Beebe & Steele, 2013; Isabella & Belsky, 1991). Within this context, maternal sensitivity is described as the mother being able to perceive and understand an infant's signals, as well as to respond contingently and adequately to the infant's needs - which makes maternal sensitivity an important prerequisite for attuning to their infant (Beebe & Steele, 2013; Thompson & Trevathan, 2009). Moving into preschool age, maternal sensitivity continues to be an important predictor of a child's social and cognitive development, especially regarding theory of mind abilities (Lemelin, Tarabulsy, & Provost, 2006; Symons & Clark, 2000). Consequently, maternal sensitivity might be instrumental in establishing neural synchronization. Interestingly, meta-analyses provided evidence that maternal sensitivity, even though important, is not an exclusive condition of attachment security, suggesting that current contextual factors, like stress, could undermine sensitive caregiving behavior and consecutively affect the parent-child relationship (Booth, Macdonald, & Youssef, 2018; Wolff & Ijzendoorn, 1997).

As children develop beyond infancy and toddlerhood, synchronous interactions are increasingly symmetric, as children improve in communication skills and social competences (Harrist & Waugh, 2002). Preschool children become more autonomous as they gain agency during social interactions (Harrist & Waugh, 2002). Both parental and teacher agency support and child agency as such have been proposed to be indicative behaviors for high interaction quality during (pre-)school age (Houen, Danby, Farrell, & Thorpe, 2016; Rocissano, Slade, & Lynch, 1987). While evidence suggests that mothers who follow the child's lead can uphold reciprocal interactions much longer than mothers who try to control the interaction, there are only few studies that consider child agency.

Given that children differ in their emotional, motor, and attentional reaction to stimulation (Putnam, Sanson, & Rothbart, 2002), personality differences might also affect their ability to synchronize with their caregivers. There is growing evidence that children prone to negative emotionality, also described as having a difficult temperament, have difficulties synchronizing with their mothers (Feldman, 2003). However, empirical evidence also suggests that children showing negative emotionality benefit most from sensitive, responsive caregiving behavior (Ellis, Boyce, Belsky, Bakermans-Kranenburg, & van Ijzendoorn, 2011; Kochanska & Kim, 2013). Indeed, negative emotionality has been shown to strengthen the relation between reciprocal interactions and positive developmental outcomes (Feldman, Greenbaum, & Yirmiya, 1999). According to Belsky (2013), children differ in their susceptibility to both adverse and beneficial rearing environments and negative emotionality is proposed to be one of the susceptibility factors. Children can benefit tremendously from optimal caregiving, but can also be much more affected by risky environments.

We used dual-fNIRS to investigate a naturalistic caregiver-child interaction during a tangram puzzle-solving task by contrasting a cooperative problem-solving condition to individual problem-solving. The problem-solving task was designed to be challenging for a preschool child in order to encourage mutual task engagement during joint problem solving, require mutual perspective-taking and communication, and activate maternal caregiving. When the mothers and children both take turns moving the puzzle pieces, we expected the dyad to attune their behavior to one another as characterized by behavioral reciprocity. We measured neural synchrony through fNIRS in temporo-parietal areas implicated in social cognitive processes such as mentalization and shared intentionality, also referred to as the sharing of psychological states (Miller et al., 2019; Saxe, 2010; Tomasello & Carpenter, 2007). Furthermore, we assessed synchrony in prefrontal areas related to executive functioning, complex decision making, and effective communication (Reindl et al., 2018; Stephens, Silbert, & Hasson, 2010; Tsujimoto, 2008). We expected higher neural synchrony in both areas to be present during joint problem solving compared to individual problem solving and to manifest itself in concordance with behavioral reciprocity.

Furthermore, we predicted higher neural synchronization to be associated with successful joint problem solving. We also expected maternal sensitivity and child agency to be related to higher synchronization, whereas we predicted maternal stress and children's difficult temperament, namely negative emotionality, to mitigate synchronization. Taken together, we suggest that during problem solving in caregiver-child dyads, neural coupling is a fundamental mechanism supporting behavioral coordination through processes of facilitated shared intentionality, affect attunement, and communication. Probing the relation between neural synchrony and interaction quality in a naturalistic context will thus advance our understanding of the neural underpinnings to caregiver-child interactions.

2. Material and methods

2.1. *Participants*

Data from forty-two mothers (mean age 36.26 years; *SD* = 4.81 years; *range* = 28–46 years) and their preschool children (19 boys and 23 girls; mean age 5; 08 years; *SD* = 0; 04 years; *range* = 5; 00–6; 01) were analyzed for the present study. From the initially recruited forty-six mother-child pairs, four were excluded due to either technical problems or children not complying with the given instructions. Fifty-seven percent of mothers graduated with a university degree, while the remaining mothers graduated from vocational school. Each mother-child pair was biologically related. The pairs were all caucasian and children were typically developing. Participants were recruited from a pre-existing database of volunteers and mothers gave written consent for both themselves and their children before participating in the study. Procedures were approved by the local ethics committee.

2.2. *Experimental procedure*

During the experiment, mother and child sat face-to-face (see Fig. 1), separated by a table. The dyads were guided through the following sequence: Task – Rest – Task – Rest – Task – Rest – Task – Verbal Conversation. For the task phase, dyads participated in a tangram puzzle-solving task during which they were asked to arrange seven geometric shapes to recreate different templates (abstract forms, objects, animals; see SI Appendix, Figure S1). The task comprised two different experimental conditions that were equally distributed. In the cooperation condition, both caregivers and children were instructed to jointly solve the templates. The specific instructions are included in SI Appendix, Section 1. In the individual condition, an opaque screen separated the mothers and children to prevent them from interacting with each other and to provide a non-competitive context. In both conditions, four puzzle templates were provided to each dyad, and participants were instructed to recreate all of them. Each task lasted 120 s and the condition order was counterbalanced. Participants were instructed to rest (eyes closed) for 80 s in between each task. After performing all task conditions, the mothers and children were instructed to engage in an additional free verbal conversation for 240 s (not reported here). The complete procedure was video recorded from three different angles.

2.3. *fNIRS data acquisition*

We used a NIRScout 8–16 (NIRx Medizintechnik GmbH, Germany) Optical Topography system to record oxy-hemoglobin (HbO) and deoxy-hemoglobin (HbR) concentration changes for each dyad. The four 2 × 2 probe sets were attached to an EEG cap with 10–20 configuration. The standard electrode locations allowed us to place the probes more precisely, as the probe sets over the left and right dorsolateral prefrontal cortex

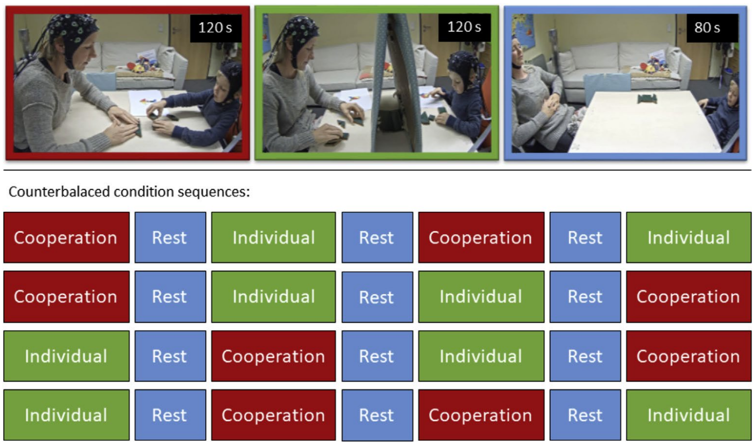


Fig. 1 – Study set-up during cooperation (left) and individual (middle) problem solving as well as the rest phase (right). Rows indicate possible sequences to counterbalance (Latin square) the order of tasks.

(dlPFC) surrounded AF3 and AF4, whereas the probes on the left and right temporo-parietal junction (TPJ) surrounded CP5 and CP6 (see Fig. 2). ROIs were based on previous work involving social mentalizing in a cooperative setting (Jiang et al., 2012; Liu et al., 2016; Miller et al., 2019; Reindl et al., 2018). In each probe set, eight sources and eight detectors were positioned, which resulted in 16 measurement channels with equal distances of 3 cm between the optodes. The absorption of near-infrared light was measured at wavelengths of 760 and 850 mm and the sampling frequency was 7.81 Hz.

2.4. *fNIRS data processing*

Before analyzing the fNIRS measurements, raw data were visually inspected during an initial quality check procedure. In so doing, all channels that did not show a clear heart band were removed, which resulted in 93.4% of the channels from the whole sample being included in further analyses. In addition, we had an inclusion threshold of two channels per region of interest, which all participants passed. After this initial step, data were subsequently pre-processed using MATLAB-based functions derived from Homer 2 and SPM-fNIRS. Raw optical density data were motion corrected with MARA, a smoothing procedure based on local regression using weighted linear least squares and a 2nd degree polynomial model (Scholkmann, Spichtig, Muehlemann, & Wolf, 2010), then band-passed filtered with low- and high-pass parameters of .5 and .01 (Baker et al., 2016; Miller et al., 2019). Next, the filtered data were converted to HbO and HbR values based on Beer–Lambert Law. For later statistical analyses, we only focused on HbO values, which were reported to be more sensitive to changes in the regional cerebral blood flow (Miller et al., 2019; Reindl et al., 2018).

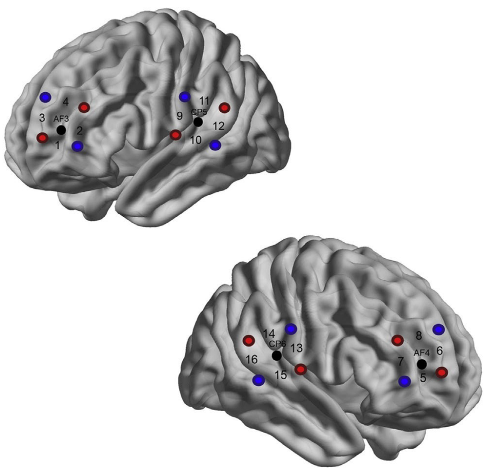


Fig. 2 – Cap Configuration. Red circles mark sources, while blue circles mark detectors. Numbers (1–16) mark measurement channels between sources and detectors. Black circles mark EEG 10–20 channel positions for orientation. The top graphic shows the left hemisphere, while the bottom graphic shows the right hemisphere.

2.4.1. *General linear model analysis*

The differential patterns of individual cortical activation that occurred throughout the different conditions were assessed using a general linear model (GLM) approach. The evoked hemodynamic responses were modelled as a boxcarr function convolved with a canonical hemodynamic response (Issard & Gervain, 2018), with the onset and duration of each condition modeled in seconds. As a result, standardized beta coefficients for each condition we estimated. The sign and magnitude of each beta coefficient provide an indicator of the direction (positive/negative) and intensity of HbO change (i.e., cortical activity) that occurred during each condition.

2.4.2. *Wavelet transform coherence analysis*

Neural synchrony was calculated with wavelet transform coherence (WTC) (for more information see Chang & Glover, 2010; Grinsted, Moore, & Jevrejeva, 2004). WTC was used to assess cross-correlation between the fNIRS time series in each dyad and each channel as a function of frequency and time. WTC considers global coherence patterns of brain activity and offers another advantage, as it considers phase-lagged correlations in addition to in-phase correlations. This type of coherence calculation fits well with the literature (e.g., Liu et al., 2016; Baker et al., 2016) thus far, suggesting that both concurrent and sequential behavioral synchrony might be linked with neural synchronization. Based on the duration to complete one template, visual inspection, and spectral analyses, task duration was established and the frequency band of .02 Hz–.10 Hz (corresponding to 10 - 50 sec) was identified as task-related. Average neural coherence (i.e., neural synchrony) was then calculated for the two cooperation conditions, the two individual conditions, and the three resting phases in each channel, which resulted in 3 (conditions) x 16 (channels) coherence values for each dyad. For all three conditions the same length of data, namely 240 s, were included the calculation. The resting period was included to explore two different non-interactive control conditions and to allow the dyad to have a “reset time” after each task, as well as the possibility to start off on a similar footing into each task condition.

