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Relations between dynamics of parent-infant interactions and baseline EEG functional connectivity

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ABSTRACT

Parent-infant interactions are one of the most critical and enduring aspects of infants' experience. Qualities of parent-infant interactions are related to social-emotional and cognitive developmental outcomes, yet how parent-infant interactions shape the functional organization of the brain is only beginning to be understood. Functional connectivity provides information about how brain regions communicate. Patterns of functional connectivity, thus far understudied in infants, have emerged as markers of abnormalities in the organization of the brain in at-risk infants as well as individuals with neurodevelopmental and neurodegenerative disorders. The current study sought to inform our understanding of relations between qualities of parent-infant interactions and functional connectivity. We report relations between responsiveness, reciprocity, and emotional tone and functional connectivity in theta, alpha, beta, and gamma in infants ranging from 6 to 11 month of age ($N = 51$). Results showed frontal-posterior connectivity in theta was inversely related to all three dimensions of parent-infant interactions. Gamma and alpha connectivity were positively associated with responsiveness and emotional tone, respectively. Results are discussed in the context of the experience-dependent nature of brain development, emphasizing how parent-infant interactions might be leveraged to structure early organization of the brain to foster healthy social-emotional and cognitive developmental outcomes.

1. Introduction

The dynamics of parent-infant interactions represent critical and enduring aspects of a child's experience (Bernier, Calkins, & Bell, 2016). It has been established that qualities of parent-infant exchanges predict social-emotional and cognitive development outcomes (e.g., Blair, Raver, & Berry, 2014; Hane & Fox, 2006). How parent-infant interactions shape the neural underpinnings of such outcomes, however, remains poorly understood. The nature of such interactions should be expected to shape the early organization of the brain given experience-dependent processes play a foundational role in brain development (Kolb et al., 2018). Indeed, a number of studies have now shown that variability in the quality of maternal caregiving behaviors is associated with individual differences in brain activity during infancy as well as developmental changes in brain activity from infancy into early childhood (Bernier et al., 2016; Hane & Fox, 2006; Swingler, Perry, Calkins, & Bell, 2014). Individual differences in brain activity during infancy are often measured using baseline electroencephalography (EEG). There has been much recent interest in extracting measures of functional connectivity – the degree to which different brain regions communicate – from baseline EEG. Functional connectivity in the EEG has

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provided insight into developmental processes (Bell & Fox, 1996; Corbetta, Friedman, & Bell, 2014) as well as the role interactivity across brain regions might have in neurodevelopmental disorders and neurodegeneration (e.g., Engles et al., 2015; Murias, Swanson, & Srinivasan, 2007). Given the pervasive role of parent-infant interactions in infant and child development, we should expect that different interaction factors be related to how various regions of the brain interact. Here, we test whether parent-infant interactions are related to functional connectivity during baseline EEG recorded from infants ranging from 6 to 11 months of age.

We begin with an overview of baseline EEG and key brain-behavioral relations found in the extant infant literature. Next, we review functional connectivity and what is known about patterns of connectivity in early development. Finally, we describe qualities of parent-infant interactions and established ties to infants' brain activity measured via EEG, which will set the stage for the current study.

1.1. Baseline EEG

Baseline EEG is a recording of the brain's electrocortical rhythms while no assigned task is being performed. Baseline EEG is widely used across the lifespan and provides a window into the organization of the brain at the level of the individual. For children and adults, baseline EEG is normally recorded while participants sit quietly with their eyes closed or else sit quietly and look at a simple stimulus (e.g., fixation cross). Baseline EEG is recorded from infants in a calm, alert state while they watch a dynamic display or a live actor manipulate an object (e.g., Bell & Fox, 1992; Benasich, Gou, Choudhury, & Harris, 2008; Marshall, Bar-Haim, & Fox, 2002), and is usually of short duration ranging from 1 to 5 min (e.g., Atzaba-Poria, Deater-Deckard, & Bell, 2017; Benasich et al., 2008; Brooker, Canen, Davidson, & Goldsmith, 2017; Levin, Varcin, O'Leary, Tager-Flusberg, & Nelson, 2017; MacNeill, Ram, Bell, Fox, & Pérez-Edgar, 2018; Mize & Jones, 2012; St. John, Kao, Liederman, Grieve, & Tarullo, 2016; Tomalski et al., 2013; Wolfe & Bell, 2007). EEG provides a measure of the synchronized firing of neuronal ensembles across a range of frequencies that are normally divided into bands that reflect different cortical rhythms, including theta (4–8 Hz), alpha (8–13 Hz), beta (13–30 Hz), and gamma (30–50 Hz). Theta and alpha are known to be slower in infancy than during childhood and adulthood (Marshall et al., 2002; Orekhova, Stroganova, Posikera, & Elam, 2006) and are typically defined as 3–6 Hz and 6–9 Hz, respectively. Gamma is consistently defined in the 30–50 Hz frequency range across the lifespan. Beta has been studied less during infancy and has been inconsistently defined, but in adults is generally represented by the frequencies between alpha and gamma (for a review, see Anderson & Perone, 2018).

