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RESEARCH ARTICLE

Maternal hair cortisol predicts periodic and aperiodic infant frontal EEG activity longitudinally across infancy

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Abstract

Maternal stress is known to be an important factor in shaping child development, yet the complex pattern of associations between stress and infant brain development remains understudied. To better understand the nuanced relations between maternal stress and infant neurodevelopment, research investigating longitudinal relations between maternal chronic physiological stress and infant brain function is warranted. In this study, we leveraged longitudinal data to disentangle between- from within-person associations of maternal hair cortisol and frontal electroencephalography (EEG) power at three time points across infancy at 3, 9, and 15 months. We analyzed both aperiodic power spectral density (PSD) slope and traditional periodic frequency band activity. On the within-person level, maternal hair cortisol was associated with a flattening of frontal PSD slope and an increase in relative frontal beta. However, on the between-person level, higher maternal hair cortisol was associated with steeper frontal PSD slope, increased relative frontal theta, and decreased relative frontal beta. The within-person findings may reflect an adaptive neural response to relative shifts in maternal stress levels, while the between-person results demonstrate the potentially detrimental effects of chronically elevated maternal stress. This analysis offers a novel, quantitative insight into the relations between maternal physiological stress and infant cortical function.

KEYWORDS
development, EEG, infant, stress

1 | BACKGROUND

1.1 | Introduction

Caregiving environments characterized by high stress are known to place infants at an increased risk of psychopathologies later in life (Blair & Raver, 2012; Kessler et al., 2010; VanTieghem & Tottenham, 2018). The majority of research in this domain has examined subjective measures of early life stress with cross-sectional and behavioral outcomes in children (Deater-Deckard, 1998; Pierce et al., 2019; Vaughan et al., 2013), which has limited use for drawing developmental inferences. However, the pathways by which caregiver physiological stress predicts differences in children's brain development are only recently being examined (Pierce et al., 2019; St. John et al., 2017; Troller-Renfree et al., 2020). Here, we aim to extend the developmental literature by examining the role of maternal chronic physiological stress, measured at multiple time points across infancy, in predicting differential change in infant electroencephalography (EEG) power on both the between- and within-person levels. In doing so, we hope to explore a malleable proximal environmental factor that may differentiate trajectories of neurocognitive development.

1.2 | Characterizing sensitive periods in infancy

Infants undergo a sensitive period of neurodevelopmental plasticity in the first years of life when environmental experiences during this time have the potential to significantly shape brain structure and wiring (Gabard-Durnam & McLaughlin, 2020; Takesian & Hensch, 2013). As the infant brain goes through important morphological and functional changes, the quality of the child's rearing environment is particularly important (Hensch, 2005). It is critical that we characterize the effects of caregiver stress on infant cortical function throughout this early sensitive period, as experience-driven neurodevelopment has important long-term implications (Gabard-Durnam & McLaughlin, 2020).

The prefrontal cortex (PFC) is a cortical region particularly susceptible to the effects of stress due to the structural and functional neurobiological linkage between the PFC and hypothalamic–pituitary–adrenal (HPA) axis (Arnsten, 2009; Liston et al., 2009; Perry et al., 2018). The PFC coordinates with the HPA axis to regulate and respond to environmental demands (Arnsten, 2009; Pruessner et al., 2010), and demonstrates disproportional plasticity and susceptibility to the effects of stress during the first years of life (Hensch, 2005). Research has used resting or baseline EEG power as a measure of cortical function to study the proximal effects of experience during infancy (Anderson & Perone, 2018). Indeed, EEG power in the frontal cortex has been shown to be a sensitive marker of environmental influence across infancy, which supports evidence of a region-specific sensitive period of increased plasticity (Marshall et al., 2002; Schaworonkow & Voytek, 2021; Voytek et al., 2015). As such, this brain region is a suitable candidate for studying the association between maternal stress and infant brain development.

1.3 | Environmental experience and infant EEG

The importance of studying stress during sensitive periods is evident when considering how acute cases of environmental stress predict differences in infant brain activity. For example, toddlers raised in impoverished environments, such as institutions, show an abundance of lower frequency (delta, theta) power and reductions in higher frequency (alpha, beta, gamma) power (Marshall et al., 2004), a pattern of EEG activity that has been linked to risk for subsequent psychopathology (Tottenham et al., 2010; Zeanah et al., 2009). More normative variations in caregiving behaviors have also been associated with differences in infant EEG power. For example, individual differences in caregiver sensitivity have been linked to right frontal alpha asymmetry (a neural index of emotion regulation; Hane & Fox, 2006; Hane et al., 2010) and functional connectivity (Perone & Gartstein, 2019) and are even longitudinally predictive of resting alpha and theta power during infancy (Bernier et al., 2016). Infants are sensitive to stress cues from their parents (Feldman, 2007), and chronically high levels of stress can impede a caregiver's ability to respond to their infant's cues in a sensitive and reliable manner (Crnic et al., 1983). As such, caregivers are the main source of stress exposure or stress regulation for infants (Callaghan et al., 2021; Sheridan et al., 2012; Tottenham, 2012).