All neural synchrony values were standardized with Fisher’s z-Transformation prior to statistical analyses (Baker et al., 2016). To rule out effects due to spurious correlation, we conducted a random pair analysis with 1,000 permutations. Coherence values of original dyads in each condition were tested against a distribution of randomized pair coherences in the same condition. Resulting *p*-values were then corrected with a false discovery rate (FDR) for multiple comparisons (Benjamini & Hochberg, 1995).

2.5. *Behavioral ratings*

The caregivers’ and children’s behavior during the cooperation condition was rated from video recordings by trained graduate students to assess interaction quality using a customized coding scheme based on the Coding System for Mother–Child Interactions (CSMCI) (Healey, Gopin, Grossman, Campbell, & Halperin, 2010). In addition, a German instrument was used to assess mother-child interactions, labeled INTAKT (an agglomeration of the German word Interaktion meaning interaction, and intakt, meaning intact - referring to an intact mother child relationship; Hirschmann, Kastner-Koller, Deimann, Aigner, & Svecz, 2011). For this study, ratings of maternal supportive presence and respect for autonomy, child agency, behavioral reciprocity (CSMCI), and maternal sensitivity (INTAKT) were performed. First, maternal supportive presence was rated as high when mothers voiced encouragement or praise and showed emotional support throughout the interaction. Additionally, respect for autonomy indicated if the mothers acted in a way that recognized and respected the validity of the children's individuality, motives, and perspectives. We further included a general maternal sensitivity scale to assess whether mothers adequately and promptly responded to children, as well as was whether they were able to take over the children's perspective (Hirschmann et al., 2011). The scale used is a German variation of Ainsworth's sensitivity scale and was adapted to the preschool age range. In addition, child agency was coded for how active and confident children approached working on the task and initiated goal-directed behavior. Behavioral reciprocity was furthermore marked by contingent responses resulting in a turn-taking quality of interactions as behavioral flow. Finally, communicative reciprocity was marked as turn-taking quality of verbalizations. Each subscale was rated on a 7-point Likert-type scale (1 = no occurrence, 7 = continuous occurrence). The cooperation tasks were coded for each block and coding values were averaged over both blocks. To calculate coding reliability, we selected 20% of the interactions and compared observations by intraclass correlations (ICC). ICC estimates and their 95% confidence intervals were calculated based on consistency employing a 1-way mixed-effects model. Coders showed moderate to excellent reliability over all assessed scales, ranging from *ICC* = .76-.93 and averaging at *ICC* = .86. When coders disagreed on ratings, the scores of the most experienced coder were used. We further assessed the number of templates solved in each condition.

2.6. *Maternal stress*

Maternal current stress levels were assessed with the General Stress Level Questionnaire (Bodenmann, 2000). This self-report questionnaire comprises questions on stressors regarding general issues, relationship, family, and finances on a 5-point scale ranging from 1 (not at all) to 5 (very strong). Internal consistency was adequate with Cronbach's a = .80.

2.7. *Child temperament*

To measure individual differences in temperamental negative affectivity in children, the very short form of the Children's Behavior Questionnaire (CBQ) (Putnam & Rothbart, 2006) was used. Temperament scores are based on parent's report on a 7-point scale ranging from 1 (extremely untrue of your child) to 7 (extremely true of your child). We only used the subscale Negative Affectivity (NA), which is marked by Sadness, Fear, Anger, Frustration, Discomfort, and Difficulties in Soothing. Internal consistencies of the subscales were high with Cronbach's a = .86.

2.8. *Statistical analysis*

Statistical analyses were calculated with R packages. In particular, linear mixed models were fitted with package "lme4" (Bates, Mächler, Bolker, & Walker, 2015). Raw data was examined prior to any calculations and if necessary corrected for normal distribution as well as outliers. This step was deemed necessary for maternal stress and child temperament scores due to their right skewed distribution. Outliers were defined by values over or under three standard deviations (SD) from the mean. Outliers were then winsorized to the respective lower and/or upper boundaries in each subscale and over all coherence values (Wilcox, 2017).

To analyze individual cortical activation patterns, standardized beta coefficients were entered as the response variable in a linear mixed effects model with condition (cooperation vs. individual vs. rest) and region of interest (ROI; four per dyad) as predictors and with random slopes for each ROI and condition in each dyad and channel. The grouping of channels in our statistical model was done to enhance reliability of region specification accounting for minimal variance in optode positioning during testing. Channel clustering provides a more meaningful and realistic interpretation of the results (Azhari et al., 2019). The results for individual brain activation analyses are reported in the supplements (SI Section 3).

For neural synchrony analyses, WTC values were entered as the response variable in a separate linear mixed effects model with condition (cooperation vs. individual vs. rest) and region of interest (ROI; four per dyad) as fixed factors and with random slopes for each ROI and condition in each dyad. To test for the effects of individual differences on neural synchrony, we extended the above mentioned linear mixed model by the predictor variable of interest and its random slope. To derive effects for single predictors we used a Kenward-Roger approximation and parametric bootstrap approach (Halekoh & Højsgaard, 2014). To further examine significant effects, contrasts of factors were conducted by using post-hoc analyses with Tukey's Honest Significant Difference to correct for multiple comparisons (Abdi & Williams, 2010). When significant, we then calculated multiple linear mixed models to further analyze the relations according to our hypotheses and corrected *p*-values with a false discovery rate (FDR) when multiple conditions were compared ($q < .05$). Behavioral data analysis was conducted with Pearson correlations and we corrected *p*-values with FDR ($q < .05$) for multiple comparisons.

3. Results

3.1. *Behavioral results*

Correlational analyses for task performance, behavioral reciprocity, maternal sensitivity, child agency, and maternal stress level are reported in Table 1, while descriptive and correlational analyses for all assessed ratings and

Table 1 – Correlation Statistics for Task Performance, interaction qualities, and questionnaire variables.

	1	2	3	4	5	6
Dyadic task performance	–	–	–	–	–	–
Individual task performance (child)	β = -.61,-.88 R^2 = .04	–	–	–	–	–
Behavioral reciprocity	r = .22 R^2 = .02	β = -.18,-.27 R^2 = -.05	–	–	–	–
Maternal sensitivity (rating)	r =-.09 R^2 = −.02	β = .17–.76 R^2 = .02	r = .64** R^2 = .39	–	–	–
Child agency	r = .21 R^2 = .02	β = -.20,0.27 R^2 = −.04	r = .33 R^2 = .09	r = .29 R^2 = .06	–	–
Maternal stress	r = -.17 R^2 = .01	β = -.45,-.05 R^2 = .02	r = -.14 R^2 = .00	r = -.04 R^2 = −.02	r = -.30 R^2 = .07	–

Note. Pearson correlations were corrected with FDR for multiple comparisons. ** = $q < .01$, * = $q < .05$. Adjusted R^2 are reported underneath correlation coefficients. Due to the factor structure of individual task performance, linear regressions were calculated and also corrected with FDR.

questionnaires are presented in supplementary Tables S1 and S2. Overall, task performance was associated with no other behavioral measure, $q > .24$. Behavioral reciprocity was related to maternal sensitivity, $r = .64$, $q = .08$, as well as weakly related to child agency, $r = .34$, $q = .08$, but not related to other assessed measures, $q > .24$.

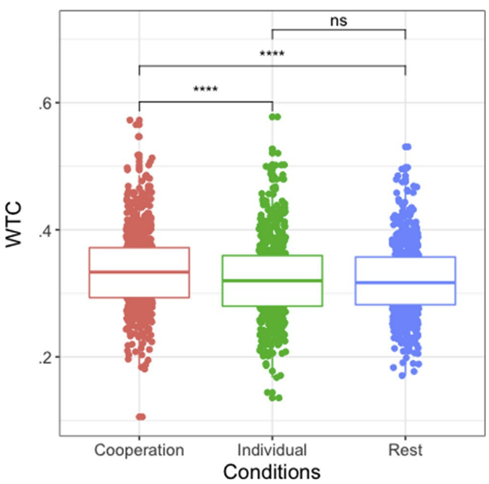
3.2. Neural synchrony during problem solving

We used fNIRS to assess brain activity from temporo-parietal and prefrontal areas in mother and child simultaneously. WTC was used to assess cross-correlation between the fNIRS time series in each dyad and measurement channel as a function of frequency and time. First, we examined whether neural synchrony during the cooperative problem-solving task was higher in comparison to individual problem solving and resting phases. Analyzing neural synchrony across all three conditions revealed a strong main effect of condition, estimate±SE = −.008 ± .003, $F(2,2015) = 8.52$, $p = .001$, 95% CI = −(.023–.008), and no effect of region, $p = .12$. In a subsequent exploratory analysis, we also found no significant interaction effect of condition and region, $p = .44$ (see SI Appendix, Section 3 and Figure S2). Post-hoc analysis showed that neural synchrony averaged over all regions of interest (ROI) was higher during cooperation in contrast to the individual condition, estimate±SE = .014 ± .005, $t(1340) = 3.29$, $p = .006$, 95% CI = .009–.02, which is depicted in Fig. 3. Additionally, neural synchrony during cooperation was higher than during resting phases, estimate±SE = .017 ± .004, $t(1340) = 3.76$, $p < .001$, 95% CI = .01–.02. These effects remained significant when we further controlled for child sex, mother and child age, maternal education, task order and familiarity with the task during conditions.

To control for spurious correlations between both neural signals, we conducted a random validation analysis. 1,000 permutations of neural synchrony between a mother's and a random child's signal were calculated and compared to neural synchrony of original dyads using Welch t-tests with FDR corrected p-values ($p < .05$). Results revealed that neural synchrony in original dyads was significantly higher than in random pairings during the cooperation condition only, $t(781.19) = 3.21$, $p = .001$ (see supplementary Figure 3). In the two other conditions, findings showed lower neural synchrony in original dyads as compared to random dyads, $t(776.23) = 2.11$, $p = .04$ and $t(834.67) = 2.65$, $p = .01$ respectively. To conclude, the random validation analysis further supported our findings of higher neural synchrony selectively in the cooperation condition.

3.3. Interaction qualities and neural synchrony

Identifying interaction qualities during cooperative problem solving (see Table 1), which are either facilitating or mitigating neural synchrony, was one of our main research questions in



aged across all ROIs). ns = non-significant, **** = p < .0001.

the present study. Thus, we assessed whether specific interaction qualities, measured from video recordings of the cooperation condition, were linked to increased neural synchronization during the cooperative task. To test the hypotheses, we entered behavioral reciprocity as a fixed effect into the above mentioned linear mixed model, which resulted in a main effect of behavioral reciprocity, *estimate* ± SE = .005 ± .003, *F*(1,1871) = 4.45, *p* = .003, 95% CI = .0002–.0112, and an interaction effect with condition, estimate±SE = .008 ± .003, *F*(2,1871) = 3.69, *p* = .02, 95% CI = −.0151–.0013. Post-hoc analysis conducted with a further specified linear model revealed that the interaction was driven by the effect of behavioral reciprocity in the cooperation condition. This means that only when the dyad was instructed to work together, neural synchrony was positively correlated with behavioral reciprocity, *t(624)* = 6.51, *p* = .01, 95% CI = .0001–.0121. These findings are depicted in Fig. 4A.

