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More than meets the eye: The neural development of emotion face processing during infancy

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Abstract

This study explored the impact of infant temperament and maternal stress on the development of the infant medial prefrontal cortex (mPFC) among sixteen 6–8-month-old infants. Functional Near Infrared Spectroscopy (fNIRS) was used to measure activation of the infant mPFC in response to angry, happy, and sad faces. Infant temperament and dimensions of maternal stress were measured with the Infant Behavior Questionnaire and the Parenting Stress Index Respectively. Infants with high negative emotionality demonstrated increased mPFC activation in association with all emotion face conditions. Negative emotionality moderated the effect of total maternal stress on mPFC activation to angry and sad faces. Mother-infant dysfunctional interaction was related to increased mPFC activation associated with happy faces, supporting the "novelty hypothesis", in which the mPFC responds more strongly to unique experiences. Therefore, this study provides additional evidence that infant temperament and the quality of the mother-infant relationship influence the development of the mPFC and how infants process emotions.

Keywords

Infant; Mother; Medial prefrontal cortex; fNIRS; Maternal stress; Infant temperament; Infant emotional development; Mother-infant relationship; Infant brain development

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.infbeh.2020.101430.

1. Introduction

With limited visual and motor skills and an inability to care for themselves, the relationship between caregiver and infant is central to the human infant's survival (Grossmann, Oberecker, Koch, & Friederici, 2010). Therefore, it is no surprise that infant brains are specialized to process faces and the first expressions they respond to are those of their mother (Field, 1984). Although, at first, infants may discriminate between emotion faces based on structural information, such as facial features (Kestenbaum & Nelson, 1990), they later attach affective meaning to facial expressions and utilize this emergent emotional understanding to process social cues as well as to regulate their own emotional responses (Grossmann, Striano, & Friederici, 2007). The process of imbuing facial expressions with emotional meaning centers on the development of the amygdala-medial prefrontal cortex (mPFC) circuit (Tottenham, 2015).

The prefrontal cortex (PFC) is the anterior portion of the frontal lobe and is primarily responsible for many complex brain processes. The PFC sends and receives information from almost all other structures in the brain and organizes thoughts and behaviors in an attempt to accomplish internal goals (Miller & Cohen, 2001). In order to regulate emotions, the PFC exerts inhibitory control on the amygdala through the mPFC, the area of the cortex directly connected to the amygdala (Urry et al., 2006). The amygdala pairs environmental input with emotional responses, such as fear in response to loud noises (Cardinal, Parkinson, Hall, & Everitt, 2002). This pairing categorizes stimuli according to various emotions—both negative and positive (Tottenham et al., 2010). Over time, the mPFC and the amygdala become part of a larger network of emotion processing and regulation. Infant temperament and the quality of mother-infant interaction are two factors that have been found to influence infant responsivity to emotion face processing (Calder, Ewbank, & Passamonti, 2011; Krol, Rajhans, Missana, & Grossmann, 2015; Tottenham, 2014). The primary goal of the current study was to identify the underlying neural mechanisms involved in emotion face processing in infants aged 6–8 months, and then to examine the relations between neural responsivity to various emotion faces as well as infant temperament and the quality of the mother-infant relationship.

1.1. Evidence of the neural underpinnings of emotion face processing

A handful of electroencephalogram (EEG) studies have examined the neural development of emotion face processing in infants, and how emotion processing may differ as a function of infant temperament and the early caregiving context. Although EEG research is unable to pinpoint the exact brain structures involved in emotion face processing due to constraints in spatial resolution, these studies reveal striking evidence of the relations between individual differences in infant emotional development and neural activation.

EEG studies focusing on the temperamental correlates of infant neurological activation to emotion faces have found that infants rated highly on negative emotionality showed greater reactivity to happy faces than fearful faces, possibly relating to a lack of habituation to nonthreatening stimuli (Martinos, Matheson, & de Haan, 2012). Similarly, another EEG study examining the association between maternal mood and infant emotion face processing demonstrated that when the reactivity of infants of depressed and non-depressed mothers

was compared, infants of non-depressed mothers demonstrated more frontal activation during the sad versus happy trials; one explanation being that sad faces were less familiar to the infants of non-depressed mothers (Field, Pickens, Fox, Gonzalez, & Nawrocki, 1998). A third study demonstrated that infants raised by highly positive mothers are more reactive to fearful faces than happy faces (De Haan, Belsky, Reid, Volein, & Johnson, 2004). The results of these studies suggest that infants appear to be more reactive to emotional expressions that are the most novel to their actual experiences.

In contrast, the opposite activation pattern was demonstrated in another EEG study (Parker, Nelson, & Bucharest Early Intervention Project Core Group, 2005). Infants raised in extreme circumstances with very little adult caregiving, such as institutionalization, displayed greater reactivity to fearful faces versus sad and happy faces. In contrast to previous studies, these groups of infants were more reactive to familiar emotions. These results may be due to an overly reactive amygdala in infants who have experienced institutionalization, as they likely have had more reason to identify and respond to fear, suggesting that brain responses may be emotion specific and vary based on population.