Research has begun to investigate links between maternal psychosocial stress and differences in infant brain activity. Pierce et al. (2019) found that higher reported levels of perceived maternal stress were negatively associated with higher frequency EEG power (beta and gamma) at 2 months of age. Along with subjective measures of stress, studies have started to include measures of physiological stress, primarily indexed via cortisol, as a predictor of infant brain activity (St. John et al., 2017; Troller-Renfree et al., 2020). A study from St. John et al. (2017) examined longitudinal associations between maternal salivary cortisol and infant EEG power. A steeper maternal cortisol slope when infants were 6 months old predicted lower infant EEG alpha power at 12 months. However, cortisol measured through saliva represents acute, momentary experiences of stress and is prone to situational factors and arbitrary fluctuations (Egliston et al., 2007).

On the other hand, cortisol extracted from hair samples has been validated as a measure of cumulative flowing cortisol circulation over the 3 months prior to sample collection (Flom et al., 2017; Meyer et al., 2014). Hair cortisol reliably correlates with various environmental and physiological stress measures (Short et al., 2016; Ursache et al., 2017). As such, researchers have started to rely on hair cortisol to index physiological chronic stress. Research from Troller-Renfree et al. (2020) demonstrated associations in caregiver hair cortisol with infant EEG power, where higher concentrations of maternal hair cortisol were associated with greater relative theta power and lower relative alpha and gamma power for infants between 6 and 12 months of age. Collectively, the reviewed findings have demonstrated that maternal stress experiences tend to be related to an abundance of lower frequency EEG power and a dearth of higher frequency power.

1.4 | Characterizing EEG power

Much of the prior research examining experience-driven change in EEG during infancy has investigated power spectral density (PSD) measures in the traditional periodic frequency bands (Brito et al., 2016; Pierce et al., 2021; St. John et al., 2017; Troller-Renfree et al., 2020). Periodic EEG can be characterized with both relative and absolute metrics. While there are benefits of each approach, there are several reasons to favor relative EEG power measures in developmental studies. First, relative power has the advantage of offsetting issues related to artifacts introduced from skull thickness and individual differences in impedance. In addition, relative power is thought to be more sensitive to developmental change (Marshall et al., 2002). Relative EEG power captures relational shifts between higher and lower frequencies, a common measure of interest in neurodevelopmental research (Benninger et al., 1984). Studies measuring relative EEG power have demonstrated that lower frequencies tend to decrease across development, while higher frequencies are though to become more abundant (Cuevas & Bell, 2022; Marshall et al., 2002; Troller-Renfree et al., 2020).

EEG power is composed of periodic (oscillations) and aperiodic signals (Donoghue et al., 2020). Differences in mean oscillatory firing rates (captured by indexing frequency bands) are thought to support distinct neurocognitive processes (Haegens, Händel, et al., 2011; Haegens, Nácher, et al., 2011; Saby & Marshall, 2012). Despite the advantages of studying EEG power across development using fixed frequency bands, there are limitations to this approach. First, the definition of such frequency ranges is arbitrary and not consistent across developmental studies (Noreika et al., 2020). In addition, oscillatory bands demonstrate age-related shifts in frequency across development (Cellier et al., 2021; Chiang et al., 2011). For example, alpha peaks demonstrate age-dependent variation in peak frequencies, which is problematic for intraindividual, longitudinal analyses.

Examining aperiodic parameters of EEG power can address these issues. The EEG power spectrum follows a 1/f-like pattern, allowing for the extraction of an aperiodic exponent that reflects the exponential decrease of PSD. Extracting the PSD slope negates commonly encountered problems associated with shifts in alpha peaks across development (Donoghue et al., 2020). While the neural and physiological contributions of the PSD slope are still being studied, it is thought to reflect the integration of underlying synaptic activity and balance of inhibitory to excitatory synaptic currents (Gao et al., 2017; Voytek et al., 2015). A flatter PSD slope represents more excitatory currents over inhibitory ones and has been linked with information processing and other aspects of cognitive control (Barry et al., 2009; Voytek & Knight et al., 2015). Similarly, developmental studies have found that the PSD slope shows a marked decrease across childhood; however, this has yet to be replicated in infants (Hill et al., 2022; Schaworonkow & Voytek, 2021). Finally, the PSD slope shows defined individual differences (Demuru & Fraschini, 2020) and is predictive of multiple behavioral and cognitive outcomes (Ostlund et al., 2022). Nonetheless, research has yet to examine how experience predicts individual differences in PSD slope in infancy.