As we hypothesized that higher neural synchrony should indicate successful task performance, we examined whether neural synchrony was associated with the number of templates solved together in the cooperation phase. Results suggested that regardless of experimental condition, neural synchrony indeed significantly predicted overall mutual task performance, estimate±SE = .008 ± .003, *F(1,1967) = 6.26, p = .003, 95% CI = .001–.013* (see Fig. 4B). Looking further into condition-related neural synchrony, we found that neural synchrony during the cooperation condition specifically was significantly related to overall task performance, *F(1,656)* = 7.30, *p* = .007, 95% CI = .002–.013 (*q* = .02). Neural synchrony during individual problem solving and rest showed no or just a weak effect on cooperative problem-solving success, *p* = .12-.88 (*q* = .18-.88). When correlating task performance with behavioral reciprocity, we did not find any significant effect, *q* = .24.

3.4. *Individual factors to neural synchronization*

3.4.1. *Maternal factors*

First, we predicted that neural synchronization should be facilitated by maternal sensitivity, because sensitivity is proposed to be essential for behavioral synchrony. Our findings, however, showed that *interaction-based maternal sensitivity* did not significantly predict neural synchrony, *p* > .40, despite its strong correlation with behavioral reciprocity, *β* = .74, *p* < .001. Next to a caregiving measure, we probed into the role of *maternal stress* on neural synchrony. Interestingly, our results displayed a weak main effect of the self-reported general maternal stress level on neural synchrony, estimate±SE = −.004 ± .003, *F*(1,1992) = 1.97, *p* = .05, 95% CI = −.009–.002, and a weak interaction effect of maternal stress with condition, estimate±SE = .008 ± .003, *F*(3,1992) = 3.52, *p* = .03, 95% CI = −.002–.014. During the cooperation condition, general maternal stress seemed to somewhat attenuate neural synchrony, *t*(672) = 1.94, *p* = .05, 95% CI = −.004–.003. General maternal stress levels showed no effect on neural synchronization during individual problem solving and resting phases, *p* = .12, *p* = .38, respectively. Findings are illustrated in Fig. 5A.

3.4.2. *Child factors*

We also investigated whether *child agency* positively influenced neural synchrony. We found that child agency was weakly associated with neural synchrony, estimate±SE = .006 ± .003, *F*(1,1848) = 1.92, *p* = .05, 95% CI = .001–.012 (see Fig. 5B), but the interaction effect with task was not significant, *p* = .47. When the child engaged autonomously in the joint task, the dyad thus showed indications of overall increased neural synchrony. In an exploratory post-hoc analysis, the regressions showed that child agency was again weakly related to neural synchrony in the cooperation condition, *F*(1,624) = 1.92, *p* = .09, 95% CI = .000–.012, but not in the individual or resting conditions, *p* > .50. The trending effect in the cooperation condition, however, was estimated as non-robust. In further analyses we found no indications for an effect of child temperament in terms of negative affectivity on neural synchrony, *p* = .34.

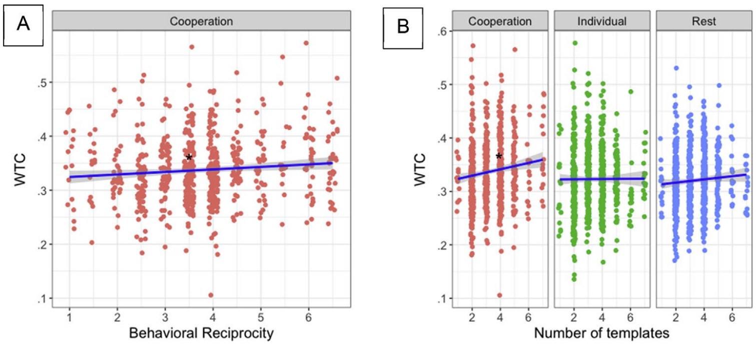


Fig. 4 – (A) Plot of the association between behavioral reciprocity and neural synchrony during the cooperation condition. When mother and child acted more reciprocally during cooperation (x-axis), the dyad also displayed higher neural synchrony (y-axis). (B) Illustration of the relation between neural synchrony in each condition (y-axis) and overall task performance (x-axis). * = *p* < .05.

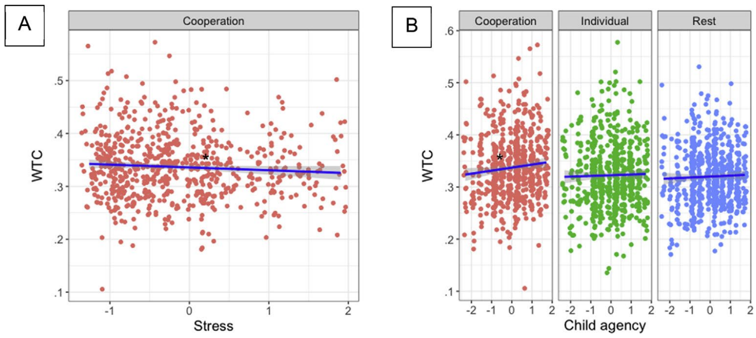


Fig. 5 — (A) High levels of maternal stress (x-axis) correlated negatively with neural synchrony during the cooperation condition (y-axis). This pattern of association was found across all ROIs. (B) The plot of the association between child agency (x-axis) and overall neural coherence (y-axis) highlights a positive linear relation between the two variables across all ROIs with the strongest indication in the cooperation condition.

3.5. *Cortical activation patterns*

3.5.1. *Child cortical activation patterns*

Extending neural synchrony analyses, we explored individual cortical activation patterns. Child brain activation analyses showed a different pattern between conditions. The linear mixed effect model revealed a significant effect of condition, $F(2, 1872) = 4.84$, $p = .008$, as well as a significant interaction of condition with region, $F(6, 1872) = 2.72$, $p = .01$. Post-hoc contrasts of conditions depict higher cortical activation patterns in both resting phases as compared to the individual condition, $t(1612) = 2.62$, $p = .02$. The cooperation and resting condition did not differ significantly in cortical activation patterns, $p > .15$. When we separated the contrast of conditions by ROI, the results show a higher cortical activation in resting phases in right temporo-parietal areas in comparison to cooperation and individual task phases, $t(1612) = 2.80–3.61$, $p = .01$ and $p = .001$. The other ROI showed no separation in cortical activation regarding conditions, $p > .16$.

We also included individual as well as dyadic task performance, behavioral reciprocity and agency as predictor variables in the model, which yielded a significant interaction between condition and individual task performance, $F(4, 1628) = 3.33$, $p = .01$. Only children, who were able to solve the task by themselves from the beginning, showed higher brain activation in frontal and temporo-parietal areas during the cooperation condition in comparison to individual and resting phases, $t(1628) = 2.57–3.89$, $p = .000-.027$, respectively. Child brain activation patterns were also related to dyadic task performance in interaction with condition and ROI, $F(6,1760) = 2.33$, $p = .03$. Particularly, higher cortical activation in the left frontal region during the cooperation condition was associated with more templates solved. Agency and behavioral reciprocity showed no effect on child cortical activation patterns, $p > .23$.

3.5.2. *Mother cortical activation patterns*

When individual mother brain activation were analyzed, the linear mixed effect model revealed a significant effect of condition, $F(2, 1672) = 4.82$, $p = .01$. Post-hoc contrasts of conditions show higher cortical activation patterns in all ROI in the cooperation condition as compared to the individual condition, $t(1733) = 2.99$, $p = .01$. Brain activation in resting phases were only marginally lower than in the cooperation condition, $t(1733) = 2.20$, $p = .07$.

Here, we again included dyadic task performance, but also maternal sensitivity, behavioral reciprocity and general stress level as predictor variables, which yielded a significant interaction between condition and maternal sensitivity, $F(2, 1680) = 3.32$, $p = .04$. Mothers, who had higher sensitivity ratings, showed lower brain activation in all ROI. Maternal brain activation patterns were marginally related to dyadic task performance in interaction with condition, $F(2,1672) = 2.62$, $p = .07$. Higher cortical activation in all ROI during the cooperation condition were marginally associated with more templates solved. Furthermore, behavioral reciprocity and general stress level showed no effect on maternal cortical activation patterns, $p > .16$.

4. Discussion

In the present study, we aimed to clarify the relation between interaction quality and neural synchrony during a naturalistic caregiver-child interaction involving cooperative problem solving. In contrast to previous studies, we tested whether interpersonal neural synchrony between mothers and children can be measured during a complex task without an inherent rhythmicity — in comparison to control conditions without direct engagement. Here, we integrated measures of complex social behavior with concurrent brain imaging to gain new insights into caregiver-child interactions. By concentrating on interaction quality and individual differences in the functioning of the caregiving system in the mother as well as temperament in the child, our goal was to measure how such dyadic and individual differences would be related to neurobehavioral synchronization during induced cooperation. In line with previous studies using more controlled and artificial tasks (Miller et al., 2019; Reindl et al., 2018), our findings demonstrate that mother-child dyads showed higher neural synchrony in the temporo-parietal and lateral prefrontal areas when solving a naturalistic task in cooperation, in comparison to when they solved the same task individually. Extending these findings, we found that neural synchronization was accompanied by higher behavioral reciprocity during joint problem solving in caregiver-child dyads. Strikingly, only neural synchronization but not behavioral reciprocity was associated with the dyad's task performance. This indicates that the function of neural synchrony may go beyond behavioral attunement as far as it can be assessed from video-recorded behavior. In other words, neural synchrony may indicate levels of mutual task engagement and shared attention that cannot be easily inferred from the observed behavior alone. Regarding individual factors on neural synchronization, we found that interaction-based measures, such as child agency, even though only marginally, correlated positively with neurobehavioral synchrony, while trait-like, self-report measures did not seem to be linked to synchronization. Hence, these results further highlight the complexity and time-specificity of neural synchronization between two individuals (Hasson et al., 2012), particularly in the caregiver-child context.

First, our results confirm the role of frontal and temporal areas for neurobehavioral synchronization in caregiver-child interactions. Neural synchrony in temporal areas has been previously linked to adequate and effective cooperation within a dyad (Jiang et al., 2012; Miller et al., 2019). While cooperating, mother and child constantly engage in mentalizing processes to predict each other's intentions while attending to the same object (Baimel, Severson, Baron, & Birch, 2015). Understanding the other person might thus have been facilitated by higher neural synchronization, meaning that when the mothers' and children's brain activity was temporally aligned, less effort may have been required to reason about and react to the other person (Keller et al., 2014; Koban, Ramamoorthy, & Konvalinka, 2019). At the same time, mother-child dyads displayed neural synchrony in frontal areas. Interactive social decision making and effective communication have previously been associated with interpersonal synchrony in the dlPFC (Zhang, Liu, Pelowski, Jia, & Yu, 2017). Our results thus corroborate earlier studies showing the involvement of frontal and temporal areas in caregiver-child interactions (Miller et al., 2019; Reindl et al., 2018), but the functions of neural synchronization in specific regions are to be tested in future studies.

