Social Touch is 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 across mammalian species, yet its potential role as a communicative signal in human parent-infant interactions has been sparsely investigated this far. We assessed whether touch enhances neural and physiological synchrony in caregiver-infant dyads. We simultaneously measured brain activity (through functional near-infrared spectroscopy) and respiratory sinus arrhythmia (through electrocardiography) of 69 4- to 6-month-old infants and their mothers in distal and proximate non-interactive conditions vs. an interactive condition. Findings revealed that neural synchrony was highest during the interaction, next in the proximate, and lowest in the distal non-interactive condition. Physiological synchrony was highest during the interaction and lower in both non-interactive conditions. Furthermore, maternal affectionate touch during the interaction was positively related to neural but not physiological synchrony. This is the first evidence showing that touch mediates mutual attunement of brain activities in infants and their caregivers in naturalistic interactions.

Keywords: Mother-infant interaction; functional near-infrared spectroscopy; hyperscanning; synchrony; respiratory sinus arrhythmia; touch

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We begin to encounter the world by the sense of touch, one of the earliest developing senses (Hertenstein, 2002). In the first months of an infant's life, social touch is an essential signal for caregiver and infant to communicate with one another and form their unique bond (Feldman, Singer, & Zagoory, 2010). In contrast to the known long-term physiological and psychosocial benefits of touch on infants' development, its more transient role in caregiver-infant synchrony has only recently been suggested (Feldman, 2007; Markova, Nguyen, & Hoehl, 2019). Caregiver-infant synchrony is defined as "the matching of behavior, affective states, and biological rhythms between parent and child that together form a single relational unit" (Feldman, 2017). Temporally aligning with another person facilitates mutual prediction, interpersonal coordination and allostasis, i.e. the ongoing interpersonal physiological regulation required to meet the changing demands of the environment (Atzil, Gao, Fradkin, & Barrett, 2018; Hoehl, Fairhurst, & Schirmer, 2020; Koban, Ramamoorthy, & Konvalinka, 2019). In these embodied interactions infant and caregiver typically fluctuate between aligned and misaligned states (Montirosso & McGlone, 2020). Touch could be one of the main tools enabling the dyad to "repair" such misaligned states.

Recently, Feldman (2007) proposed that behavioral interactional alignment was associated with interpersonal neural synchrony (INS) and interpersonal physiological synchrony (IPS). Studies on INS and IPS mainly examined adult dyads (Babiloni & Astolfi, 2014; Czeszumski et al., 2020; Dumas, Lachat, Martinerie, Nadel, & George, 2011; Gvirts & Perlmutter, 2020; Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012). The exact conditions under which INS and IPS arise in caregiver-infant dyads are still to be determined (Nguyen, Bánki, Markova, & Hoehl, 2020). In simultaneous measurements of brain activity and physiology in adults, affectionate touch, i.e. handholding, between couples is related to both increased INS and IPS (Goldstein, Weissman-Fogel, Dumas, & Shamay-Tsoory, 2018; Goldstein, Weissman-Fogel, & Shamay-Tsoory, 2017; Reddan, Young, Falkner, López-Solà, & Wager, 2020). Yet there are no studies to date examining the role of social touch during caregiver-infant INS and IPS during the first months. Here, we simultaneously measured the brain activity and physiology of 4- to 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 on caregiver-infant neural and physiological synchrony.

Interpersonal neural synchrony

Recent research with adults using simultaneous recordings of brain activities from several persons, so-called "hyperscanning", suggests that interactive synchrony also manifests itself as interpersonal synchronization of oscillatory brain activities (Czeszumski et al., 2020; Dumas et al., 2011; Konvalinka & Roepstorff, 2012). Interpersonal synchronization of brain activities has been proposed as a fundamental mechanism allowing for precisely timed turn-taking interactions (Wilson & Wilson, 2005) and interpersonal transmission of information through verbal and non-verbal communication (Dumas et al., 2011; Hasson et al., 2012). A growing body of evidence suggests that interpersonal neural synchrony is associated with successful communication and affective co-regulation in adults (Goldstein et al., 2018; Hasson et al., 2012; Schippers, Roebroeck, Renken, Nanetti, & Keysers, 2010). Beyond this correlational evidence, multi-brain stimulation has been used to artificially enhance INS leading to increased behavioral coordination and social learning (Novembre, Knoblich, Dunne, & Keller, 2017; Pan, Novembre, Song, Zhu, & Hu, 2020), corroborating the notion that neural synchrony functionally promotes social coordination and exchange.

By contrast, the neural mechanisms of social exchanges in early child development are still poorly understood as few developmental hyperscanning studies exist to date(Nguyen, Bánki, et al., 2020). The emerging evidence shows that adults and children synchronize their brain activities in interactive contexts that require mutual engagement. INS has been mainly identified in frontal and temporal brain regions associated with socio-cognitive processes (Gvirts & Perlmutter, 2020; Hoehl et al., 2020; Redcay & Schilbach, 2019), including mutual attention (prefrontal cortex), affect sharing (inferior frontal gyrus), mutual prediction, mentalizing and shared intentions (temporo-parietal junction). Additionally, high interaction quality, marked by joint attention, infant positive affect and/or turn-taking, is associated with increased interpersonal neural synchrony (Nguyen, Schleihauf, et al., 2020a; Piazza, Hasenfratz, Hasson, & Lew-Williams, 2020; Reindl, Gerloff, Scharke, & Konrad, 2018), suggesting that INS could be a sensitive biomarker for successful mutual attunement between caregivers and their infants. However, the role of touch in establishing caregiver-infant INS has been neglected so far.