Baseline EEG has long been used to study the dynamics of the infant brain (Hagne, 1972), and a growing body of evidence indicates early patterns of neural activity recorded in this manner are related to cognition and emotion regulation. Power in the 6–9 Hz alpha band is the most commonly reported measure in the infant baseline EEG literature (Bell & Fox, 1992; Fox, Henderson, Rubin, Calkins, & Schmidt, 2001; MacNeill et al., 2018; Wolfe & Bell, 2007). Alpha during infancy has been linked to basic cognitive processes (e.g., working memory; Bell, 2001; Bell & Fox, 1992; MacNeill et al., 2018) and shown to predict cognitive developmental outcomes during childhood (e.g., executive function; Kraybill & Bell, 2013; see also, Cuevas, Hubble, & Bell, 2012; Kühn-Popp, Kristen, Paulus, Meinhardt, & Sodian, 2016; Wolfe & Bell, 2007). A growing literature is beginning to investigate the role of power in other cortical rhythms during early development. For example, higher frontal gamma has been linked to better attention and inhibitory control abilities at 24 months of age (Benasich et al., 2008; see also Gou, Choudhury, & Benasich, 2011; Tarullo et al., 2017), and lower levels of frontal gamma were observed in infants developing in a low socioeconomic context (Tomalski et al., 2013). Lower levels of theta and higher levels of beta and gamma have also been linked to attention and regulatory processes during infancy (Perone & Gartstein, 2019) and childhood (Perone, Palanisamy, & Carlson, 2018). EEG power is more commonly studied in early childhood than functional connectivity. We turn to what is known about functional connectivity during early development next.

1.2. Functional connectivity

Functional connectivity is a measure of statistical interdependencies in the EEG between electrode sites and indicates the degree to which different brain regions are communicating (for review, see van Diessen et al., 2014). The result of functional connectivity analysis is a numerical value ranging from 0 (weakly connected) to 1 (strongly connected) for each electrode pair. This analysis yields an electrode-by-electrode connectivity matrix which can be used to describe functional networks by computing connectivity over regions of interest (e.g., frontal), visualizing the topography of connectivity over the scalp, or using graph theory to describe information flow through a large set of interconnected sites over the scalp (e.g., Orekhova et al., 2014; Miskovic et al., 2015; Rubinov & Sporns, 2010). In the current study, we focused on long-range connectivity over frontal and posterior regions. We selected these regions because several studies have now reported links between cortical activity in multiple rhythms over frontal and posterior regions with attention and regulatory processes in infants and young children (e.g., Benasich et al., 2008; Gou et al., 2011; Ezekiel, Bozma, & Morton, 2013; Tarullo et al., 2017; Tomalski et al., 2013; Perone et al., 2018). Moreover, long-range connectivity represents a viable indicator of individual differences in the organization of the brain, including deviations observed in the context of neurodevelopmental disorders and cognitive decline (e.g., Anguera et al., 2013; Fleck, Kuti, Brown, Mahon, & Gayda-Chelder, 2016; Righi, Tierney, Tager-Flusberg, & Nelson, 2014).

The few studies reporting functional connectivity with infants have provided unique insight into developmental processes. For instance, Bell and Fox (1996) found functional connectivity in alpha changed as a function of motor learning experience. Functional connectivity was higher for beginning crawlers than for infants who had not yet begun to crawl and those infants who were experienced crawlers, and a similar pattern was also observed for new and experienced walkers (Corbetta et al., 2014). This inverted u-shape pattern of change in functional connectivity as it corresponds to the acquisition of a new motor skill has been interpreted as the

building of connections to support motor learning followed by pruning of unused connections as infants fully acquire the new motor skill.

Studies with non-typically developing infants have yielded insight into the important role functional connectivity might have in neurodevelopmental disorders as well as patterns of connectivity that might be expected in typically developing infants. For example, Orekhova et al. (2014) found alpha connectivity over frontal and central regions was elevated in 14-month-old infants at high risk for autism who were subsequently diagnosed with autism relative to high-risk infants who did not receive an autism diagnosis later or low-risk infants. They also found elevated levels of connectivity in high-risk 14-month-old infants who were later diagnosed with outcomes associated with restricted and repetitive behaviors at 36 months of age (for similar results, see Haartsen et al., 2019). Atypical patterns of connectivity in children at risk for autism are not limited to alpha activity. For instance, Righi et al. (2014) found frontal-posterior gamma connectivity while listening to speech sounds increased from 6 to 12 months for low risk infants but decreased for high risk infants. At 12 months of age, high-risk infants who were ultimately diagnosed with autism exhibited lower levels of gamma connectivity than high-risk infants who did not receive a diagnosis as well as low-risk infants. These studies suggest low levels of connectivity in alpha but high levels of connectivity in gamma are indicators of typical brain development.

The aforementioned research indicates functional connectivity is experience-dependent and patterns of functional connectivity during infancy represent important predictors of developmental outcomes. Identifying experiential influences on functional connectivity, then, can inform our understanding of how early organization of the brain is shaped and is likely to have translational implications. Qualities of the parent-infant relational dynamic have been linked to cortical activity measured during baseline EEG, which we turn to next.

