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Longitudinal Associations between the Quality of Mother-Infant Interactions and Brain Development across Infancy

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Abstract

The aim of this study was to investigate if normative variations in parenting relate to brain development among typically-developing children. A sample of 352 mother-infant dyads came to the lab when infants were 5, 10, and 24 months of age (final $N = 215$). At each visit, child resting EEG was recorded. Mother-infant interactions were videotaped at the 5-month visit. The results indicated that higher-quality maternal behavior during mother-infant interactions predicted higher frontal resting EEG power at 10 and 24 months, as well as increases in power between 5 and 10 months, and between 10 and 24 months. These findings provide rare support for the hypothesis that normative variation in parenting quality may contribute to brain development among typically-developing infants.

Inspired by Greenough, Black, and Wallace's (1987) influential propositions pertaining to the experience-dependent nature of brain development, many scientists have been intrigued by the possibility that early relational experiences could influence children's brain development. These ideas have gained in popularity with the advent of modern brain imaging techniques that have enabled scientists to appreciate the remarkable plasticity of the developing brain, especially during the first years of life, which are characterized by over-production of synapses followed by a period of gradual pruning (Huttenlocher, 2002). During this period, experience is considered to determine to a large degree which synaptic connections persist and are strengthened by frequent use, and which are selectively eliminated as a result of inactivity (Singer, 1995). In this context, there is a substantial window of time for environmental input to influence the developing brain (Kolb et al., 2012). Such observations have led many to suggest that early caregiving relationships should be centrally implicated in children's brain development (e.g., Belsky & de Haan, 2011; Cicchetti, 2002; Gunnar, Fisher, & the Early Experience Stress and Prevention Science Network, 2006; Nelson, 2000). Empirical evidence supporting these claims is, however, still remarkably scarce. Tackling this gap, this longitudinal study investigated the prospective links between the quality of maternal behavior during early mother-infant interactions and infant brain development.

As one of the earliest, most intense, and most enduring experiences of childhood, the parent-child caregiving relationship appears to be a prime candidate to account for environmentally-driven individual differences in children's brain development. Decades of empirical research have provided overwhelming support for the classic notion that early parent-child relationships exert an exceptional influence on child development. As documented by longitudinal studies spanning infancy to early adulthood (Frale, Roisman, & Haltigan, 2013; Grossmann, Grossmann, & Waters, 2005; Jaffee, Caspi, Moffitt, Belsky, & Silva, 2001), by meta-analytic reviews (Fearon, Bakermans-Kranenburg, Van IJzendoorn, Lapsley, & Roisman, 2010; Groh, Roisman, Van Ijzendoorn, Bakermans-Kranenburg, & Fearon, 2012; Pallini, Baiocco, Schneider, Madigan, & Atkinson, 2014), and by experimental studies (Guttentag et al., 2014; Kochanska, Kim, Boldt, & Nordling, 2013), the quality of caregiving relationships forecasts child outcomes as diverse as social and emotional adjustment (see Thompson, 2008), moral development (Dunn, Brown, & Maguire, 1995), cognitive functioning (Tamis-LeMonda, Bornstein, & Baumwell, 2001), sleep/wake cycles (Bordeleau, Bernier, & Carrier, 2012), and sympathetic and parasympathetic response (Luijk et al., 2010). Such pervasive effects on socio-emotional, cognitive and biological functioning are often believed to transit through children's neural circuitry (Belsky & de Haan, 2011; Gunnar, 2003).

In this context, the dearth of studies directly examining the prospective links between early caregiving experiences and children's brain development is striking. Nearly all knowledge on this crucial topic is based on the study of grossly inadequate environments, characterized by neglect, abuse (Curtis & Cicchetti, 2007; De Bellis, 2001, 2005; Teicher, Tomoda, & Andersen, 2006), or extreme relational deprivation in orphanages (Chugani et al., 2001; Marshall & Fox, 2004; Rutter & O'Connor, 2004). These studies show the profound impact that severely unfavorable conditions can have on normal brain development, from both anatomical and functional standpoints. Hence, brain growth appears to be very susceptible to extreme adversity.

It is expected that the converse be true as well, such that favorable environmental experiences should have a positive impact on healthy brain development (e.g., Nelson & Bloom, 1997). Attempts at "enrichment" activities for children in deprived environments provide some support for this view. Children in Mauritius receiving an enriched preschool intervention and institutionalized children in Bucharest placed into foster care appear to exhibit some changes in brain electrical activity indicative of brain maturation, relative to care-as-usual groups of children (Marshall, Reeb, Fox, Nelson, & Zeanah, 2008; Raine et al., 2001). It is also expected that typical positive social influences, especially those embedded within early caregiving relationships, should foster optimal brain development (e.g., Schore, 2001). Surprisingly however, there is almost no empirical work to date to support such claims in the context of non-extreme or pathological parenting. The time appears to be ripe to investigate whether normative variations in parenting affect brain development among typically-developing children.

Animal research suggests that this may be the case: enriched maternal nurturance promotes increased dendritic branching, enhanced neurogenesis, and greater dendritic spine density in a number of brain areas (for reviews see Belsky & de Haan, 2011; Markham & Greenough,

2004; Meaney, 2001). Reviewing such studies on maternal care in animal populations, Francis and Meaney (1999) concluded that variation within the normative range of human maternal care, much less dramatic than abuse or neglect, could have a profound influence on normal brain development. Over fifteen years later, the dearth of research properly investigating these questions with human populations is remarkable. Studies to date have almost exclusively used distal proxies rather than direct measures of actual parenting, and/or cross-sectional designs with concurrent or retrospective measures.

Studies using distal indicators such as family socio-economic status (e.g., Jednoróg et al., 2012; Noble, Houston, Kan, & Sowell, 2012), stressful life events in the family (Luby et al., 2013), or maternal depression (Ashman, Dawson, & Panagiotides, 2008; Diego, Jones, & Field, 2010; Lupien et al., 2011) converge to suggest that such indices of familial risk predict non-optimal brain development in children, whether considering structure or function. Importantly, the authors of these studies argue that such distal factors have the power to impact children's brain development because they are likely to influence the quality of parent-child interactions, which in turn is presumed to be the key factor influencing children's brain development. The current study addresses this key factor directly among typically-developing children.