1.2. fNIRS: a method for imaging infant brain activation

At present, the advent of Functional Near-Infrared Spectroscopy, or fNIRS, a non-invasive neuroimaging technology has allowed researchers an additional and critical tool to investigate the development of the prefrontal cortex during infancy. Other forms of imaging technology, such as functional magnetic resonance imaging, or fMRI, which requires the infant to be very still or sleeping, are either too invasive or too limiting of movement to permit exploration of infant brain activation to emotional experiences. fNIRS can accommodate movement and allows infants to sit upright, creating a much more normative environment in which to assess brain responses to social and emotional stimuli (Grossman, 2013; Lloyd-Fox, Széplaki-Kőollőd, Yin, & Csibra, 2020). fNIRS is also similar to an EEG set-up, in that it involves placing a cap on the infant's head but utilizes the Blood Oxygenation Level Dependent (BOLD) Signal like fMRI, which allows researchers to target specific Regions of Interest (ROI) with respect to brain structures (e.g., mPFC).

In a recent study, Ravicz, Perdue, Westerlund, Vanderwert, and Nelson (2015) utilized fNIRS to examine differences in the hemodynamic responses to happy, fearful, and angry faces based on the infant's temperamental characteristics. Twenty-four 7-month-old infants were divided into temperament-based groups based on high or low scores of negative emotionality (NE), surgency/ extraversion (S/E), and orienting/regulating (O/R). When examining the PFC as a whole, these authors found that infants with lower S/E or NE scores demonstrated greater activation in response to the happy face trials. Low NE infants also showed greater responsivity in the left hemisphere of the PFC during the happy face trials. These results provided initial support for the use of fNIRS to examine individual differences in infant neural responses to emotion faces and potential underlying neural mechanisms. The current study was an attempt to replicate portions of Ravicz et al. (2015) utilizing happy, sad, and angry faces rather than happy, fearful, and angry faces in line with our interest in looking at the links between infant brain activation to emotion faces and infant temperamental characteristics and the quality of the maternal caregiving environment.

In one other recent study (Azhari et al., 2019), fNIRS was used to show that maternal stress was associated with less brain-to brain synchrony in the medial left cluster of the prefrontal cortex when mother and child watched animated videos together. This brain region overlaps with the inferior frontal gyrus and the dorsolateral prefrontal cortex, which are implicated in inference of mental states and social cognition. This finding demonstrates the negative impact of parenting stress on mother-child synchrony at the brain-to-brain level.

There is still much to be learned about the development of the emotion regulation mechanisms in the infant brain and the mechanisms that induce brain activation. In addition to infant temperamental characteristics, both maternal characteristics and the caregiving environment no doubt are important in how infants process emotional expressions. A recent functional Near Infrared Spectroscopy (fNIRS) study examined the relations between infant fearfulness, maternal empathy, and infant brain activation to emotional body expressions. Highly fearful infants with empathic mothers showed decreased brain activation to fearful body expressions in relation to happy body expressions (Krol et al., 2015) indicating that both infant and maternal characteristics may explain the development of emotion face processing. More research is clearly needed on the neural development of infant emotion face processing within the context of social relationships.

1.3. The current study

The current study focused on defining further the underlying neural activation in regions of the mPFC as it is related to emotion face processing for 6- to 8-month-old infants, and whether this activation is associated with infant temperament and caregiver stress. We chose to focus on the mPFC based on previous infant fNIRS studies finding increased activation in the mPFC during emotional processing tasks (Naoi et al., 2012; Saito et al., 2007; Schore, 2015; Tottenham, 2015), and this developmental period because 7-month-old infants demonstrate increased specificity of attention to negative emotions (Peltola, Forssman, Puura, van IJzendoorn, & Leppänen, 2015). Additionally, it has been hypothesized that between 5–7 months of age, the brain's detection of emotion matures significantly (Grossmann et al., 2010). The overall purpose of this study was to investigate the neural signature of emotion face processing among infants of varying temperaments with varying caregiving environments. The first aim was to focus on the mPFC to explore the neural correlates of infant emotion face processing. We hypothesized that the mPFC is the neural correlate of emotion face processing during infancy and will be significantly activated during the emotion faces task.

The second aim was to examine whether brain activation during the emotion face processing task differed for infants with different temperaments. Based on the results of the majority of emotion face processing studies that found infants are more activated by emotions most novel to their experiences (De Haan et al., 2004; Field et al., 1998; Martinos et al., 2012; Ravicz et al., 2015), we hypothesized that infants high on negative emotionality would demonstrate greater brain activation to happy faces than infants rated low on negative emotionality, whereas infants who score highly on surgency/extraversion will display greater brain activation to the sad and angry faces.

The third aim was to investigate the impact on brain activations for infants in highly stressful caregiving environments. We hypothesized greater mPFC activation during presentations of happy faces than sad faces because infants of highly stressed mothers have more than likely experienced more negative emotions during mother-infant interactions than infants of low stressed mothers, and hence, have more familiarity with negative emotions (Feldman et al., 2009). These infants were tested at 7 months, a critical time in the development of their emotion regulation skills. From previous research we know that infants with high negative emotionality and highly stressed mothers are adept at regulating their emotions over time (Copian, Bowker, & Cooper, 2003; Crnic, Greenberg, Ragozin, Robinson, & Basham, 1983).