Our findings also indicate, in line with previous proposals (Hasson et al., 2012), that neural coupling is essential to social information exchange. Overall neural synchronization in the caregiver-child dyads was associated with task performance as an interactional outcome of the problem-solving task. This finding corroborates recent similar findings in more controlled caregiver-child interactions (Miller et al., 2019; Reindl et al., 2018) and a tangram puzzle task with adults (Fishburn et al., 2018). The more the dyads synchronized in their brain activity, the more tangram templates they solved, which underlines the role of neural synchronization for optimal information exchange and cooperative task performance. Moreover, we find that neural synchrony occurs not only during verbal communication, but expands to non-verbal information exchange, similar to the multi-modal turn-taking behavior reported in adults earlier (Fishburn et al., 2018; Jiang et al., 2012). Particularly responsive and contingent turn-taking behavior, i.e., reciprocity, in a dyad was related to co-ordination between caregivers and children. More reciprocally behaving dyads showed higher neural synchronization. Interestingly, reciprocity was exclusively related to neural synchrony between mother and child, while task performance could also be predicted by cortical activation patterns of the child (see SI Section 3). Our findings extend results from an earlier study (Levy, Goldstein, & Feldman, 2017) during which mothers and their 9-year old children watched vignettes of their own interactions. The perception of social synchrony in those interactions was linked to interpersonal neural coupling in the superior temporal sulcus of mother and child. Here, we were able to identify additional cortical regions beyond the temporo-parietal area, i.e., the dlPFC, involved in the perception and active engagement of reciprocity, as mother and child were concurrently assessed in a live social interaction. This set of findings on the one hand highlights the necessity to take behavioral coordination into account when investigating neural synchrony, as behavioral processes may facilitate interpersonal synchronization of brain activities (Markova, Nguyen, & Hoehl, 2019). On the other hand, our findings emphasize the need for second-person neuroscience approaches to investigate the mechanisms of social interaction (Redcay & Schilbach, 2019).

When we looked closer into the effect of neural synchrony on joint problem solving, we found that both neural synchrony during cooperation as well as during resting phases, even though the latter only weakly, was related to task performance. This finding raises an important question: might there be a default coherence between caregivers and children at rest, which increases or decreases by context? The assumption of a default synchrony between mothers and children is supported by studies showing physiological synchrony in cortisol responses within families (Papp, Pendry, & Adam, 2009; Pratt et al., 2017): Synchrony in cortisol responses increased in interactive contexts but was still evident in non-interactive contexts. Moreover, physiological synchrony declined when the relationship between caregivers and children was disrupted, for instance in cases of maternal depression or child disorganized attachment (Leclère et al., 2014). Therefore, synchrony in physiological markers is discussed to be involved in the intergenerational transfer of stress physiology, and neural synchrony may serve a similar function in the development of attachment (Vrticka, 2017). We also observed a relatively high overlap in coherence between conditions. Resting phase neural synchrony between mothers and children could therefore stem from sustained processing or layover effects from participation in the whole task procedure. Mothers and children might still have engaged in thought processes regarding the other person as well the task as such. As Trapp, Havlicek, Schirmer, and Keller (2018) illustrate, attentional entrainment to stimuli only disintegrates gradually after the stimuli disappear. Thus, resting phase neural synchrony in our study could include layover effects from the mutual engagement in the tangram puzzle task. Layover effects could also stem from the experience of task order, as Over and Carpenter (2013) suggest that initial context information can induce either a focus on social or learning goals in a given task setting. More studies will have to be conducted to probe whether there is a function to resting phase neural synchrony within dyads and to tease apart possible layover effects from prior conditions.

Our findings showed high interdyadic variance within neural synchronization during caregiver-child interaction. Hence, we investigated individual factors that have previously been related to behavioral reciprocity (Harrist & Waugh, 2002). We looked at both state-like measures assessed by video-based ratings, as well as trait-like measures assessed by self-reports. We found that child agency was linked to neural synchronization, indicating the role of autonomy in social interactions during preschool age. The greater a child's agency, the more a child is able to engage in a task instead of being led by others (Clark & Ladd, 2000). Thus, mutual task engagement might have led to better behavioral coordination and in turn successful joint-problem solving, as previous studies display evidence for such a link between autonomy support and problem-solving (Bernier, Carlson, & Whipple, 2010; Clark & Ladd, 2000; Raver, 1996). This comes to show that encouraging child agency at preschool age might have important implications, especially in a challenging problem-solving situation. In addition, this finding supports the notion of a more balanced interaction from preschool age on, as children's social-cognitive abilities mature (Harrist & Waugh, 2002). Interestingly, the effects of child agency acted on the general neural synchronization of the dyad and were not specific to the cooperation condition. These findings might point towards a layover effect of neural synchronization from the mutual task engagement in the cooperation condition, as found for sustained neural entrainment in an attention task (Trapp et al., 2018). To conclude, neural synchrony might be a biomarker for mutual task engagement and therefore create an optimal learning environment for the child (Hoehl & Markova, 2018).

In addition to these interaction-based measures of reciprocity and agency, we tested the effects of maternal self-reported stress on neural synchrony in caregiver-child dyads. Even though our findings do not replicate the relation between maternal stress and maternal sensitivity as shown in earlier literature (Booth et al., 2018), they are in line with the reported effects of stress on bio-behavioral processes (Swain et al., 2017). Particularly, neural alterations show that parental stress affects brain regions connected to reflective self-awareness and the decision-making neurocircuitry, which may mitigate a parent's ability for perspective taking. In line with these results, we find that self-reported parental stress was related to reduced neural synchronization between mothers and their children.

There were, however, no effects of broader, trait-like factors related to attachment and caregiving on mother-child neural synchrony in our data. There could be several reasons for this result. As proposed by Hasson et al. (2012), neural coupling occurs via signal transmission through the environment. This model thus points towards a time-localized occurrence of neural synchronization, which is rather influenced by concurrent, immediate behavior, such as the role of eye gaze and vocalizations as found in a study by Leong et al. (2017), as well as concurrent physiological processes (Feldman et al., 2011; Pratt et al., 2017). To further explore the role of various variables indicating different components of interaction quality, it would be important to assess event-related measures of behavioral synchrony, enabling the relation of certain behaviors to events of neural synchronization. This approach could lead to further insights into what leads to neural coupling. For instance, assessing mind-related comments could yield further insight into the relation between stress and neural synchrony (Zeegers, Colonnesi, Stams, & Meins, 2017). The measures we used as maternal attachment and caregiving variables, as well as the lack of a direct child attachment measure pose another limitation. The self-report measures are efficient to assess and share variance with the underlying constructs, but it might be indispensable to use additional tools derived from attachment research, such as semi-structured narrative interviews like the adult attachment interview or the story stem battery in children to more precisely assess parent-child attachment processes (George, Kaplan, & Main, 1996). It should also be noted that the maternal sensitivity subscale (Hirschmann et al., 2011) is normally used for much longer interactions and might not be as reliable when rated in shorter interactions like in our case. Finally, the lack of variance in our sample with overall middle to high economic status may have attenuated the range of shown behavior and personality factors (Roubinov & Boyce, 2017). The missing variation, therefore, might have impeded our investigation of dyadic and individual factors.

Here we demonstrated interpersonal neural synchronization in frontal and temporal areas during mother-child cooperative problem solving in comparison to individual problem solving. We showed that neural synchronization between mothers and children also occurs in a naturalistic cooperation task, thus increasing external validity beyond highly standardized and artificial settings used previously (Miller et al., 2019; Reindl et al., 2018). Critically, the naturalistic task enabled us to look for variations in dyadic behavior that modulate neural synchrony and task performance. We showed that behavioral reciprocity, an important indicator of caregiver-child interaction quality, was positively associated with neural synchrony. In addition, we found a relation of neural synchrony with cooperative task performance beyond behavioral reciprocity, and we identified first potential factors, namely child agency and maternal stress, influencing neurobehavioral synchronization. Our results shed light on cooperation as a function of neural synchronization during caregiver-child interaction and point towards neural synchrony being a neurobiological marker of mutual engagement and successful coordination in social interactions.

To reach a better understanding of neural synchrony in caregiver-child dyads, it will be indispensable to extend the investigation of individual and dyadic factors for neural synchronization (Hoehl & Markova, 2018). Future research may examine father–child interactions as well as how individual risk-factors such as postnatal depression and preterm birth (Feldman, Rosenthal, & Eidelman, 2014; Granat, Gadassi, Gilboa-Schechtman, & Feldman, 2017) may attenuate neural synchronization. Our study also offers a first glimpse into potential neural implications of attachment-based constructs. Overall, hyperscanning may be able to provide important insights into neurobiological mechanisms underlying dynamic processes in caregiver-child interactions from a second-person approach (Hoehl & Markova, 2018; Redcay & Schilbach, 2019). More specifically, our findings highlight the potential in yielding a deeper understanding of the mechanism and preconditions of how caregivers can support children to not only understand themselves, but also others and the world around them.

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Open practices

The study in this article earned Open Materials and Open Data badges for transparent practices. The preregistration for the study is available at: https://aspredicted.org/i7k95.pdf.

NIRS, demographics, questionnaire and behavioral data as well as all digital study materials are stored on OSF: https://osf.io/75fet/.

MATLAB analysis code has been made publicly accessible here: https://github.com/tnguyen1992/MPI-CBS_Caregiver-Child-Interactions.

The conditions of our ethics approval do not permit public archiving of video data. Readers seeking access to the data should contact the lead author Trinh Nguyen. Access will be granted to named individuals in accordance with ethical procedures governing the reuse of sensitive data. Specifically, requestors must meet the following conditions to obtain the data: completion of a formal data sharing agreement.

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

Declaration of Competing Interest

The authors assert that they have no competing interests.

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Supplementary data

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Interpersonal Neural Synchrony During Father–Child Problem Solving: An fNIRS Hyperscanning Study

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Interpersonal neural synchrony (INS) has been previously evidenced in mother–child interactions, yet findings concerning father–child interaction are wanting. The current experiment examined whether fathers and their 5- to 6-year-old children ($N = 66$) synchronize their brain activity during a naturalistic interaction, and addressed paternal and child factors related to INS. Compared to individual problem solving and rest, father–child dyads showed increased INS in bilateral dorsolateral prefrontal cortex and left temporo-parietal junction during cooperative problem solving. Furthermore, the father's attitude toward his role as a parent was positively related to INS during the cooperation condition. These results highlight the implication of the father's attitude to parenting in INS processes for the first time.

During the last decades, the paternal role has evolved substantially alongside major societal changes. It is widely agreed upon and supported by scientific studies today that children benefit from their fathers in numerous ways (Lamb, 2010). For example, fathers' presence is associated with better cognitive development and greater perceived competence (Dubowitz et al., 2001). These new insights have been accompanied by the increasing recognition of fathers as caregivers and attachment figures by attachment theory where an important paradigm shift has occurred during the last two decades (Ahnert & Schoppe-Sullivan, 2020), entailing a surge in research exploring the father–child dyad including father–child interactions (Bakermans-Kranenburg, Lotz, Dijk, & van IJzendoorn, 2019). A recent study provided the first evidence for an association between fathers' interactive behavior and variation in infant brain anatomy (Sethna et al., 2019), and other research linked experiencing fatherhood with neural changes in the father in brain areas associated with mentalizing and emotion processing (i.e., superior temporal sulcus or inferior frontal gyrus; see Bakermans-Kranenburg et al., 2019). At the same time, and despite

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increasing knowledge on the relation between father–child interaction and children's outcomes, little is known about the behavioral dynamics and brain mechanisms that possibly underlie this association. With the advancements of hyperscanning in parent–child interactions, interpersonal neural synchronization (INS)—suggested to support behavioral coordination and communication—has so far mostly been evidenced in mother–child interactions (Nguyen, Bánki, Markova, & Hoehl, 2020). Here, we present a functional near-infrared spectroscopy (fNIRS) hyperscanning study investigating interpersonal neurobehavioral synchrony in father–preschool child dyads specifically.

