Variation in infant EEG power across social and nonsocial contexts

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A R T I C L E I N F O

A B S T R A C T

To understand the infant social brain, it is critical to observe functional neural activation *during* social interaction. Yet many infant electroencephalography (EEG) studies on socioemotional development have recorded neural activity only during a baseline state. This study investigated how infant EEG power (4–6 Hz and 6–9 Hz) varies across social and nonsocial contexts. EEG was recorded in 12-month-olds across controlled conditions to disentangle the neural bases of social interactions. Four conditions—nonsocial, joint attention, language-only, and social engagement—were designed to tease apart how different environmental inputs relate to infant EEG power. We analyzed EEG power in frontal, central, temporal, and parietal regions. During the joint attention condition compared with the other conditions, 4–6 Hz frontal, central, and parietal power was lowest, indexing greater neural activation. There was lower 4–6 Hz and 6–9 Hz power in the temporal region in both the joint attention and social engagement conditions compared with the nonsocial condition. In 6–9 Hz, the pattern was consistent with 4–6 Hz findings for the frontal region such that 6–9 Hz frontal power was lower, indexing greater neural activation, in the joint attention condition compared with the nonsocial condition. There were no differences between conditions in central and parietal regions in 6–9 Hz. Findings highlight the methodological importance of recording functional brain activity in multiple controlled contexts to explicate the neural bases of the infant social brain.

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Introduction

Social interactions are essential for infant development such that infants who experience social deprivation show neural, social, and emotional deficits (Marshall, Reeb, Fox, Nelson, & Zeanah, 2008; Tarullo, Garvin, & Gunnar, 2011). However, the neural underpinnings of social engagement during infancy are not well understood. Although baseline measures of neural activity have been widely used with infants, less research has explored functional neural activity *while* infants are engaged in social interactions. To better understand the development of what has been termed the *social brain* (Adolphs, 2003; Grossmann, 2015), it is important to measure functional neural activity as infants socially interact. By understanding how patterns of neural activation differ across various social and nonsocial contexts, we can begin to disentangle the neural bases of social interaction, with implications for understanding the physiological processes underlying social development.

Infant EEG and recording context

Electroencephalography (EEG) has been widely used to measure infant brain activity. Electrodes are placed on the scalp to assess electrical activity released from neuronal communication, mostly in the cerebral cortex. EEG power measures voltage at an electrode site and is a continuous EEG measure as it assesses global neural activity across a period of time (Molfese, Molfese, & Kelly, 2001). EEG is noninvasive and allows for robust movement, an advantage in research with infants. Furthermore, the use of high-density EEG allows for greater spatial resolution. EEG can be compared across brain hemispheres (called *asymmetry*), brain regions, and conditions.

Dominant frequency bands in infant EEG research are 4–6 Hz and 6–9 Hz (Calkins, Fox, & Marshall, 1996; Marshall, Bar-Haim, & Fox, 2002). They reflect slow wave brain activity, so lower power in these frequency bands is thought to index greater neural activation (Allen, Coan, & Nazarian, 2004; Davidson, 1988).

Baseline EEG

Disentangling the neural bases of social interaction is a crucial step toward understanding the neural circuitry underlying the social brain. However, in infant research, continuous EEG measures are commonly recorded during a baseline or resting state rather than during social learning or social engagement. Operationalization of baseline varies across studies, but the common goal is that infants maintain a state of quiet visual attention to ensure usable EEG data. In some cases, EEG is recorded as infants watch an experimenter spin a Bingo wheel (Fox, Henderson, Rubin, Calkins, & Schmidt, 2001; Mundy, Card, & Fox, 2000; Nichols, Martin, & Fox, 2005), watch an experimenter blow bubbles (Mize & Jones, 2012), watch an experimenter shake a rattle (Field, Fox, Pickens, & Nawrocki, 1995; Jones, Field, Fox, Lundy, & Davalos, 1997), or watch a video clip (Tomalski et al., 2013). These baseline conditions do not clearly differentiate between social and nonsocial input because infants may attend to the experimenter or the object.

Recording EEG in controlled social and nonsocial contexts would enable researchers to assess how aspects of social interaction differentially relate to neural activation. Social interaction involves various components such as engaging in joint attention, hearing language, and face-to-face interaction. Joint attention includes coordinating attention with a social partner to an object or event and is an essential form of social learning (Mundy & Acra, 2006). Responding to another individual's bids for joint attention has been related to language ability (Morales et al., 2000) and emotion and attention regulatory behaviors (Morales, Mundy, Crowson, Neal, & Delgado, 2005). Furthermore, face-to-face social interaction is associated with experiencing positive affect and decreased distress and negative affect (Abe & Izard, 1999). Despite the importance of social interaction, to our knowledge no study has systematically compared EEG recorded across all of these different social contexts. By comparing infant EEG power in a nonsocial condition with various social conditions such as engaging in joint attention, hearing language, and face-to-face interaction, we can begin to elucidate the neural bases of social engagement during infancy.

Sensitivity of continuous EEG to context

Research on infant neural activation in other domains demonstrates sensitivity of EEG to recording context. For example, maternal depression has been related to right frontal EEG asymmetry during infancy across different recording contexts (Dawson et al., 1999; Field et al., 1995; Jones et al., 1997; Lusby, Goodman, Bell, & Newport, 2014). These studies illustrate that infant EEG is sensitive to the broader environment (i.e., maternal depression), but they did not directly compare infant EEG across specific recording contexts.

Other studies have compared how infant EEG varies depending on context. For example, infant EEG is sensitive to stimuli valence such that infants show greater left hemisphere activation when shown positive stimuli and show greater right hemisphere activation when shown sad or fearful stimuli (Davidson & Fox, 1982; Missana & Grossmann, 2015).

Infant EEG is also sensitive to observing actions, performing actions, and imitation as evidenced by the mu rhythm, thought to index activation of the motor system (for reviews, see Cuevas, Cannon, Yoo, & Fox, 2014; Fox et al., 2016; Marshall & Meltzoff, 2011). Infants show a decrease in mu, recorded in 6–9 Hz over central electrodes, in numerous contexts compared with a baseline (also called event-related desynchronization). For example, infants show a decrease in mu while watching another individual perform goal-directed actions (Cannon et al., 2016; Southgate, Johnson, Karoui, & Csibra, 2010), while performing actions themselves (Cannon et al., 2016), and while watching someone imitate their own recent action (Saby, Marshall, & Meltzoff, 2012). The mu rhythm is relevant to the social brain because it shows neural sensitivity to a social partner, specifically action understanding and imitation. Therefore, it is important to consider the mu rhythm when assessing differences in infant EEG power across social and nonsocial contexts. It is possible that EEG power differences between these contexts could in part reflect mu rhythm suppression in the social context compared with the nonsocial context.

These results indicate that EEG is sensitive to the content of sensory input, specifically stimuli valence, observation and execution of actions, and imitation. However, these studies assessed infant neural responses to stimuli in short time-locked windows. Therefore, two major gaps remain. First, it is unclear how infant EEG power varies as a function of different types of social input. For example, does infant EEG power differ in a face-to-face social interaction compared with an infant hearing language without the face-to-face component? Second, we do not know how infant EEG power measured continuously would relate to social input. Because infant mu research typically assesses neural responses in short time windows, it is unclear how infant EEG power assessed over the course of minutes varies as a function of social input.