Recently there have been several reports of associations between maternal behaviors during infancy and later childhood performance on executive function tasks (e.g., Bernier, Carlson, Deschênes, & Matte-Gagné, 2012; Cuevas et al., 2014; Kraybill & Bell, 2013). Given that executive function is inextricably linked to the prefrontal cortex (Stuss, 2011), these findings provide further indirect evidence for a potential link between early parenting and subsequent brain development, perhaps especially in the frontal areas. In light also of evidence that early experiences affect prefrontal circuitry (Kolb et al., 2012), this study focuses on frontal brain regions.

Other studies have used adults' retrospective accounts of their childhood experiences. Some of these studies found that perceived maternal care in childhood was related to structural brain measures in adulthood (Buss et al., 2007; Kim et al., 2010), whereas others found no links (Narita et al., 2012). Of note, however, is that these studies were cross-sectional, thus leaving open the possibility that the observed brain markers were in fact responsible for adults' recollections of their childhood. This is of special concern in light of the fact that retrospective accounts of childhood experiences are notoriously inaccurate (Henry, Moffitt, Caspi, Langley, & Silva, 1994; Roisman, Haltigan, Haydon, & Booth-LaForce, 2014).

Other, mostly cross-sectional studies have used electroencephalography (EEG) to assess regional brain activity among infants, along with measures of parent-infant relationships. These studies focused on resting frontal EEG asymmetry, a well-documented marker of emotional and motivational tendencies (Davidson, 2000), with right frontal asymmetry typically associated with stress. Dawson, Klinger, Panagiotides, Spieker, and Frey (1992) found no direct link between frontal asymmetry and concurrent mother-infant attachment security, as assessed with the Strange Situation Procedure (SSP) when infants were between 11 and 17 months of age. In contrast, Dawson and colleagues (2001) observed that infants aged 13–15 months who were insecurely attached to their mothers were more likely to

exhibit right frontal EEG asymmetry recorded during a resting baseline condition prior to the SSP assessment. Jones, McFall, and Diego (2004) found that infants of depressed mothers who had been breastfed until their third month of life were less likely than their bottle-fed counterparts to show the right frontal EEG asymmetry usually associated with maternal depression. Diego, Field, Jones, and Hernandez-Reif (2006) further reported that infants of depressed mothers exhibiting a withdrawn interactive style at 6 months showed greater right frontal asymmetry in EEG recordings at 3 to 6 months of age than those of depressed mothers characterized by an intrusive style. Hane and Fox (2006) assessed mother-infant home interactions when infants were aged 9 months, and found relations to infants' concurrent resting frontal EEG asymmetry when considering extreme groups of maternal behavior (± 1 standard deviation above or below the mean): infants exposed to very low-quality maternal behavior were more likely to show right frontal asymmetry. In a subsequent study with the same sample, Hane, Henderson, Reeb-Sutherland, and Fox (2010) found no significant association between the quality of 9-month maternal behavior and subsequent resting frontal asymmetry at 3 years of age, when considering the whole distribution of maternal behavior scores (an analysis not reported in Hane & Fox, 2006); however, they did find relations between 3-year frontal EEG asymmetry and the extremes of maternal behavior, similar to that found when infants were aged 9 months. It is unknown, however, whether the 3-year results held above the previously documented associations at 9 months.

Despite some inconsistency in results, the findings of these studies are noteworthy in that they provide rare evidence that the quality of parent-child relationships, as measured directly and objectively, may in some circumstances relate to an important aspect of infants' brain functioning: infant right frontal asymmetry reflects a disposition toward anxiety and generally negative emotionality (Davidson, 2000). They may be, however, less telling with respect to brain development per se, given their cross-sectional designs or lack of statistical control for prior EEG data, and in that frontal asymmetry is considered to be a trait-like disposition, presumed to reflect stable individual differences in affective style. On the other hand, EEG power has a long tradition as a measure of brain development (see Bell, 1998; Bell & Fox, 1994, for reviews). The EEG signal reflects post-synaptic activity and EEG power (level of mean square microvolts of the EEG signal resulting from Fourier analysis) reflects the excitability of groups of neurons (Bell & Cuevas, 2012). With respect to brain development during infancy, more neural activity translates into higher EEG power. Frontal EEG power has clear functional implications, in that it consistently relates to infant cognitive performance, for instance working memory and inhibitory control (e.g., Bell, 2001; Cuevas, Bell, Marcovitch & Calkins, 2012). Importantly for our purposes, frontal resting EEG power is also considered indicative of brain *development*, given that it increases almost linearly with age across infancy (Bell & Fox, 1992; Cuevas & Bell, 2011). Accordingly, an age-related increase in resting frontal EEG power may be a strong indicator of brain development during infancy, and thus constitutes a particularly relevant outcome to consider when assessing parenting influences on infants' brain development. To our knowledge, however, research has never examined relations between parenting and infant EEG power, whether in cross-sectional or longitudinal designs. Addressing this gap was the primary aim of the current study.

The current study

This longitudinal study used an observational measure of the quality of maternal behavior during mother-infant interactions when infants were aged 5 months, along with concurrent and subsequent EEG recordings at 10 and 24 months, to investigate whether the quality of maternal parenting behavior relates to infant brain development, as indicated by frontal resting EEG power as well as age-related increases in frontal resting power. It was expected that infants whose mothers showed higher-quality behavior while interacting with them at 5 months would show higher frontal EEG power at 10 and 24 months, as well as more pronounced increases in power between 5 and 10 months, and between 10 and 24 months.

Method

Participants

Participants were part of an ongoing longitudinal study examining individual differences in cognitive and emotion processes across early development. Data were collected from 352 mother-infant dyads (185 girls) recruited by two research locations (Blacksburg, VA; Greensboro, NC), with each location recruiting half of the total sample. Dyads first came to the research labs when infants were 5 months of age ($M = 162$ days, $SD = 8$ days). All infants were born after at least 36 weeks of pregnancy, had a normal birth weight (> 5.5 pounds), and none suffered from a known developmental disorder diagnosed in early childhood. Of the 352 infants, 272 were Caucasian, 48 African American, 15 multiracial, 2 Asian, 13 were other, and two did not report; with respect to ethnicity, 22 were Hispanic and one did not report. Mothers and fathers were 29 and 32 years old on average ($SD = 6$ and 7 years) when infants were born. Sixty-five percent of mothers and 56% of fathers had a college education or higher. Infants were recruited via commercial mailing lists, newspaper birth announcements, and word of mouth. This sample was drawn from a larger pool of 410 dyads who participated in the lab visit at 5 months. Given the goals of the current study, we excluded participants who had unusable EEG data or unusable/unavailable mother-infant interactions.