1.5 | Current study

To better understand patterns of context-dependent individual-level change in neurodevelopment, the current study investigates whether repeated measures of maternal hair cortisol predict aperiodic and periodic parameters of infant brain function at 3, 9, and 15 months. Given that we were interested in developmental and stress-related shifts between higher and lower frequencies, we calculated PSD slope and relative EEG power as measures of aperiodic and periodic fit, respectively. Using longitudinal data, we can disaggregate *between-* from *within*-person relations of maternal cortisol and infant neural function. Investigating these research questions using longitudinal data is critical for understanding both population-level trends between maternal stress and infant neural power and dynamic responses in infant EEG power to changes in maternal stress levels. Specifically, the between-person analysis is expected to address the question: what is the effect of higher average cortisol levels (relative to the sample) on average EEG power, across infancy? On the other hand, the within-person analysis aims to address the question: when moms are experiencing higher than their own average level of cortisol, what is the resulting effect on their infant's EEG power? To expand our understanding of stress-related individual differences in infant PFC function, we (1) use maternal hair cortisol as an index of chronic maternal physiologic stress, (2) compare both aperiodic and periodic parameters of frontal EEG power outcomes, and (3) disaggregate within- from between-person longitudinal change and associations. We hypothesize that infant PSD slope and lower relative EEG frequencies will decrease across infancy, while higher relative frequencies will increase. Similarly, we hypothesize that maternal hair cortisol levels will be negatively associated with each respective EEG measure. Given the prior literature linking infant alpha asymmetry with stress and emotion regulation outcomes (Hane & Fox, 2006; Hane et al., 2010), we include exploratory models investigating relations between maternal cortisol and infant alpha asymmetry in the Supporting Information S1.

TABLE 1 Sociodemographics.

	Mean (*SD*; range) or *N* (%)
Infant age at visit 1 (years)	3.46 (0.37)
Gestational age (weeks)	39.23 (1.21)
Income-to-needs at visit 1	5.45 (5.14)
Maternal education (years)	15.98 (4.01)
Infant sex (male)	43 (53%)
Ethnicity	
Hispanic/Latino	48 (55%)
Not Hispanic/Latino	36 (41%)
Unreported	3 (3%)
Race	
White	30 (31%)
Black/African-American	10 (15%)
Asian	8 (9%)
Two or More/Other	35 (37%)
Unreported	4 (8%)

2 | METHODS

2.1 | Participants

The current sample included 87 infants (43 males) who were recruited from community events, family services, healthcare providers, and flyers posted at local businesses around New York City, NY, USA. Participants were excluded from participating in the present study on the basis of birth before 36 weeks' gestation, multiple births, or presence of developmental disorders. Families were invited to participate in the study when infants were 3 months of age. Participant demographics are reported in Table 1. The present study was conducted according to guidelines laid down in the Declaration of Helsinki, with written informed consent obtained from a parent or guardian for each child

before any assessment or data collection. All research procedures were approved by the New York University IRB.

2.2 | Protocol

Infants and their caregivers visited the lab at 3 (M_{age} = 3.46, SD = 0.37), 9 (M_{age} = 9.57, SD = 0.63), and 15 months (M_{age} = 15.29, SD = 0.45). At each time point, infant EEG, maternal hair cortisol, and responses to sociodemographic questionnaires were collected. Eighty-seven infants visited the labs at 3 months and 68 of those infants provided usable EEG at the 3-month time point, 37 provided usable EEG at the 9-month time point, and 25 provided usable EEG at the 15-month time point. Attrition in the study sample is primarily attributed to the onset of the COVID-19 pandemic. Testing for the current study began in March 2018 and was halted in March 2020. To assess for attrition-related bias, we ran multiple *t*-tests to assess for differences in caregiver income-to-needs ratio (ITN) and cortisol levels between each time point; *t*-tests did not reveal any significant differences in caregiver ITN or cortisol between the infants that provided usable EEG at the 9 and 15-month time points and those that did not.

2.2.1 | Family and household characteristics

Families were given questionnaires to obtain demographic information including maternal and infant age, race, and ethnicity. Caregivers also reported on their highest level of education attained and annual household income. Family ITN is the total household income divided by the federal poverty line for the corresponding number of adults and children in the home and used as the measure of socioeconomic status within the analyses.

