

MANUSCRIPT IN PRESS, *Trends in Cognitive Sciences*

Interpersonal neural entrainment during early social interaction

Wass, S.V.(1), Whitehorn, M.(1), Marriott Haresign, I.(1), Phillips, E.(1), Leong, V.(2,3)

1 - University of East London, London, UK

2 - University of Cambridge, UK

3 – Nanyang Technological University, Singapore

*Correspondence: Dr Sam Wass, Department of Psychology, University of East London, Water Lane, London E15 4LZ. Email: s.v.wass@uel.ac.uk

Abstract (100-120 words)

Currently, we understand much about how children’s brains attend to and learn from information presented while they are alone, viewing a screen – but less about how interpersonal social influences are substantiated in the brain. Here, we consider research that examines how social behaviors affect not one, but both partners in a dyad. We review studies that measured interpersonal neural entrainment, considering two ways of measuring entrainment: concurrent entrainment (e.g. ‘when A is high, B is high’ – also known as synchrony) and sequential entrainment (‘changes in A forward-predict changes in B’). We discuss possible causes of interpersonal neural entrainment, and whether it is merely an epiphenomenon, or may play an independent, mechanistic role in early attention and learning.

Keywords: Early learning, attention, synchrony

NOTE: IN THIS ‘WORKING’ VERSION THE GLOSSARY, SIDE BOXES AND FIGURES ARE INCLUDED AT THE END OF THE TEXT. IN THE EVENTUAL PUBLISHED MANUSCRIPT, THESE SIDE BOXES WILL BE INTERSPERSED THROUGH THE TEXT.

Tracking dynamic, social influences on early attention and learning

During the first years of our lives, in particular, our waking hours are spent almost entirely in the company of others. Yet currently, and paradoxically, most of our knowledge of how the developing brain functions during social interaction comes from studies that examine individual humans in isolation [1-4]. From early life, however, we know that social factors influence how we allocate our attention and learn. For example, nine-month-old infants learn new speech sounds better through live interaction with an adult than through watching an equivalent video of someone speaking [5]. When a 16-month-old infant initiates an exchange by pointing to an object, their memory retention for functions subsequently demonstrated on that object is increased [6]. And when a parent pays attention to a particular object whilst interacting with their 12-month-old infant, this immediately increases the infants’ own duration of attention to that object [7]. Yet we presently understand little about how these transient, interpersonal influences are substantiated in the brain.

Recent research, building on advances in adult [3] and animal [8] social neuroscience, has begun to explore these dynamic, social influences by doing two things differently: first, rather than recording from one individual brain in isolation, they record from two interacting brains concurrently (sometimes known as **hyperscanning**) [9]; second, rather than examining uni-directional influences using pre-designed, screen-presented experimental stimuli, they examine naturally occurring moments of reciprocal influence during free-flowing interpersonal naturalistic interactions (see Figures 1, 2). This research is starting to uncover a range of important new discoveries about which brain regions are active during social interaction, that illustrate the importance of studying social interaction in ecologically valid contexts. For example, mentalizing and reward networks show markedly different patterns of

activity during live interaction, compared to when passively viewing equivalent social stimuli on a screen [3, 4].

Here, we examine a different question: what this research has taught us about the *neural temporal dynamics* of early social interactions. In the first part of the review, we consider two important and well-researched aspects of social interaction: **ostensive cues** (signals that are sent during social interaction to indicate communicative intent), and **contingent responsiveness** (behaviors that indicate communicative sensitivity within an interaction). We conclude that the uni-directional neural correlates of both - i.e. how one partner transiently influences the other, with both partners considered independently – are fairly well understood; but that our understanding of how ostensive cues and contingent responsiveness alter the interpersonal neural dynamics of the interaction – i.e., how the partners inter-relate to one another - is currently limited.

In the second part of the review, we consider research that has directly examined interpersonal neural dynamics by measuring interpersonal neural **entrainment** during social interaction. We describe key methodological challenges in measuring entrainment and outline the evidence for the different types of entrainment that emerge during early social interaction. Building on the evidence for uni-directional influences described in part 1, we also consider the mechanisms through which bi-directional interpersonal neural entrainment could be achieved and maintained. In the final section, we discuss whether interpersonal neural entrainment is merely an epiphenomenon; or whether it may play a mechanistic role during early attention and learning.

Ostensive signals

Social interactions are complex, fast-moving and multi-layered: they require the brain to process rapidly changing information from multiple visual and auditory sources in a time-sensitive manner. During social interaction, we use signals known as ostensive cues (see Glossary) to indicate communicative intent; these tend to be concentrated on moments where the ‘sender’ wants to convey particularly important information to the ‘receiver’ [10]. Historically, the majority of previous research has examined how adults use ostensive cues towards children, consistent with pedagogical approaches that primarily emphasize a flow of

information from an adult ‘sender’ to a child ‘receiver’. However, more recent research has recognized that even young infants also use ostensive cues, too [11, 12]. Rather than acting as purely passive recipients of information ‘sent’ by an adult, they also play an active role as ‘senders’ of information (such as interrogative cues), which influence learning exchanges [13-15] [16, 17]. Thus, in addition to studying the direction of influence from adult ‘sender’ to child ‘receiver’, recent approaches are acknowledging that children can also act as ‘senders’ of social information, and adults as ‘receivers’ [13].

Ostensive cues lead to a range of changes in behavior during the time period immediately following the cue [10]. Although ostensive signals are uni-directional by definition (insofar as they are signals ‘sent’ from partner a to partner b), extensive research suggests that they also affect the *relationship* between partner a and partner b. Specifically, research has shown that ostensive cues lead to increased behavioral entrainment (see Glossary and Box 1) in the time period following the ostensive cues. For example, ostensive cues such as direct eye gaze lead to increases in behavioral mimicry [18] and the mirroring of facial affect [19]. Similarly, in language, increased vocal mirroring is observed following the use of child-directed speech contours [20]. Direct eye gaze [21], child-directed speech [22], and pointing [23] all lead to increases in gaze following, which is another form of sequential behavioral entrainment (see Box 2).

Considerable research has investigated the transient *uni*-directional effects of ostensive cues (i.e. how the ‘receiver’, considered independently, is affected by the ‘sending’ of a social signal). This research has suggested that both child and adult brains are highly sensitive to ostensive cues [24]: for example, infants show larger neural **ERP** responses (specifically, a larger amplitude N170 component) to images of faces showing direct compared to averted gaze even shortly after birth [25]. During live adult-infant play, cortical activity (measured from the level of oxyhemoglobin in the medial prefrontal cortex) increases in seven-month-old infants during direct gaze compared with averted gaze [26, 27]. Similarly, child-directed speech (CDS) evokes greater neural responses (a larger amplitude N250 ERP component) in 6-12-month-old infants compared with adult-directed speech [28], and during live interactions, fluctuations in the child-directedness of speech correlate with fluctuations in prefrontal cortex activity in 9-15-month-old infants [29]. And in addition to neural activity directly in response to the gaze cue, neural responsiveness is also increased for objects presented immediately following an ostensive cue. For example, when an adult gazes first to a nine-month-old infant’s face before

looking to a screen-presented object, the infant's evoked neural responses to the subsequently presented object are greater (measured as a larger amplitude Nc ERP component) [30] (see also [31]).

As yet, though, and despite the evidence reviewed above that ostensive cues cause immediate changes in the relationship between partner a's and partner b's behavior, little research has investigated the *bi*-directional neural effects of ostensive cues (i.e. how ostensive cues alter the relationship between the two partners' neural activity in the time period following the cue). In order to assess how ostensive cues alter the interpersonal neural dynamics of the interaction, it is necessary to examine change from the perspective of not one, but both members of the dyad.

Contingent responsiveness

Another strand of research has investigated the role of contingent responding during a social interaction: how the 'receiver' indicates communicative sensitivity within an interaction by consistently responding to behaviors from the 'sender'. Considerable evidence suggests that both children and adults are highly sensitive to whether or not their partner is responding contingently to their social signals [14, 24, 32, 33]. For example, one study observed 6.5- and 9.5-month-old infants' reactions to adults who either responded to the infants' gaze cues by following their gaze towards an object ('congruent looking') or looked in the opposite direction ('incongruent'). Older, but not younger, infants showed a visual preference for the congruent actor and showed greater neural reactivity to the stimulus cued by the congruent (compared to the incongruent) adult [34].