Proximity and touch are often intuitively used by caregivers to down-regulate infant distress or up-regulate positive engagement (Feldman, Magori-Cohen, Galili, Singer, & Louzoun, 2011; Hertenstein, 2002; Provasi, Anderson, & Barbu-Roth, 2014). Infants might perceive both stroking and cardiorespiratory patterns as forms of interpersonal rhythms when engaged in skin-to-skin contact. These rhythms could either induce and/or reflect interpersonal entrainment (Wass, Whitehorn, Marriott Haresign, Phillips, & Leong, 2020), allowing the dyad to attune to each other more easily and share their affective and mental states with one another (Hoehl et al., 2020).

The facilitative function of touch for INS is highlighted by a study showing that hand-holding in adults increases INS in networks in central and parietal areas, which are associated with analgesia (Goldstein et al., 2018). Social touch has, however, not yet been considered in caregiver-infant neural synchronization. Similar to adults, affectionate touch elicits specific behavioral, physiological and neural responses in infants as well (Fairhurst, Löken, & Grossmann, 2014; Jönsson et al., 2018; Pirazzoli, Lloyd-Fox, Braukmann, Johnson, & Gliga, 2019; Tuulari et al., 2019). More specifically, stroking increases parasympathetic activity in the physiological domain (Fairhurst et al., 2014) and activates brain areas such as the postcentral gyrus, posterior insular cortex and inferior frontal gyrus (Pirazzoli et al., 2019; Tuulari et al., 2019). Importantly, the inferior frontal gyrus is also implicated in INS processes, previously evidenced in adult dyads during cooperation and singing (Osaka et al., 2015; Zhang, Ding, Jia, & Yu, 2018).

Physiological synchrony

Synchronous interactions on the behavioral level have also been related to synchrony of various physiological parameters, such as arousal (Interbeat-intervals; IBIs) or intra- and interpersonal regulation (respiratory sinus arrhythmia; RSA). RSA is an index of the vagus nerve and the functioning of the vagal system. The regulation of the vagal system allows us to adapt to our ever-changing social environments, which is key to adaptive socioemotional functioning (see (Porges, 2007), for discussion of Polyvagal Theory). The attunement of cardio-respiratory rhythms between mother and child has been shown to emerge very 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 (Provasi et al., 2014). Feldman and colleagues (2007) suggest that early physiological attunement functions as a scaffold for infants' still immature physiological systems. The coupling of physiological states thereby supports the development of infants' self-regulation and various other neurobehavioral and physiological functions (Bell, 2020; Feldman, 2007).

In face-to-face-interactions at 3 months of age, infants' heart rhythms were synchronous with maternal heart rhythms (IBI) within lags of less than 1 second (Feldman et al., 2011). Especially moments of high physiological synchrony were matched with vocal and affect concordance in the dyad. Wass and colleagues (2020) report that mother-infant IPS was stronger after instances of infants showing high arousal and negative affect. Positive RSA synchrony between 4- to 6-month-old infants and their mothers was associated with co-regulation during a still-face paradigm (Abney, da Silva, & Bertenthal, under reviewb). Furthermore, three-year-old children and their mothers showed stronger RSA synchrony during higher levels of maternal teaching and weaker synchrony when mothers were disengaged (Skoranski, Lunkenheimer, & Lucas-Thompson, 2017). On the other hand, negative RSA synchrony in a video watching situation was related to higher child-reported empathy at ages 9-14 years, while positive RSA synchrony was associated with lower levels of empathy among the dyads (Creavy, Gatzke-Kopp, Zhang, Fishbein, & Kiser, 2020). The disparate results emphasize the critical nature of context and age for physiological synchrony and suggest that the potential function of physiological synchrony is not straightforward. Physiological synchrony can be both positive and negative during caregiver-child interactions and is not uniformly associated with adaptive outcomes (Abney et al., under reviewb; Ham & Tronick, 2009; Woody, Feurer, Sosoo, Hastings, & Gibb, 2016).

When looking specifically at the role of social touch and physical contact for IPS, there is some preliminary evidence for synchrony in situations with close physical contact underpinning autonomic regulation (Goldstein et al., 2017; Van Puyvelde et al., 2015; Waters, West, Karnilowicz, & Mendes, 2017; Waters, West, & Mendes, 2014). In a study by Waters and colleagues (Waters et al., 2017) caregivers were subjected to an affective arousal manipulation. Upon reunion with their 12- to 14-month-old infants, the mothers in the negative affect manipulation displayed physiological covariation with their infants when the infant was seated on the caregiver's lap in comparison to a no-touch condition. It must be noted, however, that covariation in RSA was only marginally significant and must be taken as preliminary. Still, the findings highlight a potential role of touch in affect contagion through physiology. Interestingly, physiological covariation is much more well-established in newborns in the context of skin-to-skin contact. In a study by Van Puyvelde and colleagues (Van Puyvelde et al., 2015), mothers were instructed to manipulate their respiratory rhythm when the infant was laying on their body. The results revealed that newborns were able to adjust their cardio-respiratory patterns to the pattern of their mother. Further evidence for the role of social touch is provided by research with adults. Hand holding between adults was shown to increase cardiovascular coupling, especially under conditions of pain (Goldstein et al., 2017). Across age, there is growing evidence pointing towards the role of touch in IPS in caregiver-infant dyads in both neutral and distressing situations. Yet, a systematic investigation of the role of spontaneous maternal touch on IPS during a naturalistic interaction with the infant is still lacking.