Of the 352 dyads, 304 (86.4%; 155 girls) returned for a second laboratory visit when infants were aged 10 months ($M = 314$ days, $SD = 11$ days). Finally, 215 of the original dyads (61.2%; 116 girls) returned for a third lab visit when children reached 24 months of age ($M = 25$ months, $SD = 20$ days). Eighteen of these 215 dyads had not taken part in the 10-month visit; therefore, complete data at all three time points are available for 197 dyads (105 girls). Attrition was mainly due to families moving out of the local regions. Mothers were paid \$50 for each visit and children received a small toy.

Attrition analyses revealed that the 197 families with complete data differed from the 155 families for whom data were missing at the 10-month visit, 24-month visit, or both, on mother's age at infant birth. Mothers who completed all visits were older ($M = 30.16$) at their infant's birth than mothers who failed to complete one or both follow-up visits ($M = 28.45$; $t(350) = 2.93$, $p = .004$). These groups did not differ on child sex ($p = .73$), maternal education ($p = .13$), or any of the four dimensions of maternal parenting behaviors assessed at 5 months (described below; p 's between .68 and .77).

Data were collected in both research locations using identical protocols. Research teams were trained together by the 3rd author on protocol administration, as well as on behavioral and psychophysiological coding. To ensure that identical protocol administration was maintained between the labs, the Blacksburg site team periodically viewed video recordings and EEG files collected by the Greensboro lab and provided verification of artifact screening for EEG data collected and coded by the Greensboro lab. The Blacksburg team coded all behavioral data collected by both labs.

Procedures

Upon arrival at the research labs for the 5-month visit, mother and infant were greeted by a research assistant who explained the study procedures and obtained signed consent. After a brief warm-up period, the infant sat on mother's lap and was distracted with toys while research assistants placed the EEG cap on the infant's head. Resting EEG was recorded for 1 minute while the infant sat and watched an experimenter manipulate a toy with colorful bouncing balls on top of a table and did not interact with the infant. This procedure quieted the infant and yielded minimal eye movements and gross motor movements for the EEG recording (Bell, 2001, 2012; Cuevas et al., 2012), which was digitally recorded for later coding purposes. After the EEG recording, the infant was placed in an infant seat. Mothers were instructed to interact with their infants as they normally would at home with two simple infant toys (keys, rattle) for 2 minutes; maternal behaviors were later coded from this videotaped interaction. When the dyads returned at 10 months, resting EEG was again recorded for 1 minute while the infants watched the experimenter manipulate the toy with colorful bouncing balls. When the dyads returned at 24 months, resting EEG was recorded for 1 minute while the toddlers sat in a high chair and watched *Finding Nemo* (sea turtles riding the East Australian Current).

EEG Recordings at 5, 10, and 24 Months

Based on publication guidelines for studies using EEG methodology (Keil et al., 2014), we report the following details for the EEG recordings obtained at 5, 10, and 24 months. EEG recordings were made from 16 left and right scalp sites [frontal pole (Fp1, Fp2), medial frontal (F3, F4), lateral frontal (F7, F8), central (C3, C4), temporal (T7, T8), parietal (P3, P4, P7, P8), and occipital (O1, O2)]. All electrodes were referenced to Cz during the recordings. The recordings were obtained using a stretch cap (Electro-Cap, Inc.; Eaton, OH; E1-series cap) with tin electrodes in the 10/20 system pattern. After the cap was placed on the infant's head, a small amount of abrasive gel was placed into each recording site and the scalp was gently rubbed. Conductive gel was then added to the recording sites. Electrode impedances were measured and accepted if they were below 20 k Ω . The electrical activity from each lead was amplified using separate James Long Company Bioamps (James Long Company; Caroga Lake, NY). During data collection, the high pass filter was a single pole RC filter with a 0.1 Hz cut-off (3 dB or half-power point) and 6 dB per octave roll-off. The low pass filter was a two-pole Butterworth type with a 100 Hz cut-off (3 dB or half-power point) and 12 dB octave roll-off.

Activity for each lead was displayed on the monitor of the acquisition computer. The EEG was digitized on-line at 512 samples per second for each channel to eliminate the effects of

aliasing. The acquisition software used was Snapshot-Snapstream (HEM Data Corp., Southfield, MI) and the raw data was stored for later analyses. Prior to the recording of each participant a 10 Hz, 50 uV peak-to-peak sine wave was input through each amplifier. This calibration signal was digitized for 30 seconds and stored for subsequent analysis.

Spectral analysis of the calibration signal and computation of power at the 9 to 11 Hz frequency band was accomplished. The power figures were used to calibrate the power derived from the subsequent spectral analysis of the EEG. Then, EEG data were examined and analyzed using EEG Analysis software developed by the James Long Company. Data were re-referenced via software to an average reference configuration and then artifact scored for eye movements using a peak-to-peak criterion of 100 μ V or greater. Gross motor movements over 200 μ V peak to peak were also scored. These artifact scored epochs were eliminated from all subsequent analyses. No artifact correction procedures were used. The data were then analyzed with a discrete Fourier transform (DFT) using a Hanning window of 1 second width and 50% overlap. The mean number of artifact-free DFT windows was 77 ($SD = 23$) at 5 months, 57 ($SD = 32$) at 10 months, and 65 ($SD = 29$) at 24 months. Power was computed for the 4-6 Hz and 6-9 Hz frequency bands and expressed as mean square microvolts. The 6-9 Hz band, typically considered to be “infant alpha” (Saby & Marshall, 2012), has been associated with infant working memory and inhibitory control (e.g., Bell, 2001; Cuevas et al., 2012). The 4-6 Hz band, typically considered to be “infant theta” (Saby & Marshall, 2012), has been associated with infant attention and emotion (e.g., Bazhenova, Stroganova, Doussard-Roosevelt, Posikera, & Porges, 2007; Henderson, Fox, & Rubin, 2001). Power values in each frequency band were transformed using the natural log (ln) to normalize the distributions.

