

Review

Interpersonal Neural Entrainment during Early Social Interaction

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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 during early social interaction, 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 consider whether it is merely an epiphenomenon, or whether it plays an independent, mechanistic role in early attention and learning.

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, 9-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 while interacting with their 12-month-old infant, this immediately increases the infant's 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**, see [Glossary](#)) [9]; second, rather than examining unidirectional influences using pre-designed, screen-presented experimental stimuli, they examine naturally occurring moments of reciprocal influence during free-flowing interpersonal naturalistic interactions. 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 this 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

Highlights

Social factors exert transient influences on the brains of both partners during an interaction.

Interpersonal neural entrainment during early learning interactions has been documented at multiple temporal scales, replicating findings with adults and animals.

Neural entrainment can be a consequence of behavioral coordination, but it can also arise in the absence of behavioral coordination: shared understanding involves temporally co-occurring patterns of brain activity.

Neural entrainment may influence learning in multiple ways; for example, by allowing the sender to ensure information delivered arrives at an optimal time for encoding by the receiver.

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that indicate communicative sensitivity within an interaction). We conclude that the unidirectional neural correlates of both – that is, how one partner transiently influences the other, with both partners considered independently – are well understood; but that our understanding of how ostensive cues and contingent responsiveness alter the interpersonal neural dynamics of the interaction – that is, 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 unidirectional influences described in the first section, we also consider the mechanisms through which bidirectional 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 multilayered: 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 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 [11, 12]; and that, 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 [13–17]. 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 unidirectional 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 (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 (Box 2).

Considerable research has investigated the transient unidirectional 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 evoked-response or event-related potential (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 7-month-old infants during direct gaze compared with averted gaze [26, 27]. Similarly, child-directed speech evokes greater neural responses (a larger amplitude N250 ERP component)

Glossary

Allotaxis: process by which internal equilibrium is maintained.

Contingent responsiveness: behaviors that indicate communicative sensitivity within an interaction.

Cross-correlation: 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.

Electroencephalography: 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.

Functional near-infrared spectroscopy: method for recording blood oxygenation levels near the scalp.

Granger causality: 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 cues: signals from a communicator to generate an interpretation of communicative intention in an addressee.

Partial directed coherence: 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: abrupt shift (e.g., advancement or delay) in the phase of ongoing oscillatory activity, usually in response to perturbation by a sensory cue.

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]. 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 9-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) [30,31].

Currently, however, little research has investigated the bidirectional 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.

Phase-locking value: 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: technique that can be used to measure both concurrent and sequential synchrony of two signals in the time-frequency plane.