Behavioral research also suggests that interactions featuring greater behavioral contingency in both members of the dyad are also more effective as teaching exchanges. For example, in a task in which adults presented word labels either contingently in response to infant vocalizations or non-contingently, only infants who received labels contingently in response to their own attention learned the association [35] (see also [6, 13, 14, 36]). However, not all forms of contingency are equally effective: during videoed interaction only particular types of contingent responding (mirroring, and marking with a smile) were predictive of the growth of these behaviors over time [18].

Considerable research has investigated the *uni*-directional correlates of contingent responding (i.e. how the ‘receiver’ of a social signal is influenced by the ‘sender’). This research has suggested that observing someone else perform an action involves neural activity in the ‘observer’ becoming more like neural activity in the person performing the action [37, 38]. This pattern is similar to the actor-observer correspondences documented while watching and performing actions [39] and while watching someone else experience pain, anger and reward [40, 41]. There is also some evidence that, in more contingently responsive social partners, these actor-observer correspondences are stronger [38] (see also [42]).

Recent research also suggests that similar principles might also apply in different contexts, such as when considering how adults’ brain activity tracks infants’ attention patterns during naturalistic play. The study recorded dual-EEG from parents and 12-month-old infants during free-flowing play (see Figure 1a, 1b). By tracking the continuous fluctuations of brain activity in the adult and attention patterns in the infant, their results suggested that adults’ neural activity entrained to fluctuations in the child’s attention, independent of the adult’s own attention [43] (Figure 2). Where the adult showed greater neural entrainment to the child’s attention, the child was more attentive [43].

As yet, though, and although contingent responsiveness is inherently a bi-directional behavioral phenomenon (because it describes the relationship *between* the two partners’ behaviors), little research has investigated how contingent responding alters the bi-directional neural dynamics of the interaction. Previous research has mainly considered actor-observer similarities by recording separately from actors and observers; in order to investigate interpersonal neural dynamics, it is necessary to record from both partners concurrently.

Measuring interpersonal neural entrainment in development

So far, we have considered two well-researched topics within early social interaction: ostensive cues and contingent responsiveness. We have concluded that the uni-directional neural correlates of both of these - i.e., influences of the ‘sender’ on the ‘receiver’, with the two partners considered independently – are fairly well understood. But we have also concluded that our understanding of how ostensive cues and contingent responsiveness alter the

interpersonal neural dynamics of the interaction – i.e., how the partners’ neural activity inter-relates to one another - is currently limited.

In this section, we consider another strand of research that has directly investigated interpersonal neural dynamics, by measuring interpersonal neural entrainment. In side box 1 we present a formal definition of entrainment, distinguishing two ways of measuring entrainment: concurrent entrainment (e.g., ‘when A is high, B is high’ – also known as **synchrony**), and sequential entrainment (‘changes in A are followed by changes in B’). We discuss several crucial methodological caveats in measuring entrainment. In side boxes 2 and 3 we summarize recent research into interpersonal entrainment at the other levels - behavior (box 2) and physiology (see box 3). As we emphasize in these boxes, previous research suggests that behavioral and physiological entrainment is not ‘all-or-none’. Rather, during social interaction, the parent-child dyad oscillates between states of high and low synchrony [44]. Different types of entrainment are observed at different spatiotemporal scales; and interactions can show excessive as well as insufficient entrainment.

Research with adults [3, 45] and animals [8, 46] has also already shown that interpersonal entrainment develops during social interaction, independent of features such as shared entrainment to common environmental influences (see box 1). Previous research with adults has also suggested that interpersonal neural entrainment influences learning [47, 48].

Interpersonal entrainment at the second-to-minute scale

Of the range of methods available to researchers for studying *in vivo* neural activity in infants and children, the two most commonly used techniques are **fNIRS** and **EEG**. **fNIRS**, which measures changes in blood oxygenation in the cortex [49], has a relatively high spatial resolution but a low temporal resolution: the hemodynamic response lags neural activity by approximately 2 seconds and takes approximately 5 seconds to reach its peak value [50], meaning that this technique is best equipped to examine the co-fluctuation of brain activity over time-scales of seconds or minutes.

Building on a rapidly emerging body of research in adults (reviewed [45]), a number of studies have used fNIRS to examine how brain activity co-fluctuates between children and adults during social interaction. For example, one study [29] used fNIRS to examine entrainment between 9-15-month-old infants and an unfamiliar adult, and to examine how this differed

between social interaction and when conducting separate activities in the same room. Concurrent and sequential entrainment was measured by calculating the **cross-correlation** in deoxy-hemoglobin levels. Relative to bootstrapping analyses (see Box 2), significant concurrent entrainment was observed only during interaction in 11 of 57 channel pairs (mainly in frontal areas); of note, however, the bootstrapping analyses would not have controlled for shared entrainment to the audio-visual environment (see box 1), which was more similar during the interaction condition. Peak associations were observed with infant brain activity forward-predicting adult brain activity by ~3 seconds.

Another study [51] used **wavelet transform coherence** to examine concurrent entrainment in the 0.02-0.1Hz range between 5-year-old children and their parents while solving a Tangram puzzle either together or individually, separated by a screen. They recorded from right and left frontal and temporo-parietal areas and observed entrainment that was strongest in the right frontal and temporo-parietal areas. Stronger neural entrainment correlated with increased behavioral synchrony, and with better problem-solving success while working together. Of note, however, visual sensory input would also have been more similar during the cooperation condition (see box 1 and further discussions below). A third study controlled for this by positioning 5-9-year-old children and adults facing forwards, in silence, conducting a computer task that involved either cooperative or competitive behavior (see Figure 1a). Using wavelet transform coherence they observed greater concurrent entrainment in 0.08-0.5Hz power fluctuations across left prefrontal and frontopolar optode pairings between children and their parents only during the cooperative condition, and not with an unfamiliar adult – even though the conditions were otherwise tightly matched: auditory and visual information would have been identical between conditions, mutual gaze was not permitted, and movements were not more synchronous during the cooperation condition [52]. These replicate other findings using the same paradigm [53, 54].

Interpersonal synchrony at the sub-second scale

EEG measures electrical brain activity at the sub-second scale but has a low spatial resolution, making strong conclusions about the neural generators of entrainment hard to draw [55]. Studies using EEG generally decompose neural activity into frequency bands, the most commonly studied of which in developmental research are theta (c.3-6Hz/4-7Hz in young children/adults) and alpha (c.6-9Hz/8-12Hz in children/adults). Activity in these bands has been associated with attention and learning [56, 57].

Building on a large body of dual EEG research with adults [58], one recent study examined the relationship between social learning and concurrent neural entrainment in adult – 12-month-old infant dyads [59]. Parents modelled positive or negative emotions towards objects, and infants' subsequent choices were examined. Some infants tended to choose the positively-modelled object, and others the negatively-modelled; but for both groups, parent-infant neural entrainment (phase synchrony in 6-9Hz, corresponding to the infant alpha band) during teaching predicted the likelihood of social learning on a given trial. Interpersonal entrainment was most predictive of learning across central and parietal electrodes [59]. Finally, trial-to-trial increases in interpersonal neural entrainment were associated with greater maternal use of ostensive signals such as eye contact and speech pitch modulation.

Another recent study recorded concurrent and sequential entrainment in neural activity in eight-month-old infants and adults while an adult recited nursery rhymes while alternating between direct gaze and indirect gaze with the infant [60] (see Figure 1a and 1f). A control condition, direct-oblique, was also presented in which adults' face angle was the same as for indirect gaze, but their eyes were looking at the infant. Recording at the vertex only, separate bi-directional **Granger-causal** influences (child->adult and adult->child) were identified during live interaction that were stronger during direct and direct-oblique compared to indirect gaze in both theta and alpha bands. The auditory environment did not differ between conditions, and speech-brain entrainment also did not differ between conditions, suggesting that entrainment was independent of the shared environment. Infants who vocalized for longer also had a stronger neural influence on the adult [60].