We focused our analyses on the EEG at the frontal scalp locations because of the associations mentioned above between maternal behaviors during infancy and later childhood cognitive performance on executive function tasks (Bernier et al., 2012; Cuevas et al., 2014; Kraybill & Bell, 2013), and evidence linking early experience to prefrontal circuitry (Kolb et al., 2012). Owing to this study's focus on brain development and thus EEG power rather than asymmetry, we averaged across hemispheres for the three frontal scalp locations: Fp1/Fp2 (frontal pole), F3/F4 (medial frontal), and F7/F8 (lateral frontal). Given the absence of prior data that might suggest specific links between parenting and particular frontal areas, the analyses were exploratory; we thus examined each frontal region separately.

Maternal Behavior at 5 Months

Mothers were asked to play with their infants for a period of 2 minutes. In this unstructured interaction, two simple toys were available for play. Mother was told to play as she wished, but that she could not remove her infant from the seat. The experimenter left the room during the interaction.

Maternal behaviors were scored using a coding scheme developed by Calkins, Hungerford, and Dedmon (2004) for assessing maternal interactive style during a 2-minute toy play. Maternal interactive style is a multifaceted construct that includes sensitivity to infant's signals, facilitation of attention, lack of intrusive behavior, appropriate physical stimulation,

appropriate vocal stimulation/excitement, appropriate pacing of activities, and praise. Four dimensions of maternal behaviors are used in the current study. The first dimension, *maternal sensitivity*, included the extent to which the mother's interactions were correlated with the infant's behavior. This variable included such behaviors as well-timed and synchronous responses, acknowledgment of infant's affect, appropriate levels of stimulation, soothing, picking up on the infant's interests, and attention-directing behaviors. The second dimension, *maternal intrusiveness*, was the extent to which the mother displayed overcontrolling behavior or was focused on her own agenda, ignoring the infant's cues. Maternal intrusiveness included such behaviors as failing to modulate the pace or intensity of her behavior when the infant withdrew or turned away, appearing to force toys or self on infant, and intrusive physical interactions. The third dimension, *maternal positive affect*, was the extent to which the mother expressed positive emotions during the task through her tone of voice and facial expressions. Coding included the level of intensity of positive emotion, including brief or slight smiles as well as prolonged smiles or laughter. The fourth dimension, *maternal physical stimulation*, assessed the extent to which mother directed stimulated her infant's body for the purpose of heightening the infant's level of arousal. Examples of physical stimulation included tickling the infant, exercising the infant's limbs, rubbing mother's face on infant or rubbing toy on infant. Physical stimulation also included touching the infant with toys or dropping toys on the infant.

Maternal behaviors were coded every 30 seconds using a 4-point scale (1 = none, 4 = high) for each dimension. Values were summed across epochs and divided by the number of epochs. Inter-rater reliabilities (intraclass correlations; 20% coding overlap) were acceptable for all maternal behaviors (all ICC's = .74 – .92).

Results

Preliminary analyses

Table 1 shows the descriptive statistics for EEG and maternal behavior data. All variables showed satisfactory variability, and EEG frontal power showed the expected age-related increases: power was significantly higher at 10 than 5 months, and at 24 than 10 months, in both alpha and theta bands for all three groupings of frontal electrodes (all p 's < .001).

In order to reduce the number of data points and thus the risk of Type-I error, the four dimensions of maternal behavior were submitted to a principal component analysis. This analysis yielded a two-factor solution (Eigen values > 1.0), which explained 74.7% of the variance. These factors were then submitted to a principal axis rotation (oblimin). Factor loadings indicated that the first factor (43.6%) was composed of lack of maternal sensitivity ($\lambda = -.94$) and maternal intrusiveness ($\lambda = .92$), whereas the second factor (31.1%) was comprised of lack of physical stimulation ($\lambda = -.81$) and maternal positive affect ($\lambda = .74$). No cross-loadings were observed (highest cross-loaded $\lambda = .20$). We thus derived two averaged scores to summarize the quality of maternal behavior, which for ease of understanding were labeled based on the positively-loading dimensions: maternal intrusiveness and maternal positive affect. These two factors were negatively but weakly correlated, $r = -.13$, $p = .011$. They are used in all subsequent analyses.

We then examined the extent to which socio-demographic variables (maternal age at infant's birth, maternal education, and infant sex) were related to key study variables. As displayed in Table 2, maternal age at infant's birth was unrelated to frontal alpha or theta EEG power, but associated with intrusiveness, such that younger mothers were more intrusive when interacting with their infants. Maternal education was positively linked to theta power at 10 and 24 months and alpha power at 24 months, as well as with one of the electrode groupings at 10 months for alpha power. It was also related to the two aspects of maternal behavior: more educated mothers showed more positive affect and were less intrusive. Finally, infant sex was related to alpha, but not theta, EEG power at 5 and 10, but not 24 months, with girls showing higher power than boys. Infant sex was, however, unrelated to maternal behavior. Given these results, and with the aim of running conservative analyses, infant sex and maternal age and education were co-varied in all final models.

Main analyses

Zero-order correlations between the two aspects of maternal behavior and infant EEG frontal power are also displayed in Table 2 (columns 13 and 14 for alpha EEG; rows 13 and 14 for theta EEG). A first observation is that maternal intrusiveness is clearly unrelated to EEG alpha or theta power: all 18 correlations are not only non-significant, but in fact they are consistently near-zero. Given this pattern of null findings, maternal intrusiveness is not considered further. A very different pattern of results emerges with the other aspect of parenting considered. Maternal positive affect is virtually unrelated to concurrent, 5-month EEG frontal power, but it is positively and significantly associated with subsequent power at most frontal electrode pairs and both ages. Furthermore, in the case of alpha power, the relations of maternal positive affect to the most distal (24 months) EEG assessment appear somewhat more compelling than with 10-month EEG. Together with the age-related increases in EEG power presented above, this pattern of results suggests that maternal positive affect may be associated with increases in frontal EEG power between 5 and 10 months, and 10 and 24 months. Note that although our analyses were focused on frontal electrodes, we explored potential links between parenting and all other electrode sites. This yielded an essentially null pattern of findings for the alpha EEG power values, with 28 non-significant correlations on the 30 that were computed. The two exceptions were at 10 months, with maternal positive affect correlating positively with power at T7/T8 and at O1/O2. For the theta EEG power values, there were 23 non-significant correlations on the 30 that were computed. Central, temporal, and occipital theta power values at 10 and 24 months were correlated with maternal positive affect.