Current study

This study is the first to integrate the concurrent assessment of INS and IPS in a multi-level hyperscanning paradigm with a large sample of mother-infant dyads interacting with each other naturally. We tested whether attunement through physical closeness and touch between mother and infant is associated with interpersonal neural and physiological synchrony at an age when the infant is still very much dependent on their caregiver. Interpersonal neural synchrony was assessed in 4- to 6-month-old infants and their primary caregivers by using dual-functional near-infrared spectroscopy (dual-fNIRS). We focused on prefrontal and inferior frontal regions because frontal regions were consistently shown to be implicated in both adult-adult and parent-child INS (Czeszumski et al., 2020; Nguyen, Bánki, et al., 2020). 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; Stern, Hofer, Haft, & Dore, 1985). We further assessed RSA synchrony through electrocardiogram (ECG) and performed video recordings of the dyads that were subsequently coded offline. According to our pre-registered hypotheses, we expected caregiver-infant dyads to show increased INS and IPS when we experimentally manipulated whether mother and infant were able to touch each other. We, therefore, contrasted their INS and IPS during interactive and non-interactive activities including social touch in comparison to when both were attending to the same visual stimulation passively but were distant from one another. Subsequently, we assessed whether individual differences in the use of social touch would be related to differences in INS and IPS as well. We hypothesized that increased durations of active social touch, i.e. affectionate, stimulating/playful touch, but also static touch, would be associated with increased INS and IPS.

We also contrasted individual cortical activation as well as RSA responses in the three different conditions. In light of theoretical accounts proposing 1) both INS and IPS to underpin behavioral synchronization (Atzil et al., 2018; Feldman, 2017) and 2) a general potential link between brain (prefrontal areas) and physiological oscillations (RSA), we further examined whether INS was correlated with IPS in the mother-infant dyad. Based on the few and contrasting existing findings concerning IPS between caregiver and infant, the affective context of the interaction seemed to play a role. Accordingly, we studied infant affect in association with IPS.

Results

Participants and procedures

Seventy-two mother-infant dyads participated in the experiment. The experiment included three different conditions (see *Figure 1*). In the first two non-interactive conditions, mother and infant jointly watched a calm and silent video for 90 seconds, while either being seated apart in the distal watching condition or together (the infant sat on the mother's lap) in the proximal watching condition. The sequence of these two conditions was counterbalanced. Following these two conditions, mother and infant engaged in an interactive face-to-face free play interaction without toys for five minutes.

We simultaneously measured fNIRS and ECG of the dyad to calculate neural synchrony and physiological synchrony of RSA estimates. The dyad was also video recorded throughout the whole experiment and subsequently coded for maternal touch and infant affect (see Methods section and Table S1 for further details). We excluded nine dyads due to infant fussiness, mother-reported developmental delays and refusal to wear the fNIRS caps and/or have the ECG electrodes attached.

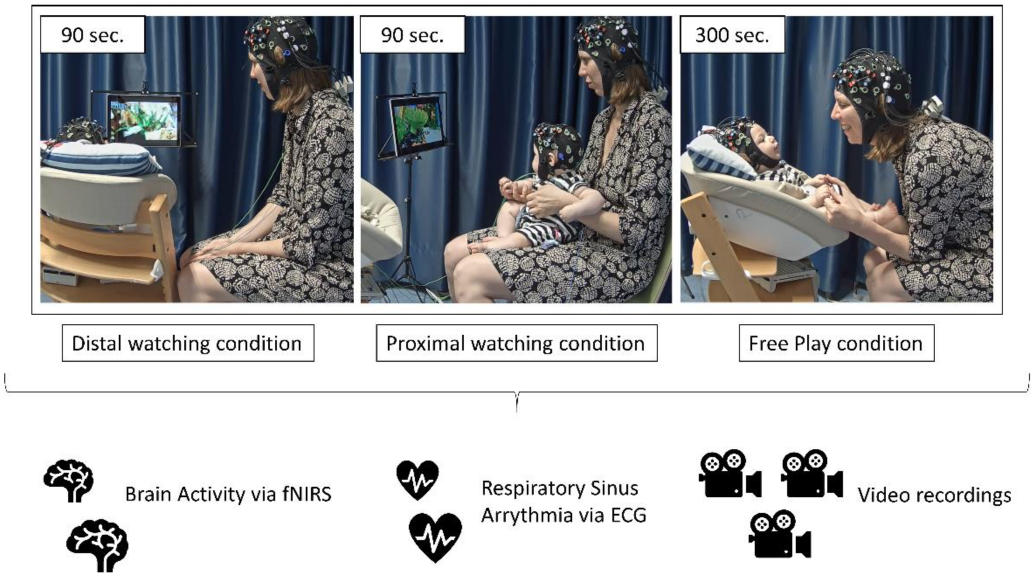

Figure 1. An exemplary mother-infant dyad during the non-interactive watching conditions with and without physical contact (90 seconds) and the free play interaction condition (300 seconds) (from left to right). Throughout the whole experiment, we simultaneously measured brain activity via functional near-infrared spectroscopy (fNIRS), respiratory sinus arrythmia 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.