A third study measured how both concurrent and sequential entrainment differed between parental positive and negative affect [61]. Graph theory analyses suggested that parents' and 12-month-old infants' interpersonal neural networks were more closely connected during maternal positive affect, and that mother to infant directional influences were stronger during positive affect.

These studies have shown that fine-grained (sub-second) neural entrainment develops during social interaction. Next, we consider *how* this entrainment develops.

How is entrainment achieved and maintained?

Building on work already conducted with adults and animals, the studies reviewed above have suggested that aspects of interpersonal neural entrainment develop during early adult-child interaction. As yet, however, our understanding of how entrainment is achieved and maintained is limited. Here, building on the discussion of uni-directional influences in part one of the review, we speculate about two complementary, but distinct, possible causes of neural entrainment. First, we discuss how the evoked responses that both children and adults show in response to ostensive cues such as gaze onsets could involve concurrently **phase resetting**, leading to **phase entrainment**. In the second, we discuss how actor-observer correspondences could lead to concurrent patterns of neural activity, potentially causing neural entrainment even in the absence of behavioral entrainment.

Neural entrainment as a consequence of behavioral cues

Social interactions involve the development of behavioral entrainment, both concurrent and sequential – including movements, gaze patterns, vocalizations and facial expressions (see Box 2). Evidence reviewed above also suggests that ostensive cues cause immediate, transient increases in behavioral entrainment. Since brain-behavior correspondences are equivalent across different individuals, this behavioral entrainment is also likely to cause neural entrainment. Indeed, some of the studies we reviewed have noted significant correlations between the degree of behavioral synchrony observed in dyads, and the neural synchrony observed [51].

The EEG studies reviewed above have, consistent with adult [58] and animal studies [8, 46], also documented phase entrainment during social interaction at much finer time-scale (up to 9Hz) than the second-to-second scale over which behavioral entrainment has been observed. This more fine-grained entrainment may also, however, have behavioral causes. As described above, behavioral ostensive cues are known to cause strong neural evoked responses, even in newborn infants. One possibility is that ostensive cues might operate as ‘edges’ in a similar way to the acoustic ‘edges’ (i.e. sharp increases in signal intensity) in the speech amplitude envelope that are known to drive theta- and delta-rate phase entrainment to cause speech-brain synchrony [62]. Phase resetting could take place in both partners to ostensive cues such as gaze onsets and vocalizations, and this could be one driver that allows phase entrainment to be achieved and maintained (see Figure 3). One prediction that would test this hypothesis would

be to assess whether interpersonal neural entrainment, on both a second-to-second and a sub-second scale, shows transient increases in the time window immediately following ostensive cues (see Outstanding questions).

Neural entrainment arising from higher-order cognitive processes?

Some of the studies reviewed above have [52, 54], however, also documented neural entrainment that cannot be explained solely by behavioral entrainment – consistent with recent animal research that observed neural activity in socially interacting mice under conditions in which behavioral synchrony and shared entrainment to external sensory input were tightly controlled for [8]. Using *in vivo* recordings from populations of neurons in the dorsomedial prefrontal cortex, the results of this animal research suggested that concurrent entrainment (synchrony) was driven by behavior-encoding neurons that show overlapping activity when an action is performed by themselves, and when the same action is performed by a social partner [8] (see section above, on contingent responsiveness and actor-observer correspondences).

Adult studies have further built on this, by suggesting in addition that neural entrainment may reflect higher-order cognitive processes such as comprehension, engagement and shared understanding [63, 64]. In one study, for example, concurrent inter-participant entrainment in neural activity was recorded while adult participants listened to a real-life auditory narrative compared to a temporally scrambled version; inter-participant entrainment was increased in default mode network areas (including medial prefrontal cortex) when participants had a shared understanding of a story [65] (see also [66]). These results suggest that entrainment is not just a consequence of concurrent brain-behavior correspondences and sensory cue-based phase-resetting, as described above; rather, that neural entrainment may also be a consequence of temporally concurrent patterns of activity, driven shared understanding in addition to shared entrainment to sensory cues [37, 67, 68]. As yet, however, no research has investigated this from the perspective of early learning.

As we describe further in the Outstanding Questions, further work also remains to uncover whether, and if so how, these separate causes contribute to neural entrainment during early learning. For example, one area for future investigation is the degree to which interpersonal entrainment may potentially affect later stages of information processing more than earlier stages [38, 69]. Research with five-month-old infants has shown that different ostensive cues

(eye gaze and vocalizations) show differing patterns of activation in low-level processing regions, but overlapping patterns of activation in frontal areas [70]. It is possible that similar patterns would be observed for interpersonal entrainment – but no research has yet investigated this.

Is synchrony ‘just’ an epiphenomenon?

In this final section, we consider whether interpersonal neural dynamics, quantified by measuring entrainment, are best seen ‘simply’ as epiphenomena – as secondary consequences of common entrainment to behavioral cues and of actor-observer correspondences. Alternatively, we hypothesize two possible mechanistic routes through which interpersonal neural entrainment might play a causal role during early learning.

First, there are inherent differences in brain function between infants and adults: developing brains are intensely stochastic [71, 72], with altered intra-brain connectivity [73] and entrainment to external stimuli [74]. One key function of social interaction is **allostasis** (helping to maintain a stable state) [75], achieved via bi-directional, dynamical mutual adaptation within the dyad (see also [19, 76]). For children, then, entrained states might involve more mature patterns of functional activity; transient phases of child-adult entrainment could thus serve as a transitional stage towards mature function.

Second, human perception is known to rely on oscillatory processes which shape conscious experience [77]. Research has suggested that the phase of neural activity at the time of stimulus presentation may relate systematically to the excitability of neural populations and the magnitude of event-related responses [78, 79] (although see [80]); accordingly, perceptual stimuli that are delivered during a high excitability oscillatory phase may be more likely to be detected and encoded than stimuli that arrive at an inhibitory oscillatory phase [79, 81]. During an interaction, we may use social cues to ‘nudge’ our partner into a transient state of entrainment – such that, for example, parent-initiated mutual gaze might trigger a short-term increase in parent-child phase synchrony. The effect of this would be to ensure that, for the duration of the existence of a high synchrony state, high excitability oscillatory phases co-occur, thus ensuring that information (e.g. word labels) is presented at optimal phases for

encoding by the ‘receiver’ (see Figure 3). In the Outstanding Questions section, we outline some predictions to test these hypotheses.

Concluding remarks

In this review, we have evaluated the evidence for how social behaviors affect not one, but both partners in a dyad. We have concentrated on two important and well-researched aspects of early social interaction: ostensive cues (signals that are sent during social interaction to indicate communicative intent), and contingent responsiveness (behaviors that indicate communicative sensitivity within an interaction). We have concluded that the uni-directional effects of each - i.e. how one partner transiently influences the other, with both partners considered independently - are well understood. But we have concluded that our understanding of how ostensive cues and contingent responsiveness alter the interpersonal neural dynamics of the interaction – i.e., how the partners inter-relate to one another - is currently limited.

We have also reviewed a smaller corpus of more recent research that has taken a different approach, by recording from two individuals concurrently during social interaction and measuring interpersonal neural entrainment. We concluded that, consistent with animal and adult research, this evidence suggests that interpersonal neural entrainment does develop during social interaction. Building on the discussion of uni-directional influences in part one of the review, we have discussed how concurrent and sequential neural entrainment may arise as a result of two causes: first, as a consequence of shared entrainment to behavioral cues such as ostensive cues, and, second, as a consequence of actor-observer correspondences and shared understanding. And we have hypothesized two possible mechanistic routes through which interpersonal neural entrainment may play a causal role during early learning.

Our understanding of how early social interaction affects the bi-directional neural dynamics of the two partners (i.e. how the two patterns of brain activity relate to one another) is still at an early stage. Many important and fundamental questions remain (see Outstanding Questions). Perhaps the two most important aspects of the results hitherto are, first, that social influences affect early learning exchanges at a variety of different temporal scales, including both sub-second as well as second-to-minute temporal scales; and, second, that these interactions are a

consequence of bi-directional sensitivity, in which *both* partners - child and adult – influence each other.