To test the above hypothesis that maternal positive affect may be associated with age-related increases in frontal power, the data were submitted to a series of hierarchical regression analyses predicting EEG power while controlling for prior power. In each equation, maternal age and education as well as infant sex were entered in a first block, to account for their shared variance with maternal behavior or EEG power, described above. To focus on increases in frontal EEG power and thus run very conservative analyses, previous EEG power at the corresponding electrode grouping was entered in a second block, followed by maternal positive affect in a third block. Analyses were conducted separately for alpha and theta frequency band data.

The results of the equations predicting 10-month alpha power are displayed in Table 3. The first model, predicting power at Fp1/Fp2, was significant, $F(5,304) = 15.26, p < .001$. Together, the covariates and 5-month alpha power accounted for 19.1% of the variance, while maternal behavior accounted for a modest yet significant 1.4% of additional variance in 10-month power. In contrast, the second model, while also significant overall ($F(5,304) = 12.83, p < .001$), revealed that maternal behavior did not explain a significant portion of the variance at F3/F4 after accounting for previous power at the same location. Finally, the third model (F7/F8) was also significant, $F(5,304) = 10.30, p < .001$. Together, the covariates and 5-month power accounted for 11.8% of the variance, and maternal behavior added a significant 3% ($p < .001$) to the prediction. Overall, the models explained between 14.7 and 20.5% of the variance in 10-month alpha power.

Table 4 presents the results of the regression analyses predicting 24-month alpha power, this time accounting for 10-month alpha power and the same set of covariates as above. In the first model ($F(5,197) = 12.34, p < .001$), maternal behavior accounted for only a marginal portion (1.4%; $p = .061$) of unique variance in power at Fp1/Fp2. In contrast, in both the second ($F(5,197) = 6.01, p < .001$) and the third models ($F(5,197) = 10.75, p < .001$), maternal behavior accounted for significant increments (a little over 3%, $p < .01$) in explained variance in power, above and beyond that explained by the covariates and by 10-month power at the same electrode grouping. Overall, the models explained between 13.1 and 23.7% of the variance in 24-month alpha power.

The results of the equations predicting 10-month theta power are displayed in Table 5. The first model, predicting power at Fp1/Fp2, was significant, $F(5,304) = 14.65, p < .001$. Together, the covariates and 5-month theta power accounted for 13.7% of the variance, while maternal behavior accounted for a significant 6.1% of additional variance in 10-month power. The second model (F3/F4), also significant overall ($F(5,304) = 9.81, p < .001$), revealed that maternal behavior explained a significant 4.6% of additional variance after accounting for the 9.5% of variance explained by the covariates. Finally, the third model (F7/F8) was also significant, $F(5,304) = 12.80, p < .001$. Together, the covariates and 5-month power accounted for 11.1% of the variance, and maternal behavior added a significant 6.6% to the prediction. Overall, the models explained between 14.1% and 19.8% of the variance in 10-month theta power.

Table 6 presents the results of the regression analyses predicting 24-month theta power, accounting for 10-month theta power and the same set of covariates as above. In the first model ($F(5,197) = 14.84, p < .001$), maternal behavior did not account for unique variance in power at Fp1/Fp2, even though the model account for 27.9% of variance. In contrast, in both the second ($F(5,197) = 5.01, p < .001$) and the third models ($F(5,197) = 7.29, p < .001$), maternal behavior accounted for significant increments (a little over 3%, $p < .01$) in explained variance in power, above and beyond that explained by the covariates and by 10-month power at the same electrode grouping. Overall, the models explained between 11.5 and 27.9% of the variance in 24-month theta power.

All in all, despite the covariates and prior power accounting for between 8.1% and 27.3% of the variance in alpha and theta power at different frontal electrode groupings, maternal

behavior made unique additional contributions that were significant in nine of the twelve models, and marginal in one of the other three.

Discussion

As critical catalysts of child development, parent-child relationships are often assumed to play a crucial role in brain development. And yet, as reviewed in the introduction, the evidence to support these claims is sparse and often indirect. The aim of the current report was to investigate the prospective links between the quality of maternal behavior during mother-infant interactions and infants' subsequent brain development, as indicated by resting EEG frontal power. The results indicated that mothers who interacted with their 5-month-old infants in a style characterized by more positive affect and less physical stimulation had infants whose frontal resting alpha and theta EEG power was higher at 10 and 24 months, and increased more rapidly between 5 and 10 months, as well as between 10 and 24 months.

We focused on the EEG at the frontal scalp locations because of associations between maternal behaviors during infancy and later childhood performance on executive function tasks (Bernier et al., 2012; Cuevas et al., 2014; Kraybill & Bell, 2013) and because frontal EEG values are related to performance on those tasks (Cuevas et al., 2012; Morasch & Bell, 2011). EEG power reflects synchronized postsynaptic potentials and power values reflect the excitability of groups of neurons (Jackson & Bolger, 2014). Thus, development of the EEG likely reflects underlying changes in the number of synapses as well as the efficiency of the underlying neural networks.

We see the results pertaining to age-related increases in power as particularly meaningful, for both empirical and developmental reasons. From a strictly empirical point of view, the possibility to control for prior power makes for stringent analyses. Perhaps more importantly, age-related increases in power are regarded as a key index of brain *development*, given the almost linear relations between power and age across infancy (Bell & Fox, 1992; Cuevas & Bell, 2011). There are also, however, substantial individual differences in this developmental progression, with some infants reaching higher power levels more rapidly than others, which in turn has implications for cognitive functioning (e.g., Cuevas et al., 2012). The origins of these individual differences remain largely unknown, with biological and maturational factors assumed to play the central role, but no contributing environmental factor identified thus far. The current results suggest that the quality of maternal behavior during mother-infant interactions may be one of the factors contributing to these individual differences, with infants exposed to higher-quality interactions with their mothers showing more pronounced increases in frontal power than their peers. Hence, the findings of this study provide rare evidence that normative variation in parenting quality may contribute to brain development among typically-developing young children. This is consistent with classic (Greenough et al., 1987) and recent propositions (e.g., Lupien et al., 2011), with animal studies (see Meaney, 2001), and with research on highly traumatized children populations (see Belsky & de Haan, 2011). To our knowledge however, it has not been observed before in samples of healthy infants.