Neural synchrony in hemodynamic brain activity

First, we tested interpersonal neural synchrony (estimated with Wavelet Transform Coherence [WTC]) in oxygenated Hemoglobin (HbO) concentration changes in the three experimental conditions: the non-interactive distal watching condition vs. the non-interactive proximal watching condition and the interactive face-to-face free play condition. The frequency-averaged coherence value between 0.031 and 0.125 Hz was calculated and then further averaged across each condition (see Methods section). WTC was entered as the response variable in the Generalized Linear Mixed Effects (GLME) model, 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 neural synchrony during free play and proximal watching in comparison to distal watching that were detected in bilateral lateral prefrontal (lPFC) and medial prefrontal areas (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 neural synchronization during free play, $t>3.06$, $p<.006$. None of the conditions differed in neural synchrony in bilateral inferior frontal gyri (IFG), $p>.071$. The results are depicted in *Figure 2A*. For HbR, we were able to replicate the main results we found for INS in HbO (see Supplemenary Information).

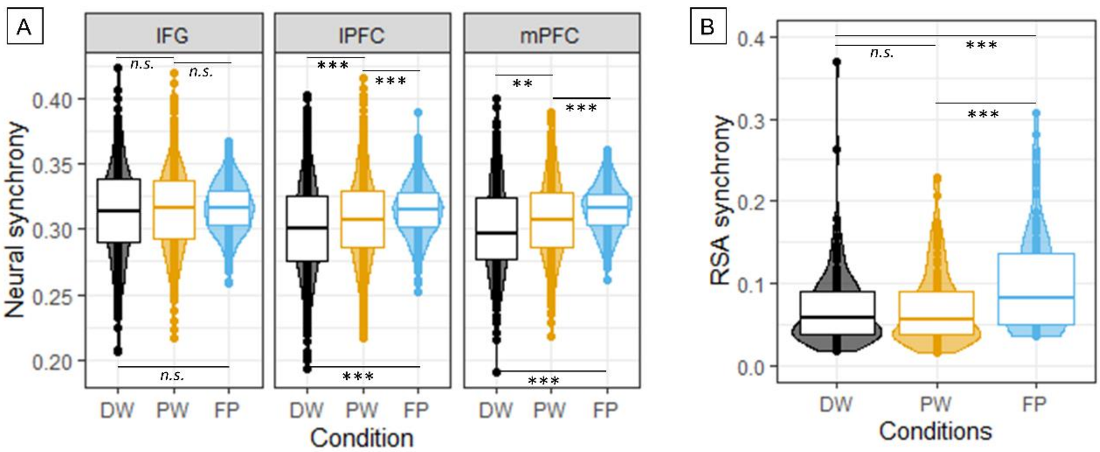

Figure 2. (A) Plot of the interaction effect of condition (x-Axis) and region (facets) for INS. Neural synchrony (y-Axis) during free play was significantly higher than during distal and proximal joint watching phases in lateral and medial prefrontal areas, but not in the inferior frontal gyrus. Neural synchrony during proximate joint watching was higher than during distant joint watching. (B)

Physiological synchrony (y-Axis) during free play was significantly higher than during distal and proximal joint watching phases. n.s.= non-significant, **= *p*<.010, ***= *p*<.001.

Individual differences of spontaneous social touch and INS

To assess whether variation in social touch relates to variation in INS, we calculated a GLME model for the assessed qualities of maternal social touch. 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 (*Figure 3A*), and stimulating touch durations, $\chi^2(1)=6.24$, *p*=.012 (*Figure 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]. Passive touch and functional touch durations were non-significant, *p*>.122.

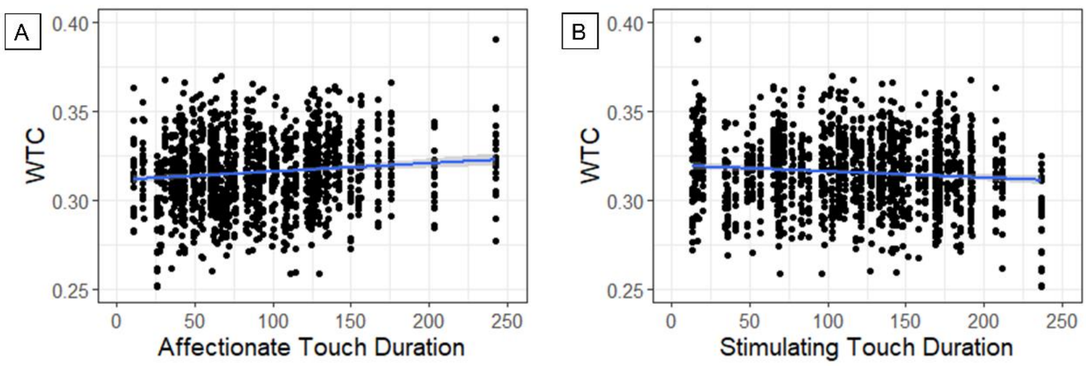

Figure 3. Graphs depict (A) the positive correlation between durations of affectionate touch (x-Axis) and (B) the negative correlation between durations of stimulating touch (x-Axis) and neural synchrony (y-Axis) during the free play condition.