EEG power compared across contexts

A few studies have tried to explicitly vary social stimulation by comparing EEG across different conditions (Jones, Venema, Lowy, Earl, & Webb, 2015; Orekhova, Stroganova, Posikera, & Elam, 2006). One study assessed a small sample of 8- to 12-month-olds and found that 3.6 to 5.6 Hz power increased predominately in frontal regions during social interaction and toy manipulation conditions compared with a bubbles baseline (Orekhova et al., 2006). Although this study included face-to-face interaction, it is difficult to determine the role of social context. The baseline involved the experimenter blowing bubbles, which could be more social for some infants and less social for others depending on whether the infant attended to the experimenter or the bubbles.

Finally, Jones and colleagues (2015) assessed 3–6 Hz and 6–9 Hz power in 6- and 12-month-old infants. First they compared infant EEG power during a social movie with that during a nonsocial movie. Next they recorded EEG in a live action condition while a woman was singing and holding objects. EEG was then parsed depending on whether the infant was looking at the experimenter or the objects she was holding. Frontal 3–6 Hz power was greater during the social movie compared with the nonsocial movie and was also greater when infants attended to the experimenter compared with the nonsocial objects. In 6–9 Hz, there was no difference in power between the social and nonsocial movies. However, 6–9 Hz power was lower during attention to the experimenter compared with the nonsocial objects in temporal and occipital regions. To our knowledge, this is the only study so far to explicitly vary social and nonsocial input given that the movies were clearly social and nonsocial. However, a few gaps remain. First, although the infants could look at the experimenter or objects,

the live action condition always involved language—the experimenter singing—so this condition included both social and nonsocial elements. Second, the live action condition was parsed each second based on where the infant was looking, so it is not a comparison between sustained conditions.

These studies suggest that there are emerging differences in infant EEG power across various social contexts; however, the specific role of various environmental inputs, such as face-to-face interaction and language, still remains unclear. To our knowledge, no studies have directly compared EEG power during a contingent face-to-face social interaction with EEG power during a nonsocial condition. Comparing EEG power recorded during clearly nonsocial and varying social conditions would help to elucidate how infant brain activity varies during social engagement. Furthermore, to our knowledge no studies have assessed EEG power while infants engage in joint attention, an important aspect of social learning.

Neural correlates of social interaction in adults

Given the lack of infant research, adult studies can help to inform which brain regions may be important during infant social interaction. Adult neural activation measured with EEG (Lachat, Hugueville, Lemaréchal, Conty, & George, 2012) and functional magnetic resonance imaging (Redcay, Kleiner, & Saxe, 2012; Williams, Waiter, Perra, Perrett, & Whiten, 2005) shows involvement of frontal (Redcay et al., 2012; Williams et al., 2005), temporal (Lachat et al., 2012; Redcay et al., 2012; Williams et al., 2005), and parietal (Lachat et al., 2012; Redcay et al., 2012) regions during joint attention. Frontal regions are involved in orienting and shifts of attention (Petersen & Posner, 2012), suggesting that frontal activation may be particularly important for joint attention. Temporal regions are involved in facial processing, including direction of another individual's gaze (Emery, 2000), indicating that temporal regions could be involved in face-to-face social interaction in general and in joint attention specifically. Parietal regions are involved with orienting spatial attention and gaze following (Emery, 2000; Petersen & Posner, 2012), suggesting that parietal activation could be required for joint attention as opposed to other forms of social engagement. Although these studies do not compare joint attention with other aspects of social interaction, the proposed roles suggest likely involvement of frontal, temporal, and parietal regions in infant social engagement. Finally, based on evidence of central regions for 6–9 Hz EEG power (i.e., mu rhythm) for imitation (Fox et al., 2016), it is possible that central regions are relevant for social interaction, such as responding to joint attention, which involves imitating gaze direction.

The current study

The aim of this study was to assess infant EEG power in 4–6 Hz and 6–9 Hz across controlled social and nonsocial contexts in frontal, central, temporal, and parietal regions. Conditions were designed to disentangle the various components of social interaction, including joint attention, language input, and face-to-face interaction.

We included four conditions: *nonsocial*, where the infant could not see or hear the experimenter; *joint attention*, where the experimenter directed the infant's attention to pictures while commenting on the pictures; *language-only*, where the experimenter spoke from behind a curtain; and *social engagement*, where the experimenter sang songs and played "peek-a-boo." These conditions allowed us to see how different aspects of social interaction influenced functional neural activation. For instance, if infants demonstrated similar neural activation during the joint attention and language-only conditions compared with the nonsocial condition, we could attribute the effect to language. Similarly, if infants had similar neural activation during the joint attention and social engagement conditions, we could attribute the effect to face-to-face interaction. We focused on 4–6 Hz and 6–9 Hz frequency bands, which have been widely used in infant EEG literature (e.g., Calkins et al., 1996; Schmidt, Fox, Perez-Edgar, & Hamer, 2009).

We expected that infants would have globally lower 4–6 Hz and 6–9 Hz EEG power, representing greater neural activation, in the joint attention condition compared with the nonsocial, language-only, and social engagement conditions. We also expected regional differences. Based on frontal involvement in orienting and shifting attention, we expected that infants would show the greatest frontal

activation in the joint attention condition. Because the temporal region is associated with facial processing, we expected that infants would show greater activation in the joint attention and social engagement conditions because both involve face-to-face interaction with the experimenter. Because the parietal region is associated with spatial orientation, we expected greater parietal activation only in the joint attention condition due to the spatial orienting demands in responding to the experimenter's bids for attention. Finally, based on evidence for mu desynchronization during action observation and imitation, we assessed EEG power in central regions to rule out the possibility that the mu rhythm explained our results.

Method

Participants

Laboratory visits were conducted with 94 mother–infant dyads when infants were approximately 12 months old. Of these, 21 were excluded because they lacked usable EEG data due to excessive movement during EEG recording ($n = 12$), technical difficulties ($n = 6$), or participant declining EEG ($n = 3$). The final sample included in analyses was 73 infants (M_{age} = 12.18 months, SD = 0.68; 38 boys). All were singletons with no known hearing, visual, neurological, or developmental disorders and whose mothers were fluent in English (see Table 1 for demographic information).

General procedure

Participants were recruited from a department-maintained database of families interested in participating in research, from publicly available state birth records and online advertising, and through face-to-face recruitment events. This study was approved by the university institutional review board.

Visits were scheduled for when the infant would be alert and well rested. On arrival, a female experimenter greeted the mother, offered her the opportunity to feed the infant before beginning, and obtained informed parental consent. Next the experimenter placed the EEG net on the infant's head as the infant sat in the mother's lap. Following EEG recording, the mother completed a questionnaire. The visit lasted approximately 90 min.

Table 1
Demographic information.

Maternal age (years)	
M (*SD*)	33.61 (0.71)
Infant age (months)	
M (*SD*)	12.18 (0.68)
Infant ethnicity (%)	
Caucasian	69.9
Black	12.3
Asian	6.8
Hispanic	4.1
Middle Eastern	1.4
Multiracial	2.7
Maternal education (%)	
At least a 4-year college degree	85.2
Number of children in the household	
M (*SD*)	1.59 (0.71)
Income-to-needs ratio[a]	
M (*SD*)	5.58 (3.93)

[a] Income-to-needs ratio represents how much greater a family's income is compared with the federal poverty line (according to household size). It was calculated by dividing the family income by the federal poverty line, thereby indexing how many times greater a family's income is compared with the federal poverty line.

Four EEG conditions were administered while continuous EEG was recorded. Each condition was administered twice for a total of eight blocks, with blocks alternating every 2.5 min to maintain infant attention. Blocks followed the following sequence: social engagement, nonsocial, joint attention, language-only, joint attention, nonsocial, social engagement, and language-only. The infant was seated on the mother's lap facing two adjacent computer monitors (measuring 14.5 × 12 inches) spaced 18 inches apart in an electrically shielded booth to prevent interference with the EEG signal. They were seated 48 inches from the computer monitors. The mother was instructed to remain silent and not to make face-to-face contact with the infant or interact socially. The experimenter was in the booth behind the computer screens, facing the infant.