2.2.2 | Chronic caregiver cortisol

A small hair sample was collected from caregivers, with each sample weighing at least 15 mg. Each hair sample was trimmed to be approximately 3 cm long (measured from the end closest to the root). As human hair grows approximately 1 cm per month, each sample contains cortisol deposited during roughly the first 3 months postpartum. The samples were stored at −40°C until sent for analysis. Each sample was weighed, washed twice in isopropanol to remove external contaminants, ground to a fine powder, and extracted with methanol. The methanol extract was evaporated, re-dissolved in an assay buffer, and analyzed along with standards and quality controls by a sensitive and specific enzyme-linked immunosorbent assay. Assay readout was converted to picogram cortisol per milligram dry hair weight. Intra- and interassay coefficients of variation for this assay are <10%. Three samples were calculated to have no cortisol levels detected and were excluded from further analysis. Hair cortisol values were log10-transformed to correct for skew.

2.2.3 | EEG data acquisition and processing

At each time point, resting EEG data were acquired while infants watched a video of engaging, nonsocial stimuli (e.g., bubbles, spinning wheel) while seated on their caregivers' laps. The recording room was dimly lit and an experimenter was nearby to soothe the infant with bubbles or a toy if the infant became too fussy. Infants provided between 40 and 550 s of resting data. EEG was recorded using a 64-channel HydroCel Geodesic Sensory Net (Electrical Geodesic, Inc., Eugene, OR) and amplifier (Electrical Geodesic, Inc., Eugene, OR; EB NEURO S.p.A., Firenze, Italy). Electrode impedances were kept below 100 KΩ and the sampling rate was recorded at 1000 Hz.

All EEG files were processed in batch using an EEG automated processing platform (BEAPP) software to ensure standardization in data processing and cleaning across all files (Levin et al., 2018). Continuous resting EEG files were converted from NetStation format to Matlab format. Data preprocessing was carried out using the Harvard Automated Processing Pipeline for EEG (HAPPE V.1), an automated preprocessing pipeline designed for infant EEG data (Gabard-Durnam et al., 2018). First, a 1-Hz high-pass and 100-Hz low-pass filter was applied to each EEG recording. Second, the data, which were originally sampled at 1000 Hz, were resampled with interpolation to 250 Hz, following guidelines for further HAPPE processing. The third step involved artifact removal and included CleanLine's multitaper approach to removing 60 Hz electrical noise, bad channel rejection, and wavelet-enhanced independent component analysis (ICA) for artifact rejection with automated component rejection through the Multiple Artifact Rejection Algorithm (Winkler et al., 2014) in EEGLAB. A subset of spatially distributed electrodes was selected for analysis with MARA: 2, 3, 5, 6, 8, 9, 10, 11, 12, 13, 14, 18, 20, 24, 25, 28, 30, 31, 34, 35, 39, 40, 42, 44, 48, 50, 52, 57, 58, 59, and 60 (NetStation Geodesic 64- Channel Net). Bad channels that were initially rejected were repopulated using spherical interpolation to reduce bias in re-referencing and the signal was mean detrended. Finally, each EEG file was segmented into 2-s windows and each segment was assessed for remaining artifacts. Segment rejection thresholds were determined according to HAPPE's automated rejection criteria (Gabard-Durnam et al., 2018), which uses amplitude thresholding and assessment of segment likelihood using joint probability calculations.

EEG power decomposition was accomplished using fast Fourier transformation using a multitaper windowing (three windows) to decompose power into 2-s segments for each channel. PSD slope and relative power were then calculated for channels in the frontal region (electrode #: 2, 3, 5, 9, 10, 11, 12, 13, 14, 18, 57, 58, 59, and 60; see Figure 1a). PSD slope was calculated using the *fooof* package within eeglab (Donoghue et al., 2022). PSD slope was computed within the 1–20 Hz frequency range at each frontal cortex channel by fitting the log–log least-square line after removing peaks associated with rhythmic oscillatory components (see Figure 1b). PSD slope was then averaged across channels in the right frontal and left frontal hemisphere. Individuals with PSD slope model fit less than R^2 = .95 were excluded from further analyses. The average model fit for PSD slope