1.3. Links between EEG activity and parent-infant interactions

Infant neurobehavioral development is necessarily interactive in nature, with parent-infant interaction dynamics exerting direct and indirect effects (Calkins, 1994). For example, parents may be more or less effective in soothing infants, helping them to lower their level of arousal, and can also aid or disrupt child regulation by shaping the context of an emotionally-eliciting event (e.g., via their own display of emotions). Parent-infant interactions in early childhood are typically characterized by variability along three most prominent dimensions: responsiveness, positive emotional tone, and reciprocity (see Table 1).

Maternal responsiveness has been examined most widely in infancy, and linked with a variety of positive outcomes, perhaps most notably secure attachment, and also advanced attention/regulatory capacity (Ainsworth, Blehar, Waters, & Wall, 1978; Gartstein, Crawford, & Robertson, 2008). Mothers who are highly responsive appropriately interpret their infant's communication attempts, providing prompt, contingent, and supportive responses, engaging their infant in a genuinely interested and emphatic, rather than intrusive, fashion. Positive emotional tone represents another key aspect of higher quality exchanges with the infant, also found predictive of attachment security (Ainsworth et al., 1978). Positive emotional tone involves displays of enjoyment, affection, and enthusiasm while interacting with the infant, and is closely related to the dynamic of parent-child exchanges referred to as parental warmth (focused on the positive affective quality), also associated with child self-regulation and compliance (Colman, Hardy, Albert, Raffaelli, & Crockett, 2006; Dennis, 2006). Importantly, warmth/positive emotional tone predict more advanced effortful control (Eiden, Edwards, & Leonard, 2004; see also, Cipriano & Stifter, 2010), widely defined as the ability to inhibit a prepotent response in favor of an adaptive novel response, with established neurophysiological correlates (e.g., frontal lobe activation; Posner, Rothbart, Sheese, & Voelker, 2012). Reciprocity is another prominent attribute of parent-infant interactions related to attunement and turn-

Table 1
Parent-Infant Interaction Coding Scheme.

Scales	Codes/Descriptions		
	1	4	7
Responsiveness/ sensitivity	Extremely non-responsive/sensitive: lacks genuine empathy and interest in infant. Parent does not a) initiate play; b) reinforce infant activities; c) draw infant into joint activity; d) give encouragement; e) allow infant independent activity; f) effectively extends infant activity	Moderately responsive/ sensitive: moderate empathy and interest in infant. Parent periodically a) initiates play b) reinforces infant activities; c) draws infant into joint activity; d) gives encouragement; e) allows infant independent activity; f) effectively extends infant activity	Extremely responsive/ sensitive: prompt, regular, genuine empathy and interest in infant. Parent consistently a) initiates play; b) reinforces infant activities; c) draws infant into joint activity; d) gives encouragement; e) allows infant independent activity; f) effectively extends infant activity
Reciprocity/ synchrony	Extremely asynchronous/ non-reciprocal: a) low frequency of simultaneous movement; b) low tempo similarity; c) low coordination/ smoothness	Moderately synchronous/ reciprocal: a) moderate frequency of simultaneous movement; b) moderate tempo similarity; c) moderate coordination/ smoothness	Extremely synchronous/ reciprocal: a) high frequency of simultaneous movement; b) high tempo similarity; c) high coordination/ smoothness
Emotional tone	Extremely negative emotional tone: a) frequent critical/ negative comments; b) frequent expressions of distress; c) frequent negative physical displays	Neutral emotional tone: a) mostly neutral verbal exchanges; b) few, if any, expressions of affect; c) few, if any, physical displays of affect	Extremely positive emotional tone: a) frequent enthusiastic/positive comments; b) frequent expressions of positive emotion/joy/pleasure; c) frequent positive physical displays

Note. All coding scales based on 7-point Likert Scales (1–7).

taking, with a mutual nature of responding central to this dimension (Tronick, 1989). Reciprocity in parent-child exchanges has also been shown to predict superior cognitive and social-emotional outcomes (Leclère et al., 2014; Lewis & Coates, 1980; Lindsey, Cremeens, Colwell, & Caldera, 2009). Greater quality of caregiving is generally characterized by high levels of all three attributes: responsiveness, positive emotional tone and reciprocity, yet these dimensions have distinct features and, critically, may be differentially related to infant brain activity.

Parent-infant interactions have not previously been investigated in relation to functional connectivity. However, several studies demonstrated that parent-infant interactions were related to cortical activity during baseline EEG. For example, Swingler et al. (2014) reported that 5-month-old infants who exhibited greater left frontal alpha activity – a neural correlate of approach-oriented motivational bias - and also had highly responsive mothers were better able to regulate their emotions during an arm-restraint task than infants with highly responsive mothers who exhibited greater right frontal alpha activity (see also Hane & Fox, 2006). Developmental change in EEG power is also linked to parent-infant interactions. Bernier et al. (2016) showed mothers who exhibited higher quality caregiving behaviors (higher levels of positive emotional tone and less intrusiveness) had infants demonstrating increases in baseline theta and alpha power from 5 to 10 months of age and again from 10 to 24 months of age. We should expect qualities of parent-infant interactions to be related to functional connectivity given connectivity is experience-dependent (Bell & Fox, 1996) and parent-infant-interactions are a prevalent piece of infants' experience. Probing such relations can inform our understanding of how dynamics of parent-infant exchanges help structure the emerging functional organization of the brain - this was the goal of the current study.