Acknowledgement

This research was funded by Leverhulme Project Grant RPG-2018-281. We wish to thank Chiara Bulgarelli, Trinh Nguyen, Carina de Klerk, Vanessa Reindl and Louise Goupil for reading and commenting on earlier versions of this manuscript.

Side Box: Glossary (450 words)

Allostasis: The process by which internal equilibrium is maintained.

Contingency: The dependent temporal relationship between the occurrence of two events.

Cross-correlation: A measure of the similarity between two time-series as a function of the displacement of one relative to the other. Cross-correlations examine whether changes in one time-series tend to anticipate, or follow on from, changes in another.

Dyadic attention: Two-way sharing of attention - either between a person and an object, or a person and another person.

EEG: Electro-encephalography – a method for recording naturally occurring electrical brain activity.

Entrainment: In this paper we consider two forms of entrainment. The first is concurrent entrainment (a zero-lag relationship between two time series, e.g. ‘when A is high, B is high’ or ‘when A is high, B is low’), which is commonly known as synchrony. The second is sequential entrainment (‘changes in A forward-predict changes in B’). See Box 1 for further details of how these terms are quantified.

ERP: Evoked response potential or event-related potential.

fNIRS: Functional Near-Infrared Spectroscopy – a method for recording blood oxygenation levels near the scalp.

Granger causality: A method for quantifying sequential entrainment by analyzing how one time-series influences another; similar to cross-correlations, but incorporating information about the self-similarity of each time series.

Hyperscanning: Neuroimaging studies that record brain activity in two individuals at the same time.

Ostensive signals: Cues from a communicator to generate an interpretation of communicative intention in an addressee.

Partial directed coherence: A technique to examine cross-spectral Granger-causal relationships in multivariate time series.

Phase entrainment: Concurrent entrainment in the phase of ongoing oscillatory activity.

Phase resetting: An abrupt shift (e.g. advancement or delay) in the phase of on-going oscillatory activity, usually in response to perturbation by a sensory cue.

Phase-locking value: A technique for estimating concurrent entrainment between the phase series of two signals.

Synchrony: In this paper, we treat the term synchrony as synonymous with concurrent entrainment. See Box 1 for further details.

Triadic attention: Three-way sharing of attention – generally between two people and an object.

Wavelet transform coherence: A technique that can be used to measure both concurrent and sequential synchrony of two signals in the time-frequency plane.

Side box 1: types of interpersonal entrainment and measurement caveats (400 words)

The concept of entrainment, and the related concept of synchrony, are immensely rich topics that have been studied across all domains of knowledge [82-85]. Within cognitive neuroscience, extensive previous research has examined how different units within a brain, (from individual neurons to brain regions), entrain to one another (*intra*-personal entrainment) [86-88]. Previous research has also examined entrainment between individual brains and temporal structures in the environment (stimulus-brain entrainment) [89].

In this article we focus on two forms of interpersonal entrainment [19, 90]:

- *Concurrent entrainment* (see Figure 1c) – a zero-lag relationship, e.g. ‘when X is high, Y is high’ – measured using techniques including **Phase-Locking Value** [91], Wavelet Coherence [92] and others. Concurrent synchrony is undirected ($A \rightarrow B$ is indistinguishable from $B \rightarrow A$). Concurrent entrainment is treated as synonymous with the term ‘synchrony’.
- *Sequential entrainment* (see Figure 1d) – ‘changes in X forward-predict changes in Y’ – measured using techniques derived from Granger Causality [93], including Generalized **Partial Directed Coherence** [94]. Sequential entrainment is directional ($A \rightarrow B \neq B \rightarrow A$).

Entrainment can also be estimated based on different aspects of the signal:

- *amplitude*. Some fNIRS studies [95] and most fMRI studies [96] measure co-fluctuations in the amplitude of the signal – which, depending on the method, measures blood oxygenation/deoxygenation (fNIRS), the BOLD signal (fMRI)), or voltage (for EEG).
- *phase*. Many EEG studies measure the alignment of oscillatory phase between two signals. [59, 61].
- *combinations*. Many fNIRS studies measure wavelet coherence, which includes both amplitude and phase [51, 52]. Other studies measure e.g. phase-amplitude coupling (see [97]).

In the case of child-adult interactions, one complication is that adults and children have different dominant frequency bands of naturally occurring brain activity [98]. Although the majority of studies hitherto have not addressed this, techniques for measuring cross-frequency coupling are available [55].

Researchers measuring interpersonal neural entrainment face a number of methodological caveats [90]:

The first is that common intrinsic properties of the neural signal itself can create a false impression of entrainment [90]. For example, two adults, each with a dominant alpha rhythm

of 10Hz, might show consistent phase relationships between their alpha rhythms even in the absence of any communication [90]. Similar considerations apply when considering variability in amplitude and power of the signal, where co-occurring oscillatory activity may be attributable to other sources (such as autonomic activity [99]).

A second problem is that neural activity is also influenced by common environmental perturbations. For example, neural activity synchronizes to temporal structures in speech [89], and differentiating neural interpersonal entrainment from synchrony attributable to shared external perturbation can be highly challenging [100]. This is particularly true for naturalistic paradigms where factors such as the acoustic environment cannot be completely controlled for.

Common techniques for addressing these problems often use bootstrapping approaches in which corresponding epochs from each dyad are either temporally translocated ('shuffled') or phase scrambled and the entrainment analysis is performed repeatedly. In this way, it is possible to estimate how the observed entrainment would differ from the entrainment observed by chance (e.g. [29]). Of note, however, this approach does not control for environmental influences in naturalistic studies where the environment differs between dyads. Because of this inherent problem, most hyperscanning studies do not measure absolute levels of synchrony, but rather examine relative changes in coupling between different experimental conditions (such as the presence or absence of mutual gaze) – while keeping other factors constant (such as the acoustic environment).

Side box 2: behavioral entrainment (400 words)

Research into concurrent and sequential behavioral entrainment in parent-child dyads has a long history [101, 102], and includes investigations using both qualitative [103] and quantitative [104] methods. Entrainment has been investigated at multiple levels of behavior, including:

Vocalizations. Patterns of sequential entrainment during vocal exchanges between adults and infants have been identified at multiple scales [105, 106]. Weaker adult-infant coordination

has been associated, for example, with increased attachment problems and poorer cognitive outcomes [106, 107].

Facial affect. Concurrent and sequential entrainment in facial affect has been identified during tabletop play [19] that changes over time and differs between fathers and mothers [108]. Stronger child->parent and parent->child influences associate with, for example, later child self-control [109] and symbolic competence [110]. Not all findings associate increased entrainment with positive outcomes [111] (see Box 3).

Eye gaze. Two principal types of eye gaze entrainment are of interest:

- a) Concurrent partner gaze, referred to a ‘mutual gaze’. Mutual gaze during infancy positively correlates with later attention control [112] and is reduced in some atypical dyads [113] [114].
- b) Sequential entrainment in object gaze, referred to as ‘gaze following’ – i.e. that one partner’s look towards an object forward-predicts the other partner’s look. Although gaze following has been extensively investigated using simplified screen-based paradigms, research suggests that in ‘real-world’ naturalistic settings (see e.g. Figure 1) infants actually follow parents’ gaze only rarely [115].

Both types of gaze entrainment, concurrent mutual gaze and sequential gaze following, are often combined as joint, or **triadic attention** –the three-way sharing of attention between a partner and an object, which involves both mutual gaze and gaze following [116].

Touch. Current research may over-emphasize the role of gaze during shared parent-child attention and learning: gaze is a predominant feature of Western parent-child interaction, but less so in other cultures [117]. Similar to the distinction between mutual gaze and joint attention, research has examined both touching one another during parent-child interactions [118], and combined touch to an object [115].

Inducing behavioral entrainment. Some research has experimentally induced behavioral entrainment – suggesting, for example, that this can be effective at promoting shared understanding in adult-child dyads [119, 120]

Side box 3: physiological entrainment (400 words)

Whereas some research into parent-child interactions has examined how, for example, individual heart-beats become coordinated over time [121], most research has studied how autonomic arousal co-varies across time windows (both concurrent, and sequentially - see Box 1). Some research has administered how patterns of change co-vary within dyads by administering experimental stressors in the lab [122, 123]; other research has examined how autonomic arousal levels co-fluctuate in naturalistic, home settings [124, 125].