Physiological synchrony in vagal tone

Physiological synchrony between mother and infant were compared in the three experimental conditions with %DETerminism (%DET) from Cross-Recurrence Quantification Analysis (CRQA) of detrended RSA values as the dependent measure. %DET scores were entered into the GLME model as the response variable, while 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, $\chi^2(2)=34.62$, $p<.001$ (*Figure 2B*). 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 non-interactive conditions, however, did not differ from one another, $p=.978$.

Individual differences of spontaneous social touch and IPS

Next, we modeled a regression analysis to test the association between social touch and IPS. The linear regression model comprised %DET scores as 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, $\beta=0.571$, $SE=0.237$, *95% CI*=[0.091 1.051], $t=2.48$, $p=.084$.

Relation between neural and physiological synchrony

We assessed a potential relation between neural and physiological synchrony by testing if INS was related to IPS (both scores were averaged over each condition). HbO WTC values were entered as the response variable into the GLME model. Condition, IPS (%DETerminism) 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 interpersonal physiological synchrony nor its interaction with conditions and/or region of interest in the brain on interpersonal neural synchrony in HbO, p>.136.

Supplementary analyses

Firstly, we assessed individual cortical activation and RSA responses in all three conditions. The results revealed no difference in individual responses comparing the three conditions. We also examined the role of infants' affect to shed light on the affective context of the interaction. Overall, we find higher mother-infant IPS, 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.

Discussion

Touch is thought to fundamentally support caregiver-infant attunement and co-regulation. In the present study, we tested whether mother-infant INS and IPS differentiate between three naturalistic experimental conditions with varying physical proximity and mutual engagement. Also, we examined whether variations in spontaneous social touch during free play can explain variations in INS and IPS between a mother-infant dyad. Firstly, the findings revealed that both INS and IPS emerged in the communicative context of a free play situation. The interactive free play allowed mother and infant to see each other and respond to one another in a timely and contingent manner. Our findings thus support the notion that caregiver-child INS fundamentally depends on mutual engagement and contingent adaptation to one another (Nguyen, Schleihauf, et al., 2020a, 2020b). In contrast, the dyads did not show INS and IPS when they only shared a situation with the same visual input and were distanced from one another. The mother-infant dyads also displayed increased INS when the infant was seated on the mother's lap while watching the videos. We suggest that the micro-adjustments of bodily contact, as well as the perception of heart rhythms and respiration, contributed to mother-infant neural synchronization during this condition. Supporting the experimentally revealed relation of mother-infant INS with touch, we identified active forms of touch that correlate with INS during free play. IPS, on the other hand, was neither related to the experimentally induced proximity during the non-interactive watching conditions nor the spontaneous touching behavior of the mother during free play. The findings thus indicate that neural and physiological synchrony might arise in part in similar contexts, i.e. during mutual engagement of the mother-infant dyad but could diverge in their functionality as they seem to arise by different processes. Still, the results show that INS and IPS can differentiate the three conditions beyond single-subject analyses of individual cortical activation or RSA responses.

A growing body of evidence indicates that interacting partners show INS during various social contexts, such as cooperation, conversation or joint musical activities (Czeszumski et al., 2020; Dumas et al., 2011; Hasson et al., 2012; Jiang, Zheng, & Lu, 2020). In the developmental domain, the present study is the first study to date that provides evidence for INS in infants, as young as 4 months of age, and their primary caregiver. We replicate findings from research with adults (Fishburn et al., 2018) showing that passively viewing the same visual stimulation is related to lower levels of INS in comparison to an interactive face-to-face interaction and a passive viewing condition with physical contact. The findings thus indicate that INS might be a unique neural process underpinning the transmission of interactional signals through the environment, instead of merely reflecting common neural reactions towards the same perceptual stimulation (Fishburn et al., 2018). We suggest that both free play and the proximate watching conditions offer the mother-child dyad opportunities to exchange communicative signals with one another and engage in a “dance” of back and forth to coordinate with one another (Markova et al., 2019; Wass et al., 2020). This finding is in line with previously evidenced links between INS and reciprocal behavior in caregiver-preschool child interactions (Nguyen, Schleihauf, et al., 2020a, 2020b; Quiñones-Camacho et al., 2019).