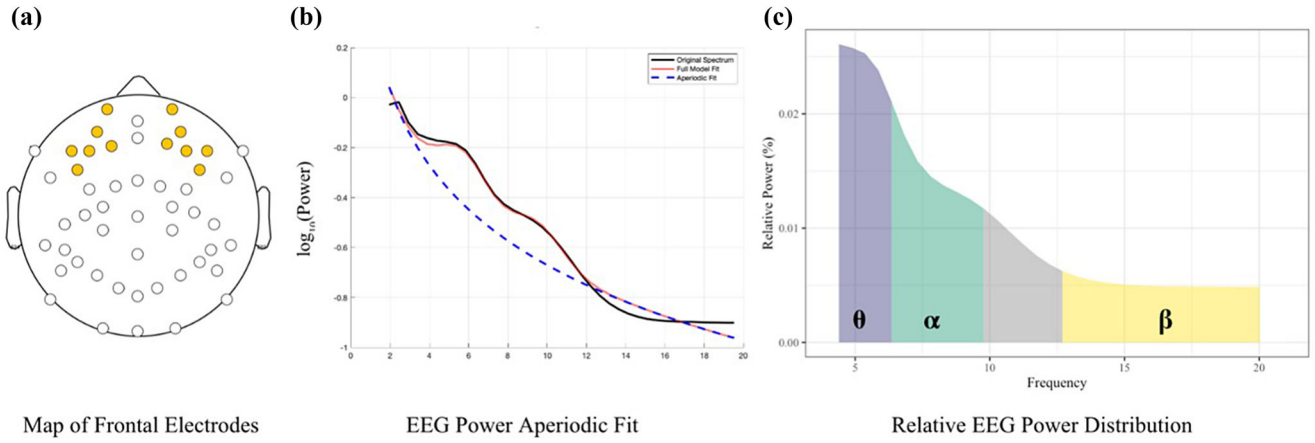

FIGURE 1 Conceptual schematic illustrating how longitudinal EEG parameters were collected and analyzed. Panels (b) and (c) represent EEG parameters averaged across infants at 3 months of age. (a) Map of frontal electrodes included in subsequent analysis; (b) aperiodic spectral component between 1 and 20 Hz was calculated; (c) periodic relative power in each discrete frequency band was calculated.

$R^2 = .99$ (±.2 *SD*), indicating that the model fit the aperiodic data well. To assess relative power in discrete frequency bands, spectral power was computed for theta (4–6 Hz), alpha (6–9 Hz), and beta (13–20 Hz). At each channel, summed power within each frequency band was averaged across all segments and divided by the total power spectrum (2–50 Hz; see Figure 1c). Relative power was then averaged across channels in the frontal cortex. As an exploratory aim of the study, we also calculated frontal alpha asymmetry scores by subtracting log-transformed right frontal hemisphere power values from left frontal hemisphere power values (see Supporting Information S1; Brooker et al., 2017; Hane & Fox, 2006).

The amount of usable data provided by infants at each time point varied. At the 3-month time point, eight infants did not complete the EEG task due to fussiness or declined to be scanned and 11 EEG files were rejected during processing due to quality. At the 9-month time point, 10 infants did not complete the EEG task due to fussiness or declined to be scanned and four EEG files were rejected during processing due to quality. At the 15-month time point, eight infants did not complete the EEG task due to fussiness or declined to be scanned and one EEG file was rejected during processing due to quality.

2.3 | Analysis plan

We constructed multiple two-level mixed models with random intercepts. Time-varying level 1 predictors were group-mean (i.e., within-person) centered and time-invariant level 2 predictors were grand-mean (i.e., between-person) centered. At level 1, we modeled PSD slope and each discrete relative frequency band as the dependent variable and included group-mean-centered maternal hair cortisol and age centered at 0 as the time-varying within-person independent predictors. At level 2, we included grand-mean-centered maternal hair cortisol and grand-mean-centered ITN as time-invariant between-person independent variables. Level 1 analysis describes the within-person changes in EEG power and level 2 describes the between-person differences in EEG power. We also tested several other covariates that might influence EEG power including race, maternal education, and gestational age. None of these variables had significant effects on any EEG power measures and were not included in subsequent models. Caregiver cortisol is included in both level 1 and level 2 analyses to disaggregate within- from between-person contributions. Participants were included in the analytic sample if the caregiver provided a usable cortisol sample and the infant had usable EEG data from at least one visit. Models were fitted using the "lme4" package in R.

3 | RESULTS

3.1 | Aperiodic EEG power (PSD slope)

First, on the within-person level, there was a significant negative effect of age indicating that infant frontal PSD slope decreases (or flattens) from 3 to 15 months (see Figure 1a). There was also a significant negative within-person association between maternal cortisol and frontal PSD slope such that relative increases in a mother's cortisol level (above their average) were associated with flattening of frontal PSD slope. On the between-person level, there was a significant positive association between caregiver cortisol and frontal PSD that suggests that average caregiver cortisol levels from 3 to 15 months were associated with steeper frontal PSD slopes, on average (see Table 2).