Parents use diverse tactics to maintain allostasis

One central aim of social interaction is thought to be to help individuals (particularly young individuals) to maintain a stable state - a process known as allostasis [75]. How parents respond to changes in their child in order to maintain allostasis is thought to vary contingent on context. Short-term increases in concurrent parent-child physiological entrainment were observed, for example, negative affect vocalizations from the child [124]. When the initial arousal level of the parent is low, parent increase their own arousal in response to increases in child arousal – matching their own arousal state to their child’s; but when the initial arousal level of the parent is high, parents respond to increases in the child’s arousal in the opposite way - by decreasing their own arousal [124]. This suggests that adults employ diverse tactics to maintain allostasis within the dyad [72, 75] – dynamically connecting, or disconnecting, their own level of arousal from their child’s [76].

‘There when you need me’ vs ‘Always on’

Arousal levels in typical dyads do not routinely co-fluctuate in naturalistic settings [124]. Instead, typical parents selectively respond to ‘peak’ changes in their child’s arousal, but not otherwise. Parents with depression under-respond to ‘peak’ moments of child arousal [111] (see [126] for comparable neuroimaging results). In contrast, parents with higher anxiety showed no difference in responsivity to ‘peak’ child arousal moments but were *more* responsive to small-scale fluctuations in their child, and showed higher parent-child entrainment overall [125]. These observations echo similar behavioral findings [111] and question whether optimal outcomes always associate with greater parent-child entrainment.

Side box: Outstanding questions [2000 chars]

- Intra-brain entrainment has been shown to play an important role in attention and learning; how does inter-brain entrainment relate to intra-brain entrainment?
- Are later stages of stimulus processing relatively more influenced by interpersonal influences than earlier stages?
- Do concurrent and sequential entrainment reflect the same or distinct phenomena, in terms of underlying causes and consequences?
- Does interpersonal entrainment show transient increases in the time window immediately following an ostensive cue? And are these increases driven by temporally co-occurring phase resetting in response to the ostensive cue?
- Does greater adult-child neural entrainment at the time of a learning event associate with more effective learning? If so, are differences mediated by an increased likelihood of learning items (e.g. word labels) being presented during high excitatory oscillatory phases?
- How does inter-personal entrainment change over development? Other aspects of development show a transition from co-regulation (within the dyad) to self-regulation (within the individual) over time. Is the same true for early learning? If so, is interpersonal neural entrainment more important during early learning than later on?
- Does atypical development manifest unusual patterns of neural responsivity and entrainment? Certain clinical populations show excessive behavioral and physiological entrainment (see Boxes 2 and 3); is more interpersonal neural entrainment always better?

Figures

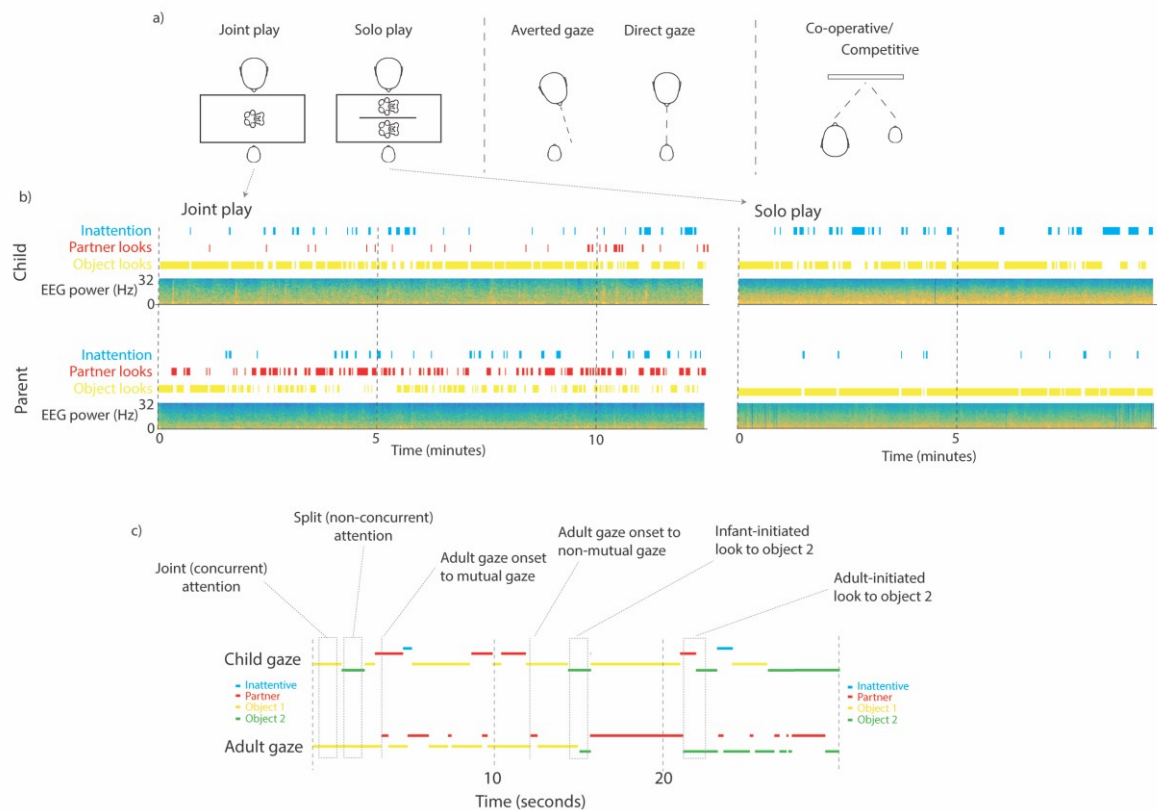


Figure 1: Behavioral paradigms used to measure interpersonal neural entrainment. a) examples of the experimental set-ups described in the main text, used by: left [43, 127]; middle [60]; right [52]; b) examples of raw data collected using the paradigms from [43, 127]; even from this raw data sample some significant patterns noted overall data can be seen – such as that parents pay more attention to infants during joint play than vice versa [115], and that infants are more inattentive during solo play than joint play [127]. c) example of a 30-second segment of data illustrating the further range of different types of events that can be identified in naturalistic interactions.

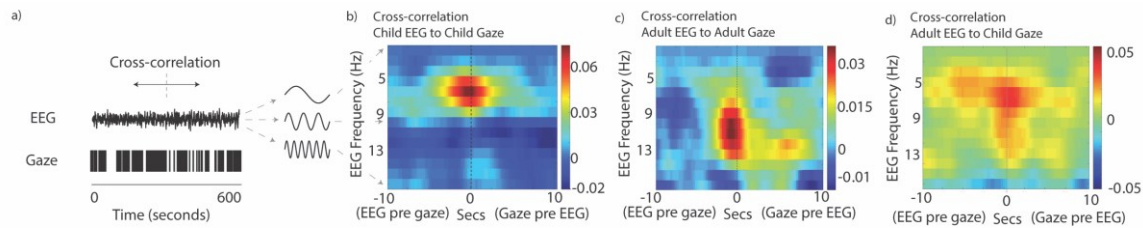


Figure 2: Neural activity in the parent entrains to attentional fluctuations in the child. From [43]: a) schematic illustrating the analysis; b) cross-correlation between child EEG and child gaze, showing an association between child neural activity and child attention; c) cross-correlation between adult EEG and adult gaze, also showing an association between adult neural activity and adult attention; d) cross-correlation between adult EEG and child Gaze, showing an association between the adult's neural activity and the child's attention. Subsequent analyses showed that the association between the adult's neural activity and the child's attention was independent of the adult's own attention. Whereas the child EEG-child gaze and adult EEG-adult gaze relationships were predictive (i.e. the strongest associations were found between neural activity at a given moment and attention c.750ms after that moment), the adult EEG-child gaze associations were reactive (i.e. the strongest associations were found between the child's attention at a given moment and the adult's neural activity c.750ms after that moment).