The longitudinal design with repeated EEG measures, along with the analyses controlling for prior EEG power, provide some degree of confidence in the direction of the associations found, in that the underlying developmental sequence appears more likely to proceed from maternal behavior to infant EEG power than the converse. The fact remains, however, that this design was non-experimental, and thus causality cannot be inferred. In this context, findings from experimental studies with biologically at-risk infants are noteworthy. Using a randomized control trial, Milgrom and colleagues (2010) found that a 9-session intervention aimed at enhancing sensitivity among mothers of preterm babies (< 30 weeks gestation), administered at the NICU while the babies were still hospitalized, improved infant cerebral white matter maturation and connectivity. Along similar lines, Welch et al. (2014) implemented a randomized control trial to test an NICU-based intervention focusing on the quality of affective communication between mothers and their preterm (26–34 weeks gestation) babies. The authors found positive effects of the intervention on sleep EEG: babies who had been exposed to the intervention showed higher frontal EEG power than infants in the control group during quiet and active sleep (no waking EEG data was reported). Although these two studies were conducted with medically vulnerable and extremely young infants, their experimental designs are strongly suggestive of causal links. Combining these experimental results with those obtained here with normally-developing infants in a longitudinal design, we would argue that emerging evidence is beginning to support the long-standing suggestion that normative variations in maternal care can influence young children's brain development, and that such effects are not restricted to extreme cases of abuse, neglect, or institutionalization. Nonetheless, the current findings should not be interpreted as unambiguously demonstrating a causal influence of mothering on infant brain development. The non-experimental design does leave other hypotheses open, notably bidirectional processes. An especially exciting hypothesis is that the links identified here may reflect more complex, reciprocal influences, such that more mature infants may trigger more optimal parenting, which in turn would contribute to further brain development, and so on. Longitudinal cross-lagged designs, entailing multiple assessments of both parenting and child EEG, are needed to test such transactional mechanisms.

It is important to note that the magnitude of the relations observed here between maternal parenting and infant EEG power was small. Part of this, of course, is likely due to the controls implemented, with both previous power and key socio-demographics held constant in the regression models. Still, the unique contributions of maternal behavior after accounting for these covariates, while robust (significant in nine of the twelve models, and marginal in one other), were modest in magnitude, and may have gone unnoticed with a smaller sample size and thus lower statistical power. On the one hand, this may partly reflect the nature of the parenting assessment used: only two minutes of mother-infant interaction were used for coding, while some scholars argue that at least a few *hours* of structured observation are necessary to properly measure the quality of mother-infant relationships (Pederson & Moran, 1995; Waters & Deane, 1985). In this context, one may argue that finding reliable links between maternal behavior assessed in a brief free play and infant EEG power several months later is remarkable, and could suggest that the underlying links between maternal parenting and children's brain development are especially robust. On the other hand, the small effect sizes observed almost certainly also indicate that many other

(biological and environmental) factors influence brain development, several of which are likely to carry more predictive power than parenting. Overall, we would argue that the current findings highlight both the reliability and the potentially modest magnitude of the links between parenting and infant brain development. Studies using longer and more numerous parenting assessments, and also considering fathers or other important caregivers, might reach greater but still modest predictive power, given the numerous other factors contributing to brain development. For instance, infant general maturation, physical health, nutrition, as well as instrumental types of stimulation (e.g., quality and diversity of available toys, music, etc.) and other social influences (grand-parents, daycare experiences, older siblings) are all likely to explain incremental variance in infant brain development.

Another direction for future studies pertains to the identification of the exact aspects of parenting that may impact infant brain development. Decades of research have shown that the quality of parent-child interactions is multidimensional, with different dimensions making unique contributions to child functioning (see Grusec & Davidov, 2010, for a review). In the case of this study, the first dimension of maternal behavior to emanate from the principal component analysis was composed of high sensitivity and low intrusiveness. Both have in common the central role of infant cues in the coding, with sensitivity indicating mothers' capacity to perceive and interpret infant cues accurately and to respond appropriately, and intrusiveness rather indicating disregard for, or difficulty respecting, infant cues. It is thus sensible that the two tend to load (in opposite directions) on one factor. In contrast, the second dimension appears to mostly reflect mother-initiated behavior, whether of an emotional (positive affect) or physical nature (physical stimulation), with less weight given to infant cues in the coding. It may be worth to note that excessive physical stimulation has been identified by attachment research as a strong marker of a maternal interactive style precursor of insecure mother-child attachment: notably, the item "Mother subjects baby to constant and unphased barrage of stimulation" is one of the 90 items of the Maternal Behavior Q-Sort (Pederson & Moran, 1995) that is most strongly indicative of low maternal sensitivity, with a score of 1.25 on a 1–9 scale (with 9 indicating highly sensitive behaviors). Likewise, low positive affect is characteristic of mothers of insecurely attached infants (Main & Weston, 1982; see also Ainsworth, Blehar, Waters, & Wall, 1978, chapter 8). It appears sensible, then, that high positive affect and low physical stimulation would load together, and this might suggest that mothers who are comfortable expressing positive emotions through facial expression and tone of voice do not need to revert to physical stimulation to initiate and maintain contact with their infants.

Why, however, such a parenting style would be especially relevant to infant brain development remains unclear at this point. In fact, we would argue that the other dimension of mothering assessed here, consisting of mothers' capacity to perceive, interpret, and follow their infant's cues, appears just as likely to play a role in infant neural development. This study's failure to find links between these aspects of maternal behavior and infant EEG may reflect a methodological issue, such that the observation context (brief free play) was not ideally suited to assess complex behaviors like sensitivity and intrusiveness. Some mothers who have a tendency to be intrusive in daily caretaking activities may not have enough time, in 2 minutes, to display this tendency, which may become more manifest as they settle in in the interaction and become less self-conscious. Likewise, coders often need to observe

caregivers' responses to numerous infant cues in order to assess sensitivity. Hence, the observation context of this study may have been ill suited to capture the full spectrum of natural variability in maternal sensitivity and intrusiveness – and indeed, the rating scales for these behaviors were not fully used, in contrast to those for positive affect and stimulation (Table 1). It may also be that the role of such aspects of maternal behavior is more salient in other contexts, such as infant distress, or at later ages as infants become increasingly skilled at detecting cause-and-effect relations and thus social contingencies. All in all, owing to these developmental, contextual, and methodological issues, and given how extremely young the literature on parenting and brain development is, we would argue that it is much too soon to conclude that central aspects of parenting like sensitivity and intrusiveness do not play a role in infant brain development. Likewise, although we did not expect compelling results when considering non-frontal electrodes, and that indeed the protracted post-natal development of frontal areas (Giedd et al., 1999) makes them especially susceptible to environmental influences, the current results should not be taken as excluding possible caregiving influences on non-frontal brain regions.