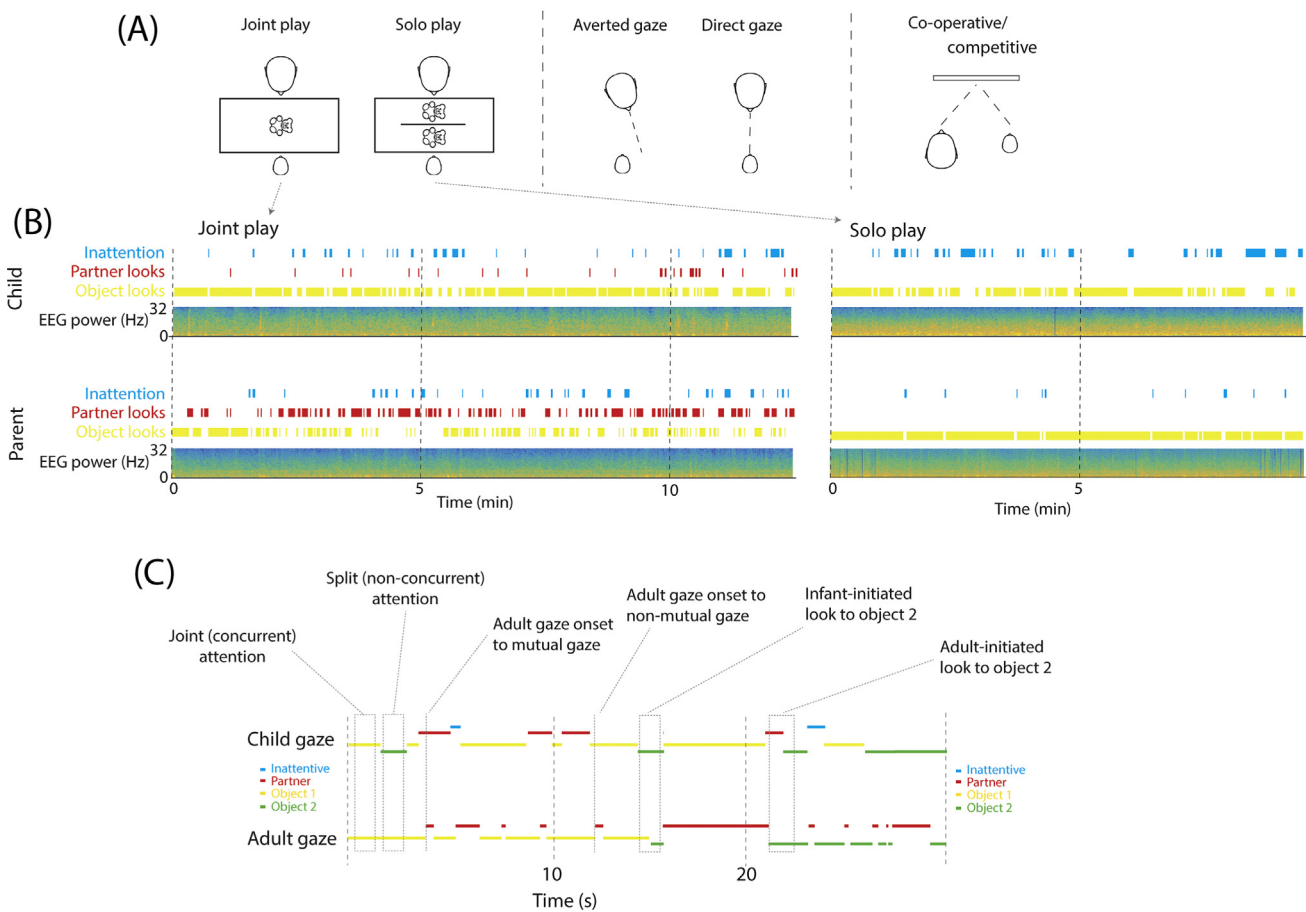


Figure 1. Behavioral Paradigms Used to Measure Interpersonal Neural Entrainment. (A) examples of the experimental setups described in the main text, used by: left [43,126]; middle [60]; right [52]. (B) Examples of raw data collected using the paradigms from [43,126]; even from this raw data sample, some significant patterns noted that overall data can be seen – such as, parents pay more attention to infants during joint play than vice versa [114], and infants are more inattentive during solo play than joint play [126]. (C) Example of a 30-s segment of data illustrating the further range of different types of events that can be identified in naturalistic interactions. Abbreviation: EEG, electroencephalography.

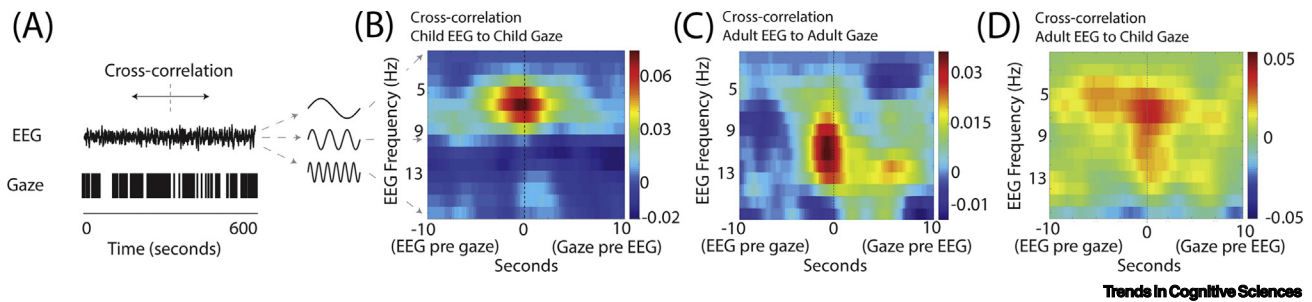


Figure 2. Neural Activity in the Parent Entrain to Attentional Fluctuations in the Child. (A) Schematic illustrating the analysis; (B) cross-correlation between child EEG and child gaze, showing an association between child neural activity and child attention; (C) cross-correlation between adult EEG 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., strongest associations were found between neural activity at a given moment and attention c. 750 ms after that moment), the adult EEG–child gaze associations were reactive (i.e., strongest associations were found between the child's attention at a given moment and the adult's neural activity c. 750 ms after that moment). Reproduced, with permission, from [43]. Abbreviation: EEG, electroencephalography.