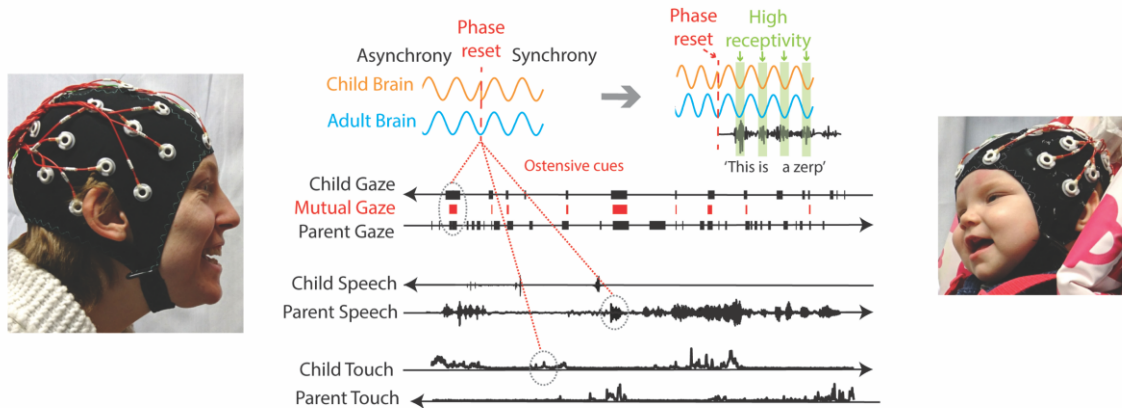


Figure 3. Schematic illustrating a mechanistic role for interpersonal entrainment during early learning. In a mutual responsive interaction, there is a mutual timely exchange of phase-resetting cues between partners. Social ostensive signals may act as synchronizing cues that trigger transient increases in interpersonal entrainment through phase-resetting, leading subsequently produced maternal speech to arrive at a high receptivity phase for optimal encoding by the infant.

References (max 120)

1. Schilbach, L., et al., *Toward a second-person neuroscience 1*. Behavioral and brain sciences, 2013. **36**(4): p. 393-414.
2. Wheatley, T., et al., *Beyond the Isolated Brain: The Promise and Challenge of Interacting Minds*. Neuron, 2019. **103**(2): p. 186-188.
3. Redcay, E. and L. Schilbach, *Using second-person neuroscience to elucidate the mechanisms of social interaction*. Nature Reviews Neuroscience, 2019: p. 1.
4. Redcay, E. and K.R. Warnell, *A social-interactive neuroscience approach to understanding the developing brain*, in *Advances in child development and behavior*. 2018, Elsevier. p. 1-44.
5. Kuhl, P.K., F.M. Tsao, and H.M. Liu, *Foreign-language experience in infancy: Effects of short-term exposure and social interaction on phonetic learning*. Proceedings of the National Academy of Sciences of the United States of America, 2003. **100**(15): p. 9096-9101.
6. Begus, K., T. Gliga, and V. Southgate, *Infants learn what they want to learn: Responding to infant pointing leads to superior learning*. PloS one, 2014. **9**(10): p. e108817.
7. Yu, C. and L.B. Smith, *The social origins of sustained attention in one-year-old human infants*. Current Biology, 2016. **26**(9): p. 1235-1240.
8. Kingsbury, L., et al., *Correlated Neural Activity and Encoding of Behavior across Brains of Socially Interacting Animals*. Cell, 2019.
9. Dumas, G., et al., *Inter-Brain Synchronization during Social Interaction*. PLoS ONE, 2010. **5**(8): p. e12166.
10. Csibra, G. and G. Gergely, *Natural pedagogy*. Trends in cognitive sciences, 2009. **13**(4): p. 148-153.
11. Albert, R.R., J.A. Schwade, and M.H. Goldstein, *The social functions of babbling: acoustic and contextual characteristics that facilitate maternal responsiveness*. Developmental science, 2018. **21**(5): p. e12641.
12. Lucca, K. and M.P. Wilbourn, *Communicating to learn: Infants' pointing gestures result in optimal learning*. Child development, 2018. **89**(3): p. 941-960.
13. Begus, K. and V. Southgate, *Curious Learners: How Infants' Motivation to Learn Shapes and Is Shaped by Infants' Interactions with the Social World*, in *Active Learning from Infancy to Childhood*. 2018, Springer. p. 13-37.
14. Murray, L. and C. Trevarthen, *The infant's role in mother-infant communications*. Journal of child language, 1986. **13**(1): p. 15-29.
15. Stahl, A.E. and L. Feigenson, *Observing the unexpected enhances infants' learning and exploration*. Science, 2015. **348**(6230): p. 91-94.
16. Goupil, L., M. Romand-Monnier, and S. Kouider, *Infants ask for help when they know they don't know*. Proceedings of the National Academy of Sciences, 2016: p. 201515129.
17. Goupil, L. and S. Kouider, *Behavioral and neural indices of metacognitive sensitivity in preverbal infants*. Current Biology, 2016. **26**(22): p. 3038-3045.

18. Murray, L., et al., *The functional architecture of mother-infant communication, and the development of infant social expressiveness in the first two months*. Scientific Reports, 2016. **6**: p. 39019.
19. Feldman, R., *Parent–infant synchrony and the construction of shared timing; physiological precursors, developmental outcomes, and risk conditions*. Journal of Child psychology and Psychiatry, 2007. **48**(3-4): p. 329-354.
20. Gratier, M. and E. Devouche, *Imitation and repetition of prosodic contour in vocal interaction at 3 months*. Developmental Psychology, 2011. **47**(1): p. 67.
21. Arco, C.M., P.A. Self, and N. Gutrecht, *The effect of increased maternal visual regard on neonatal visual behavior*. Journal of Clinical Child & Adolescent Psychology, 1979. **8**(2): p. 117-120.
22. Senju, A. and G. Csibra, *Gaze Following in Human Infants Depends on Communicative Signals*. Current biology, 2008. **18**(668-671).
23. Butterworth, G. and S. Itakura, *How the eyes, head and hand serve definite reference*. British Journal of Developmental Psychology, 2000. **18**(1): p. 25-50.
24. Young, K.S., et al., *The neural basis of responsive caregiving behaviour: Investigating temporal dynamics within the parental brain*. Behavioural brain research, 2017. **325**: p. 105-116.
25. Farroni, T., et al., *Eye contact detection in humans from birth*. Proceedings of the National Academy of Sciences, 2002. **99**(14): p. 9602-9605.
26. Urakawa, S., et al., *Selective medial prefrontal cortex responses during live mutual gaze interactions in human infants: an fNIRS study*. Brain topography, 2015. **28**(5): p. 691-701.
27. Grossmann, T., et al., *Early cortical specialization for face-to-face communication in human infants*. Proceedings of the Royal Society of London B: Biological Sciences, 2008. **275**(1653): p. 2803-2811.
28. Zhang, Y., et al., *Neural coding of formant-exaggerated speech in the infant brain*. Developmental science, 2011. **14**(3): p. 566-581.
29. Piazza, E.A., et al., *Infant and adult brains are coupled to the dynamics of natural communication*. Psychological Science, in press.
30. Striano, T., V.M. Reid, and S. Hoehl, *Neural mechanisms of joint attention in infancy*. European Journal of Neuroscience, 2006. **23**(10): p. 2819-2823.
31. Hoehl, S., et al., *Eye contact during live social interaction modulates infants' oscillatory brain activity*. Social Neuroscience, 2014. **9**(3): p. 300-308.
32. Grossmann, T., S. Lloyd-Fox, and M.H. Johnson, *Brain responses reveal young infants' sensitivity to when a social partner follows their gaze*. Developmental Cognitive Neuroscience, 2013. **6**: p. 155-161.
33. Bourvis, N., et al., *Pre-linguistic infants employ complex communicative loops to engage mothers in social exchanges and repair interaction ruptures*. Royal Society open science, 2018. **5**(1): p. 170274.
34. Rayson, H., et al., *Building blocks of joint attention: Early sensitivity to having one's own gaze followed*. Developmental Cognitive Neuroscience, 2019: p. 100631.
35. Goldstein, M.H., et al., *Learning while babbling: Prelinguistic object-directed vocalizations indicate a readiness to learn*. Infancy, 2010. **15**(4): p. 362-391.
36. Lavelli, M. and A. Fogel, *Interdyad differences in early mother–infant face-to-face communication: Real-time dynamics and developmental pathways*. Developmental Psychology, 2013. **49**(12): p. 2257.