As hypothesized, INS in mother-infant dyads occurred predominantly in lateral and medial frontal areas and the results thus replicate earlier adult-infant as well as adult-children fNIRS hyperscanning studies (Nguyen, Schleihauf, et al., 2020a; Piazza et al., 2020; Reindl et al., 2018). INS in frontal areas has been related to the “mutual social attention system” of interacting partners (Gvirts & Perlmutter, 2020). While attending to one another, but not to the same visual stimulation, mother and infant showed alignment in their brain activations. Synchrony in medial frontal areas is further associated with the general detection of communicative signals directed toward the self, mentalizing and reward, all processes which are implicated in mutually engaged interactions (Redcay &

Schilbach, 2019). On the other hand, INS inferior frontal areas did not differ between conditions and was neither increased in free play nor the proximate watching condition. The many functions associated with inferior frontal areas, such as language, inhibition and empathy, make it difficult pinpoint as to why mother-infant dyads did not show neural synchronization in that area (Khalil, Karim, Kondinska, & Godde, 2020; Shamay-Tsoory, Aharon-Peretz, & Perry, 2009; Wang, Yang, Zhao, Zuo, & Tan, 2020). It seems that INS in the IFG as part of the social interaction network proposed by Redcay and Schilbach (Redcay & Schilbach, 2019) was not yet synchronized during these early caregiver-infant interactions.

While the free play condition was associated with the highest levels of INS between mother and infant in comparison to the non-interactive conditions, joint watching of a calm video was also associated with higher neural synchrony when the infant was seated on the mother's lap instead of next to her. Even though there is preliminary evidence for caregiver-infant INS in non-interactive proximate situations (Azhari et al., 2019; Minagawa, Xu, & Morimoto, 2018), this is the first study to our knowledge to explicitly contrast the same non-interactive joint watching conditions, while the proximity of mother and infant was experimentally manipulated. There is limited empirical evidence on the effects of caregiver-infant proximity (Botero, Langley, & Venta, 2019), even though theoretical accounts maintain that physical contact is beneficial to infants' secure attachment relationship and healthy development (Berecz, Cyrille, Casselbrant, Oleksak, & Norholt, 2020; Norholt, 2020). The proposed mechanisms to physical contact are enhanced caregiver responsiveness to infants and stimulation from parent locomotion (Little, Legare, & Carver, 2019). Accordingly, we suggest that the micro-adjustments of bodily contact and the perception of heart rhythms and respiration are reciprocally related to neural synchronization during this non-interactive condition (Cascio, Moore, & McGlone, 2019). Holding the infant could additionally be related to the activation of specific sensory nerve fibers through "pleasant deep pressure" similar to the activation of C-tactile fibers through affectionate touch (Case et al., 2020; Norholt, 2020). Our finding holds many implications in the social domain such that proximity allows the caregiver to co-regulate their infant even when their attention is directed away from the infant. Situations in proximity, such as holding, carrying and sitting on the lap are much more common in infancy and these situations decrease throughout development (Jean, Stack, & Fogel, 2009). Future studies could therefore investigate whether infant and caregiver might decrease in INS during non-interactive proximity as 1) these situations occur less frequently and 2) the infant starts to select more specifically what and who to attune to with increasing age (Van Puyvelde et al., 2015).

In the free play condition, communicative signals are visibly exchanged between caregiver and child using various behavioral modalities, such as gaze, vocalizations and touch (Markova et al., 2019; Wass et al., 2020). Here, we identified social touch as one of the communicative signals related to INS. Specifically, our findings show that affectionate touch was related to higher INS in a mother-infant dyad. By eliciting infant attention and regulating infant's affect (Della Longa, Gliga, & Farroni, 2019; Stack & Muir, 1992), affectionate touch might help mother and infant to establish and maintain engagement with one another. Generally, affectionate touch has been highlighted for its beneficial effects in child development (Bales et al., 2018). Reduced rates of affectionate touch were found in clinical populations, such as mothers with postpartum depression disorder or infants with a feeding disorder (Feldman, Keren, Gross-rozval, & Tyano, 2004; Peláez-Nogueras, Field, Hossain, & Pickens, 1996). The link between affectionate touch and INS thus supports the notion that INS might be a biomarker for interaction quality and could be attenuated in clinical samples with anxious or depressed caregivers (Leong & Schilbach, 2019). Interestingly, we find a negative association for stimulating touch and INS. The results indicate that stimulating touch might be disruptive to the interaction and thus be related to lower INS. These results tie in with research underlining diverging functions to different touch qualities (Mantis, Mercuri, Stack, & Field, 2019; Moreno, Posada, & Goldyn, 2006). Moreno and colleagues (Moreno et al., 2006) show that co-regulation between mother and infant is more likely to be associated with higher amounts of affectionate and lower amounts of stimulating touch. Especially, higher frequencies of stimulating touch have been related to intrusive caregiving behavior, as sometimes shown by anxious caregivers (Field, 2010; Granat, Gadassi, Gilboa-Schechtman, & Feldman, 2017; Malphurs, Raag, Field, Pickens, & Pelaez-Nogueras, 1996). Overall, the involvement of social touch in neural synchronization processes of adults (Goldstein et al., 2018) and the caregiver-infant dyads in our study highlights the importance of touch in early interactions. Our results further show the need to further investigate the role and effects of social touch for child development outcomes and, maybe even more importantly, how the lack of touch affects infants' development (Ardiel & Rankin, 2010).