1.4. The current study

The current study examined relations between functional connectivity in infants ranging from 6 to 11 months of age in relation to parent-infant interaction dynamics during free play. The infant functional connectivity literature is sparse. However, the larger infant and child baseline EEG literatures indicates parent-infant interactions and related qualities of the social context (e.g., SES) are linked to theta, alpha, and gamma (Bernier et al., 2016; Tomalski et al., 2013). Moreover, these rhythms are robustly related to social-emotional and cognitive development (Benasich et al., 2008; MacNeill et al., 2018; Perone et al., 2018). We expect that parent-infant interactional dynamics will be related to functional connectivity in these rhythms as well.

We focused on three key measures of parent-infant interactions: responsiveness, emotional tone, and reciprocity because of predictive relations with these qualities of exchange demonstrated in existing research. Responsiveness has been linked to EEG activity (Swingler et al., 2014; Hane & Fox, 2006) and utilized as a “vehicle” in early interventions facilitating development for at-risk infants (Landry, Smith, Swank, & Guttentag, 2008; Rogers et al., 2014). Similarly, emotional tone has been linked to EEG activity (Bernier et al., 2016) and predictive of long-term outcomes, including effortful control (Cipriano & Stifter, 2010; Eiden et al., 2004). Reciprocity has not previously been examined in relation to EEG activity. However, as noted, synchronous parent-child interactions, characterized by reciprocity and contingency, promote cognitive and social-emotional development (e.g., Lewis & Coates, 1980; Lindsey et al., 2009; Leclère et al., 2014). For example, synchrony between mothers and infants at 3 and 9 months independently predicted symbolic play and internal state-related talk in the toddler period (Feldman & Greenbaum, 1997). Therefore, relations between this interactional dynamic and early organization of the brain can also be expected. The current study is expected to inform our understanding of critical links between parent-infant interactions and functional connectivity, setting the stage for subsequent inquiry into the real-time processes by which parent-infant interactions structure brain development and relations with advances in behavioral functioning (e.g., emotion regulation).

2. Method

2.1. Participants

The final sample consisted of 51 infants ranging from 6 to 11 months of age, including four 6-month-olds ($M = 27.29$ weeks, $SD = .20$ weeks), 11 7-month-olds ($M = 33.03$ weeks, $SD = 1.22$ weeks), 11 8-month-olds ($M = 36.73$ weeks, $SD = 1.40$ weeks), 12 9-month-olds ($M = 40.43$ weeks, $SD = 1.23$ weeks), seven 10-month-olds ($M = 46.27$ weeks, $SD = 1.08$ weeks), and six 11-month-olds ($M = 49.64$ weeks, $SD = 1.55$ weeks). Twenty-eight additional infants participated but were excluded because they did not participate in parent-infant interaction ($n = 8$), equipment malfunction ($n = 2$), fussiness ($n = 1$), unusable EEG due to experimenter/recording error ($n = 2$), or missing data due to experimenter/computer error ($n = 15$). Mothers with infants were recruited via social media advertisements, local birth centers/parent-infant programs, and pamphlets distributed in locations frequented by families with infants in two neighboring communities in the Pacific northwest. We only recruited families with children who did not have significant medical or birth complications, were born full-term (> 37 weeks of gestation), and with no developmental delays or disabilities. Non-English speaking caregivers were also not recruited, as instruments utilized for a larger project families participated in are not available in languages other than English. All families received an infant T-shirt (about \$10 value) incentive at the end of their laboratory visit as a thank-you for participation in the study. Participating families were largely Caucasian (90%). Mothers were primarily married (91%), and educated ($M = 16.01$ years, $SD = 2.04$ years), with family income above \$30,001 (81%). Mothers were between 21 and 42 years of age ($M = 28.72$, years, $SD = 4.64$ years).

2.2. Design and procedure

Parent-infant interactions involved a two-minute free play session. Mothers were instructed to play as they normally would with

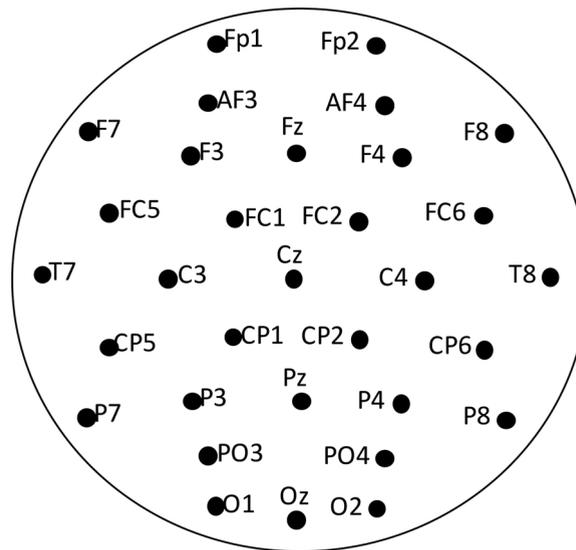


Fig. 1. 32 electrode locations and labels EEG was recorded from.

their infants at home. The dyad used a toy phone as a prop, provided by the experimenter. Video records of the free play session were scored for responsiveness, reciprocity, and emotional tone on a Likert scale ranging from 1 to 7, as previously described (Gartstein et al., 2008; Gartstein, Iverson, Desmarais, & Hancock, 2017; Gartstein, Hancock, & Iverson, 2018). Table 1 provides a description of low, moderate, and high scores for each category of parent-infant interactions. Inter-rater reliability was computed on 20% of the sample (e.g., Bernier et al., 2016; Kiel & Buss, 2012; Tsotsi et al., 2018) and was satisfactory for all three parent-child interaction factors (Responsiveness: ICCs .62–.98, mean ICC = .83; Reciprocity: ICCs .65–.98, mean ICC = .81; Emotional Tone ICCs .62–.98, mean ICC = .84).