In each condition, a series of 10 photographs of objects appeared on the computer monitors with the same object displayed on each screen using E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA, USA). All objects were nonsocial (e.g., flower, glove), and the same 10 categories of objects were repeated across blocks but were counterbalanced for order and color. In each block, objects appeared at variable interstimulus intervals (0.5–2.0 s) and remained on the screen for 13.0 to 14.5 s. A sound alerted the experimenter to trial onset, and blocks were separated by a blank white screen and a bell sound. A black curtain separated the experimenter and infant during the nonsocial and language-only conditions and was open during the joint attention and social engagement conditions.

Nonsocial

The experimenter was behind a curtain and remained silent while the infant saw identical objects on the two computer monitors.

Joint attention

The curtain was pulled back. The experimenter was face-to-face with the infant between the two computer monitors and directed the infant's attention toward pictures on the computer screens while commenting on the pictures. To ensure that the infant had the opportunity to engage in joint attention, the experimenter made eye contact with the infant at the start of each trial and continued bids for the infant's attention until the infant was looking directly at the experimenter. Next the experimenter turned her head in a specified direction (left or right), looked at the appropriate screen, and pointed at the picture while saying a specific utterance for each trial. Each utterance involved a comment on the picture and a question directed at the infant (e.g., "Look at the cool picture over here! Do you think it's a cool picture too?"). The experimenter then looked back at the infant. If the trial was not over, the experimenter continued to alternate gaze between the screen and the infant's face. The 10 scripted utterances were the same in each joint attention block but were presented in a variable order.

Language-only

The experimenter was behind the curtain and commented on the pictures with the same utterances and tone of voice as in the joint attention condition. The infant, therefore, could hear the experimenter's voice but was unable to see the experimenter. The order of comments followed those in the preceding joint attention block, and utterances were linked to trial onset.

Social engagement

The curtain was open, and the experimenter was face-to-face with the infant. The goal was to keep the infant's attention on the experimenter's face and not on the screens (as identical objects continued appearing). The experimenter did not look or point at the screens, and if the infant initiated joint attention (e.g., by pointing at the computer monitors), the experimenter did not follow the infant's gaze and tried to pull the infant's attention back. Experimenter utterances were not linked to trials or scripted. The experimenter talked warmly to the infant throughout the block and responded contingently to the infant. Strategies included playing peek-a-boo and singing songs (especially those with hand motions, e.g., *Itsy Bitsy Spider*). If the infant was bored, the experimenter adapted to recapture the infant's interest.

Measures

Infant looking behavior

To verify that infants were engaging in joint attention and social interaction as intended during the joint attention and social engagement conditions, looking behavior was micro-coded, frame by frame, using Noldus Observer 11.5 (The Vaggenigen, Netherlands). Looking behavior codes included when the infant looked at the left screen, the right screen, the experimenter, the mother's face, or elsewhere (anywhere other than the screens, experimenter, or mother) and was missing (when the infant was out of camera view). Percentage looking time for each code was then computed. To assess whether infants were following the experimenter's point and gaze during the joint attention condition, percentage looking time was computed separately for the correct screen (e.g., looking at the left screen during a trial when the experimenter was pointing to the left screen) and the incorrect screen (e.g., looking at the left screen during a trial when the experimenter was pointing to the right screen). Five coders were trained to a reliability threshold of .80 kappas, and 20% of videos were double coded to assess interrater reliability, yielding an overall kappa for infant gaze of .84.

Electrophysiological recording and analysis

EEG was recorded to a vertex reference using NetStation acquisition software and a Net Amp 300 amplifier (Electrical Geodesics, Eugene, OR, USA) connected to a Geodesic Sensor Net with 128 electrodes spaced approximately 1 cm apart over the scalp. Prior to use, the 128 lead high-density net was soaked for 10 min in an electrolyte solution (6 cc potassium chloride/liter distilled water) to facilitate electrical contact between the scalp and electrodes. Prior to recording, impedances were lowered by administering small amounts of the electrolyte solution to electrodes with poor contact. The mother was asked to distract the infant while the experimenter put on the net.

Data were sampled from all channels at 500 Hz. The raw data were exported from NetStation, and MATLAB was used to process the EEG data. Data were notch filtered at 60 Hz, and then a highpass filter of 0.1 Hz was applied. An automatic artifact rejection paradigm excluded electrodes with excessive artifact generally from participant movement. Data were analyzed in 30-s epochs, and electrodes were excluded from each epoch if the root mean square of the EEG voltage data exceeded 175 μV or if the amplifier was saturated at any time within the epoch. Epochs with more than 20 excluded electrodes were rejected from further analyses. Data were re-referenced to the average reference of the remaining electrodes prior to power analyses. EEG power was computed for each electrode using fast Fourier transformations for each 30-s epoch in 3 Hz frequency bands. Regional EEG power averages were computed for each region (left and right frontal polar, frontal, central, temporal, parietal, and occipital regions) to reduce multiple comparisons. Good epochs were combined to yield average power values for condition, region, and frequency band. Power values were log transformed using the natural log. We analyzed EEG power in frontal, central, temporal, and parietal regions. Regional demarcation was adapted based on past research (Cannon et al., 2016; Welch et al., 2014) (see Fig. 1 for a map of electrodes by region).

To be included in analyses for a given condition, infants needed to have at least one good 30-s epoch of EEG recording within that condition. Of the 94 infants, 73 had usable EEG recordings for at least one condition. Of those 73, the percentage of usable EEG data within each condition was as follows: 78.10% (57 infants) in nonsocial, 71.20% (52 infants) in language-only, 91.80% (67 infants) in joint attention, and 87.85% (63 infants) in social engagement. All infants with sufficient EEG recordings were used in each analysis, so the sample size varied across analyses depending on conditions included.

We assessed power in 4–6 Hz and 6–9 Hz frequency bands, which have been widely studied in infant research (Calkins et al., 1996; Henderson, Yoder, Yale, & McDuffie, 2002; Marshall et al., 2002). Both bands have been related to constructs of interest in the current study; 4–6 Hz power has been related to joint attention behaviors (Henderson et al., 2002; Mundy et al., 2000), and 6–9 Hz power has been related to social interaction (Jones et al., 2015). Inclusion of multiple frequency bands in the same study can be particularly helpful to facilitate interpretation of a new paradigm (Bell, 2002; Jones et al., 2015).
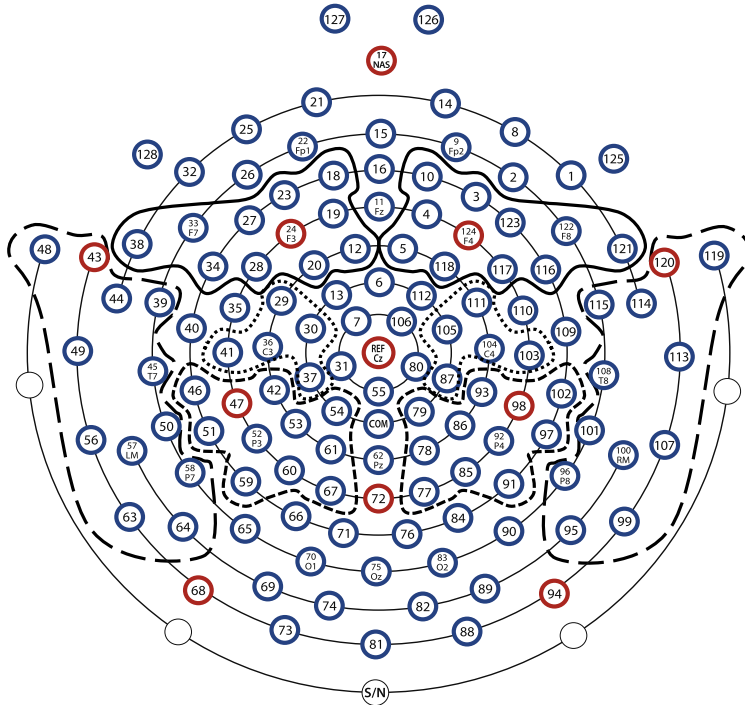
Fig. 1. Regional demarcation used to compute EEG power values for the left and right frontal (solid line), central (dotted line), temporal (long dashed line), and parietal (short dashed line) regions. This view is looking down on the head with the nose positioned near Electrode 17.