37. Gallotti, M., M.T. Fairhurst, and C.D. Frith, *Alignment in social interactions*. Consciousness and cognition, 2017. **48**: p. 253-261.
38. Hasson, U. and C.D. Frith, *Mirroring and beyond: coupled dynamics as a generalized framework for modelling social interactions*. Philosophical Transactions of the Royal Society B: Biological Sciences, 2016. **371**(1693): p. 20150366.
39. Meltzoff, A.N. and P.J. Marshall, *Human infant imitation as a social survival circuit*. Current Opinion in Behavioral Sciences, 2018. **24**: p. 130-136.
40. Bernhardt, B.C. and T. Singer, *The neural basis of empathy*. Annual review of neuroscience, 2012. **35**: p. 1-23.
41. Singer, T., et al., *Empathy for pain involves the affective but not sensory components of pain*. Science, 2004. **303**(5661): p. 1157-1162.
42. Leerkes, E.M., et al., *Pathways by which mothers' physiological arousal and regulation while caregiving predict sensitivity to infant distress*. Journal of Family Psychology, 2016. **30**(7): p. 769.
43. Wass, S.V., et al., *Parental neural responsivity to infants' visual attention: how mature brains influence immature brains during social interaction*. PLoS biology, 2018. **16**(12): p. e2006328.
44. Gianino, A. and E.Z. Tronick, *The mutual regulation model: The infant's self and interactive regulation and coping and defensive capacities*. 1988.
45. Gvirts, H.Z. and R. Perlmutter, *What Guides Us to Neurally and Behaviorally Align With Anyone Specific? A Neurobiological Model Based on fNIRS Hyperscanning Studies*. The Neuroscientist, 2019: p. 1073858419861912.
46. Zhang, W. and M.M. Yartsev, *Correlated Neural Activity across the Brains of Socially Interacting Bats*. Cell, 2019.
47. Davidesco, I., et al., *Brain-to-brain synchrony predicts long-term memory retention more accurately than individual brain measures*. bioRxiv, 2019: p. 644047.
48. Pan, Y., et al., *Interpersonal synchronization of inferior frontal cortices tracks social interactive learning of a song*. Neuroimage, 2018. **183**: p. 280-290.
49. Reindl, V., et al., *Conducting Hyperscanning Experiments with Functional Near-Infrared Spectroscopy*. JoVE (Journal of Visualized Experiments), 2019(143): p. e58807.
50. Hong, K.-S., N. Naseer, and Y.-H. Kim, *Classification of prefrontal and motor cortex signals for three-class fNIRS-BCI*. Neuroscience letters, 2015. **587**: p. 87-92.
51. Nguyen, T., Schleichauf, H., Kayhan, E., Matthes, D., Vrtička, P. & Hoehl, S., *The effects of interaction quality on neural synchrony during mother-child problem solving*. Cerebral Cortex, in press.
52. Reindl, V., et al., *Brain-to-brain synchrony in parent-child dyads and the relationship with emotion regulation revealed by fNIRS-based hyperscanning*. Neuroimage, 2018. **178**: p. 493-502.
53. Pan, Y., et al., *Cooperation in lovers: An fNIRS-based hyperscanning study*. Human brain mapping, 2017. **38**(2): p. 831-841.
54. Miller, J.G., et al., *Inter-brain synchrony in mother-child dyads during cooperation: An fNIRS hyperscanning study*. Neuropsychologia, 2019. **124**: p. 117-124.
55. Noreika, V., et al., *14 challenges and their solutions for conducting social neuroscience and longitudinal EEG research with infants*. Infant Behavior & Development, in press.

56. Jones, E.J., et al., *Developmental changes in infant brain activity during naturalistic social experiences*. *Developmental psychobiology*, 2015. **57**(7): p. 842-853.
57. Orekhova, E.V., et al., *EEG theta rhythm in infants and preschool children*. *Clinical Neurophysiology*, 2006. **117**(5): p. 1047-1062.
58. Liu, D., et al., *Interactive Brain Activity: Review and Progress on EEG-Based Hyperscanning in Social Interactions*. *Frontiers in Psychology*, 2018. **9**: p. 1862.
59. Leong, V., et al., *Mother-infant interpersonal neural connectivity predicts infants' social learning*. 2019.
60. Leong, V., et al., *Speaker gaze increases information coupling between infant and adult brains*. *Proceedings of the National Academy of Sciences*, 2017: p. 201702493.
61. Covarrubias, L.S., et al., *Emotional valence modulates the topology of the parent-infant inter-brain network*. *NeuroImage*, in press: p. 623355.
62. Doelling, K.B., et al., *Acoustic landmarks drive delta–theta oscillations to enable speech comprehension by facilitating perceptual parsing*. *Neuroimage*, 2014. **85**: p. 761-768.
63. Fishburn, F.A., et al., *Putting our heads together: interpersonal neural synchronization as a biological mechanism for shared intentionality*. *Social cognitive and affective neuroscience*, 2018. **13**(8): p. 841-849.
64. Stolk, A., et al., *Cerebral coherence between communicators marks the emergence of meaning*. *Proceedings of the National Academy of Sciences*, 2014. **111**(51): p. 18183-18188.
65. Simony, E., et al., *Dynamic reconfiguration of the default mode network during narrative comprehension*. *Nature communications*, 2016. **7**: p. 12141.
66. Liu, Y., et al., *Measuring speaker–listener neural coupling with functional near infrared spectroscopy*. *Scientific Reports*, 2017. **7**: p. 43293.
67. Nummenmaa, L., et al., *Emotions promote social interaction by synchronizing brain activity across individuals*. *Proceedings of the National Academy of Sciences*, 2012. **109**(24): p. 9599-9604.
68. Hu, Y., et al., *Inter-brain synchrony and cooperation context in interactive decision making*. *Biological psychology*, 2018. **133**: p. 54-62.
69. Konvalinka, I. and A. Roepstorff, *The two-brain approach: how can mutually interacting brains teach us something about social interaction?* *Frontiers in human neuroscience*, 2012. **6**: p. 215.
70. Parise, E. and G. Csibra, *Neural responses to multimodal ostensive signals in 5-month-old infants*. *PloS one*, 2013. **8**(8): p. e72360.
71. Robertson, S.S., *Empty-headed dynamical model of infant visual foraging*. *Developmental psychobiology*, 2014. **56**(5): p. 1129-1133.
72. Beebe, B., et al., *A systems view of mother–infant face-to-face communication*. *Developmental psychology*, 2016. **52**(4): p. 556.
73. Grayson, D.S. and D.A. Fair, *Development of large-scale functional networks from birth to adulthood: A guide to the neuroimaging literature*. *Neuroimage*, 2017. **160**: p. 15-31.
74. Vakorin, V.A., S. Lippé, and A.R. McIntosh, *Variability of brain signals processed locally transforms into higher connectivity with brain development*. *Journal of neuroscience*, 2011. **31**(17): p. 6405-6413.
75. Atzil, S., et al., *Growing a social brain*. *Nature Human Behaviour*, 2018: p. 1.