During early social exchanges, behavioral coordination—such as synchrony—has been suggested to be essential to a child's social, cognitive, and affective development (Feldman, 2012). More recently, this account was extended to also include synchrony on the physiological (e.g., heart rate, cortisol secretion) and neural (e.g., brain activity) levels (Feldman, 2017; Leclère et al., 2014). Focusing specifically on neural synchrony, the rhythmicity in behavioral coordination has been proposed to be reflected in the synchronization of neural oscillations (Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012; Markova, Nguyen, & Hoehl, 2019). As the behavioral communicative rhythms are transmitted through the environment (e.g., as speech sounds), the sensory system of one person is coupled to the motor system of another person. In both individuals of an interacting dyad, entrainment of internal neuronal oscillations to external rhythms has been shown to enable optimal processing of rhythmic stimuli, because sensory input is then sampled during phases of high neuronal co-excitability (Calderone, Lakatos, Butler, & Castellanos, 2014). Accordingly, INS has been proposed as an essential mechanism to facilitate the transmission of information through verbal and non-verbal communication between a dyad (or within groups; Dumas, Lachat, Martinerie, Nadel, & George, 2011; Hasson et al., 2012). A growing body of research indeed provides evidence for higher levels of INS during cooperative interactions to be associated with higher task performance in terms of joint goal achievement in adults as well as adult–child dyads (see Hoehl, Fairhurst, & Schirmer, 2020). These findings underscore facilitated coordination and communication in relation to increased INS for parent–child dyads. The above said, data on the neural aspect of bio-behavioral synchrony during social interaction remain scarce. This generally applies for parent–child dyads, but particularly so for father–child dyads.

Existing hyperscanning studies using fNIRS have mostly investigated INS in mother–child dyads (Nguyen, Bánki, et al., 2020). fNIRS allows to measure brain activity, indicated by oxygenation changes in hemoglobin, in naturalistic interactions. It is less susceptible to motion artifacts while compromising on cortical depth and temporal resolution in comparison to fMRI and EEG/MEG, respectively (refer to Lloyd-Fox, Blasi, & Elwell, 2010 for more information). In a growing body of research, INS in caregiver–child dyads—involving children of different ages from infancy to school age—has been observed during naturalistic problem solving (Nguyen et al., 2020a; Quiñones-Camacho et al., 2019), non-verbal dyadic interaction (Piazza, Hasenfratz, Hasson, & Lew-Williams, 2020), free verbal conversation (Nguyen et al., 2020b), as well as standardized cooperative button-press tasks (e.g., Reindl, Gerloff, Scharke, & Konrad, 2018). These studies provide first evidence for INS during caregiver–child interaction for different child age groups from infancy to adolescence and across a range of different interaction contexts. Common to all published studies with children is that INS varied as a function of mutual engagement across different behavioral modalities (i.e., gaze, speech, motor) in the given task or interaction. In contrast, when assessing behavioral coordination, the relevant modalities change in their relevance as children develop. For example, conversational coordination only emerges when children can verbalize themselves (Feldman, 2012). We thus propose INS as a useful biomarker for mutual engagement in parent–child interaction. Studying INS in father–child dyads can help us better understand the unique features and commonalities in mother–child and father–child interactions and may unveil essential mechanisms to interpersonal behavioral coordination throughout early childhood.

Studies on mother–child cooperation and communication consistently report INS in the temporoparietal junction (TPJ) and lateral prefrontal cortex (PFC), even though different estimation methods for INS were used (see Nguyen, Bánki, et al., 2020). INS in the TPJ has been implicated in interpersonal behavioral coordination, which is essential to parent–child interactions (Hoehl et al., 2020; Leclère et al., 2014). Interpersonal alignment of rhythms during coordination depends on various influencing factors, notably their socio-emotional value, computed in temporoparietal regions including the TPJ (Koster-Hale & Saxe, 2013). Besides the tracking of socio-emotional value of incoming visual information and engagement in mental state representation associated with TPJ functions, cooperation also involves top-down cognitive control over emotional processes in social contexts. This function is associated with the engagement of a cognitive control system mainly localized in lateral prefrontal areas (i.e., dorsolateral prefrontal cortex [dlPFC]; Balconi & Pagani, 2015; Long, Verbeke, Ein-Dor, & Vrticka, 2020). Thus, INS in the dlPFC is suggested to represent a potential biomarker for mutual attention and shared intentionality during social interactions, as well as to reflect emotion regulation abilities (Gvirts & Perlmutter, 2020; Reindl et al., 2018). Overall, the emerging findings suggest a prominent role of the TPJ and dlPFC in INS during caregiver–child interactions.

Although fathers are increasingly recognized as caregivers and attachment figures to their children, parent–child hyperscanning studies focusing on or including father–child interactions are scarce. The available behavioral data suggest that fathers' and mothers' interactional behavior toward their children should in principle not substantially differ. For example, father– and mother–child dyads appear to show similar levels of interpersonal behavioral synchrony during their interactions (de Mendonça, Bussab, & Kärtner, 2019; Feldman, 2003), and father– and mother–child interaction quality seems to be comparable more generally (e.g., Piskernik & Ruiz, 2020). These results suggest that father–child dyads might show comparable associations of INS to state-like factors, such as behavioral reciprocity, as mother–child dyads.

Besides state-like factors relating to behavioral synchrony of the dyad, other state-like factors concerning parent characteristics have been probed. Two studies revealed maternal stress to attenuate INS in mother–child dyads independent of the interactive context (Azhari et al., 2019; Nguyen et al., 2020a). Conversely, maternal sensitivity as another predictor of parent–child relationship quality (Leclère et al., 2014) could so far not be linked to INS—although such lack of association may be due to too little variance in the assessed high socioeconomic status sample (Nguyen et al., 2020a). Similar qualities of paternal behavior also seem to affect children's development (Brown, Mangelsdorf, & Neff, 2012). More precisely, fathers' involvement in child care is related to fathers' sensitivity in caregiving and subsequent positive outcomes in child development (Cowan, Cowan, Pruett, & Pruett, 2019; Flouri, Midouhas, & Narayanan, 2016). More generally, the trait-like factor of father involvement is not only suggested to positively affect fathers' caregiving behavior but also to change fathers' physiology (Bakermans-Kranenburg et al., 2019). In contrast, perceptions of distress related to parenting may shape fathers' behavior in ways that have a negative impact on children and may even put them at risk for psychopathology (e.g., Barker, Iles, & Ramchandani, 2017). Taken together, these findings emphasize the need to take state-like factors like paternal sensitivity and distress, as well as trait-like factors like father involvement into account when studying father–child interactions using hyperscanning in the context of bio-behavioral synchrony.

Additionally, results from other fNIRS hyperscanning studies corroborate findings from behavioral research highlighting the increasingly active role of the child during interactions at preschool age (Harrist & Waugh, 2002; Nguyen et al., 2020a). While Nguyen et al. (2020a) observed that child agency, a state-like factor, could facilitate INS within mother–child dyads, Quiñones-Camacho et al. (2019) emphasize the role of child irritability during recovery phases of stressful interactions as potentially inhibiting task-related INS. Moreover, the biological sex of the child seems to be related to the interaction qualities of father–child dyads (de Mendonça et al., 2019). Crucially, however, the evidence here is somewhat inconsistent. For example, while father–daughter dyads were observed to be more attuned with fathers showing more sensitive, structuring, and non-intrusive behavior toward their daughters (e.g., de Mendonça et al., 2019), other observations indicated that fathers are more involved with and responsive to their sons (Feldman, 2003). Also, earlier studies suggest that fathers are more likely to support active play in boys than in girls (Tauber, 1979) and father–son interactions are marked by higher child agency without getting into conflict or competition (Buss, 1981). Combined, there seem to be some inconsistencies in behavioral findings indicating that father–child dyads may be characterized by similar—but not necessarily equal—patterns in INS and interaction quality as compared to mother–child dyads. At the same time, available findings indicate that father–child dyads may likely show sex differences in their interaction qualities. Henceforth, it appears that child biological sex needs to be considered in the investigation of father–child INS.

In the present study, we specifically focused on the question of whether father–child dyads show INS during cooperative problem solving measured with fNIRS hyperscanning. The task was contrasted with an individual problem-solving control condition as well as rest phases. We were able to build on the preexisting literature with mother–child dyads using the tangram puzzle task (Nguyen et al., 2020a) to test whether father–child dyads would show similar patterns of INS during problem solving, including the state- and trait-like factors already assessed within this context. The fact that we exclusively focused on fathers as the caregiver during these interactions allowed us to deepen our understanding of the neurobiological underpinnings of parent–child interactions in general, and provided the opportunity to investigate potential factors specific to father–child dyads either facilitating or attenuating neurobehavioral synchronization. Moreover, understanding how similar patterns in both behavior and brain-activity may conform but also differ between mother–child and father–child dyads may hopefully shed light on the unique contribution of fathers for child development.

We investigated the following main research questions:

1. Do fathers and children show increased INS during the cooperative problem-solving task in comparison to individual and resting phases? Given above-cited evidence that increased INS in the TPJ and dlPFC has been found in several mother–child studies with a range of child ages (e.g., Nguyen et al., 2020a; Reindl et al., 2018), we expected INS in the same brain areas to be the highest during the cooperation condition (in comparison to all other conditions).
2. Is INS during cooperation related to dyadic behavioral variables, that is, task performance and behavioral reciprocity? The link between INS and task performance has not only been evidenced in mother–child studies but also adult dyads in various forms of cooperative tasks ranging from button-press to problem solving (Nguyen, Bánki, et al., 2020). We therefore also predicted a positive link between task performance and INS in all regions of interest during cooperation in father–child dyads. Furthermore, evidence from recent developmental research suggests higher levels of behavioral reciprocity to be associated with higher levels of INS in the TPJ and dlPFC during cooperative mother–child problem solving (Nguyen et al., 2020a; Quiñones-Camacho et al., 2019). We therefore hypothesized father–child dyads to show the same association in the same brain areas.
3. Is there an association between INS during cooperation and child agency? The role of child agency was previously evidenced by an association with higher INS in the TPJ and dlPFC during mother–child cooperation (Nguyen et al., 2020a). We therefore assumed that this association would show in father–child cooperation as well.
4. What are the parental state-like behavioral and self-report markers of INS in father–child cooperation? We assumed paternal sensitivity to be positively related to INS during cooperation. Although maternal sensitivity was not significantly related to INS during cooperation in a previous study (Nguyen et al., 2020a), we expected fathers' sensitive caregiving to provide unique individual differences in association with INS in both the TPJ and dlPFC during cooperative problem solving. Conversely, according to previous literature indicating that maternal stress may be associated with decreased INS in the TPJ and dlPFC during cooperation (Azhari et al., 2019; Nguyen et al., 2020a), we predicted a similar pattern in the present father–child dyads.
5. Are there any associations between INS during cooperation and more trait-like characteristics associated with fatherhood? As fathers' sensitivity and involvement in child care were found to be related to positive outcomes in child development more generally (Cowan et al., 2019; Flouri et al., 2016), we also expected a positive relation between fathers' appreciation of their role as a parent (measured with the Role of the Father Questionnaire [ROFQ]—see below) and INS in all regions of interest during cooperation.