Data analysis plan

We first assessed infant looking behavior during the social engagement and joint attention conditions to verify that infants were engaging in the conditions as intended. We compared looking times between conditions and time spent looking at the correct versus incorrect screen in joint attention using paired-samples t-tests.

To assess differences in neural activation between conditions, we conducted separate repeated-measures analyses of variance (ANOVAs) for 4–6 Hz and 6–9 Hz with condition, region (frontal, central, temporal, or parietal), and hemisphere (left or right) as within-participants factors. In the initial models, we included the joint attention and nonsocial conditions because they differ on several dimensions. The joint attention condition includes language, face-to-face interaction, and the presence of joint attention, whereas the nonsocial condition has none of these dimensions. Whenever condition main effects or interactions with condition were observed in the initial ANOVA, we repeated the model including the language-only and social engagement conditions to examine which dimensions of environmental input explained the increase in neural activation from the nonsocial condition to the joint attention condition. In other words, a difference in EEG power between the joint attention and nonsocial conditions could be due to various social inputs. By including the language-only condition in the model, we could determine whether joint attention and language-only showed similar activation. The difference between the joint attention and nonsocial conditions, therefore, could be attributed to language input. Next we would include social engagement in the model. If the joint attention and social engagement conditions showed similar activation, this would suggest that the face-to-face interaction explains the difference in EEG power between the joint attention and nonsocial conditions.

For all ANOVAs, post hoc analyses followed significant main effects, using Bonferroni corrections for multiple testing. In ANOVAs where the assumption of sphericity was violated, we used Greenhouse–Geisser corrections.

Results

Looking behavior during EEG recording

In the joint attention condition, infants spent 2.88 times more looking at the correct screen ($M = 34.14\%$, $SD = 8.53$) compared with the incorrect screen ($M = 11.85\%$, $SD = 4.56$), $t(58) = 19.88$, $p < .001$, Cohen's $d = 2.480$, and all infants spent more time looking at the correct screen compared with the incorrect screen (binomial $p < .001$). Joint attention is defined as sharing attention between an object or event and a social partner. In the joint attention condition, infants spent the majority of the time (67.93%) looking at either the correct screen or the experimenter.

In the social engagement condition compared with the joint attention condition, infants spent a significantly lower percentage of time looking at the computer screens, $t(48) = -13.510$, $p < .001$, Cohen's $d = -1.77$, and a significantly higher percentage of time looking at the experimenter, $t(48) = 15.018$, $p < .001$, Cohen's $d = 2.30$; see Table 2 for average percentage of time of infant looking behavior within the joint attention and social engagement conditions.

EEG power differences between conditions: 4–6 Hz

Primary analysis: 4–6 Hz power in the nonsocial versus joint attention condition

We performed a repeated-measures ANOVA with condition (nonsocial or joint attention), region (frontal, central, temporal, or parietal), and hemisphere as within-participants factors. There was a main effect of condition, $F(1, 51) = 14.470$, $p < .001$, $\eta_p = .221$, such that there was lower 4–6 Hz power in the joint attention condition, reflecting higher neural activation, compared with the nonsocial condition. There was a main effect of region, $F(3, 132) = 149.657$, $p < .001$, $\eta_p = .77$. Post hoc tests showed that regions differed significantly from each other ($ps < .001$) except that there was no difference in 4–6 Hz power between the frontal and parietal regions. Power in 4–6 Hz was greatest in the temporal region, followed by the frontal and parietal regions, and lowest in the central region.

There was also a Hemisphere × Region interaction, $F(3, 153) = 6.948$, $p = .001$, $\eta_p = .120$. Follow-up analyses showed that in the frontal region 4–6 Hz power was lower in the right hemisphere compared with the left hemisphere ($p = .001$) and in the parietal region 4–6 Hz power was lower in the left hemisphere ($p = .004$). There were no differences in 4–6 Hz power between hemispheres in the central and temporal regions. There were no other interactions. See Fig. 2 for a summary of 4–6 Hz findings by condition and region.

This primary analysis demonstrates that there was significantly lower 4–6 Hz power in the joint attention condition compared with the nonsocial condition.

Table 2
Descriptive statistics for percentage of time of infant looking behavior.

Infant looking behavior	Joint attention % [M (SD)]	Social engagement % [M (SD)]
Total screen looking***	45.99 (10.63)	23.45 (10.42)
Experimenter***	33.80 (9.61)	60.06 (13.97)
Elsewhere	16.32 (10.20)	13.42 (8.20)
Mother	0.15 (0.63)	0.34 (0.93)
Missing	3.88 (5.92)	3.34 (4.87)

Note. Mean percentages of time for looking behavior during the joint attention and social engagement conditions are shown. During the social engagement condition compared with the joint attention condition, infants spent on average a significantly lower percentage of time looking at the screens and a higher percentage of time looking at the experimenter.
*** $p < .001$.

Follow-up analysis: the impact of language input on 4–6 Hz power

To assess whether language input was explaining the difference in power between the joint attention and nonsocial conditions, we repeated the original ANOVA while adding the language-only condition to the model. There was a main effect of condition, $F(2, 88) = 13.081$, $p < .001$, $\eta_p = .229$. Post hoc tests showed that there was less 4–6 Hz power in the joint attention condition compared with the language-only ($p < .001$) and nonsocial ($p = .008$) conditions but no difference in power between the nonsocial and language-only conditions. This demonstrates that the difference between the joint attention and nonsocial conditions was not just due to the presence versus absence of language input.

There was a Condition × Region interaction, $F(6, 264) = 3.544$, $p = .009$, $\eta_p = .075$. Follow-up ANOVAs were conducted separately for each region. There was a main effect of condition in each region: frontal, $F(2, 88) = 11.842$, $p < .001$, $\eta_p = .212$; central, $F(2, 88) = 5.502$ $p = .01$, $\eta_p = .111$; temporal, $F(2, 88) = 15.151$, $p < .001$, $\eta_p = .256$; and parietal, $F(2, 88) = 8.093$, $p = .002$, $\eta_p = .155$. Post hoc tests conducted for each ANOVA indicated that there was significantly less power in the joint attention condition compared with the language-only condition ($ps < .05$), with no difference in power between the language-only and nonsocial conditions.

In sum, this follow-up analysis showed that 4–6 Hz power was significantly lower in the joint attention condition compared with the language-only condition both overall and within each region. There was no difference in power between the language-only and nonsocial conditions. This shows that the presence of language input does not explain the difference in power between the joint attention and nonsocial conditions.

Follow-up analysis: the impact of social engagement on 4–6 Hz power

Finally, to assess whether the presence of face-to-face interaction accounted for the 4–6 Hz power differences between the nonsocial and joint attention conditions, we repeated the ANOVA while adding the social engagement condition to the model. There was a main effect of condition, $F(2, 94) = 7.307$, $p = .002$, $\eta_p = .135$. Post hoc tests showed that there was significantly less power in the joint attention condition compared with the social engagement ($p = .004$) and nonsocial ($p = .003$) conditions, with no difference in power between the nonsocial and social engagement conditions. This demonstrates that the difference between the joint attention and nonsocial conditions was not solely attributable to the presence versus absence of face-to-face social interaction.