2. Methods

2.1. Participants

Sixteen 6–8-month-old infants (7 Female, M = 215.7 days, SD = 31.5) and their mothers participated in the study. Seven additional infants were also recruited and tested but were excluded from the study for various reasons including movement artifacts ($n = 4$; see fNIRS section below for details), equipment failure ($n = 1$), and failure to complete the task ($n = 2$). This attrition rate is comparable to previous infant studies using fNIRS (Lloyd-Fox, Blasi, & Elwell, 2010). All infants were full-term without histories of medical complications or neurological problems. Mothers provided informed consent prior to participation in the study, and the *blinded for review* Institutional Review Board for Behavioral and Health Sciences approved the protocol. Mother-infant dyads were recruited from *website blinded for review*, the Women's Mental Health Registry from the Department of Obstetrics and Gynecology, as well as through flyers at local libraries, businesses, parks, and Women, Infants & Children (WIC) offices. See Table 1 for sample characteristics.

2.2. Session overview

Mothers arrived with their infants to a university laboratory and were escorted to a child friendly waiting area by the experimenter who described the sequence of events that would take place during the visit. The mother then read and signed consent forms and completed two short surveys; one assessing infant temperament and another evaluating maternal stress. Another member of the research staff engaged the infant during this time to allow the infant time to become comfortable within the lab setting; infant head measurements were also taken during this time. In concordance with the 10–20 international system (Jasper, 1958), the infant's head circumference and distance between inion and nasion were noted for correct cap placement.

The mother and infant were then directed to the fNIRS room for the emotion faces task. The infant sat on the mother's lap during the entire task, including cap placement. The fNIRS cap was placed on the infant's head according to the measurements previously recorded (see Fig. 1). Video-recordings (iPad mini version 2, Apple, Cupertino, CA) of the entire task were recorded to ensure that cap and optodes were covering the correct brain regions throughout the task and that the infants were looking at the stimuli at a rate of greater than 50 % of the task (Ravicz et al., 2015). Because of the young age of the infants, infants were not separated from mothers and as a result, mothers were not blind to the face stimuli.

Mothers were asked to sit silently and not move or talk to the infant during the presentation of the stimuli Instances where the mother did not follow these procedures were not considered valid trials, and these trials were not included in analyses.

2.3. Emotion faces task

In order to assess emotion face processing, infants were shown a series of pictures of women with happy, sad, or angry facial expressions chosen from the NimStim Face Stimulus Set, of which the overall validity and reliability have been reported to be high (.81 and .84) (Tottenham et al., 2009). Each trial included three short blocks of each emotion, with five different women expressing the same emotion shown for one second, for a total of five seconds (see Fig. 2). Eight seconds of black and white shapes including a square, circle, star, and triangle, were shown in between each emotion block. Therefore, each trial contained fifteen seconds of face pictures with a randomly generated 200–400 ms inter-stimulus time, and twenty-four seconds of shapes. Emotions were pseudo-randomized across the task (random, but in the same order for each participant). In total, there were ten trials of each emotional type resulting in 30 trials altogether (Fig. 2). The faces were presented using the E-Prime Application Suite for Psychology (E-Prime 2.0, Psychology Software Tools, Sharpsburg, PA, USA). The session was terminated if the infant became too upset or the mother requested to discontinue, which she was told she could do at any time ($n = 2$). This set of stimuli is a modification of the methods and procedures of a previous fNIRS study by Ravicz et al. (2015), in which they utilized happy, fearful, and angry expressions in a block design format. Our focus was on happy, sad, and angry faces in the current study because we had initially planned on recruiting both depressed and nondepressed mothers, but it proved difficult to screen for depressive symptoms in our attempts to recruit mothers.

2.4. fNIRS data acquisition

During the emotion faces task, a continuous wave fNIRS system (CW6; TechEn Inc., Milford, MA) was used to record the hemodynamic responses of the mPFC. Two wavelengths, 690 and 830 nm, were used during data collection with a sampling rate of 50 Hz. Fiber optic cables were used to disseminate near-infrared light to a custom-designed Easycap (GmbH, Herrsching am Ammersee, Germany) made for this study and adjusted using a velcro chin strap for each infant's head size. The cap was designed using three source- and five detector-optodes placed 2.5 cm apart forming an 9-channel array (grommets, TechEn, Inc. Milford, MA; see Fig. 1). The array was designed using the 10–20 international system (Jasper, 1958) and channels covered the Fp1–4 landmarks to capture our region of interest (Brodmann's area (BA) 10, see Fig. 1). The cables were connected to the cap before being placed on the infant's head at the beginning of the emotion faces task.

Brain regions—Brain regions were estimated using a Polhemus Patriot 6DOF Digitizer on a mannequin head. The resulting coordinates were put into AtlasViewerGUI (Aasted et al., 2015), through MATLAB to render the brain measurements in Montreal Neurological Institute (MNI) stereotactic space. These coordinates were then partitioned into 1000 voxel points that identified the midpoint between each source and detector optode (see Fig. 1) and rendered on a 3D adult brain template. To ensure the optodes would be placed to accurately

capture our regions of interest (ROI), these voxel points were converted to BA's using xjView database in Matlab (http://www.alivelearn.net/xjview).