The present study and the above-mentioned hypotheses were preregistered on aspredicted.com (https://aspredicted.org/u84z6.pdf). We furthermore exploratively evaluated the associations between father–child INS and (a) dyadic and individual behavioral patterns as the well as (b) biological child sex. These additional exploratory analyses were not preregistered.

Method

Sample

Sixty-six fathers (*M* = 39.2 years, *SD* = 5.17 years) and their preschool children (*M* = 5.32 years, *SD* = 0.31 years; 31 girls) participated in the present study. Out of the initially recruited 68 dyads, 2 were excluded due to non-compliance with the given instructions (n = 1) and refusal of the child to wear the fNIRS cap (n = 1). Optimal sample size calculations using G*Power for a medium effect size repeated measures design (groups = 3, f = .25, α = .05, 1-beta = .90) resulted in N = 36. The fNIRS assessment was combined with a subsequent fMRI experiment as well as attachment interviews (not reported here), with a predetermined sample size of N = 50 mother–child dyads with usable data available from all measurements. This cut-off was reached after performing N = 68 fNIRS scans. Data collection took place from May 2018 to July 2019. Fathers were recruited from a database of volunteers based in and around a mid-sized city in eastern Germany. All dyads were of White European origin and came from middle to upper-class families based on parental education and family monthly income. Fathers had on average 6.84 years of higher education and 66.7% of families had a monthly income higher than 3,000€. Fathers were remunerated and children received a small gift for participating. Fathers provided written consent for themselves and their children and all procedures were approved by the local ethics committee.

Procedure

Fathers and their children were welcomed to the lab and led to a testing room. After giving written informed consent the dyad was seated face-to-face, separated by a table, and was guided through a cooperative problem-solving condition (120 s), an individual problem-solving condition (120 s), and 80 s of rest with eyes closed in between each condition (see Figure 1A). Cooperation and individual

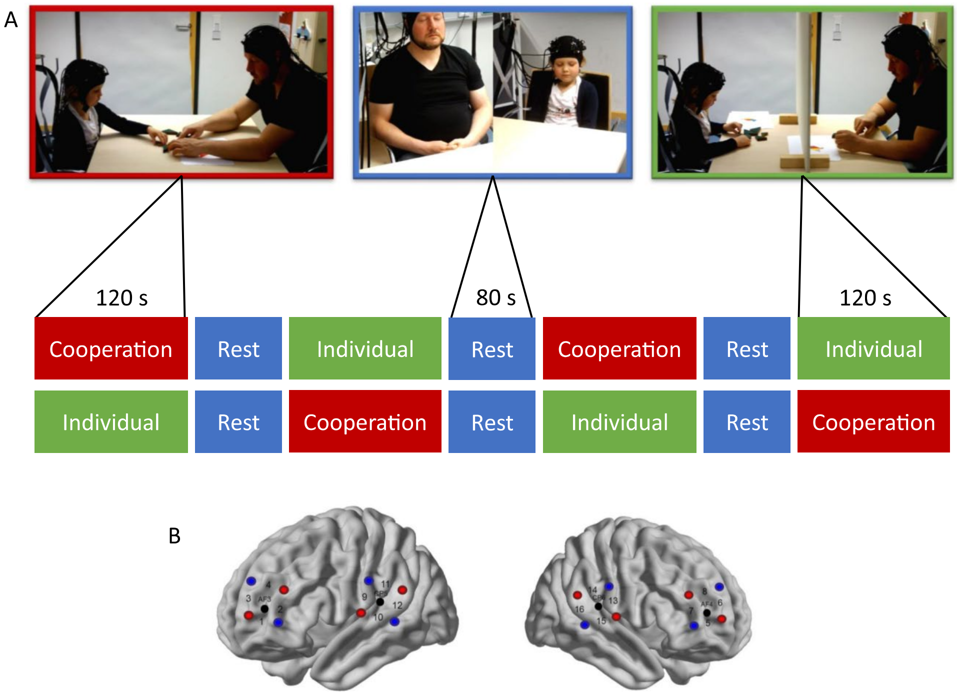


Figure 1. Experimental paradigm. (A) Illustration of the sequence of the experimental procedure showing an exemplary father–child dyad solving the tangram in cooperation (red) and individually (green). The rest phases are shown in blue. The order of conditions was counterbalanced and thus resulted in two possible sequences. (B) Illustration of the optode configuration at bilateral dorsolateral prefrontal cortex and temporo-parietal junction anatomical locations (sources = red, detectors = blue, channel = numbers, EEG position = black). The left hemisphere is visible on the left, while the right hemisphere is depicted on the right.

problem solving were repeated twice and the order was counterbalanced. In the problem-solving conditions, father and child were instructed to either cooperatively or individually arrange tangram puzzles and recreate templates of abstract forms, objects, and animals (see Nguyen et al., 2020a for more information). During the individual condition, an opaque screen was put in between the dyad to help the caregiver and the child to focus on their own puzzle. In the rest phases, father and child were instructed to close their eyes, relax, and refrain from talking to each other. Subsequently, the child had to solve a preschool form (this task will not be reported further here). The whole procedure was recorded on video from three different angles capturing frontal images from the father and the child and one of the whole dyad from the side.

fNIRS Acquisition

We recorded oxy-hemoglobin (HbO) and deoxy-hemoglobin (HbR) concentration changes for each dyad using a NIRScout 8 × 16 (NIRx Medizintechnik GmbH: Berlin, Germany) Optical Topography system. Eight light sources and eight detectors were grouped into four 2 × 2 probe sets and were attached to an EEG cap with 10–20 configuration. The probes were placed according to standard electrode locations. To assess brain activity in the left and right dlPFC electrode locations for AF3 and AF4 were used for guidance, whereas the probes over the left and right temporo-parietal junction (TPJ) were placed according to CP5 and CP6. The regions of interest (ROI) were based on previous studies investigating cooperative parent–child interactions (Nguyen et al., 2020a; Reindl et al., 2018). The four-probe sets resulted in 16 measurement channels with equal distances of 3 cm between the optodes. The absorption of near-infrared light was measured at the wavelengths of 760 and 850 nm and the sampling frequency was 7.81 Hz.

fNIRS Processing

Before analyzing the fNIRS measurements, raw data were visually inspected during an initial quality check procedure. This resulted in 2.16% of the channels from the whole sample to be removed from further analyses. After this initial step, remaining data were pre-processed using MATLAB-based functions derived from SPM for fNIRS (Tak, Uga, Flandin, Dan, & Penny, 2016). Raw optical density values were first motion-corrected with MARA, a smoothing procedure based on local regression using weighted linear least squares and a 2nd-degree polynomial model (Scholkmann, Spichtig, Muehlemann, & Wolf, 2010), and then filtered with a high-pass parameter of 0.01 Hz (Reindl et al., 2018). Next, the filtered data were converted to HbO and HbR values based on modified Beer-Lambert Law with age-dependent differential path length factors. In the following statistical analyses, we focused on HbO values, which were reported to be more sensitive to changes in the regional cerebral blood flow (Hoshi, 2016). Statistical analyses for HbR are included in the Appendix S1.

Wavelet Transform Coherence

INS was estimated using Wavelet Transform Coherence (WTC) based on the Morlet wavelet (Chang & Glover, 2010; Grinsted, Moore, & Jevrejeva, 2004 for more information). WTC estimates a coherence coefficient between two fNIRS time series based on frequency and time and thus results in a synchrony score comprising both in-phase and phase-lagged synchrony in a certain frequency band. WTC is the most commonly used estimation approach to INS (see Czeszumski et al., 2020) and includes both time-related as well as frequency-related properties of the two time-series. The frequency band of interest for this study was determined to be 10–50 period seconds (approx. 0.08–0.1 Hz) based on visual inspection and a previous study using the same paradigm (see Figure A1 in Appendix S1; Nguyen et al., 2020a). WTC values were averaged across conditions and frequency bands to result in 16 (channels) × 4 (conditions) INS values. For all four conditions the same length of data, namely 240 s, went into the calculation. We further conducted a random pair analysis with 1,000 permutations to rule out effects due to spurious correlation - please refer to the Appendix S1 for further details.

Behavioral Task Performance and Interaction Quality

Individual and dyadic task performance were indexed by the numbers of templates solved during the individual and cooperation condition, respectively. Interaction quality, namely behavioral reciprocity, parental sensitivity, and child agency, during the cooperation condition was rated by three graduate students from the video recordings using a coding scheme adapted from a previous study investigating INS during mother–child problem solving (Nguyen et al., 2020a). Shortly summarized, ratings of child agency and behavioral reciprocity were derived using a customized coding scheme based on the Coding System for Mother–Child Interactions (Healey, Gopin, Grossman, Campbell, & Halperin, 2010), and paternal sensitivity was assessed with a German instrument labeled INTAKT (an agglomeration of the German word "Interaktion" meaning interaction, and "intakt" meaning intact—referring to an intact mother child relationship; Hirschmann, Kastner-Koller, Deimann, Aigner, & Svecz, 2011). For more details on these coding scales (as well as interrater reliability from 25% of the video recordings calculated as intraclass correlations—ICC), please refer to Table 1. Each scale was rated on a 7-point Likert-type scale (1 = *no occurrence*, 7 = *continuous occurrence*) and averaged over the two cooperation conditions. Any discrepancy of more than one point on each scale between coders was reviewed and a consensus was obtained.

Additional Trait-Like Variables From Self-Reports Related to Fatherhood

Role of the Father Questionnaire

Fathers' attitudes toward fatherhood (i.e., the extent that fathers believe to play an important role for child development) were measured using a German translation of the ROFQ (Palkovitz, 1984) adapted to fathers of preschoolers. The ROFQ contains 15 items and fathers indicate their level of agreement or disagreement with each item on a 5-point scale. Higher scores reflect attitudes that fathers are capable of caring for children and that they should be involved with and act sensitively toward their children. Internal consistency was adequate with Cronbach's α = .78.

Parenting Stress Index

The current amount of fathers' parenting stress was assessed with the short German version of the Parenting Stress Index (Tröster, 2011). This self-report questionnaire evaluates the magnitude of parental stress within the child and the parenting domain. It consists of 48 items that form brief statements on stressors regarding the parent's perception of the child and the parent's functioning using a 5-point Likert scale ranging from 1 (*not at all*) to 5 (*very strong*). Internal consistency was high with Cronbach's α = .91.

Statistical Analysis

Statistical analyses were run in RStudio (RStudio Team, 2020). Behavioral and questionnaire data analysis was conducted using linear regressions for

Table 1
Scale Names, Descriptions, and Interrater Reliability Are Depicted in the Table

Subscales	Description	Intraclass correlation
Cooperative task performance	Cooperative task performance is indicated by the number of templates solved during the cooperation condition	—
Individual task performance	Individual task performance is indicated by the number of templates the child solves by him or herself during the individual problem-solving condition	—
Behavioral reciprocity	Contingent behavioral responses to the interaction partner and mutual engagement in the task. Higher ratings indicate turn-taking and that the dyads were attentive to one another. They took interest and pleasure in the mutual task completion as well as in the interaction. Furthermore, dyads with high scores displayed reciprocal behaviors coupled with signs of shared affect, such as smiling or eye contact. Dyads scoring low on the scale are characterized as being impatient or having disregard for the partner's actions, being passive, or completing the task in parallel without any shared experience	r = .74
Paternal sensitivity	The scale entails the father's prompt, appropriate, and sensitive response to his child's signals. Fathers who scored high on this scale were continuously oriented towards the child's needs and wishes. They were loving and warm and gave appropriate and supportive feedback in a way that motivated the child. Low sensitivity was characterized as low emotional engagement with the child or in the interaction, and being insensitive to the child's cognitive and emotional needs	r = .83
Child agency	This scale captures how the child approaches the task. High scores were assigned to a child that shows interest, vigor, enthusiasm, and eagerness to do the tasks. The child invested efforts in his or her activities, was confident and valued success. Moreover, high scores indicate that the child took on a leading role. Low scores imply a lack of confidence, interest or excitement, hesitant behavior, or restrained affect	r = .89

behavioral scales, that is, task performance, parental sensitivity, child agency, engagement, as well as self-report scales, that is, role of the father and parental stress. Behavioral reciprocity was analyzed using zero-inflated Poisson regressions. We corrected *p*-values with the false discovery rate (FDR; $q < .05$) for multiple comparisons. Descriptive statistics and results of linear regressions are reported in the Appendix S1.