There was a Condition × Region interaction, $F(6, 682) = 7.348$, $p < .001$, $\eta_p = .135$. Follow-up ANOVAs showed that there was a main effect of condition in each region: frontal, $F(2, 94) = 6.934$, $p = .002$, $\eta_p = .129$; central, $F(2, 94) = 5.606$, $p = .006$, $\eta_p = .107$; temporal, $F(2, 94) = 8.786$, $p = .001$, $\eta_p = .157$; and parietal, $F(2, 94) = 7.111$, $p = .002$, $\eta_p = .131$.

Post hoc tests showed that in the frontal, central, and parietal regions, 4–6 Hz power was lower in the joint attention condition compared with the social engagement ($ps < .05$) and nonsocial ($ps < .05$)
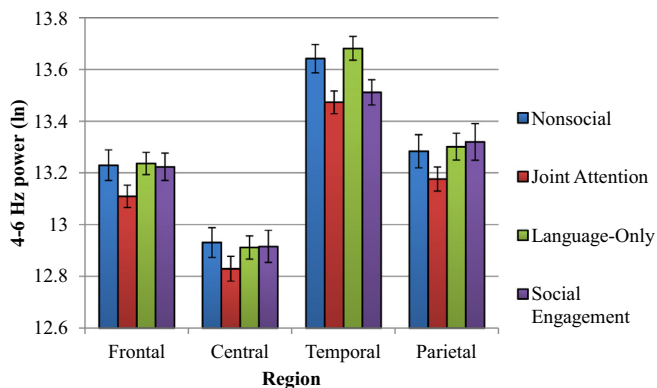

Fig. 2. Mean 4–6 Hz power in each condition and region. In the frontal, central, and parietal regions, 4–6 Hz power was lower in the joint attention condition compared with the other conditions. Temporal 4–6 Hz power was lower in both the joint attention and social engagement conditions compared with the nonsocial condition.

conditions, with no difference in power between the social engagement and nonsocial conditions. In the temporal region, 4–6 Hz power was lower in both the joint attention ($p = .002$) and social engagement ($p = .023$) conditions compared with the nonsocial condition, with no difference in 4–6 Hz power between the joint attention and social engagement conditions. Thus, lower 4–6 Hz power in the frontal, central, and parietal regions was specific to the joint attention condition. In the temporal region, there was lower 4–6 Hz power in both the joint attention and social engagement conditions.

Summary of 4–6 Hz EEG power

Frontal, central, and parietal 4–6 Hz power was lower in the joint attention condition compared with all of the other conditions (nonsocial, language-only, and social engagement). Temporal 4–6 Hz power was lower in both conditions involving face-to-face social interaction (joint attention and social engagement) compared with the nonsocial condition.

EEG power differences between conditions: 6–9 Hz

Primary analysis: 6–9 Hz power in the nonsocial versus joint attention condition

There was a main effect of condition, $F(1, 51) = 9.757$, $p = .003$, $\eta_p = .161$, because there was lower 6–9 Hz power in the joint attention condition, reflecting higher activation, compared with the nonsocial condition. There was a main effect of region, $F(3, 153) = 23.974$, $p < .001$, $\eta_p = .320$. Post hoc tests showed that regions differed significantly from each other ($ps < .05$) except that there was no difference in 6–9 Hz power between the frontal and central regions. Power in 6–9 Hz was greatest in the temporal region, followed by the parietal region, and lowest in the frontal and central regions.

There was a Condition × Region interaction, $F(3, 153) = 4.226$, $p = .028$, $\eta_p = .077$. Follow-up ANOVAs for each region showed that there was lower 6–9 Hz power in the joint attention condition compared with the nonsocial condition in the frontal region, $F(1, 51) = 11.398$, $p < .001$, $\eta_p = .183$, and the temporal region, $F(1, 51) = 21.399$, $p < .001$, $\eta_p = .296$. There was no difference in 6–9 Hz power between conditions in the central and parietal regions. See Fig. 3 for a summary of 6–9 Hz findings by condition and region.

This primary analysis demonstrates that there was significantly lower 6–9 Hz power in the joint attention condition compared with the nonsocial condition overall and within the frontal and temporal regions.

Follow-up analysis: the impact of language input on 6–9 Hz power

There was a main effect of condition, $F(2, 88) = 7.350$, $p = .002$, $\eta_p = .143$. Post hoc tests showed that there was less 6–9 Hz power in the joint attention condition compared with the language-only ($p < .001$) and nonsocial ($p = .023$) conditions but no difference in power between the nonsocial and language-only conditions. As in 4–6 Hz, this demonstrates that the difference between the joint attention and nonsocial conditions was not just due to the presence versus absence of language input.

There was a significant Condition × Region interaction, $F(6, 264) = 3.458$, $p = .020$, $\eta_p = .073$. Follow-up ANOVAs were conducted separately for the frontal and temporal regions based on the significant effects in these regions from the primary model. There was a main effect of condition for each region: frontal, $F(2, 88) = 8.349$, $p = .001$, $\eta_p = .159$, and temporal, $F(2, 88) = 15.090$, $p < .001$, $\eta_p = .255$. Post hoc tests conducted for each ANOVA indicated that there was significantly less power in the joint attention condition compared with the language-only and nonsocial conditions ($ps < .01$), with no difference in power between the language-only and nonsocial conditions.

This follow-up analysis shows that 6–9 Hz power was lower in the joint attention condition compared with the language-only condition overall and within the frontal and temporal regions. There was no difference in power between the language-only and nonsocial conditions. This shows that the presence of language input does not explain the difference in power between the joint attention and nonsocial conditions.

Follow-up analysis: the impact of social engagement on 6–9 Hz power

There was a main effect of condition, $F(2, 94) = 4.410$, $p = .021$, $\eta_p = .086$. Post hoc tests showed that there was no difference in 6–9 Hz power between the joint attention and social engagement
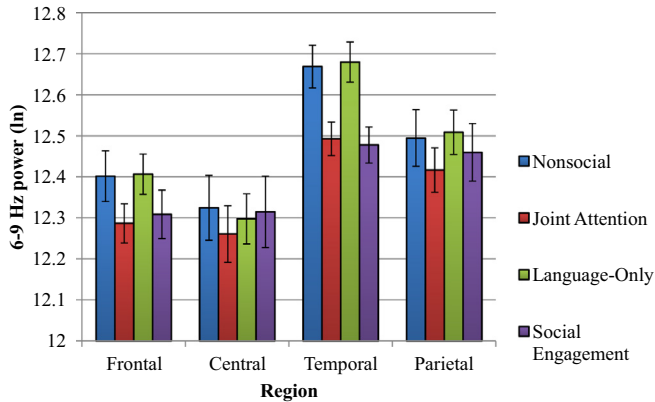
Fig. 3. Mean 6–9 Hz power in each condition and region. In the frontal region, 6–9 Hz power was lower in the joint attention condition compared with the language-only and nonsocial conditions. In the temporal region, 6–9 Hz power was lower in both the joint attention and social engagement conditions compared with the nonsocial condition.

conditions. There was lower 6–9 Hz power in the joint attention condition compared with the nonsocial condition ($p = .026$), with no difference between the social engagement and nonsocial conditions.