In addition to the limitations already mentioned (the non-experimental design and the brief parenting assessment), this study presents the shortcoming of most studies examining parenting and child outcomes: because the design is not genetically informative, we cannot rule out common genetic factors as an account of the shared variance between maternal behavior and infant EEG. There are several reasons, however, to doubt that shared genetic variance played a major role in the results reported here. Most importantly, several genetically-informed twin studies suggest that the variance in maternal behavior (Roisman & Fraley, 2008), as well as the covariance between parenting and different aspects of child functioning (Fearon et al., 2006; Roisman & Fraley, 2012; Tither & Ellis, 2008), are largely due to environmental influences, with small genetic contributions. In addition, we controlled for prior EEG power in predicting subsequent power. This was a critical control, given that genetic factors are theorized and often observed to contribute mostly to continuity in individual differences over time, rather than to age-specific variance (e.g., Kovas, Haworth, Dale, & Plomin, 2007; Petrill et al., 2004; Polderman et al., 2007). Finally, controlling for maternal education further reduced the likelihood of strong genetic influences on the results. Nonetheless, the fact that the design was not genetically informed does leave open the possibility of shared genes between mother and infant having played a role in the results reported here. Likewise, several other factors that may play a role in infant brain development were not assessed, for instance maternal and paternal mental health, parenting stress and experience, attitudes toward parenting, etc. These factors, however, are all robust predictors of parenting itself and therefore, seem likely to exert any putative influence on infant brain development through an intermediate impact on parenting, which we assessed. Nevertheless, assessing such factors in future studies is important, in that it will allow for formal testing of a mediation process transiting through parenting, which is often hypothesized (e.g., Lupien et al., 2011) but rarely tested.

This study suggests that the quality of maternal behavior during early mother-infant interactions relates to individual differences in one of the best documented markers of early brain development, namely developmental increases in resting frontal alpha and theta band EEG power across infancy. These findings are among the first to suggest that variation

within the normative range of parenting quality may be sufficient to influence the normative course of early brain development. Much remains to be investigated however, including the neurophysiological mechanisms that may account for these parenting effects, the exact dimensions of parenting involved (which may vary according to child age), and whether these effects, if they are replicated and found to be robust, are responsible for part of the numerous and profound effects of parenting on child development.

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Table 1

Descriptive statistics for core study variables

	Mean ^a	Standard ^a deviation	Range ^a	<i>n</i>
Fp1/Fp2 resting power, 5 months	1.88	.45	0.52 – 3.31	352
	2.48	.39	1.09 – 3.67	
F3/F4 resting power, 5 months	2.08	.51	0.04 – 3.92	352
	2.65	.44	0.78 – 4.50	
F7/F8 resting power, 5 months	2.13	.45	0.10 – 3.48	352
	2.63	.41	0.79 – 3.83	
Fp1/Fp2 resting power, 10 months	2.40	.43	1.34 – 3.64	304
	2.99	.50	1.84 – 5.43	
F3/F4 resting power, 10 months	2.66	.51	1.19 – 4.21	304
	3.06	.46	1.75 – 4.96	
F7/F8 resting power, 10 months	2.51	.45	0.79 – 3.71	304
	2.98	.49	1.63 – 5.16	
Fp1/Fp2 resting power, 24 months	2.71	.47	0.61 – 3.86	215
	3.07	.46	1.40 – 4.50	
F3/F4 resting power, 24 months	2.92	.56	0.80 – 4.34	215
	3.14	.52	1.06 – 4.55	
F7/F8 resting power, 24 months	2.80	.49	0.75 – 3.92	215
	3.11	.48	1.04 – 4.47	
Maternal behavior: positive affect	2.45	.55	1 – 4	352
Maternal behavior: physical stimulation	2.00	.89	1 – 4	352
Maternal behavior: sensitivity	3.42	.55	1.5 – 4	352
Maternal behavior: intrusiveness	1.39	.48	1 – 3.5	352

^aNote. EEG alpha (6-9 Hz) above; EEG theta (4-6 Hz) below

Table 2

Inter-correlations among study variables

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.
1. Fp1/Fp2 resting power, 5 months	---	.72***	.74***	.41***	.35***	.37***	.29***	.27***	.27***	.03	.04	.23***	.11*	.02
2. F3/F4 resting power, 5 months	.82***	----	.81***	.34***	.42***	.29***	.24***	.27***	.24***	.01	.04	.23***	-.04	.03
3. F7/F8 resting power, 5 months	.80***	.81***	----	.35***	.35***	.33***	.25***	.27***	.28***	.03	.07	.22***	.06	.01
4. Fp1/Fp2 resting power, 10 months	.36***	.26***	.35***	----	.79***	.83***	.48***	.30***	.43***	.02	.09	.20*	.17**	-.01
5. F3/F4 resting power, 10 months	.35***	.30***	.35***	.87***	----	.82***	.39***	.31***	.36***	.05	.05	.11*	.05	-.01
6. F7/F8 resting power, 10 months	.32***	.22***	.31***	.89***	.89***	----	.46***	.32***	.42***	.03	.14*	.10 [†]	.21***	-.02
7. Fp1/Fp2 resting power, 24 months	.27***	.16*	.25***	.50***	.43***	.45***	---	.79***	.83***	.01	.15*	.09	.24***	.01
8. F3/F4 resting power, 24 months	.24***	.17*	.22***	.28***	.26***	.28***	.75***	----	.85***	.05	.13 [†]	.05	.21**	.03
9. F7/F8 resting power, 24 months	.22***	.16*	.25***	.35***	.30***	.33***	.80***	.80***	----	.04	.15*	.07	.30***	.07
10. Mother's age at infant birth	.03	.02	.05	.01	.02	.02	.01	.02	.02	----	.48***	-.04	.02	-.16***
11. Maternal education	.06	.07	.08	.11*	.11*	.15**	.11*	.11*	.15**	.48***	----	-.07	.15**	-.14*
12. Infant sex	.09	.11*	.09	.08	.05	.01	.08	.05	.01	-.04	-.07	----	.07	.04
13. MPA	.09	.01	.11*	.29***	.23***	.30***	.26***	.24***	.30***	.02	.15***	.07	----	-.13*
14. Maternal intrusiveness	-.01	.01	-.02	.09	.03	.06	.05	.06	.07	-.16***	-.14*	.04	-.13*	----

Note. Infant sex is coded: 1 = boy; 2 = girl. MPA = Maternal positive affect.
 EEG alpha (6-9 Hz) above the diagonal; EEG theta (4-6 Hz) below the diagonal.