3.2 | Periodic EEG power (relative frequency band analysis)

There was a significant age effect on relative frontal alpha and beta power, suggesting an increase in relative power across infancy (see Figure 2b). There was also a small association between age and relative frontal theta power, suggesting a decrease in power across infancy, but this was not statistically significant. On the within-person level,

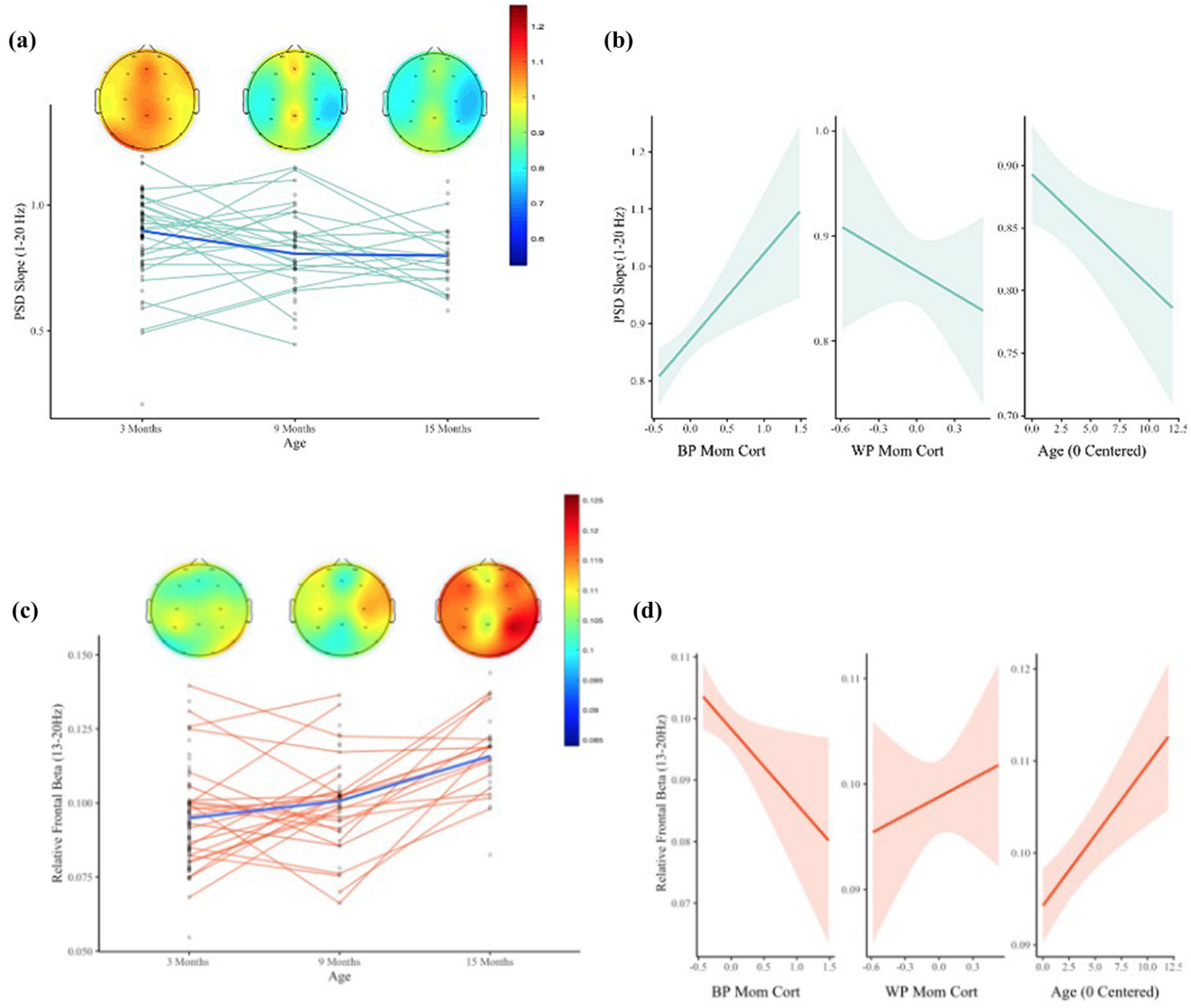

FIGURE 2 (a) Multilevel model plots of frontal PSD slope. (A) Growth trajectories from 3 to 15 months. (B) Plotted slopes from the multilevel model. (b) Multilevel model plots of relative frontal beta. (A) Growth trajectories from 3 to 15 months. (B) Plotted slopes from the multilevel model. BP, Between-person; WP, Within-person.

TABLE 2 PSD slope (1–20 Hz).