After the free play session, infants participated in baseline EEG. The EEG was recorded from 32 electrode sites (see Fig. 1). Infants sat in a high-chair and were fitted with an EEG cap (Cortech Solutions, Inc.; Wilmington, NC). Small amounts of electro-conductive gel were placed in each site and pin-type electrodes (BioSemi - Cortech Solutions, Inc.; Wilmington, NC) were then snapped into each site. The EEG was collected via the BioSemi Active Two amplifiers and initial screening via the BioSemi acquisition software at a sampling rate of 1024 Hz. The EEG was referenced to Cz online. Baseline EEG was recorded for 60 s while infants watched a segment of *Baby Einstein, Baby Mozart* video (Gartstein, 2019). This animation depicts colorful objects while classical music is played. Mothers were instructed to limit their interaction with the infant to directing their infants' attention to the screen.

2.3. EEG processing

The EEG was processed in Matlab using functions from EEGLab (Delorme & Makeig, 2004), ERPLab (Lopez-Calderon & Luck, 2014), and FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011). The continuous EEG was down-sampled to 256 Hz. A high-pass filter at 1 Hz and a 60 Hz notch filter was applied. Excessively noisy electrodes were removed and interpolated. The mean number of electrodes interpolated was 2.18 ($SD = 2.01$, $range = 0-7$). The EEG was then re-referenced to the average. The continuous EEG was divided into 1 s epochs with 75% overlap. Epochs were rejected if the absolute voltage of any electrode exceeded $100 \mu V$ for more than 100 ms. Functional connectivity was measured by the weighted Phase Lag Index (wPLI) which was computed from the Fast Fourier Transformation (FFT) in FieldTrip for theta (3–6 Hz), alpha (6–9 Hz), beta (9–30 Hz), and gamma (30–50 Hz). There are several functional connectivity metrics each with their own strengths and weakness (for detailed review, see van Diessen et al., 2014). We chose PLI because it minimizes the contribution of volume conduction which can inflate connectivity estimates. PLI is a measure of phase synchronization and serves as an indicator of neural synchrony across brain regions. PLI measures the degree to which two signals consistently lead or lag over time and varies between 0 (weak connectivity) and 1 (high connectivity). For the weighted variant, phase angle differences farther from zero or π -phase have a larger influence which minimizes the contribution of volume conduction to connectivity in a graded fashion (see Vinck, Oostenveld, van Wingerden, Battaglia, & Pennartz, 2011; for discussion, see Cohen, 2014). wPLI was extracted from artifact free epochs. The average proportion of epochs used to estimate connectivity was 88% ($SD = 12\%$).

Our main analyses focused on relations between frontal-posterior connectivity and parent-infant interactions. Frontal-posterior connectivity was computed as the average wPLI between all 56 pairs of frontal (Fp1, Fp2, AF3, AF4, F3, F4, Fz) and posterior (P3, P4, PO3, PO4, O1, O2, Pz, Oz) sites. Connectivity within each region was also computed separately for supplemental analyses. The electrodes within these regions of interest align closely with prior studies with infants and children (Gou et al., 2011; Perone et al., 2018; Tomalski et al., 2013).

2.4. Analytic strategy

We computed bivariate correlations between connectivity within the four bands (theta, alpha, beta, gamma) with the three dimensions of parent-infant interactions (responsiveness, reciprocity, emotional tone). Statistical significance of each observed correlation was evaluated against a null hypothesis distribution using nonparametric permutation testing (for detailed review, see Cohen, 2014). Nonparametric permutation testing does not make any assumptions about the underlying distribution from which the observed data was drawn, as in parametric statistics. One advantage of this method is it yields a probability by comparing the observed test statistic to what would be expected by chance given the empirical data, which can be more sensitive than parametric statistics and yield a probability of zero (for discussion of other advantages, see Exploratory Analyses).

Nonparametric permutation testing requires generating a null hypothesis distribution of the test statistic, in our case, r , from the empirical data to which the observed test statistic is compared. The null hypothesis distribution is a representation of the r statistic if parent-infant interactions and connectivity were unrelated (i.e., if the null hypothesis were true). Generating the null hypothesis distribution involved three steps. First, mothers' score on a dimension of parent-infant interactions (e.g., responsiveness) was randomly assigned to another infant. Second, Pearson's r was computed for the randomly assigned parent-infant interaction scores with frontal-posterior connectivity for a given band (e.g., theta). Third, the r statistic was stored. This process was repeated 5000 times, yielding a near Gaussian distribution of the r statistic. A p-value was obtained by dividing the number of r values in the distribution greater than (for positive correlations) or less than (for negative correlations) the observed r statistic by the total number of r statistics in the distribution. Thus, one-tail p-values are reported. Only correlations that fell in the upper or lower 2.5% ($\alpha = .05$) were interpreted as significant. This same process was applied to each dimension of parent-infant interactions and band for frontal-posterior, frontal, and posterior regions separately. Note semi-partial r distributions were generated when age was related to connectivity, which only occurred for gamma.