For the INS analysis across our four ROIs and three conditions, a linear mixed-effects model was calculated with the package lme4 (Bates, Mächler, Bolker, & Walker, 2015). As WTC values ranged from 0 to 1, they were Fisher's *z* transformed. WTC values were entered as the response variable with condition (cooperation vs. individual vs. rest) and the interaction effect of ROI (four per dyad) as fixed factors and with random slopes for each condition in each dyad. For each a priori hypothesis, an individual statistical model was calculated. To test for the effects of individual and dyadic factors on INS beyond looking at the main pattern of INS (Model 1), we estimated the following statistical models using a subset of data containing only WTC values from the cooperation condition versus the individual condition (the latter serving as an active control condition) according to our pre-registration. Model 2 (dyadic interaction variables) included the fixed and interaction effects of condition, cooperative task performance and behavioral reciprocity. Model 3 included the fixed and interaction effects of condition and child agency. Model 4 (state-like paternal variables) comprised the fixed and interaction effects of condition, paternal sensitivity and parental stress. Model 5 (trait-like paternal variables) included the fixed and interaction effects of condition and the Role of the Father. All model formulae and further details on model output are included in the Appendix S1.

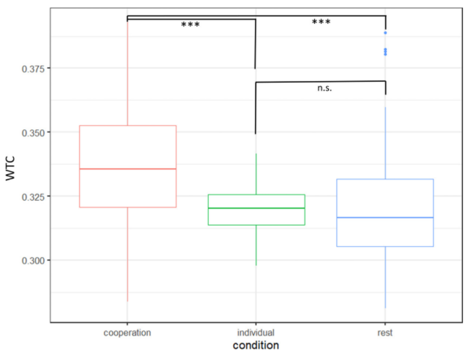
Model fit was obtained comparing the full models that included all predictors with the respective null models that only included the random effect structure using a Likelihood ratio test (Dobson, 2002). To examine the significance of fixed effect factors, we calculated confidence intervals with the function confint to estimate robustness (i.e., confidence intervals excluding 0) and post-hoc comparisons using the package emmeans to further analyze the relations according to our pre-registered hypotheses. *p*-values in post-hoc contrasts were corrected using Tukey's honest significant differences (Abdi & Williams, 2010).

Results

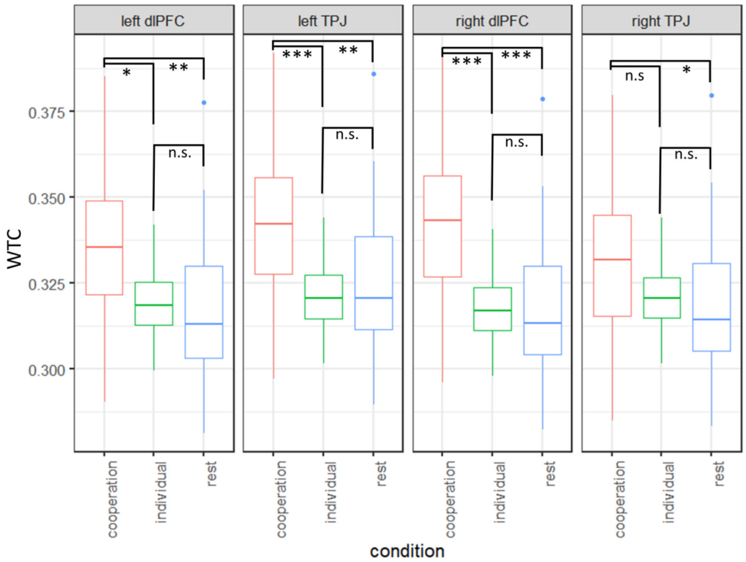
Interpersonal Neural Synchrony

First, we examined whether different father–child contexts of interaction and non-interaction affected dyadic INS in dlPFC and TPJ (Model 1). Linear mixed-effects analysis revealed a significant main effect of condition, $\chi^2(3) = 22.34$, $p < .001$ (see Figure 2). Overall, dyads showed higher levels of INS, in terms of increased WTC, during the cooperative problem-solving task in comparison to individual problem solving as well as rest, $t = 4.31–5.02$, $p < .001$. We found no significant difference between INS during individual problem solving and rest, $p = .984$.

Model 1 also resulted in a significant main effect of ROI, $\chi^2(3) = 9.13$, $p = .027$. However, the interaction between condition and ROI remained non-significant, $p = .121$. Subsequent planned exploratory contrasts between conditions were calculated in each ROI and showed significant increases in INS during the cooperation as compared to the individual and resting conditions in the left and right dlPFC as well as left TPJ, $t = 2.83–4.55$, $p < .002$ (see Figure 3). Contrasts between conditions in the right TPJ were found to be significant for cooperation versus rest, $t = 2.34$, $p = .049$, but only marginal for the cooperation versus individual condition, $p = .096$. Overall, INS was increased in the cooperation condition in all ROI in comparison to an individual condition and rest phases.



ual (green) and rest (blue) conditions (*x* axis).
***$p < .001$.



$p < .001$.

Subsequent analyses included the fixed effect of ROI to control for confounds.

Dyadic Interaction Variables

Model 2 tested the effects of dyadic interaction variables, namely task performance and behavioral reciprocity, and whether they differed in their relation to INS in the cooperation versus the individual condition (the latter serving as an active control condition). Findings revealed nonsignificant main effects and interactions for all predictors, $p > .12$, which means that in the current investigation in father–child dyads, cooperative INS was neither related to dyadic differences in behavioral reciprocity nor task performance.

Child Agency

In a third linear mixed-effects model (Model 3), we probed child agency ratings as fixed effects predictors. Results revealed that child agency was not related to INS in any condition as there were no significant main effects and interactions, $p > .221$.

Paternal Variables

State-Like Variables: Paternal Sensitivity and Parental Stress

In linear mixed-effects Model 4, we tested the effects of state-like paternal variables, that are, paternal sensitivity and parental stress in fathers. Model 4 revealed no significant main or interaction effects involving paternal sensitivity, $p > .572$, and analyses pertaining to parental stress only showed a marginal main effect, $\chi^2(1) = 2.82$, $p = .092$, estimate = −.004, $SE = .003$, 95% CI [−.009, .002]. Although there seemed to be previous indications for higher self-reported parental stress to be related with lower levels of INS during mother–child interaction, this effect did not seem to be robust enough in the present sample of father–child dyads.

Trait-Like Variables: Role of the Father

In Model 5 the effect of the trait-like variable Role of the Father on INS was analyzed. Model 5 revealed a significant main effect of the Role of the Father, $\chi^2(1) = 4.57$, $p = .033$, as well as an interaction with condition that was approaching

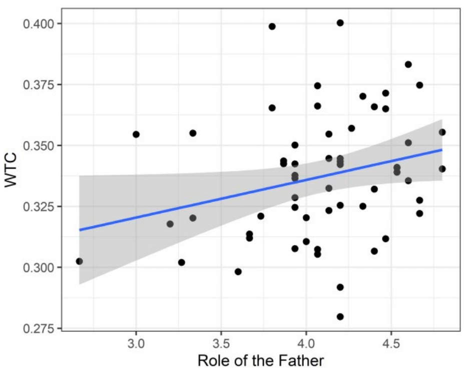


Figure 4. Illustration of the significant positive association between interpersonal neural synchronization (INS; *y* axis) in terms of Wavelet Transform Coherence (WTC) and Role of the Father Questionnaire (ROFQ) scores (*x* axis). The gray shaded area corresponds to 95% confidence intervals and each black dot corresponds to data from one dyad.

significance, $\chi^2(1) = 3.59$, $p = .058$ (see Figure 4). A subsequent post-hoc trend analysis revealed the association to be positive and the most robust in the cooperation condition, estimate = .007, *SE* = .003, 95% CI [.002, .013], while positive but not robust in the individual condition, estimate = .002, *SE* = .003, 95% CI [−.003, .008]. This pattern indicated that when the father's attitude toward his role in child-rearing was more involved, sensitive, and positive, INS in the cooperation condition was increased.

Results of the exploratively evaluated associations between dyadic and individual behavioral patterns as the well as the role of the biological sex of the child on father–child INS are reported in the Appendix S1.

Discussion

In the present study, we investigated whether father–child dyads show interpersonal neural synchronization (INS) in temporo-parietal and dorsolateral prefrontal areas in different interactive and non-interactive contexts. Furthermore, we tested a number of dyadic, parental, and child state- and trait-like characteristics hypothesized to associate with INS. Overall, father–child dyads showed increased INS in bilateral dlPFC as well as left TPJ during a cooperative problem-solving task in comparison to individual problem solving as well as rest phases. This finding specifically in father–child dyads is consistent with previous literature assessing INS during mother–child cooperation at both preschool and school age (see Nguyen, Bánki, et al., 2020). In addition, we identified a significant association between Role of the Father Questionnaire (ROFQ) scores and INS during father–child interaction, being strongest during cooperation - a pattern that again aligns with previous findings from mother–child interaction (Nguyen Kayhan, Matthes, Vrtička, et al., 2020). However, in contrast to extant studies (Nguyen et al., 2020a; Reindl et al., 2018), INS during cooperation in father–child dyads was unrelated to task performance, behavioral reciprocity or child agency. To conclude, our study is the first to underscore that differences in father–child neural synchrony could be related to differences in the trait-like parenting attitude of fathers.

In line with previous fNIRS hyperscanning studies between adults (see Czeszumski et al., 2020 for a review) and caregiver–child dyads with mostly mothers participating (Nguyen, Bánki, et al., 2020), we find that fathers and preschool-aged children show increased INS in the left TPJ as well as bilateral dorsolateral prefrontal areas (dlPFC) during cooperative problem solving. The TPJ is suggested to continuously track the socio-emotional value of temporal regularities in sensory input, such as those induced through behavioral coordination necessary for cooperation (Hoehl et al., 2020). In addition, activation of the TPJ was found to be associated with social connectedness (Eddy, 2016). The dlPFC, on the other hand, has been implicated in cognitive top-down control during cooperation to ensure that attention is directed toward task-relevant information (Gvirts & Perlmutter, 2020). Temporal contingency in cognitive control likely reflects similar, mutually adapted cognitive demands and/or effort. Interestingly, a growing body of hyperscanning research shows that synchronised activity in the TPJ and dlPFC constitutes an important component of the neural mechanisms supporting social interaction (Redcay & Schilbach, 2019).