	PSD slope (1–20 Hz)		
Predictors	***B***	***β***	***SE***
Intercept	0.86***		0.035
Age	−0.01*	−0.210	0.003
Income-to-needs	0.000	0.010	0.003
Within-person maternal cortisol	0.140*	−0.180	0.059
Between-person maternal cortisol	0.145**	0.300	0.049

Note: B = unstandardized coefficient; β = standardized coefficient.
^≤.10; *≤.05; **≤.01; ***≤.001.

maternal cortisol was significantly associated with higher relative frontal beta power. In other words, increases in maternal cortisol levels (above their average) predicted decreases in relative frontal beta power. On the between-person level, there was a significant positive association on relative frontal theta power and a negative association between maternal cortisol and relative frontal beta power. This suggests that higher average maternal cortisol from 3–15 months was associated with higher relative frontal theta power and lower frontal beta power, on average (see Table 3).

4 | DISCUSSION

4.1 | Overall findings

The current study investigated longitudinal relations between maternal hair cortisol and traditional periodic spectral power (relative

TABLE 3 Relative frequency band power.

	Relative frontal theta (4–6 Hz)			Relative frontal alpha (6–9 Hz)			Relative frontal Beta (13–20 Hz)		
Predictors	***B***	***β***	***SE***	***B***	***β***	***SE***	***B***	***β***	***SE***
(Intercept)	0.141***		0.004	0.003***		0.003	0.094***		0.002
Age	−0.001^	−0.160	0.001	0.003***	0.500	0.001	0.002***	0.483	0.000
Income-to-needs	0.001	0.140	0.000	−0.000	−0.010	0.000	−0.000	−0.093	0.000
Within-person maternal cortisol	−0.120	−0.110	0.009	−0.03	−0.060	−0.006	0.015*	0.225	0.007
Between-person maternal cortisol	0.014*	0.220	0.007	0.012	0.160	0.006	−0.011*	−0.411	0.005

^≤.10; *≤.05; **≤.01; ***≤.001.

power) in tandem with aperiodic power (PSD slope) in the frontal cortex at age 3, 9, and 15 months. Using EEG and maternal hair cortisol data collected longitudinally across infancy, we found significant associations between caregiver hair cortisol and infant EEG on both the between- and within person-level. On the within-person level, increased maternal cortisol (relative to an individual's average) predicted flattening of frontal PSD slope and decreases in relative frontal beta power. On the between-person level, higher maternal cortisol (relative to the population) was associated with a steeper PSD slope, increased relative frontal theta power, and decreased relative frontal beta power, on average. To the best of our knowledge, this is the first study to investigate associations between caregiver chronic physiological stress and multiple parameters of neural activity across infancy. The findings presented here align with existing research demonstrating infant neural associations with caregiver perceived stress (Pierce et al., 2019), salivary cortisol (St. John et al., 2017), and more recently hair cortisol (Troller-Renfree et al., 2020), but extend this research in multiple ways.

4.2 | Multilevel contributions of maternal cortisol

On the within-person level, maternal hair cortisol was negatively associated with frontal PSD slope and positively associated with relative frontal beta power. In other words, intraindividual increases in caregiver cortisol, above their typical average, were associated with a "flattening" of frontal PSD slope and an associated increase in relative frontal beta power. Flatter PSD slopes and relative frontal beta have been linked with increases in information processing and other aspects of rudimentary cognitive control (Barry et al., 2009; Voytek & Knight et al., 2015). We speculate that these findings may reflect a process of neural adaptation to experiences of increased or decreased relative threat levels, consistent with prior behavioral research showing cognitive enhancements after stress exposures (Ellis et al., 2022; Fields et al., 2021; Frankenhuis & de Weerth, 2013; Nweze et al., 2021). Our study offers a potential neural mechanism supporting past observed behavioral findings and theoretical principles of adaptive responses to stress.

On the between-person level, higher average levels of maternal hair cortisol from 3 to 15 months were associated with steeper frontal PSD slopes, higher relative frontal theta power, and lower relative frontal beta power on average. Troller-Renfree et al. (2020) similarly demonstrated that maternal hair cortisol predicts increased low-frequency power and decreased high-frequency power on the between-person level using cross-sectional data, and past studies have linked this EEG power profile to decreased top-down control (Voytek & Knight et al., 2015; Stroganova et al., 1998), hypoarousal (Barry et al., 2009), and differentiated maturational profiles of cortical function (Coming et al., 1982). The between-person analysis creates a baseline for "chronically high" cortisol levels, given that individual between-person values are relative to the population average. Thus, the between-person findings may reflect how the infant brain develops in response to chronically high levels of maternal stress, whereas the within-person findings reflect how the infant brain responds to intermittent, normative shifts in caregiver cortisol levels. Disaggregating within- from between-person levels has important implications for understanding context-dependent adaptation while highlighting the potentially detrimental effects of chronically elevated maternal stress.