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 noncontingently, only infants who received labels contingently in response to their own attention learned the association [6,13,14,35,36]. 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 unidirectional 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 [38,42].

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-electroencephalography (EEG) from parents and 12-month-old infants during free-flowing play (Figure 1A,B). By tracking the continuous fluctuations of brain

Box 1. Types of Interpersonal Entrainment and Measurement Caveats

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 (intrapersonal 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 – a zero-lag relationship, for example, ‘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→B is indistinguishable from B→A). Concurrent entrainment is treated as synonymous with the term synchrony.
- Sequential entrainment – ‘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→B ≠ B→A).

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

- Amplitude. Some fNIRS studies [29] and most fMRI studies [95] 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, for example, phase–amplitude coupling [96].

In the case of child–adult interactions, one complication is that adults and children have different dominant frequency bands of naturally occurring brain activity [97]. 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 10 Hz, 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 [98]).

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 [99]. 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 [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).

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] (see Figures 1 and 2). When the adult shows greater neural entrainment to the child’s attention, the child is more attentive [43].

Currently, however, and although contingent responsiveness is inherently a bidirectional behavioral phenomenon (because it describes the relationship between the two partners’ behaviors), little research has investigated how contingent responding alters the bidirectional 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.

Box 2. Behavioral Entrainment

Research into concurrent and sequential behavioral entrainment in parent–child dyads has a long history [100,101], and includes investigations using both qualitative [102] and quantitative [103] 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 [104,105]. Weaker adult–infant coordination has been associated, for example, with increased attachment problems and poorer cognitive outcomes [105,106].

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 [107]. Stronger child→parent and parent→child influences associate with, for example, later child self-control [108] and symbolic competence [109]. Not all findings associate increased entrainment with positive outcomes [110] (Box 3).

Eye Gaze

Two principal types of eye gaze entrainment are of interest. (i) Concurrent partner gaze, referred to as mutual gaze. Mutual gaze during infancy positively correlates with later attention control [111] and is reduced in some atypical dyads [112,113]. (ii) Sequential entrainment in object gaze, referred to as gaze following – that is, 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 Figure 1 in main text) infants actually follow parents’ gaze only rarely [114].

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 [115].

Touch

Current research may overemphasize 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 [116]. Similar to the distinction between mutual gaze and joint attention, research has examined both touching one another during parent–child interactions [117], and combined touch to an object [114].

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 [118,119].

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 unidirectional neural correlates of both of these – that is, influences of the sender on the receiver, with the two partners considered independently – are well understood. However, we have also concluded that our understanding of how ostensive cues and contingent responsiveness alter the interpersonal neural dynamics of the interaction – that is, how the partners’ neural activity inter-relates – 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 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 Boxes 2 and 3 we summarize recent research into interpersonal entrainment at the other levels – behavior (Box 2) and physiology (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

Box 3. Physiological Entrainment

Whereas some research into parent–child interactions has examined how, for example, individual heart beats become coordinated over time [120], most research has studied how autonomic arousal covaries across time windows (both concurrent, and sequentially – see Box 1). Some research has administered how patterns of change covary within dyads by administering experimental stressors in the laboratory [121,122]; other research has examined how autonomic arousal levels co-fluctuate in naturalistic, home settings [123,124].

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 [123]. When the initial arousal level of the parents is low, parents 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 [123]. This suggests that adults use 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' versus 'Always On'

Arousal levels in typical dyads do not routinely co-fluctuate in naturalistic settings [123]. 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 [110] (see [125] for comparable neuroimaging results). By 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 [124]. These observations echo similar behavioral findings [110] and question whether optimal outcomes always associate with greater parent–child entrainment.

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 (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 **functional near-infrared spectroscopy** (fNIRS) and EEG. fNIRS, which measures changes in blood oxygenation in the cortex [49], has a high spatial resolution but a low temporal resolution: the hemodynamic response lags neural activity by ~2 s and takes ~5 s to reach its peak value [50], meaning that this technique is best equipped to examine the co-fluctuation of brain activity over timescales of seconds or minutes.

Building on a rapidly emerging body of research in adults [45], a number of studies have used fNIRS to examine how brain activity co-fluctuates between children and adults during social interaction (see Figure 1). For example, one study [29] used fNIRS to examine entrainment between 9 and 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 deoxyhemoglobin levels. Relative to bootstrapping analyses (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 audiovisual environment (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 s.