2.5. Maternal report measures

2.5.1. Infant temperament (IBQ-R-SF)—Infant temperament was measured using the Revised Infant Behavior Questionnaire Short Form (Putnam, Helbig, Gartstein, Rothbart, & Leerkes, 2014), a caregiver report instrument with items designed to describe specific behaviors in infants ages 3–12 months. Mothers were asked to respond to 36 items based on their infant's behavior during the previous week. This questionnaire consists of 14 subscales that load onto three different temperament factors (Gartstein & Rothbart, 2003): (1) *Surgency/Extraversion (S/E),* which includes activity level, vocal reactivity, smiling and laughing, high intensity pleasure, perceptual sensitivity, and approach; (2) *Negative Emotionality (NE),* which includes subscales of fear, distress to limitations, sadness and falling reactivity; and (3) *Orienting/Regulation (O/R),* which includes soothability, duration of orienting, cuddliness, and low intensity pleasure. Items were averaged across scales to create mean scores. The IBQ is a widely used measure of infant temperament and has demonstrated reliability and validity with Cronbach's alphas ranging from .77 to .96 (see Gartstein & Rothbart, 2003). For this sample, $\alpha = 0.88$.

2.5.2. Parenting stress index (PSI-SF)—Parenting stress was measured with the 36-item Parenting Stress Index-Short Form (Abidin, 1990), a widely used assessment of parental stress that has been used extensively with mothers of infants, and has good to excellent reliability with a Chronbach's alpha of .84 for the total stress score, and Chronbach's alphas ranging from .69 to .85 for the subscales (Barroso, Hungerford, Garcia, Graziano, & Bagner; 2016; Beebe, Casey, & Pinto-Martin, 1993). The total stress score is used to assess an overall level of parenting stress with three subscales; (1) *Parental Distress* – the distress the individual feels in relations to their identity as a parent, (e.g. 'I feel trapped by my responsibilities as a parent'); (2) *Parental-Child Dysfunctional Interaction* – the parents' views of the child as not meeting expectations or displaying positive behaviors in response to the parent (e.g. 'My child rarely does things for me that make me feel good'); (3) *Difficult Child* – perceptions of child's demandingness and compliance (e.g. 'My child makes more demands on me than most children'). Higher scores indicate greater levels of stress (Abidin, 1990). For this sample, $\alpha = 0.98$.

2.6. Data processing and analysis strategy

Inclusion criteria were based on several factors, in stages: First, whether the infant completed the emotion faces task, then if the infant was looking at the screen the majority of the task (> 50 %) and finally, motion artifacts. Motion artifacts are artificial signals that result from participant moving during the task, which was the major reason participant data were not included in the final analyses. To examine the quality of the data, raw data were exported from the Techen fNIRS machine to Matlab (Mathworks, Inc., 2016) and Homer2 (Barker, Aarabi, & Huppert, 2013) was used to inspect the quality of the data and label each condition of the task by stimulus.

NIRS Brain AnalyzIR Toolbox (Santosa, Zhai, Fishburn, & Huppert, 2018) was also used to assess the viability of each channel. The following pre-processing steps were completed in the following order: optical density change data conversion, motion artifact detection and correction via spline interpolation, and concentration change data conversion into oxy- and deoxy-genated hemoglobin values. First, the raw data was converted into units of optical density change (OD). Next, a motion detection algorithm was applied to the OD data on a channel-by-channel basis, in order to apply the motion correction in the following step. This motion detection function identifies data points exceeding an experimenter-set threshold, thus we applied thresholds commonly used for children in the fNIRS field (see Brigadoi et al., 2014; Cooper et al., 2012; Hu et al., 2015; Scholkmann, Spichtig, Muehlemann, & Wolf, 2010). Specifically, motion artifacts were defined as signal changes with a relative amplitude greater than one standard deviation (*STDEVThresh* = 1) of the overall signal change or an absolute magnitude greater than 50 (*AMPThresh* = 50) within a half second (*tMotion* =0.5 s). Then this time point, as well as an additional second window (*tMask* = 1) around the detected motion time point (+/−), was marked as an artifact. Spline based motion correction was then used to correct the previously identified motion artifacts, interpolation parameter = 0.99 (Scholkmann et al., 2010). The spline interpolation fixes a defined motion artifact by subtracting a reconstructed polynomial interpolation function from it (Scholkmann et al., 2010). The spline interpolation method (csaps) implemented in MATLAB was used. The interpolation parameter, specified as a scalar value between 0 and 1, determines the relative weight to place on the contradictory demands of having the spline interpolation function be smooth or be close to the data.

The data were then transformed into hemoglobin concentration changes using the modified Beer-Lambert law yielding oxygenated (HbO) and deoxy-genated (HbR) hemoglobin values. If the number of channels excluded during this stage due to motion artifacts was greater than one third of all channels, these infants were omitted from the study (Filippetti, Lloyd-Fox, Longo, Farroni, & Johnson, 2015). Ultimately, four infants' data had to be excluded as they did not meet the criteria, and sixteen infants were included in the final analysis. Of the sixteen infants included in the final analysis all of their channels were included as well as all ten trials of the angry, sad, and happy face trials, in order to alter the remaining data as little as possible.