Despite prior research documenting relations between socioeconomic levels and infant neurodevelopment (Hanson et al., 2013; Tomalski et al., 2013), we did not see any significant associations of family ITN level on infant EEG power. We attribute this null association to several important factors worth considering. First, our sample's average ITN was moderately high and displayed a wide degree of heterogeneity. It is possible that if our sample was lower income, the results may have been different (Noble et al., 2015). Aside from more extreme cases of economic inequalities, ITN levels are a relatively global measure of the family environment. While a family's relative income level inevitably has downstream consequences, there is wide variability in family dynamics and experiences based on income backgrounds (Chan et al., 2018; Luby et al., 2013). Comparatively, caregiver stress is a specific experience that may have more direct effects on an infants' developmental process. This interpretation is speculative, however, and would require further experimental studies to tease apart stress from economic capital.

4.3 | Aperiodic and periodic EEG power estimates

Consistent with prior studies, our findings demonstrated that across infant development, EEG power estimates demonstrate a "flattening" of PSD slope and decreased relative lower frequencies and increased

relative higher frequencies (Cellier et al., 2021; Clarke et al., 2001; Donoghue et al., 2020; Marshall et al., 2002). In addition, the frontal PSD slope, an index of the global aperiodic components of the power spectrum, was predicted by maternal physiological stress on multiple levels. While the specific neuronal mechanisms contributing to aperiodic activity measured via PSD slope are still being investigated, PSD slope has been experimentally linked to the dynamic balance between inhibitory and excitatory neuronal currents (Gao et al., 2017). Thus, it is possible that extracting the PSD slope provides a useful measure of dynamic infant brain activity across development. Indeed, it has been hypothesized that aperiodic features of the power spectrum maximize individual variability, possibly due to removing the constraints of discrete frequency bands. Given that aperiodic components may be more sensitive to demonstrating differentiated patterns of activity, extracting PSD slopes is particularly valuable for characterizing experience-dependent neurodevelopment (Demurua & Fraschini, 2020; Donoghue et al., 2020).

In comparison to aperiodic EEG power, maternal physiological stress predicted differences in periodic relative frontal theta and relative frontal beta, but not relative frontal alpha. This could possibly be explained by prior studies demonstrating that canonical alpha band analyses may fail to capture the true oscillatory power within the defined frequency band (Donoghue et al., 2020). Further, periodic alpha band oscillations are subject to age-related biases due to the fact that older infants have higher alpha frequencies than younger infants (Chiang et al., 2011; Donoghue et al., 2020; Stronganova et al., 1998). Despite the merits of extracting aperiodic PSD slopes, the relative power findings may still be important for understanding and comparing how specific oscillations reflect the infant brain's response to stress experiences. Distinct frequency bands may be driven by unique synaptic mechanisms to support domain-specific cognitive functions (Buschman & Miller, 2007; Cardin et al., 2009; Iemi et al., 2017). Both periodic and aperiodic measures can offer valuable information into the way the brain is developing and organizing based upon environmental experiences. Overall, these findings demonstrate that changes in infant's early stress-related experiences may organize their functional neural connectivity in the frontal cortex.

4.4 | Limitations

While this study offers a number of contributions to the field, there are several limitations that need to be addressed. First, although our sample reflected sociodemographic diversity, the sample size is relatively small, particularly at subsequent time points from attrition due to COVID-19 study interruption issues. Thus, research replicating this work using a larger sample size is necessary. Despite the merits of disaggregating within- from between-person methods, causal interpretations are still only speculative as this study is observational. Future research aimed at reducing caregiver stress experimentally would help overcome this limitation. Finally, additionally work is needed to connect brain measures back to behavior. The inclusion of a behavioral outcome in early childhood to understand how stress-based differences in infant brain development are associated with subsequent differential outcomes in learning and self-regulation is needed.

5 | CONCLUSIONS

This study provides a novel contribution to the literature by tying caregiver *physiological stress* to *longitudinal* infant *neural function*. The within-person results highlight the plasticity of infant PFC, while the between-person results emphasize the population-level importance of reducing caregiver experiences of chronic stress. These findings illustrate the complex impact caregiver stress has on infant brain function and development. It is critical that we continue studying caregiver stress given that it is an important predictor of infant development *and* a malleable process, amenable to intervention and prevention efforts.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, ABA, upon reasonable request.

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