Another study [51] used **wavelet transform coherence** to examine concurrent entrainment in the 0.02–0.1-Hz 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 temporoparietal areas and observed entrainment that was strongest in the right frontal and temporoparietal 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 ([Figure 1A](#)). Using wavelet transform coherence, they observed greater concurrent entrainment in 0.08–0.5-Hz 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 Subsecond Scale

EEG measures electrical brain activity at the subsecond 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 (3–6/4–7 Hz in young children/adults) and alpha (6–9/8–12 Hz 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 modeled positive or negative emotions towards objects, and infants' subsequent choices were examined. Some infants tended to choose the positively modeled object, and others the negatively modeled; but for both groups, parent–infant neural entrainment (phase synchrony in 6–9 Hz, 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 8-month-old infants and adults while an adult recited nursery rhymes while alternating between direct gaze and indirect gaze with the infant [60] ([Figure 1](#)). 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 bidirectional **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 (subsecond) 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 unidirectional influences in the first section 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 section, 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

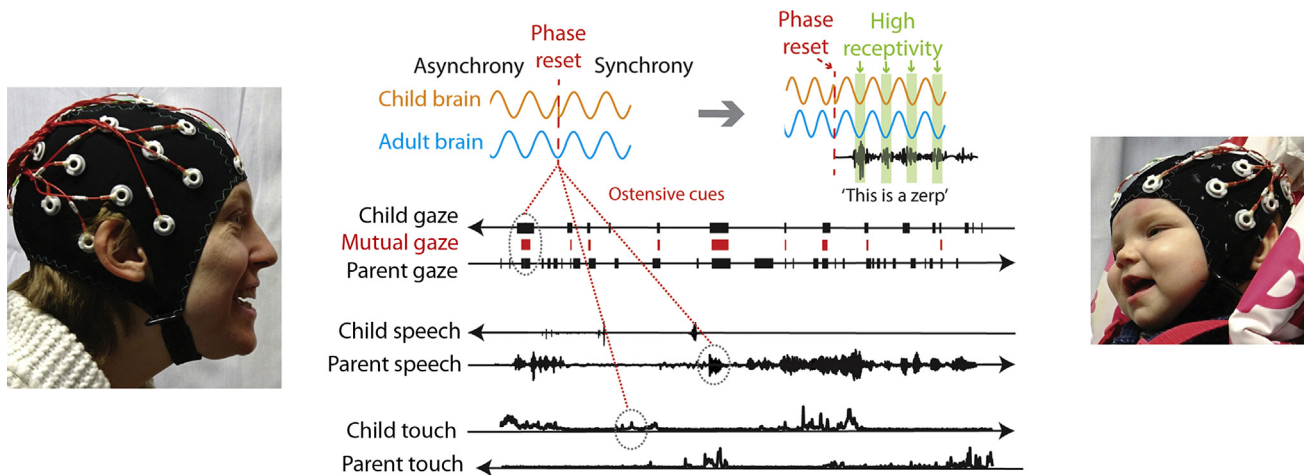
Social interactions involve the development of behavioral entrainment, both concurrent and sequential – including movements, gaze patterns, vocalizations, and facial expressions (Box 2). Evidence reviewed above also suggests that ostensive cues cause immediate, transient increases in behavioral entrainment. 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 timescale (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 (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 subsecond 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 [52,54] have, 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



Trends in Cognitive Sciences

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.

[63,64]. In one study, for example, concurrent interparticipant entrainment in neural activity was recorded while adult participants listened to a real-life auditory narrative compared to a temporally scrambled version; interparticipant entrainment was increased in default mode network areas (including medial prefrontal cortex) when participants had a shared understanding of a story [65,66]. 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 5-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 intrabrain 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 bidirectional, dynamical mutual adaptation within the dyad [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 (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 unidirectional effects of each – that is, how one partner transiently influences the other, with both partners considered independently – are well understood. However, we have concluded that our understanding of how ostensive cues and contingent responsiveness alter the interpersonal neural dynamics of the interaction – that is, 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 unidirectional influences in the first section of the review, we have discussed how concurrent and sequential neural entrainment may arise as a result of two causes: (i) as a consequence of shared entrainment to behavioral cues such as ostensive cues, and (ii) 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 bidirectional 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 subsecond as well as second-to-minute temporal scales; and, second, that these interactions involve bi-directional sensitivity, with both partners - child, as well as adult - influencing one another.

Outstanding Questions

Intrabrain entrainment has been shown to play an important role in attention and learning; how does interbrain entrainment relate to intrabrain 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 interpersonal entrainment change over development? Other aspects of development show a transition from coregulation (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 (Boxes 2 and 3); is more interpersonal neural entrainment always better?

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