The final set of infant fNIRS data included in the study (n = 16) went through preprocessing using the NIRS Brain AnalyzIR Toolbox (Santosa et al., 2018); this toolbox is similar to Homer2 in that it involves examining two major sources of noise that influence fNIRS data —physiological signals unrelated to brain responses as well as motion artifacts, but also contains a GLM function (Barker et al., 2013). The same preprocessing steps utilized previously in Homer2, with the same values (described in detail above), were then completed in the AnalyzIR toolbox and were inclusive of all channels and trials of the final sixteen infants that ultimately comprised the study. This included optical density change data conversion, motion artifact detection and correction via spline interpolation, and concentration change data conversion into oxy- and deoxy-genated hemoglobin values. Hemoglobin data can be highly contaminated by physiological noise, especially when sampled at a temporal resolution greater than 10-Hz, leading to serially correlated error terms (Barker et al., 2013). Thus, modeling the data using a multiple regression General

Linear Model (GLM) approach is one way of correcting for autocorrelations (Barker et al., 2013; Poline & Brett, 2012) and to account for statistical parametric mapping assumptions (Penny, Friston, Ashburner, Kiebel, & Nichols, 2006).

Each participant's hemoglobin data was then modeled using a GLM ordinary least squares (OLS) fit (Huppert et al., 2017). The GLM OLS assumed the dual-gamma canonical hemodynamic response function at trial onset. The GLM then estimated the response signal strength values or "activation" (β) for each condition (happy, sad, angry, and shapes) considering the percent signal change across all four conditions, which were labeled as fixed factors, across both hemoglobins (HbO and HbR).

Next, we exported hemoglobin data and carried out separate group-level analyses for each hemoglobin (HbO and HbR) in IBM SPSS Statistics v. 25 software. A one-way ANOVA was performed in order to determine if there was a statistically significant difference between HbO and HbR values for each emotion face condition. Correlations were then used to probe significant associations between HbO and HbR values during each condition and the various temperament and maternal stress scales. Multiple regressions were then used to identify significant temperament and maternal stress predictors of brain activation. Given the exploratory nature of our analyses we did not correct for multiple comparisons (Ravicz, 2015).

3. Results

To assess our first aim, the neural correlates of infant emotion face processing, the main effect of the emotion faces condition was examined using a one-way ANOVA to assess significant differences in HbO and HbR activation between the three emotion faces conditions, which proved to be non-significant (see Table 2). However, different channels were significantly activated during each emotion condition (see Fig. 3).

Table 3 presents descriptive statistics and intercorrelations between study variables. Preliminary analyses were conducted to determine whether we needed to control for any of our demographic variables (i.e., age, maternal education, household income, race/ethnicity, gender, and marital status). There were no significant correlations with demographic variables so these variables were not included in further analyses.

To preliminarily assess our second and third aims, correlations between temperament, maternal stress and total activation of HbO and HbR were computed. These analyses revealed the total stress scale of the PSI-SF was significantly positively associated with HbR activation during both the angry and sad emotion faces conditions (see Table 3). The parent-child dysfunctional interaction subscale of the PSI-SF was significantly positively associated with HbR values during the happy faces condition. Negative emotionality (a subscale of the IBQ-R-SF) was significantly associated with all conditions of the task, as well as activation in both HbO (negative correlations) and HbR (positive correlations) and was most strongly correlated with the happy faces condition in both HbR and HbO (see Table 3).

3.1. Predicting brain activation from infant and maternal characteristics

In order to further examine our second and third aims; whether infant temperament and maternal stress were unique predictors of infant brain activation during the emotion face processing task, we utilized multiple regressions, using only variables that revealed significant correlations with hemoglobin activation (i.e., negative emotionality, total parenting stress, and parent-child dysfunctional interaction). Three multiple regression models were conducted: (1) negative emotionality, total parenting stress, and the interaction of these variables in predicting HbR activation during the sad face condition, and (2) negative emotionality, total parenting stress, and the interaction of these variables in predicting HbR activation during the angry face condition, and (3) negative emotionality, parent-child dysfunctional interaction, and the interaction of these variables in predicting HbR activation during the happy face condition. Maternal reports of total stress and the parent-child dysfunctional interaction scale from the PSI-SF and maternal reports of infant temperament were centered prior to the inclusion in the analyses (see Tables 4 and 5).

The results of the first multiple regression analysis demonstrated that although only total parenting stress was a unique predictor of HbR activation during the sad face condition (see Table 4), the interaction between total parenting stress and negative emotionality was significant (see Table 4), $F(3, 12) = 8.38$, $p < .02$, $R^2 = .83$, such that for infants whose mothers rated themselves as less stressed, higher negative emotionality predicted higher HbR activation to the sad faces condition, $b = 16874.89$, $t(12) = 4.36$, $p < .01$. Additionally, for infants whose mothers self-reported an average amount of stress, higher negative emotionality also led to more HbR reactivity during the sad faces condition, $b = 10{,}125.66$, $t(12) = 4.90$, $p < .01$. For mothers who rated themselves as highly stressed, there was no significant interaction with infant temperament in predicting HbR activation during the sad faces condition, $b = 3376.42$, $t(12) = 1.31$, *ns*.