On a more general note, increased INS in TPJ and dlPFC during cooperation is suggested to be maintained to facilitate attunement and greater allocation of attention to the interaction to reap its potential benefits (Gvirts & Perlmutter, 2020). INS could not only facilitate mutual focus on the given task, but also increase salience of communication cues, thereby enhancing the predictability of social interactions. The more interactions are rhythmic and thus regular, the more they are predictable for both partners. With increased predictability through interpersonal synchrony it becomes easier for one individual to align their own rhythm to the rhythm of another person (Hoehl et al., 2020; Koban, Ramamoorthy, & Konvalinka, 2019). Accordingly, it was proposed that the rhythmic alignment of brain activity may reflect the regularity of interactive rhythms induced by social interactions (Markova et al., 2019). Increased INS in parent–child dyads during cooperation in the left TPJ and bilateral dlPFC may thus also relate to processes involved in processing and prediction of the interaction partner's behavior (see also Perner, Aichhorn, Kronbichler, Staffen, & Ladurner, 2006), which has to be continuously monitored and adjusted to one's own intentions and behavior.

Crucially, although the overall pattern of INS across bilateral dlPFC and TPJ was comparable in mother– and father–child pairs, the anatomical distribution of effects does not appear to be identical (Nguyen et al., 2020a). Father–child dyads only showed marginally significant increases in INS during cooperation in the right TPJ, which is generally linked to mentalizing and shared intention (Perner et al., 2006). Due to the limited information we have on the localization of the optodes, however, we need to proceed cautiously when speculating about the involvement of specific brain areas and their lateralization in INS processes.

Interpersonal coordination on the neural level between mothers and their children was previously found to positively correlate with successful cooperation, namely higher task performance and communication (see Nguyen, Bánki, et al., 2020). INS during the present father–child cooperative task, however, did not seem to be related to task performance. This finding underscores that the neural dynamics in father–child problem solving can diverge from mother–child problem solving although the interaction would follow similar behavioral dynamics (Conner, Knight, & Cross, 1997).

Diverging from mother–child dyads (Nguyen et al., 2020a), we did not find an association between child agency and INS in father–child cooperative problem solving. The absence of this effect is somewhat unexpected since the role of child characteristics and behavior has been described as essential for INS in previous research (Nguyen et al., 2020a; Quiñones-Camacho et al., 2019). Attempting to explain these diverging findings, we need to consider the age-range in the so far available findings on interpersonal synchrony and its role as a mechanism of dynamic mutual adjustments of behavior and brain activity. In caregiver–infant interaction during the first year of life, behavioral and neural coordination are guided by nonverbal communicative rhythms, such as touch, gaze, singing, and vocalizations, and these patterns were shown in both father– and mother–child pairs (Feldman, 2012). As language and symbolic thought emerge toward the second year of life, they become part of the repertoire of how fathers and mothers can establish interpersonal synchrony with their children (Keren, Feldman, Namdari-Weinbaum, Spitzer, & Tyano, 2005). Children further mature in their ability to deliberately engage, both physiologically and socio-emotionally, in social interactions with both parents during their preschool years (Harrist & Waugh, 2002). Concerning the role of child agency in parent–child interactions in that child age range, however, Hughes, Lindberg, and Devine (2018) showed that mothers' support for children's agency and autonomy may be higher than fathers' support. The potential implication of this finding could be that child agency during father–child interactions in that child age range might not be a driving factor for fathers to engage in a reciprocal interaction with their child (Bureau et al., 2014). Within such father–child interactions, child agency would rather map children's engagement in the task itself, which may not be related to INS per se. In future studies, additional dyadic characteristics in association with parental gender should be taken into account to further explore and clarify potential similarities and differences in mother– versus father–child interaction, child agency, and INS.

Besides child agency, we also tested for associations between behavioral reciprocity and paternal sensitivity and INS. However, these two behavioral measures were not significantly related to INS, particularly during cooperation. In previous mother–child hyperscanning studies, interaction quality, in terms of synchrony/reciprocity, during problem solving was shown to positively correlate with INS in the TPJ and dlPFC (Nguyen et al., 2020a; Quiñones-Camacho et al., 2019). Furthermore, Nguyen et al. (2020b) found increased INS to relate with higher amounts of turn-taking during mother–child conversation. However, in the current study, father–child dyads showed rather low levels of reciprocity with limited variance between dyads. The lack of variance in reciprocity between fathers and their children may thus have resulted in a non-significant relation of reciprocity with INS. The low levels of reciprocity further indicate that father–

child joint problem solving was less likely to be coordinated in a turn-taking manner. Even though this finding is in line with behavioral research that fathers are less likely to show cyclic interactions with their children (e.g., Lamb, 2010), it begs the question whether fathers establish INS with their children using different behavioral dynamics in comparison to mothers' continuous adjustments throughout the interaction (see Markova et al., 2019). Future studies should look into the effect of experimentally manipulated levels of reciprocity in a task that necessitates turn-taking behavior to examine how those affect INS.

Regarding parental sensitivity, our analyses did not reveal any association with INS during cooperation. This lack of association is consistent with previous work using the same problem-solving task in mother–child pairs (Nguyen et al., 2020a). Although parental sensitivity did relate to another behavioral measure of interaction quality during both mother– and father–child interaction, reciprocity (see also below), such positive interactional parent characteristics did not seem to translate into INS. More research is needed to unveil whether this lack of association generalizes across other social contexts and age groups. For instance, parental sensitivity may play a more prominent role in more demanding or stressful contexts and/or for younger children.

It should also be mentioned here that no specific associations involving biological child sex during the cooperation condition were present. It was therefore not possible to extend previous observations of fathers supporting their sons' agency by activating them (Paquette & Dumont, 2013) and fathers being more attuned toward their daughters and cater more toward their needs (e.g., de Mendonça et al., 2019) by means of INS in the current study. The issue of biological child sex differences, particularly during father–child interaction, nonetheless remains intriguing and should be further investigated using both behavioral as well as neuroimaging methods.

Apart from looking at associations between INS, behavioral task performance, and interaction quality from video ratings, we also assessed direct relations between the latter two behavioral measures. This revealed several interesting patterns. Behavioral task performance during cooperation was negatively related to paternal sensitivity but positively related to child agency and individual task performance. In addition, there was a positive association between paternal sensitivity and reciprocity.

Sensitive parenting in fathers was previously associated with more reciprocal behavior between fathers and their children (Harrist & Waugh, 2002; Leclère et al., 2014), and suggested to represent a marker for high interaction quality in terms of attachment security (Brown et al., 2012). In the present study, the pattern of results implies that sensitive parenting (with higher reciprocity) during cooperative problem solving was characterized by poorer task performance. In turn, higher cooperative task performance was linked to stronger child autonomy and individual task performance (i.e., child ability). Overall, these findings may suggest that father–child dyads were most successful in terms of cooperative task-performance if fathers did not engage in sensitive and reciprocal behavior but instead the child was able to lead the task as the primary agent. Accordingly, task performance during cooperative interaction was determined by how well the children engaged in and subsequently solved the task by themselves, instead of depending on coordinating dyadic efforts.

Higher sensitivity in fathers was previously associated with engagement in didactic interactions (González, 1996), and INS evidenced during didactic interactions of children with their teacher was linked to learning success rather than cooperative problem-solving success as an outcome (e.g., Bevilacqua et al., 2019). Consequently, cooperative task performance may only consider one style of interaction and thus capture only one out of many potential functions of (parent–child) INS (Hoehl et al., 2020). These considerations may potentially explain some of our findings reported here. While INS during father–child interaction was unrelated to cooperative task-performance and child agency, cooperative task performance was related to both child agency and individual child ability. At the same time, this pattern does not imply a direct link between child ability (i.e., learning success) and parental sensitivity and/or reciprocity. It may be that in the present problem-solving task, INS rather reflected the father's observation of his child leading the task and only giving intermittent, not necessarily sensitive feedback—focusing on the child's learning rather than the cooperation per se. The observed pattern differed from observations we made previously in mother–child pairs engaging in the same task where INS did relate to cooperative task performance and reciprocity (Nguyen et al., 2020a). In future studies, more than one task outcome to parent–child INS should be considered to take the caregiver's interaction role, that is, as playmate, teacher, etc., into account. In addition, it would be very interesting to test children's interactions with both their mothers and fathers, ideally in both dyadic and triadic settings. This would allow for investigating father–mother interaction patterns and relationship quality and their influence on parent–child interaction patterns and relationship quality (and vice-versa).

Besides the influence of paternal sensitivity coded from interaction videos on INS, we observed that fathers' self-reported attitude toward their role as a parent (Role of the Father Questionnaire; ROFQ) was associated with the degree of INS in father–child problem solving. To date, this is the first fNIRS hyperscanning study to find such association. Father involvement is often mentioned as very important and conducive to fatherhood as well as child development (Flouri et al., 2016). Fathers' attitude toward parenting has been shown to be a strong predictor for father involvement and more specifically parent–child interaction quality and quantity (Fox & Bruce, 2001). We assume that stronger identification with being a warm and supporting parent can help fathers in their self-efficacy as well as sensitivity when interacting with their child (Brown et al., 2012). In particular, self-efficacy is maintained to be an important mechanism to influence parenting behavior in terms of consistency, which feeds back to parents being able to engage in more harmonic interactions with their children (Giallo, Treyvaud, Cooklin, & Wade, 2013). Higher interaction quality through stronger identification with being a warm and supporting parent could thus be related to higher levels of INS in parent–child interactions (Nguyen et al., 2020a). Although our results are only preliminary to this vast field of parenting constructs, they underscore the potential factor of parental self-efficacy for future studies concerning parent–child INS.

The current study has some limitations. One limitation is the homogeneity of the participants' socioeconomic backgrounds. It may be that due to the lack of socio-economic variance in our sample, our findings are more strongly representative of a certain caregiver group rather than easily generalizable to the overall population. For example, Allport et al. (2018) report that especially low-resource families struggle with father involvement in child-rearing, which calls for future studies addressing how interpersonal synchronization and parental characteristics interact in different, more varied socio-economic groups. Another limitation is the relatively short interaction duration. The experimental conditions in the present study each lasted for 4 min in total, which is shorter than the intervals used in other studies that derive behavioral ratings from videos (e.g., Hirschmann et al., 2011). Accordingly, our coders had to evaluate the father–child interaction based on fewer observation points, which might have affected the rating results.

Conclusions and Future Directions

This fNIRS hyperscanning study investigated INS during cooperative problem solving in father–child dyads as a function of dyadic behavioral and individual trait-like variables in fathers for the first time. In line with existing results from dyadic fNIRS measurements in school-aged child-parent and preschool child-mother dyads, we report increased INS during cooperation in lateral prefrontal (dlPFC) and temporoparietal (TPJ) brain areas in father–child dyads at preschool age. This said, our data tentatively suggest that INS during cooperative problem solving in father–child dyads may reflect somewhat different underlying processes as compared to those found in mother–child dyads. For example, our findings on INS in father–child dyads weakens the notion of child agency as a central behavioral variable relating to inter-dyadic variability in INS, since it might play a more important role in mother–child than in father–child interaction. Moreover, we only observed an association between INS and cooperative task performance and reciprocity in mother– but not father–child pairs. Future studies might be able to decipher further relevant behaviors and traits in relation to INS in father–child interactions and probe possible mediation / moderation mechanisms (see Feng et al., 2020). A more detailed comparison of behavioral and INS patterns in dyads consisting of mothers and fathers with their children seems to be a promising research avenue. Specifically considering father–child interaction, our study identified fathers' self-reported attitude toward their role as a parent as a relevant factor for father–child INS during cooperation. In a broader societal context, it, therefore, seems relevant to promote the importance of paternal involvement by means of stronger identification with being a warm and supporting parent for child developmental outcomes.

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Supporting Information

Additional supporting information may be found in the online version of this article at the publisher's website:

Appendix S1. Additional analyses and full model outputs