There was a Condition × Region interaction, $F(2, 282) = 7.186$, $p < .001$, $\eta_p = .133$. Follow-up ANOVAs were conducted separately for frontal and temporal regions based on the findings from the primary model. There was a main effect of condition in each region: frontal, $F(2, 94) = 5.014$, $p = .012$, $\eta_p = .096$, and temporal, $F(2, 94) = 14.172$, $p < .001$, $\eta_p = .232$. In the frontal region, 6–9 Hz power in the joint attention condition was lower than that in the nonsocial condition ($p = .012$), with no other differences. In the temporal region, there was lower power in both the joint attention ($p < .001$) and social engagement ($p = .001$) conditions compared with the nonsocial condition, with no difference between the joint attention and social engagement conditions, consistent with findings in 4–6 Hz.

Summary of 6–9 Hz EEG power

Overall power in 6–9 Hz was lower in the joint attention condition compared with the nonsocial and language-only conditions, with no difference in power between the joint attention and social engagement conditions. Frontal 6–9 Hz power was lower in the joint attention condition compared with the language-only and nonsocial conditions. Temporal 6–9 Hz power was lower in both conditions involving face-to-face social interaction (joint attention and social engagement) compared with the nonsocial condition. There were no differences in central and parietal 6–9 Hz power between the joint attention and nonsocial conditions.

Discussion

In a within-participants design, we assessed EEG measures of functional neural activity in 12-month-old infants across controlled nonsocial and social conditions. These included *nonsocial*, where the infant could not see or hear the experimenter; *joint attention*, where the experimenter directed the infant's attention and commented on pictures; *language-only*, where the experimenter commented on pictures from behind a curtain; and *social engagement*, where the experimenter sang songs and played peek-a-boo. These conditions allowed us to decompose the effects of different elements of recording contexts, such as the presence versus absence of language and face-to-face interaction, to understand the driving contextual factors in patterns of functional neural activation. We found decreased 4–6 Hz frontal, central, and parietal power in the joint attention condition compared with all other conditions and found decreased 6–9 Hz frontal power in the joint attention condition compared with the nonsocial and language-only conditions. Results suggest widespread increases in neural activation specifically in the joint attention condition compared with all other conditions. Decreased 4–6 Hz

and 6–9 Hz power, indexing increased temporal activation, was common to joint attention and social engagement, the two conditions that involved face-to-face interaction.

The main strength of this study was the use of controlled nonsocial and social conditions, which allowed us to systematically examine functional neural activation. Our conditions were effective in changing infants' looking behavior. Infants spent the majority of the time looking at the experimenter during social engagement and sharing attention between the experimenter and the correct screen during joint attention. We also examined EEG power in two frequency bands: 4–6 Hz and 6–9 Hz. The general pattern of results was mostly consistent across analyses for both frequency bands, confirming that lower power in these bands reflected greater neural activation.

The goal of this study was to assess how infant EEG power varies across social and nonsocial contexts. We first compared EEG power in the joint attention condition with that in the nonsocial condition. Consistent with our expectations, infants showed widespread increases in activation during the joint attention condition. Because these conditions differ on several dimensions—face-to-face interaction, language input, and the presence of joint attention—we used the social engagement and language-only conditions to probe which dimensions of environmental input explained the increase in neural activation.

Supporting our hypotheses, increases in frontal and parietal activation were specific to joint attention, with no differences in activation between the social engagement and language-only conditions compared with the nonsocial condition. Frontal activation during joint attention is consistent with infant event-related potential (ERP) research (Grossmann & Johnson, 2010) and adult research (Redcay et al., 2012; Williams et al., 2005). The frontal region plays a role in orienting and shifting attention (Petersen & Posner, 2012). Thus, increased frontal activation was specific to joint attention, as expected given that this was the only condition where infants were prompted to shift attention between the computer screens. Increased parietal activation was also unique to joint attention, consistent with adult research (Lachat et al., 2012; Redcay et al., 2012). Our findings extend previous work finding that parietal activation during a Bingo wheel baseline at 14 months predicted responding to joint attention at 18 months (Mundy et al., 2000). The parietal regions are involved in orienting spatial attention and gaze following (Emery, 2000), demands required only in our joint attention condition as the experimenter made bids for the infant to look alternately at the experimenter and pictures on two computer screens.

The fronto–parietal attention network, involved in allocating attention (Corbetta, 1998; Ptak, 2012), possibly played a role in regional activation in joint attention. To investigate this, future research should examine fronto–parietal EEG coherence. Coherence indexes synchrony of cortical activity between neural regions, reflecting how different areas of the brain communicate. This could help to elucidate how frontal and parietal regions together may be involved in joint attention.

Whereas increased frontal and parietal activation was specific to the joint attention condition, increased temporal activation was common to the joint attention and social engagement conditions compared with the nonsocial condition, supporting our hypotheses. This suggests that an increase in temporal activation is due to face-to-face interaction, consistent with past research suggesting that temporal regions are involved in facial processing (Emery, 2000).

In 4–6 Hz, activation in central regions was also unique to the joint attention condition compared with the other conditions. However in 6–9 Hz, there was no difference in central activation between conditions. Therefore, the mu rhythm, assessed in 6–9 Hz, does not seem to explain our pattern of results. It is possible that the absence of condition differences in central 6–9 Hz power was due to differences in measurement. Mu desynchronization is typically calculated in small time bins (Saby et al., 2012) that are time locked to specific action events (e.g., picking up an object). In contrast, we compared global neural activation across sustained conditions.

Language input did not explain our pattern of results given that the language-only condition did not differ from the nonsocial condition in any region. This result that positive affect language alone did not make a difference for neural activation is consistent with Santesso, Schmidt, and Trainor (2007), who found that infant-directed speech with fear affect influenced infant neural activation, whereas positive affect did not. Future research should assess EEG coherence, which might be a more sensitive measure of the neural underpinnings of language. For example, lower left fronto–central and greater left fronto–occipital coherence assessed during a Bingo wheel baseline at 14 months predicted

language development at 24 months (Mundy, Fox, & Card, 2003). ERPs have also been related to infant language (Becker, Schild, & Friedrich, 2014; Friedrich & Friederici, 2008). ERPs can clarify specific neural components of processing that might be more appropriate for studying language than the global engagement and activation indexed by EEG power. Future research assessing both continuous EEG and ERPs across social and nonsocial recording contexts would provide a nuanced perspective on infant neural activation across contexts.

Our results were most pronounced in the 4–6 Hz band. The pattern was consistent in 6–9 Hz; however, not all effects were significant. This finding that condition differences were not as pronounced in 6–9 Hz is consistent with past research (Jones et al., 2015). It is possible that lower frequency power is more sensitive to social contexts during infancy (Jones et al., 2015) given that other research relating baseline EEG to joint attention behaviors focused on 4–6 Hz (Henderson et al., 2002; Mundy et al., 2000).

In addition to exploring patterns of regional activation, we also assessed hemisphere differences. There were no hemisphere effects in 6–9 Hz. In 4–6 Hz frontal activation was greater in the right hemisphere compared with the left hemisphere, whereas in the parietal region the pattern was reversed and activation was greater in the left hemisphere. However, there were no interactions of hemisphere with condition in either 4–6 Hz or 6–9 Hz, indicating that at a group level changes in neural activation with condition were bilateral. It would be interesting in future research to assess whether hemisphere by condition interactions might be observed for certain subgroups of infants. EEG asymmetry scores have been related to infant individual differences of temperament (Fox et al., 2001; Gartstein, Bell, & Calkins, 2014; LoBue, Coan, Thrasher, & DeLoache, 2011; Mize, Pineda, Blau, Marsh, & Jones, 2014) and experiences of maternal depression (Dawson et al., 1999; Field et al., 1995; Jones et al., 1997; Lusby et al., 2014). Future studies could assess how these individual differences relate to infant EEG asymmetry measured in both social and nonsocial contexts as well as whether there are hemisphere by condition interactions specific to infants with depressed mothers or infants with certain temperaments.