3. Results

We report relations among dimensions of parent-infant interactions, with age, and between functional connectivity and parent-infant interactions. We also report exploratory analyses visualizing the topography of relations between functional connectivity and parent-infant interactions.

3.1. Relations among parent-infant interactions

Responsiveness was related to reciprocity ($r = .77, p < .001$) and emotional tone ($r = .75, p < .001$), and reciprocity and emotional tone were also related ($r = .63, p < .001$).

3.2. Relations with age

Age was unrelated to parent-infant interactions (all $ps > .40$). Age was also unrelated to frontal-posterior connectivity with the exception of gamma ($r = .285, p = .042$; all other $ps > .25$), and was not associated with connectivity within frontal or posterior regions in any band (all $ps > .05$).

3.3. Relations between parent-infant interactions and connectivity

Descriptive statistics for parent-infant interactions and frontal-posterior connectivity are shown in Table 2. Frontal-posterior theta connectivity was inversely related to responsiveness ($r = -.34, p = .008$), reciprocity ($r = -.37, p = .005$), and emotional tone ($r = -.29, p = .014$). Frontal-posterior alpha connectivity was positively related to emotional tone only ($r = -.35, p = .007$; all other $ps > .25$). Frontal-posterior beta connectivity was unrelated to parent-infant interactions (all $ps > .30$). Gamma was positively related only to responsiveness ($r = .30, p = .016$; all other $ps > .05$).

To determine if relations between connectivity and parent-infant interactions were limited to long-range connectivity, for supplemental analyses we probed relations between short-range connectivity within the frontal and posterior regions of interest separately. Only frontal connectivity within the alpha band was inversely related to responsiveness, $r = -.29, p = .019$, indicating observed relations were generally limited to long-range connectivity.

Table 2
Means (SD) for Parent-Infant Interaction Variables and Functional Connectivity Across Bands.

Parent-Infant Interactions		Functional Connectivity	
Responsiveness	4.67 (1.54)	theta	.16 (.04)
Reciprocity	4.45 (1.46)	alpha	.14 (.03)
Emotional Tone	4.14 (1.36)	beta	.13 (.02)
		gamma	.12 (.01)

3.4. Exploratory analyses

Our main analyses focused on relations between frontal-posterior connectivity and parent-infant interactions. One advantage of zooming in on a small number of regions is it constrains the number of connections under investigation. However, it may also conceal highly interconnected sites or other salient patterns of connectivity related to parent-infant interaction dynamics. The goal of our exploratory analyses was to visualize patterns of connectivity in relation to dimensions of parent-infant interactions. Computing correlations for parent-infant interactions and connectivity for all pairs of electrodes increases the likelihood some relations might be due to chance – 32 electrodes yield 496 pairs of electrodes. A central advantage of nonparametric permutation testing in neuroimaging research is it can be used to identify patterns of connectivity that are related to parent-infant interactions and also have a low probability of occurring by chance.

We generated a null hypothesis distribution of the r statistic for a given behavioral variable (e.g., responsiveness) and each electrode pair (e.g., Fp1/Fp2) for a given band (e.g., theta). We then tallied up the number of r statistics with $p < .025$ (one-tailed) associated with each electrode for the behavioral variable and band. For example, Fp1 would receive a score of two if connectivity for Fp1/Fp2 and Fp1/AF4 were both positively associated with responsiveness at the $p < .025$ level. This was repeated across 5000 permutations and yielded an asymmetric distribution of the number of significant relations that could be expected between a given electrode and a behavioral variable by chance. We extracted a critical value which was the number of relations associated with a given electrode that occurred 5% of the time. To visualize networks, we plotted all significant connections linked to electrodes exceeding this threshold.

Fig. 2 shows the results. Each plot shows the topography of connections that are related to responsiveness (left panel), reciprocity (middle panel), and emotional tone (right panel). The colored electrodes represent those electrodes that exceeded the aforementioned threshold. These are color and size coded to indicate their relative importance. Blue lines reflect inverse relations and red lines reflect positive relations.

The results were largely consistent with the main analyses of frontal-posterior connectivity. All relations with theta (2A-C) and responsiveness, reciprocity, and emotional tone were inverse whereas relations with alpha and emotional tone (2F) and gamma and responsiveness (2J) were almost all positive. Additionally, associations with frontal-posterior connectivity were prevalent for theta and responsiveness (2A) as well as theta and reciprocity (2B), alpha and emotional tone (2F), and gamma and responsiveness (2J). Other patterns were also evident, as for instance, reciprocity was linked to central-posterior gamma connectivity (2K).

Visualization of functional networks provides an opportunity to identify sites especially relevant to each dimension of parent-infant interactions. For example, the link between reciprocity and gamma connectivity at FC2 and Pz were especially high. This pattern of results speaks to the prevalence of synchronized activity between FC2 and Pz with other sites distributed over the scalp in relation to aspects of mother-infant interactions. These sites may reflect hubs through which information is processed and communicated. We turn to the implications of these observations in the General Discussion.