Next to neural synchronization, we simultaneously measured and examined IPS in the mother-infant dyad. IPS, just like INS, in the caregiver-infant dyad was higher in the interactive condition than in both non-interactive conditions. Our results are therefore in line with previous studies providing evidence for IPS during moments of mutual engagement (Skoranski et al., 2017). So, while touch and proximity were related to increased INS, IPS was not related to non-interactive physical contact in the current study. Our findings concur with studies showing that mother and infant show attenuated physiological coupling responses 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). Interestingly, infants' ability to show physiological entrainment of cardio-respiratory rhythms with others seems to increase again from at least 8 months of age due to the maturation of their physiology (Suga, Uraguchi, Tange, Ishikawa, & Ohira, 2019). Future studies could therefore investigate whether IPS through physical contact could (re-)occur when infants are older. We further probed IPS for potential correlations with the mother's touching behavior. Yet, again, social touch did not correlate with IPS between mother and infant, while functional touch durations were weakly, but not significantly, associated with IPS. Instead, when examining IPS for the affective context of the interaction, we find higher IPS to be associated with higher durations of infant negative affect and lower IPS to be associated with higher durations of infant positive affect in the interactive free play condition. Even though IPS was initially associated with vocal and affect concordances of mother-infant dyads (Feldman et al., 2011), IPS was, later on, more specifically linked to instances of high arousal and negative affect (Wass et al., 2019). Our results, therefore, tie in with a co-regulatory account of caregiver-infant RSA synchrony (Abney et al., under reviewb). The mother-infant dyads more likely show IPS, when co-regulation is needed, such as during infant distress marked by negative affect (Beebe et al., 2008; Porges, 2007). Longer durations of infant positive affect could have indicated that the infant was well regulated by herself. Thus, the dyad's physiology did not need coupling for the infant to maintain allostasis (Atzil et al., 2018). Our results provide preliminary evidence in the developmental domain for an account by Mayo & Gordon (Mayo & Gordon, 2020) suggesting that a dyad needs to go in and out of physiological synchrony. IPS is maintained to be ideal when it reaches a state of meta-stability. Recent research suggesting anxious caregivers to engage in hyper-coregulation and higher IPS in comparison to healthy control caregivers provides further evidence to the account (Smith et al., in press). Overall, more research is needed on the exact behavioral correlates of IPS to understand its functionality.

Interestingly, condition means of INS and IPS were not correlated. In the theoretical account by Feldman (Feldman, 2017)both INS and IPS as well as behavioral and hormonal coordination, are maintained to underpin the formation of human attachment. In the study presented, both INS and IPS were the highest in the interactive condition in comparison to non-interactive conditions. Yet, while INS was related to the communicative signals exchanged through touch, IPS seemed to be related to co-regulatory signals associated with facial expressions of affect. The discrepancy could stem from 1) the different approaches to calculate synchrony, but also suggest 2) the discrepant role of social touch for neural and physiological synchronization, 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. Moreover, additional measures to add information on infants' brain and physiological maturation could add to the investigation of both forms of synchrony across different age groups. Importantly, we know very little about the *intraindividual* developmental trajectory of brain activation and RSA coupling, which could inform *interindividual* coupling (Beauchaine, 2015).

Conclusion and Future Directions

The present study is the first multi-level hyperscanning studies on naturalistic mother-infant interactions with infants as young as 4 months of age, which allows us to take a more holistic approach on when and how mother and infant coordinate. Our results show that 4- to 6-month-old infants and caregivers show brain synchronization associated with communicative signals, especially physical contact and touch. The link between affectionate touch as well as physical contact and INS provides crucial new insights on the aspects of interaction quality that support caregiver-infant neural alignment. Future investigations should study whether INS is involved in facilitating the social bond between caregiver and child (Atzil et al., 2018; Feldman, 2017). Additionally, 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, Jones, Mize, & Platt, 2020). Synchronization in close physical contact could also promote children's social learning just as it is suggested during social interactions (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. Both intracultural and intercultural differences in holding infants and co-sleeping could be used as factors to investigate the relation between touch and INS as well as infant development. Physiological synchrony, on the other hand, was related to dyads' coregulation, in particular when infants expressed infant negative affect. Taken together, the present study highlights the feasibility of multi-level hyperscanning with infants and their caregivers to uncover neurobiological pathways of mutual engagement and co-regulation. These first results on the different levels of synchrony pave the way to 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). Moreover, our results underscore neural synchrony as a potential biological pathway of how social touch plays into infant development and how this pathway could be used to support infant learning and social bonding.

Material and methods

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. Infants' age ranged from 4- to 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 report. The study was approved by the local ethics committee. Parents provided written informed consent on behalf of their infants. Participation was remunerated.

Experimental procedure

During the experiment, caregiver and infant were either seated next to one another or the infant sat on the caregiver's lap as both were watching a calm aquarium video on a tablet (distal watching and proximate watching conditions). 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 in a 5 min. long 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 functional near-infrared spectroscopy. We assessed respiratory sinus arrhythmia (RSA) through electrocardiography (ECG) and each dyad was filmed by three cameras (angled towards the dyad, the infant and the mother) throughout the experiment.

Data acquisition

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 x 2 probe sets were attached to an EEG cap with a 10-20 configuration (*Figure S1*). The standard electrode locations allowed us to place the probes more precisely, as 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, Schleihauf, et al., 2020a; Piazza et al., 2020; Redcay & Schilbach, 2019). In each probe set, 8 sources and 8 detectors were positioned, which resulted in 16 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.

Electrocardiogram (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.