Our study design included an alternating sequence of social and nonsocial conditions to sustain infant cooperation throughout the protocol. Nonsocial conditions were preceded and followed by social conditions. It is plausible that our condition sequence is ecologically valid and consistent with an infant's day-to-day experiences. For instance, an infant might transition from playing and engaging with his or her mother to being in a car seat without social stimulation. Thus, our results might reflect how infants are actually neurally responding and processing from day to day.

However, given the relatively rapid alternation between conditions, it is possible that infant neural responses during a given condition may have been influenced by the prior condition. For instance, during the nonsocial condition, infants may have been anticipating the return of the experimenter. One study reported decreased neural activation in infants waiting for the experimenter to reappear during peek-a-boo (Orekhova, Stroganova, & Posikera, 1999), and it is possible that during the nonsocial condition in the current study infants also were waiting for the experimenter to return from behind the curtain. Even if conditions were recorded on separate days to avoid sequencing, it would not be feasible to avoid social interaction with the infant immediately preceding a nonsocial condition due to the social interaction inherent to placing the EEG net on the infant.

Given that the current paradigm alternated social and nonsocial conditions such that a social, face-to-face condition (joint attention or social engagement) always preceded a nonsocial condition (nonsocial or language-only), it was not possible to test for potential order effects of the conditions. We alternated conditions in this way to maintain infant attention because EEG recording lasted 20 min. Future research recording EEG for a shorter amount of time or with fewer conditions could experimentally manipulate the order of conditions to test for order effects.

Relatively few infants had usable EEG data in every condition. Therefore, we did not have a large enough sample size to use an omnibus test including all four conditions. Furthermore, requiring data for all four conditions would bias the sample toward the calmer, more patient infants, which would limit both generalizability and statistical power. Thus, we maximized the use of available data by using an a priori stepwise approach, including the joint attention and nonsocial conditions in the primary model and then separately including the social engagement and language-only conditions.

Future research would benefit from a large enough sample size to include an omnibus test to compare all conditions in the same model.

It is possible that the joint attention and social engagement conditions differed in more ways than the presence versus absence of joint attention. Specifically, the social engagement condition involved nonscripted interactions, whereas the joint attention condition involved scripted language. However, in both conditions the experimenter was trained to be consistent in the emotional tone, degree of warmth, and contingent responding. Therefore, although the language used between the conditions was different, as was the timing of the utterances during the joint attention condition, the experimenter was similarly positive and engaging in both conditions.

Our pattern of greater frontal activation in the joint attention condition compared with the nonsocial condition contrasts with Jones and colleagues (2015), who found that frontal activation was lower during a social movie compared with a nonsocial movie. It is likely that neural processing in social contexts depends on whether the context is contingent and face-to-face compared with a movie. Future research is needed to explore the nuances of how neural activation varies with different elements of the social context.

For example, including a joint attention condition that did not involve language could show whether the same differences in neural activation would be present. This would further clarify how joint attention relates to the social brain. Future research should also assess whether changes in EEG power from nonsocial to social contexts predicts future outcomes. It could be that greater activation in general, and in joint attention specifically, helps infants to take advantage of social interactions to learn more about the social world. In that case, greater activation in joint attention and face-to-face interactions during infancy might predict social competence and cognitive outcomes.

Future research should build on these results and further investigate how the nature of social interaction relates to infant EEG. For example, assessing several EEG measures, including power, coherence, and asymmetry, during infant social interactions would further an understanding of the development of the social brain. Comparing EEG measures recorded during interaction with caregivers versus unfamiliar adults would allow for analysis of the influences of social partner familiarity and dyadic interaction quality on neural engagement. Furthermore, including positive and negative social interactions, as well as assessments of infant emotions, would contribute to understanding how the emotional valence of the social interaction relates to infant EEG. Finally, future research should assess how individual differences such as socioeconomic status and age relate to neural activation across social and nonsocial contexts.

Conclusion

This study assessed infant functional neural activation across controlled nonsocial and social conditions. Our results demonstrate that EEG power is sensitive to social interaction given that infants showed increased frontal, central, and parietal activation during joint attention and increased temporal activation during two forms of face-to-face interaction compared with a nonsocial condition. Our results underscore the importance of using controlled social and nonsocial conditions in EEG research to elucidate the development of the social brain during infancy.

Acknowledgments

References

Abe, J. A. A., & Izard, C. E. (1999). The developmental functions of emotions: An analysis in terms of differential emotions theory. *Cognition and Emotion, 13*, 523–549.
Adolphs, R. (2003). Cognitive neuroscience of human social behaviour. *Nature Reviews Neuroscience, 4*, 165–178.
Allen, J. J. B., Coan, J. A., & Nazarian, M. (2004). Issues and assumptions on the road from raw signals to metrics of frontal EEG asymmetry in emotion. *Biological Psychology, 67*, 183–218.

Becker, A. B. C., Schild, U., & Friedrich, C. K. (2014). ERP correlates of word onset priming in infants and young children. *Developmental Cognitive Neuroscience, 9*, 44–55.

Bell, M. A. (2002). Power changes in infant EEG frequency bands during a spatial working memory task. *Psychophysiology, 39*, 450–458.

Calkins, S. D., Fox, N. A., & Marshall, T. R. (1996). Behavioral and physiological antecedents of inhibited and uninhibited behavior. *Child Development, 67*, 523–540.

Cannon, E. N., Simpson, E. A., Fox, N. A., Vanderwert, R. E., Woodward, A. L., & Ferrari, P. F. (2016). Relations between infants' emerging reach–grasp competence and event-related desynchronization in EEG. *Developmental Science, 19*, 50–62.

Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: Identical, independent, or overlapping neural systems? *Proceedings of the National academy of Sciences of the United States of America, 95*, 831–838.

Cuevas, K., Cannon, E. N., Yoo, K., & Fox, N. A. (2014). The infant EEG mu rhythm: Methodological considerations and best practices. *Developmental Review, 34*(1), 26–43.

Davidson, R. J. (1988). EEG measures of cerebral asymmetry: Conceptual and methodological issues. *International Journal of Neuroscience, 39*, 71–89.

Davidson, R. J., & Fox, N. A. (1982). Asymmetrical brain activity discriminates between positive and negative affective stimuli in human infants. *Science, 218*, 1235–1237.

Dawson, G., Frey, K., Panagiotides, H., Yamada, E., Hessl, D., & Osterling, J. (1999). Infants of depressed mothers exhibit atypical frontal electrical brain activity during interactions with mother and with a familiar, nondepressed adult. *Child Development, 70*, 1058–1066.

Emery, N. J. (2000). The eyes have it: The neuroethology, function, and evolution of social gaze. *Neuroscience and Biobehavioral Reviews, 24*, 581–604.

Field, T., Fox, N. A., Pickens, J., & Nawrocki, T. (1995). Relative right frontal EEG activation in 3- to 6-month-old infants of "depressed" mothers. *Developmental Psychology, 31*, 358–363.

Fox, N. A., Bakermans-Kranenburg, M. J., Yoo, K. H., Bowman, L. C., Cannon, E. N., Vanderwert, R. E., Ferrari, P. F., & van IJzendoorn, M. H. (2016). Assessing human mirror activity with EEG mu rhythm: A meta-analysis. *Psychological Bulletin, 142*, 291–313.

Fox, N. A., Henderson, H. A., Rubin, K. H., Calkins, S. D., & Schmidt, L. A. (2001). Continuity and discontinuity of behavioral inhibition and exuberance: Psychophysiological and behavioral influences across the first four years of life. *Child Development, 72*, 1–21.