The second multiple regression revealed a similar pattern of results, with total parenting stress being a significant predictor of HbR activation during the angry faces condition, as well as the interaction between total parenting stress and negative emotionality (see Table 4). Again, there was a significant interaction between mothers who reported low maternal stress and high negative emotionality, $b = 14376.74$, $t(12) = 9.91$, $p < .01$, as well as mothers who reported average stress and high negative emotionality $b = 7930.74$, $t(12) = 10.22$, $p < .01$. The interaction between reports of high total maternal stress and high negative emotionality was not significant $b = 1484.73$, $t(12) = 1.53$, *ns* (see Table 4).

For the final multiple regression analysis, infant negative emotionality and parent-child dysfunctional interaction were both found to be unique predictors of HbR activation during the happy faces condition. However, the interaction between these two variables was not significant (see Table 5).

4. Discussion

Humans are an altricial species, which means that infants are vulnerable when born and require the constant care and attention of a caregiver to survive. Just as hatchlings cannot survive outside the nest and rely on their mothers for food and warmth, human infants rely

on their caregivers to provide them with safety and physiological co-regulation (Bornstein et al., 2017; Sameroff, 2009; Swain & Ho, 2017; Swain, Lorberbaum, Kose, & Strathearn, 2007; Tottenham, 2012). During the first year, the infant brain matures at a rapid pace, and the quality of early caregiving plays an essential role in facilitating growth, ultimately influencing how an individual will respond to novel and/or stressful situations throughout life (Schore, 2001). Although the long-term effects of environmental input on the brain can be observed both behaviorally and through neuroimaging, we still know little about how the brain processes emotions in infancy. This study augments the current literature by providing contextual information about the early caregiving environment and infant temperament to an understanding of emotion face processing by human infants.

With regard to our first aim, we hypothesized that the main region of interest involved in emotion face processing was the mPFC. Previous studies have focused on this area and its connection with social-emotional processing (Grossman, 2013), and the current study confirmed significant brain activation in the mPFC during the emotion faces task. The mPFC as a whole did not respond cohesively to the task, and different parts of the mPFC activated during each emotion condition (see Fig. 3). This may speak to the complexity of the mPFC as a whole, and that different regions of this structure are involved in distinctive aspects of emotion processing. Therefore, neural processing may differ for each emotion, meaning that our understanding of emotions should be based on each emotion individually, versus emotions as a whole.

Regarding our second and third aims, and hypotheses that infant temperament and maternal parenting stress would influence brain activation, we did find these factors to be associated with significant activation in HbO and HbR during the presentation of emotion faces. Total parenting stress was significantly and positively associated with HbR activation during the sad and angry faces conditions and the parent-child dysfunctional interaction subscale was significantly and positively associated with HbR activation during the happy faces condition, independent of the infant's negative emotionality. Although both total parenting stress and infant negative emotionality were positively correlated with the sad and angry faces HbR condition, only total parenting stress was a significant predictor in the regression analysis. The interaction between total parenting stress and negative emotionality was significant for both low and average maternal stress such that mothers who reported low and average stress, when combined with infant high negative emotionality predicted more HbR activation during the angry and sad faces condition. In the case of predicting happy face condition HbR activation, both negative emotionality and parent-child dysfunctional interaction were significant predictors, although the interaction between these two variables was not. These results fit with recent neuroimaging showing that a parenting intervention-related decrease in parenting stress was associated with increased child-focused responses in social brain areas that can be modulated by psychotherapy (Swain et al., 2017), and indicate how potentially plastic maternal characteristics and quality of caregiving can influence infant brain activation.

Our hypothesis that infants with high negative emotionality would demonstrate the most activation in response to happy faces was not confirmed by multiple regression analyses. Instead, we found negative emotionality to be a significant predictor of level of HbO

activation of all conditions. The pattern of significant brain activation in response to *all* emotion conditions for infants high on negative emotionality may reflect the fact that these children may be more sensitive and reactive to their environment in general (Belsky, Bakermans-Kranenburg, & Van IJzendoorn, 2007). Regardless, it is clear from the current results that infant negative emotionality was strongly linked with infants' emotion face processing, and future research is needed to examine these relations further.

Although the findings with respect to total parenting stress and the interaction between total parenting stress and negative emotionality predicting HbR activation during the angry and sad faces conditions does not support the novelty hypothesis, this may be reflective of the intersecting relationship between negative emotionality and maternal stress. Behavioral research has highlighted the strong relationship between maternal stress and negative emotionality, and this study provides evidence of this association in brain activation (Gartstein & Rothbart, 2003; Hartman, Freeman, Bales, & Belsky, 2018). This may be one reason why the interaction between total maternal stress and negative emotionality was not significant—because at a certain level the impact of maternal stress on the development of attachment and self-regulation behavior may eclipse the influence of temperament on brain activation. Finding the same pattern of impact of maternal stress of brain activation during both the angry and sad faces condition but not for the happy face condition suggests a similarity of emotional response with regard to anger and sadness that is not present during the happy face condition, providing evidence for a differential response to positive and negative emotions.