Data Analysis

fNIRS

fNIRS measurements were processed using MATLAB-based functions derived from Homer 2 (Huppert, Diamond, Franceschini, & Boas, 2009). Raw data converted into optical density. Next, optical density data were motion-corrected with a wavelet-based algorithm with an interquartile range of 0.5 (Molavi & Dumont, 2012). Motion-corrected time series were further visually inspected during a quality check procedure. Before continuing, 22.87 % of the channels 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 and a slope of 12 dB per octave. The filtered data were converted to HbO and HbR values (μMol) based on the modified Beer-Lambert Law. For later statistical analyses, both HbO and HbR synchrony are reported (Tachtsidis & Scholkmann, 2016).

Individual cortical activation

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 were 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.

Neural synchrony

We assessed the relation between the fNIRS time series in each caregiver and infant using (Morlet) Wavelet transform coherence (WTC) as a function of frequency and time (Chang & Glover, 2010; Grinsted, Moore, & Jevrejeva, 2004). WTC is more suitable in comparison to correlational approaches, as it is invariant to interregional differences in the hemodynamic response function (HRF) (Sun, Miller, & D'Esposito, 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 age) as well as different brain areas. A high correlation may be observed among regions that have no blood flow fluctuations. Accordingly, based on previous studies (Nguyen, Schleihauf, et al., 2020a), 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 neural coherence (neural synchrony) was then calculated for the distal watching condition, the joint watching condition, and 90-second epochs in the interactive free play condition in each channel, which resulted in 5 (conditions) x 22 (channels) coherence values for each dyad.

Respiratory Sinus Arrhythmia

Interbeat-intervals (IBIs) were extracted offline using ARTiiFACT (Kaufmann, Sütterlin, Schulz, & Vögele, 2011). The ECG data was 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 down-sampled 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 (Abney, da Silva, & Bertenthal, under reviewa). An 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 higher range of 1.0 Hz for mothers' respiration was used 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 & Bohrer (Porges & 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 $\ln(\mathrm{ms})^2$. At the magnitude estimation stage, a sliding window of 15 seconds 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.

Individual mean RSA analyses

To analyze infants' and mothers' individual physiological responses in each condition, we computed mean values for RSA for mother and infant for each condition. The values were then contrasted between the three conditions to analyze mother and infant responses in parasympathetic activation/deactivation. Results are reported in the supplements (S2).

Physiological synchrony

To examine physiological synchrony, we used cross-recurrence quantification analysis (CRQA) (Coco & Dale, 2014; Konvalinka et al., 2011) to identify coupling between mothers' and infants' RSA time-series. CRQA is a nonlinear method for analyzing shared dynamics between two different data series (Shockley, Butwill, Zbilut, & Webber, 2002) and has been applied successfully to investigate cardio-respiratory dynamics (Konvalinka et al., 2011; Marwan, Wessel, Meyerfeldt, Schirdewan, & Kurths, 2002; Zbilut, Webber, & Zak, 1998). The method is especially suitable to RSA synchrony estimations, as it does not assume stationarity within the data. Moreover, 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. Therefore, 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' detrended RSA as well as IBI time series. This approach allowed us to take concurrent (lag 0) physiological synchrony into account. Results for cross-correlation of RSA time-series are detailed in the supplements (S2).

Behavioral coding

To assess maternal social touch and infant affect, 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 and infant facial affect was 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 either for active, passive or functional maternal touch (adapted from (Jean et al., 2009)). Segments of active touch were subsequently divided into the two categories of affectionate and stimulating touch (Mantis et al., 2019). For infant facial affect, we distinguished between positive, negative and neutral facial expressions (refer to Table S1 for a full description of coding categories).

To establish inter-rater reliability, 25% of randomly chosen videos were coded by two trained coders. We calculated inter-rater reliability using the kappa, which resulted in overall k = .79 for social touch and k = .81 for facial affect. To control for minor variations in interaction duration, the total duration of each touch and facial affect category was divided through the total time of free-play (i.e. duration of coded free-play) to be able to control for different interactional durations between dyads. The touch and affect scores thus indicate proportions of time during each condition.

Statistical Analysis

All statistical analyses were calculated in RStudio (RStudio Team, 2020) using generalized linear mixed-effects models (glmmTMB). Wavelet Transform Coherence (WTC) values were entered as the dependent variable with condition (distal watching vs. proximate watching vs. free play epoch 1 vs. free play epoch 2 vs. free play epoch 3) and ROI (left IFG vs. right IFG vs. left lPFC vs. right lPFC vs. mPFC) as fixed factors and with random slopes for each ROI and condition and random intercepts of dyads. CRQA %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 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 permutation analyses (Nguyen, Schleihauf, et al., 2020a; Piazza et al., 2020). Mother's original data was randomly paired with infant data out of the sample for 1,000 permutations. WTC and Cross-Recurrence Analysis was calculated for each random pair. Subsequently, the average of coherence or correlation between random pairs was computed and compared against original pairs using generalized linear mixed-effects (GLME) modelling and post-hoc contrasts. The detailed random pair permutation analyses are reported in the Supplements (S1, S2).

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Author contributions

T.N. and S.H. conceived this project. T.N. and D.S. performed the experiments and collected the data. T.N. analysed the data under the supervision of S.H. D.A. contributed code on RSA estimation and physiological synchrony analyses. T.N., D.A., B.B., and S.H. wrote the manuscript.

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Competing interests

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.

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