[†] $p < .10$;
 * $p < .05$;
 ** $p < .01$;
 *** $p < .001$

Table 3

Summary of regression analyses predicting 10-month alpha (6-9 Hz) EEG power

Block	R ²	ΔR ²	F change	β when first entered	β in final model
Predicting Fp1/Fp2 resting power					
1. Covariates	.052	---	5.44 ^{**}		
Maternal age				-.03	-.01
Maternal education				.12 ^t	.09
Infant sex				.21 ^{***}	.11 [*]
2. 5-month Fp1/Fp2 power	.191	.139	50.91 ^{***}	.38 ^{***}	.37 ^{***}
3. Maternal behavior	.205	.014	5.31 [*]	.12 [*]	.12 [*]
Predicting F3/F4 resting power					
1. Covariates	.018	---	1.83		
Maternal age				.04	.05
Maternal education				.04	-.01
Infant sex				.12 [*]	.01
2. 5-month F3/F4 power	.173	.155	56.19 ^{***}	.41 ^{***}	.41 ^{***}
3. Maternal behavior	.177	.004	1.40	.07	.07
Predicting F7/F8 resting power					
1. Covariates	.034	---	3.54 [*]		
Maternal age				-.03	-.01
Maternal education				.16 [*]	.11 ^t
Infant sex				.12 [*]	.03
2. 5-month F7/F8 power	.118	.083	28.25 ^{***}	.30 ^{***}	.29 ^{***}
3. Maternal behavior	.147	.030	10.39 ^{**}	.18 ^{***}	.18 ^{***}

Note. N = 304

^t
p < .10;^{*}
p < .05;^{**}
p < .01;^{***}
p < .001

Table 4

Summary of regression analyses predicting 24-month alpha (6-9 Hz) EEG power

Block	R ²	ΔR ²	F change	β when first entered	β in final model
Predicting Fp1/Fp2 resting power					
1. Covariates	.031	---	2.13 ^t		
Maternal age				-.07	-.07
Maternal education				.14 ^t	.11
Infant sex				.12 ^t	.02
2. 10-month Fp1/pF2 power	.223	.192	49.50 ^{***}	.45 ^{***}	.42 ^{***}
3. Maternal behavior	.237	.014	3.55 ^t	.12 ^t	.12 ^t
Predicting F3/F4 resting power					
1. Covariates	.012	---	0.83		
Maternal age				.02	.01
Maternal education				.09	.10
Infant sex				.05	-.02
2. 10-month F3/F4 power	.099	.087	19.23 ^{***}	.30 ^{***}	.28 ^{***}
3. Maternal behavior	.131	.032	7.40 ^{**}	.18 ^{**}	.18 ^{**}
Predicting F7/F8 resting power					
1. Covariates	.026	---	1.76		
Maternal age				-.02	.01
Maternal education				.15 ^t	.11
Infant sex				.07	-.03
2. 10-month F7/F8 power	.179	.153	37.16 ^{***}	.40 ^{***}	.35 ^{**}
3. Maternal behavior	.214	.035	8.71 ^{**}	.20 ^{**}	.20 ^{**}

Note. N = 197

^t
p < .10;^{**}
p < .01;^{***}
p < .001

Table 5

Summary of regression analyses predicting 10-month theta (4-6 Hz) power

Block	R ²	ΔR ²	F change	β when first entered	β in final model
Predicting Fp1/Fp2 resting power					
1. Covariates	.020	---	1.99		
Maternal age				-.04	-.01
Maternal education				.13*	.08
Infant sex				.09	.02
2. 5-month Fp1/Fp2 power	.137	.117	40.34***	.35***	.33***
3. Maternal behavior	.198	.061	22.70***	.25***	.25***
Predicting F3/F4 resting power					
1. Covariates	.015	---	1.56		
Maternal age				-.03	.00
Maternal education				.12 ^t	.07
Infant sex				.06	-.01
2. 5-month F3/F4 power	.095	.080	26.35***	.29***	.29***
3. Maternal behavior	.141	.046	16.07***	.22***	.22***
Predicting F7/F8 resting power					
1. Covariates	.023	---	2.39 ^t		
Maternal age				-.06	-.03
Maternal education				.17**	.12*
Infant sex				.02	-.04
2. 5-month F7/F8 power	.111	.087	29.30***	.30***	.28***
3. Maternal behavior	.177	.066	23.99***	.26***	.26***

Note. N = 304

^t
p < .10;*
p < .05;**
p < .01;***
p < .001

Table 6

Summary of regression analyses predicting 24-month theta (4-6 Hz) power

Block	R ²	ΔR ²	F change	β when first entered	β in final model
Predicting Fp1/Fp2 resting power					
1. Covariates	.050	---	3.42*		
Maternal age				-.11	-.08
Maternal education				.18*	.12 ^t
Infant sex				.16*	.12 ^t
2. 10-month Fp1/ρF2 power	.273	.223	59.04***	.48***	.45***
3. Maternal behavior	.279	.006	1.63	.08	.08
Predicting F3/F4 resting power					
1. Covariates	.024	---	1.61		
Maternal age				.00	.01
Maternal education				.14 ^t	.12
Infant sex				.06	.03
2. 10-month F3/F4 power	.081	.056	11.81***	.24***	.19**
3. Maternal behavior	.115	.035	7.54**	.20**	.20**
Predicting F7/F8 resting power					
1. Covariates	.028	---	1.85		
Maternal age				-.02	.01
Maternal education				.14 ^t	.09
Infant sex				.11	.08
2. 10-month F7/F8 power	.121	.093	20.34***	.31***	.24**
3. Maternal behavior	.160	.039	8.90**	.21**	.20**

Note. N = 197

^t
p < .10;**
p < .01;***
p < .001