Friedrich, M., & Friederici, A. D. (2008). Neurophysiological correlates of online word learning in 14-month-old infants. *NeuroReport, 19*, 1757–1761.

Gartstein, M. A., Bell, M. A., & Calkins, S. D. (2014). EEG asymmetry at 10 months of age: Are temperament trait predictors different for boys and girls? *Developmental Psychobiology, 56*, 1327–1340.

Grossmann, T. (2015). The development of social brain functions in infancy. *Psychological Bulletin, 141*, 1266–1287.

Grossmann, T., & Johnson, M. H. (2010). Selective prefrontal cortex responses to joint attention in early infancy. *Biology Letters, 6*, 540–543.

Henderson, L. M., Yoder, P. J., Yale, M. E., & McDuffie, A. (2002). Getting the point: Electrophysiological correlates of protodeclarative pointing. *International Journal of Developmental Neuroscience, 20*, 449–458.

Jones, E. J. H., Venema, K., Lowy, R., Earl, R. K., & Webb, S. J. (2015). Developmental changes in infant brain activity during naturalistic social experiences. *Developmental Psychobiology, 57*, 842–853.

Jones, N. A., Field, T., Fox, N. A., Lundy, B., & Davalos, M. (1997). EEG activation in 1-month-old infants of depressed mothers. *Development and Psychopathology, 9*, 491–505.

Lachat, F., Hugueville, L., Lemaréchal, J.-D., Conty, L., & George, N. (2012). Oscillatory brain correlates of live joint attention: A dual-EEG study. *Frontiers in Human Neuroscience, 6*. http://dx.doi.org/10.3389/fnhum.2012.00156.

LoBue, V., Coan, J. A., Thrasher, C., & DeLoache, J. S. (2011). Prefrontal asymmetry and parent-rated temperament in infants. *PLoS One, 6*(7), e22694.

Lusby, C. M., Goodman, S. H., Bell, M. A., & Newport, D. J. (2014). Electroencephalogram patterns in infants of depressed mothers. *Developmental Psychobiology, 56*, 459–473.

Marshall, P. J., Bar-Haim, Y., & Fox, N. A. (2002). Development of the EEG from 5 months to 4 years of age. *Clinical Neurophysiology, 113*, 1199–1208.

Marshall, P. J., & Meltzoff, A. N. (2011). Neural mirroring systems: Exploring the EEG mu rhythm in human infancy. *Developmental Cognitive Neuroscience, 1*(2), 110–123.

Marshall, P. J., Reeb, B. C., Fox, N. A., Nelson, C. A. I., & Zeanah, C. H. (2008). Effects of early intervention on EEG power and coherence in previously institutionalized children in Romania. *Development and Psychopathology, 20*, 861–880.

Missana, M., & Grossmann, T. (2015). Infants' emerging sensitivity to emotional body expressions: Insights from asymmetrical frontal brain activity. *Developmental Psychology, 51*, 151–160.

Mize, K. D., & Jones, N. A. (2012). Infant physiological and behavioral responses to loss of maternal attention to a social-rival. *International Journal of Psychophysiology, 83*, 16–23.

Mize, K. D., Pineda, M., Blau, A. K., Marsh, K., & Jones, N. A. (2014). Infant physiological and behavioral responses to a jealousy provoking condition. *Infancy, 19*, 338–348.

Molfese, D. L., Molfese, V. J., & Kelly, S. (2001). The use of brain electrophysiology techniques to study language: A basic guide for the beginning consumer of electrophysiology information. *Learning Disability Quarterly, 24*, 177–188.

Morales, M., Mundy, P., Crowson, M. M., Neal, A. R., & Delgado, C. E. F. (2005). Individual differences in infant attention skills, joint attention, and emotion regulation behaviour. *International Journal of Behavioral Development, 29*, 259–263.

Morales, M., Mundy, P., Delgado, C. E. F., Yale, M., Messinger, D., Neal, R., & Schwartz, H. K. (2000). Responding to joint attention across the 6- through 24-month age period and early language acquisition. *Journal of Applied Developmental Psychology, 21*, 283–298.

Mundy, P., & Acra, F. (2006). Joint attention, social engagement, and the development of social competence. In P. Marshall & N. Fox (Eds.), *The development of social engagement neurobiological perspectives* (pp. 81–117). New York: Oxford University Press.

Mundy, P., Card, J., & Fox, N. (2000). EEG correlates of the development of infant joint attention skills. *Developmental Psychobiology, 36*, 325–338.

Mundy, P., Fox, N., & Card, J. (2003). EEG coherence, joint attention, and language development in the second year. *Developmental Science, 6*, 48–54.

Nichols, K. E., Martin, J. N., & Fox, N. A. (2005). Individual differences in the development of social communication: Joint attention and temperament. *Cogniție Creier Comportament, 9*(2), 317–328.

Orekhova, E. V., Stroganova, T. A., & Posikera, I. N. (1999). Theta synchronization during sustained anticipatory attention in infants over the second half of the first year of life. *International Journal of Psychophysiology, 32*, 151–172.

Orekhova, E. V., Stroganova, T. A., Posikera, I. N., & Elam, M. (2006). EEG theta rhythm in infants and preschool children. *Clinical Neurophysiology, 117*, 1047–1062.

Petersen, S. E., & Posner, M. I. (2012). The attention system of the human brain: 20 years after. *Annual Review of Neuroscience, 35*, 73–89.

Ptak, R. (2012). The frontoparietal attention network of the human brain: Action, saliency, and a priority map of the environment. *The Neuroscientist, 18*, 502–515.

Redcay, E., Kleiner, M., & Saxe, R. (2012). Look at this: The neural correlates of initiating and responding to bids for joint attention. *Frontiers in Human Neuroscience, 6.* http://dx.doi.org/10.3389/fnhum.2012.00169.

Saby, J. N., Marshall, P. J., & Meltzoff, A. N. (2012). Neural correlates of being imitated: An EEG study in preverbal infants. *Social Neuroscience, 7*, 650–661.

Santesso, D. L., Schmidt, L. A., & Trainor, L. J. (2007). Frontal brain electrical activity (EEG) and heart rate in response to affective infant-directed (ID) speech in 9-month-old infants. *Brain and Cognition, 65*, 14–21.

Schmidt, L. A., Fox, N. A., Perez-Edgar, K., & Hamer, D. H. (2009). Linking gene, brain, and behavior. *Psychological Science, 20*, 831–837.

Southgate, V., Johnson, M. H., Karoui, I. E., & Csibra, G. (2010). Motor system activation reveals infants' on-line prediction of others' goals. *Psychological Science, 21*, 355–359.

Tarullo, A. R., Garvin, M. C., & Gunnar, M. R. (2011). Atypical EEG power correlates with indiscriminately friendly behavior in internationally adopted children. *Developmental Psychology, 47*, 417–431.

Tomalski, P., Moore, D. G., Ribeiro, H., Axelsson, E. L., Murphy, E., Karmiloff-Smith, A., Johnson, M. H., & Kushnerenko, E. (2013). Socioeconomic status and functional brain development—associations in early infancy. *Developmental Science, 16*, 676–687.

Welch, M. G., Myers, M. M., Grieve, P. G., Isler, J. R., Fifer, W. P., Sahni, R., et alfor the FNI Trial Group. (2014). Electroencephalographic activity of preterm infants is increased by Family Nurture Intervention: A randomized controlled trial in the NICU. *Clinical Neurophysiology, 125*, 675–684.

Williams, J. H. G., Waiter, G. D., Perra, O., Perrett, D. I., & Whiten, A. (2005). An fMRI study of joint attention experience. *NeuroImage, 25*, 133–140.