4. General discussion

The current study investigated the link between qualities of parent-infant interactions and functional connectivity in infants ranging from 6 to 11 months of age. The main finding captures lower levels of frontal-posterior theta connectivity being related to higher levels of responsiveness, reciprocity, and positive emotional tone in interactions with the infant. Higher levels of frontal-posterior alpha connectivity were related to a greater expression of positive emotional tone, and higher frontal-posterior gamma connectivity was related to more responsive interactions. This study contributes to the existing literature primarily by demonstrating that parent-infant interactions are related to emerging functional networks in the brain, with implications for prevention efforts that capitalize on parental caregiving behaviors during a highly malleable period of development.

One of our most salient observations involved responsiveness, reciprocity, and emotional tone, reflective of higher quality caregiving overall, being inversely related to theta. Theta activity has been linked to regulatory processes, such as executive control, in children and adults (e.g., [Anguera et al., 2013](#); [Fleck et al., 2016](#); [Massar, Kenemans, & Schutter, 2014](#); [Perone et al., 2018](#)). Previous studies with infants have shown connectivity decreases as emerging behaviors stabilize and become more automatic (e.g., walking; [Bell & Fox, 1996](#); [Corbetta et al., 2014](#)), thus lower levels of theta connectivity could reflect a more stable pattern of activity that parent-infant interactions help structure early in development. As all three parent-infant interaction dynamics considered in this study contributed to the observed pattern, how responsive parents are when interacting with their infants, the extent to which they are able to foster reciprocal exchanges, and the positive emotional tone of play, set the stage for this aspect of connectivity. Our findings are consistent with the existing literature demonstrating the importance of these parent-child interaction factors with respect to EEG markers, as well as social-emotional and cognitive indicators more broadly (e.g., [Blair et al., 2014](#); [Cipriano & Stifter, 2010](#); [Hane & Fox, 2006](#); [Swingler et al., 2014](#)).

The direction of links between connectivity and parent-infant interactions appears to differ across bands. For example, we observed relations between higher levels of gamma and responsiveness. [Righi et al. \(2014\)](#) showed long-range, frontal-posterior gamma connectivity increases over the second half of the first year and parents who interact with their infant in a responsive fashion could be structuring higher levels of gamma connectivity. Alpha connectivity was also positively related to emotional tone in the present study. This pattern of results fits within a larger literature showing alpha is involved in emotion regulatory processes (e.g., [Buss et al., 2003](#); [Fox et al., 2001](#)) and has been tied to maternal positive affect (including tone) in previous EEG studies with infants ([Bernier et al., 2016](#)). This pattern of results also demonstrates variability in associations between infant brain organization and aspects of parent-child interactions, despite significant interrelations for the latter observed in this study. Such differential predictive links have