76. Fogel, A., *Two principles of communication: Co-regulation and framing*, in *New perspectives in early communicative development*. 2017, Routledge. p. 9-22.
77. Buzsaki, G., *Rhythms of the Brain*. 2006: Oxford University Press.
78. Lakatos, P., et al., *Entrainment of neuronal oscillations as a mechanism of attentional selection*. *science*, 2008. **320**(5872): p. 110-113.
79. Busch, N.A., J. Dubois, and R. VanRullen, *The phase of ongoing EEG oscillations predicts visual perception*. *Journal of Neuroscience*, 2009. **29**(24): p. 7869-7876.
80. Ruzzoli, M., et al., *The relevance of alpha phase in human perception*. *Cortex*, 2019.
81. Mathewson, K.E., et al., *To see or not to see: prestimulus α phase predicts visual awareness*. *Journal of Neuroscience*, 2009. **29**(9): p. 2725-2732.
82. Hagen, E.H. and G.A. Bryant, *Music and dance as a coalition signaling system*. *Human nature*, 2003. **14**(1): p. 21-51.
83. Johnson, S., *Emergence: The connected lives of ants, brains, cities, and software*. 2002: Simon and Schuster.
84. Di Paolo, E.A., *Rhythmic and non-rhythmic attractors in asynchronous random Boolean networks*. *BioSystems*, 2001. **59**(3): p. 185-195.
85. Kennedy, J., *Swarm intelligence*, in *Handbook of nature-inspired and innovative computing*. 2006, Springer. p. 187-219.
86. Engel, A.K. and W. Singer, *Temporal binding and the neural correlates of sensory awareness*. *Trends in Cognitive Sciences*, 2001. **5**(1): p. 16-25.
87. Calderone, D.J., et al., *Entrainment of neural oscillations as a modifiable substrate of attention*. *Trends in Cognitive Sciences*, 2014. **18**(6): p. 300-309.
88. Regev, M., et al., *Propagation of Information Along the Cortical Hierarchy as a Function of Attention While Reading and Listening to Stories*. *Cerebral cortex (New York, NY: 1991)*, 2018.
89. Giraud, A.-L. and D. Poeppel, *Cortical oscillations and speech processing: emerging computational principles and operations*. *Nature neuroscience*, 2012. **15**(4): p. 511-517.
90. Burgess, A.P., *On the interpretation of synchronization in EEG hyperscanning studies: a cautionary note*. *Frontiers in human neuroscience*, 2013. **7**: p. 881.
91. Lachaux, J.P., et al., *Measuring phase synchrony in brain signals*. *Human Brain Mapping*, 1999. **8**(4): p. 194-208.
92. Grinsted, A., J.C. Moore, and S. Jevrejeva, *Application of the cross wavelet transform and wavelet coherence to geophysical time series*. *Nonlinear processes in geophysics*, 2004. **11**(5/6): p. 561-566.
93. Granger, C.W., *Investigating causal relations by econometric models and cross-spectral methods*. *Econometrica: Journal of the Econometric Society*, 1969: p. 424-438.
94. Baccalá, L.A. and K. Sameshima, *Partial directed coherence: a new concept in neural structure determination*. *Biological Cybernetics*, 2001. **84**(6): p. 463-474.
95. Piazza, E.A., et al., *Infant and adult brains are coupled to the dynamics of natural communication*. *bioRxiv*, 2018: p. 359810.
96. Babiloni, F. and L. Astolfi, *Social neuroscience and hyperscanning techniques: past, present and future*. *Neuroscience & Biobehavioral Reviews*, 2014. **44**: p. 76-93.
97. Cohen, M.X., *Analyzing neural time series data: theory and practice*. 2014: MIT press.

98. Dustman, R.E., D.E. Shearer, and R.Y. Emmerson, *Life-span changes in EEG spectral amplitude, amplitude variability and mean frequency*. *Clinical neurophysiology*, 1999. **110**(8): p. 1399-1409.
99. Shmueli, K., et al., *Low-frequency fluctuations in the cardiac rate as a source of variance in the resting-state fMRI BOLD signal*. *Neuroimage*, 2007. **38**(2): p. 306-320.
100. Fairhurst, M. and G. Dumas, *Reciprocity and alignment: quantifying coupling in dynamic interactions*. 2019.
101. Kaye, K. and A. Fogel, *The temporal structure of face-to-face communication between mothers and infants*. *Developmental Psychology*, 1980. **16**(5): p. 454.
102. Tronick, E., *Social interchange in infancy: Affect, cognition, and communication*. 1982: Univ Park Press.
103. Leclère, C., et al., *Why synchrony matters during mother-child interactions: a systematic review*. *PLoS One*, 2014. **9**(12): p. e113571.
104. Cohn, J.F. and E.Z. Tronick, *Mother-Infant Face-to-Face Interaction: Influence is Bidirectional and Unrelated to Periodic Cycles in Either Partner's Behavior*. *Developmental Psychology*, 1988. **24**(3): p. 386-392.
105. Trevarthen, C., *Communication and cooperation in early infancy: A description of primary intersubjectivity*. *Before speech: The beginning of interpersonal communication*, 1979. **1**: p. 530-571.
106. Jaffe, J., et al., *Rhythms of dialogue in infancy: Coordinated timing in development*. *Monographs of the society for research in child development*, 2001: p. i-149.
107. Beebe, B., et al., *The origins of 12-month attachment: A microanalysis of 4-month mother-infant interaction*. *Attachment & human development*, 2010. **12**(1-2): p. 3-141.
108. Feldman, R., *Infant-mother and infant-father synchrony: the coregulation of positive arousal*. *Infant mental health journal*, 2003. **24**(1): p. 1-23.
109. Feldman, R., C.W. Greenbaum, and N. Yirmiya, *Mother-infant affect synchrony as an antecedent of the emergence of self-control*. *Developmental psychology*, 1999. **35**(1): p. 223.
110. Feldman, R. and C.W. Greenbaum, *Affect regulation and synchrony in mother-infant play as precursors to the development of symbolic competence*. *Infant Mental Health Journal: Official Publication of The World Association for Infant Mental Health*, 1997. **18**(1): p. 4-23.
111. Granat, A., et al., *Maternal depression and anxiety, social synchrony, and infant regulation of negative and positive emotions*. *Emotion*, 2017. **17**(1): p. 11.
112. Niedźwiecka, A., S. Ramotowska, and P. Tomalski, *Mutual Gaze During Early Mother-Infant Interactions Promotes Attention Control Development*. *Child Development*, 2017.
113. Harel, H., et al., *Gaze behaviors of preterm and full-term infants in nonsocial and social contexts of increasing dynamics: Visual recognition, attention regulation, and gaze synchrony*. *Infancy*, 2011. **16**(1): p. 69-90.
114. Field, T., et al., *Behavior-state matching and synchrony in mother-infant interactions of nondepressed versus depressed dyads*. *Developmental psychology*, 1990. **26**(1): p. 7.
115. Yu, C. and L.B. Smith, *Joint attention without gaze following: Human infants and their parents coordinate visual attention to objects through eye-hand coordination*. *PLoS one*, 2013. **8**(11): p. e79659.

116. Siposova, B. and M. Carpenter, *A new look at joint attention and common knowledge*. *Cognition*, 2019. **189**: p. 260-274.
117. Akhtar, N. and M.A. Gernsbacher, *On privileging the role of gaze in infant social cognition*. *Child development perspectives*, 2008. **2**(2): p. 59-65.
118. Gliga, T., T. Farroni, and C.J. Cascio, *Social touch: A new vista for developmental cognitive neuroscience?* *Developmental cognitive neuroscience*, 2018.
119. Cirelli, L.K., *How interpersonal synchrony facilitates early prosocial behavior*. *Current opinion in psychology*, 2018. **20**: p. 35-39.
120. Levy, J., A. Goldstein, and R. Feldman, *Perception of social synchrony induces mother-child gamma coupling in the social brain*. *Social cognitive and affective neuroscience*, 2017. **12**(7): p. 1036-1046.
121. Feldman, R., et al., *Mother and infant coordinate heart rhythms through episodes of interaction synchrony*. *Infant Behavior and Development*, 2011. **34**(4): p. 569-577.
122. Ham, J. and E. Tronick, *Relational psychophysiology: Lessons from mother-infant physiology research on dyadically expanded states of consciousness*. *Psychotherapy Research*, 2009. **19**(6): p. 619-632.
123. Waters, S.F., T.V. West, and W.B. Mendes, *Stress contagion: Physiological covariation between mothers and infants*. *Psychological science*, 2014. **25**(4): p. 934-942.
124. Wass., S.V., et al., *Parents mimic and influence their infant's autonomic state through dynamic affective state matching*. *Current Biology*, in press.
125. Smith, C.G., et al., *Anxious parents show higher physiological synchrony with their infants*. under review.
126. Azhari, A., et al., *Parenting Stress Undermines Mother-Child Brain-to-Brain Synchrony: A Hyperscanning Study*. *Scientific reports*, 2019. **9**(1): p. 1-9.
127. Wass, S.V., et al., *Infants' visual sustained attention is higher during joint play than solo play: is this due to increased endogenous attention control or exogenous stimulus capture?* *Developmental Science*, 2018.