Additionally, high parent-child dysfunctional interaction being related to increased brain activation during the happy faces condition was consistent with our hypothesis that infant brain regions will be more activated by novel experiences (i.e. infants with dysfunctional relationships with their mothers have likely experienced less happy faces). However, there are many different types of dysfunctional parent-child interactions involving both hostility and withdrawal, so we are unable to disentangle if parent-child dysfunction in the current study is assessing greater anger or sadness in the infant's home environment. Because the parent-child dysfunctional interaction subscale only assesses maternal perceptions, and not how the mother interacts with the child, future research should be completed with clinical populations and observational measures to examine how different types of dysfunctional parent-infant interactions influence the infant brain. Lastly, Azhari et al. (2019) demonstrated that hyperscanning can be used to examine brain-to-brain synchrony in mother-child dyads. Because of the transactional nature of maternal characteristics and the development of infant emotion regulation future research should consider examining brain-to-brain attunement of the mPFC to further our understanding of these mechanisms.

Lastly, inverted hemodynamic responses were observed, such that HbO activations were negative and HbR activations were positive, when the canonical hemodynamic response is an increase in HbO and decrease in HbR. This inverted response is not unusual during infancy, when a greater variety of hemodynamic responses are observed, and these patterns are still developing (Watanabe et al., 2017). Other factors, such as cortical region and complexity of stimuli, have also been found to influence the shape and value of HbO and HbR activation (Issard & Gervain, 2018). It is thought that an increase in HbR activation

may represent a less mature hemodynamic response and suggests that for infants it is important to examine both types of hemodynamic response (Bortfeld, Wruck, & Boas, 2007).

4.1. Limitations and future directions

This study has several major limitations including lack of diversity and low statistical power as a result of the small sample size, which limits the generalizability of our findings. Additionally, although fNIRS allows for more movement than other neuroimaging techniques, the equipment used in the study was not specifically designed for infants and, even with modifications, the cords attached to the infant cap were often heavy on the infants' heads. The cap itself needed to be tight enough on the infant's head so that the source and detector optodes could transmit information about brain activation for the fNIRS machine which may have also been uncomfortable for the infants and increased our termination rate. Ultimately, we wanted to be mindful and aware of the infants' experience and mothers' comfort with experimental procedures so erred on terminating the lab session at signs of infant emotional distress.

4.2. Conclusions—This study underscored the importance of examining infant brain activation in response to emotion faces, as well as additional factors such as differences in infants' emotional dispositions, maternal stress, and the larger context of parent-child dynamics. Ultimately, these variables were related to brain activation in the mPFC, a ROI found in previous research on emotion regulation (Gee et al., 2013). The development of the infant brain is a reflection of a relational environment and adding to our understanding of how "outside" factors "get under the skin" and result in internal emotional experiences will be crucial in understanding fully the infant emotional brain.

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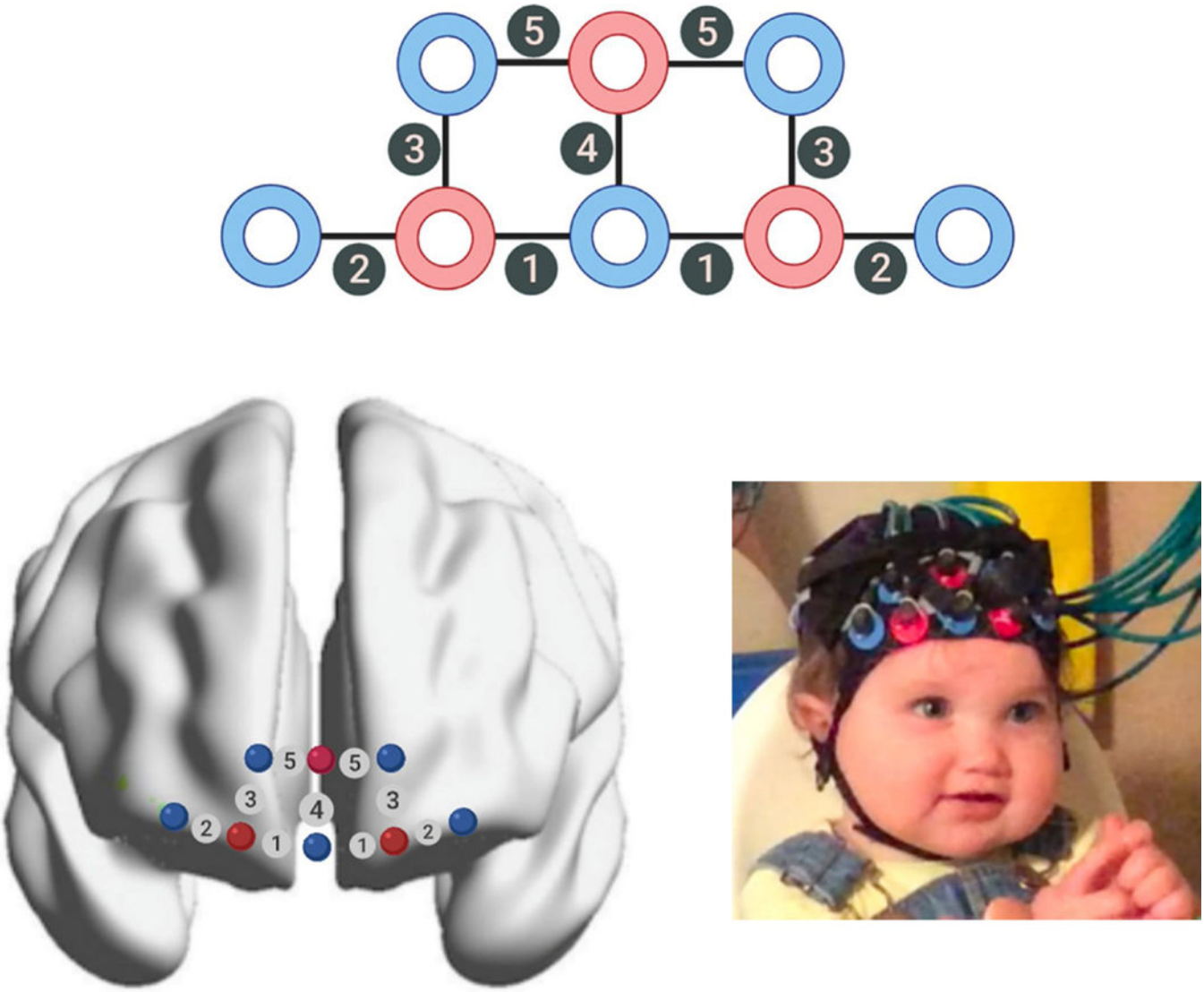