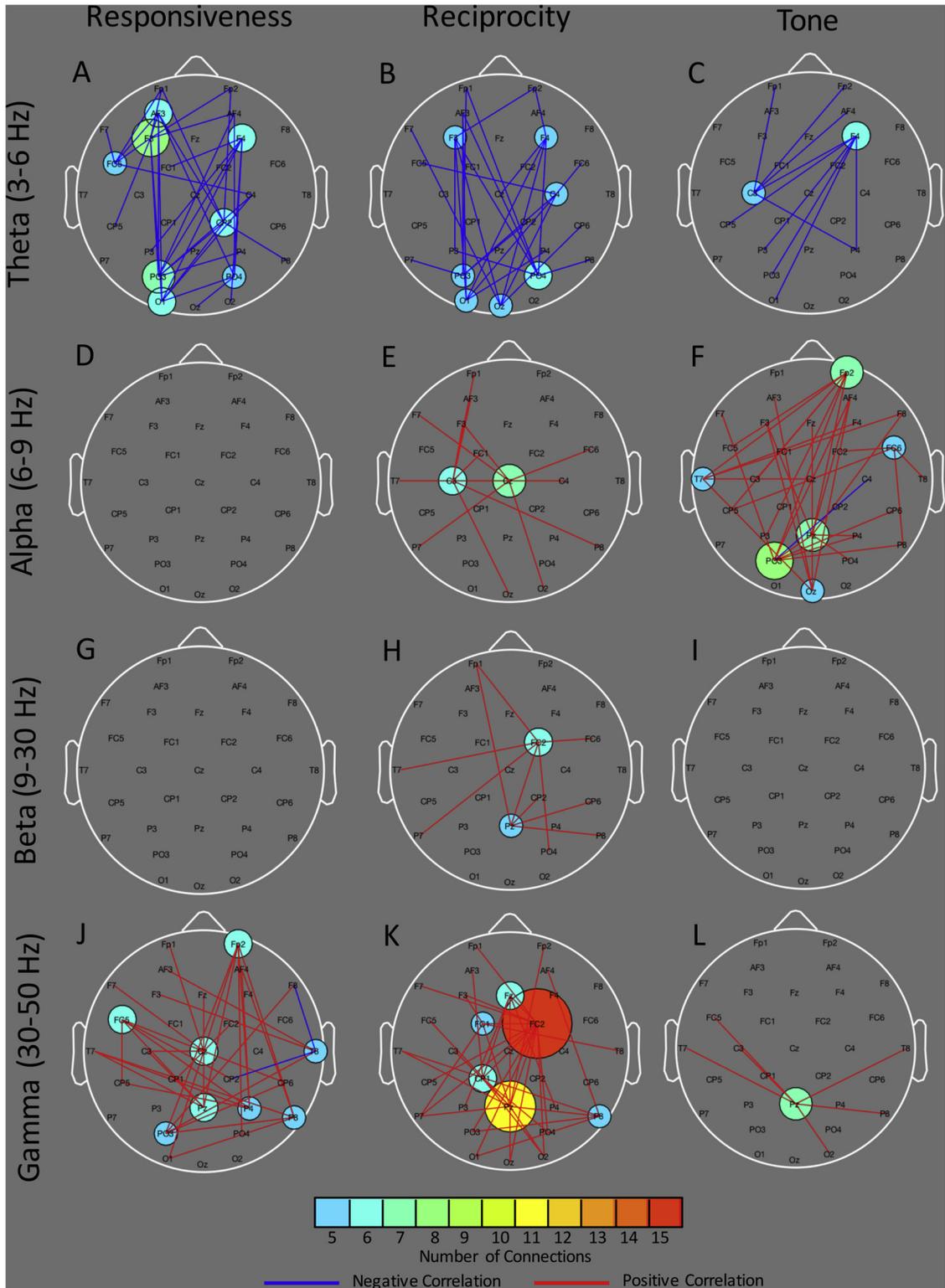


Fig. 2. Depicts results of exploratory analyses using permutation testing to identify patterns of connectivity in relation to dimensions of parent-infant interactions. The topography is shown of connections for theta (A–C), alpha (D–F), beta (G–I), and gamma (J–L) that are related to responsiveness (left panel), reciprocity (middle panel), and emotional tone (right panel). The colored electrodes represent those electrodes that were determined to be robustly interconnected, which are color and size coded to indicate their level of connectedness. Blue lines reflect inverse relations and red lines reflect positive relations between electrode x electrode connectivity and parent-infant interactions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

been demonstrated for infant behavioral development, for example, approach and avoidance motivation/emotions, as well as the associated EEG lateralization, in prior research (Gartstein et al., 2018; Gartstein, 2019).

Our main analyses revealed relations between functional connectivity and parent-infant interactions were generally constrained to long-range frontal-posterior connectivity, not short-range connectivity within the frontal or posterior regions. The integrity of long-range connectivity has been implicated for infants at-risk for autism (Righi et al., 2014; primarily frontal-central in Orekhova et al., 2014), children with autism (for review and discussion, see Vasa, Mostofsky, & Ewen, 2016), as well as declining executive control in older adults (Fleck et al., 2016), and may reflect integration of distant brain regions involved in regulatory or cognitive functioning. Our findings extend the existing literature in an important direction, demonstrating significance of long-range connectivity for typically developing infants in multiple cortical rhythms in relation to parent-infant interactions. Results of the exploratory analyses were generally consistent with our main findings, showing robust patterns of frontal-posterior connectivity. For example, connectivity within theta were largely long-range in relation to responsiveness and reciprocity. However, exploratory analyses also revealed patterns of connectivity not organized around the frontal-posterior axis, as for instance, central-posterior connectivity in gamma was robustly related to reciprocity. Exploratory analyses conducted in this study also highlight the utility of non-parametric permutations in identifying patterns of connectivity, similar to our prior research (Perone & Gartstein, 2019), that may ultimately have an important role in behavioral development.

4.1. Limitations and conclusions

Investigations of parent-infant interactions in relation to infants' brain activity are important to understand how typical every-day social experiences contribute to structuring the organization of the brain. The current study sheds new light on the links between parent-infant interactions and the emerging organization of infant brain activity. Our findings show parent-infant interaction dynamics are consistently related to functional connectivity especially in theta but also alpha and gamma bands, albeit not always in the same direction or consistent manner across the three interactional dimensions examined in this study. The current study does have some limitations, however. One limitation is the sample size is relatively small, but not atypical for EEG studies with infants (e.g., Marshall et al., 2002; Orekhova et al., 2006; Schmidt, 2008; Wolfe & Bell, 2007). Additionally, reported results are systematic and robust and should be expected to be reliable. A second limitation has to do with the cross-sectional nature of these data that does not permit us to make conclusive statements about the direction of observed effects. Third, we do not know how parent-infant interactions are linked to functional connectivity in the moment, and how these real-time associations translate into relations across developmental time. This latter point raises a bigger issue of time scale integration – how does responsiveness in the here-and-now influence the organization of functional networks in the brain concurrently and, in turn, developmentally (for discussion, see Perone & Simmering, 2017; Perone & Spencer, 2013). Finally, we were not able to discern how patterns of functional connectivity and parent-infant interactions together predict social-emotional or cognitive development. The current study provides a foundation critical for future research to address these lingering questions. Doing so will take important steps toward the long-term goal of research aimed at understanding the types of parental behaviors that structure neural networks to promote healthy outcomes and may be incorporated as part of early interventions to curtail adverse developmental trajectories, including neurodevelopmental disorders.

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