Fig. 1.

Functional NIRS probe configuration, 3D brain template with probe-set overlay. Probe set and channel configurations denote connections between sources and detectors. Red and blue optodes correspond to source and detector placement at a distance of 2.5 cm over an average brain template. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

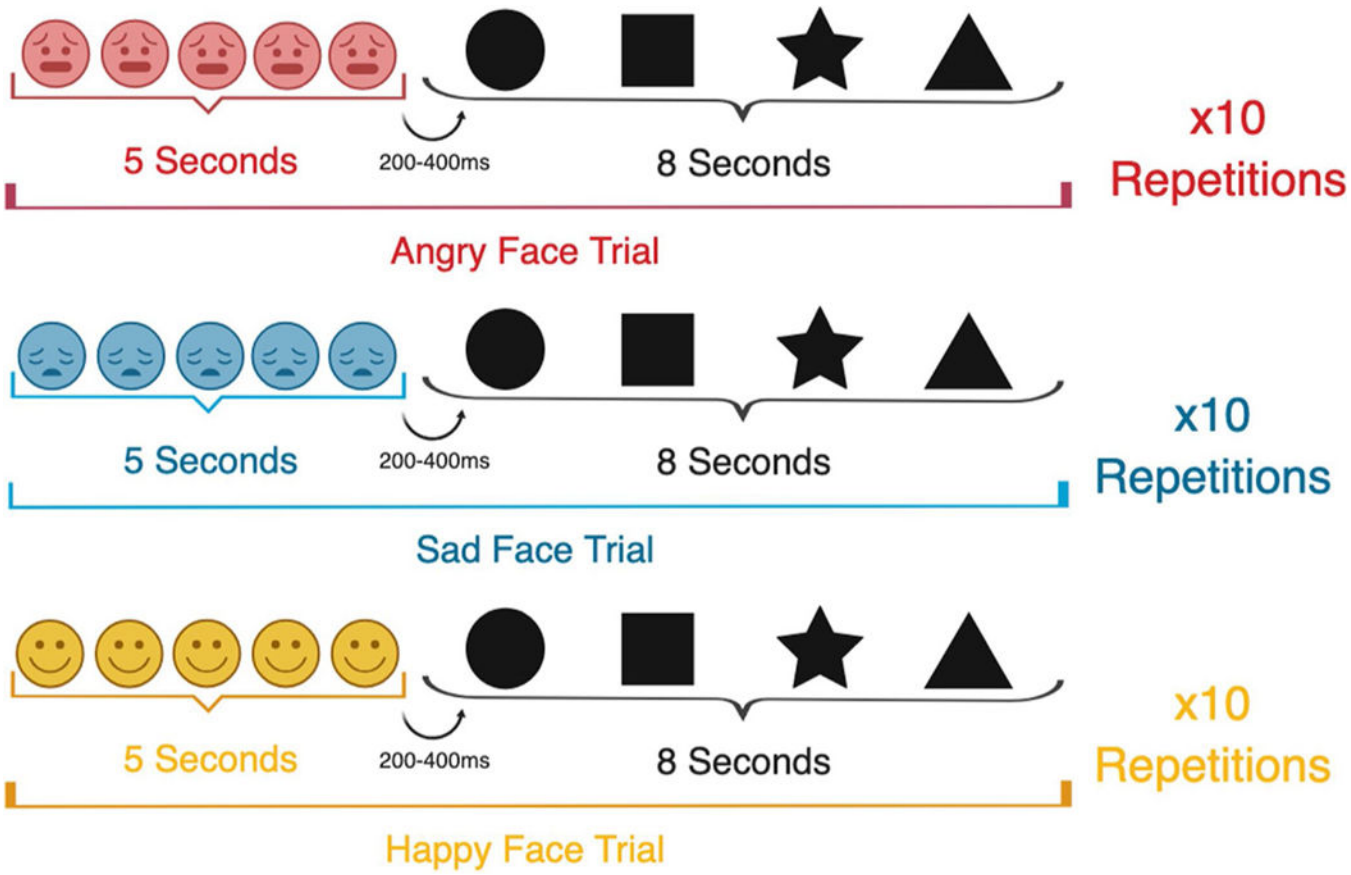

Fig. 2.
Emotion faces task trials.

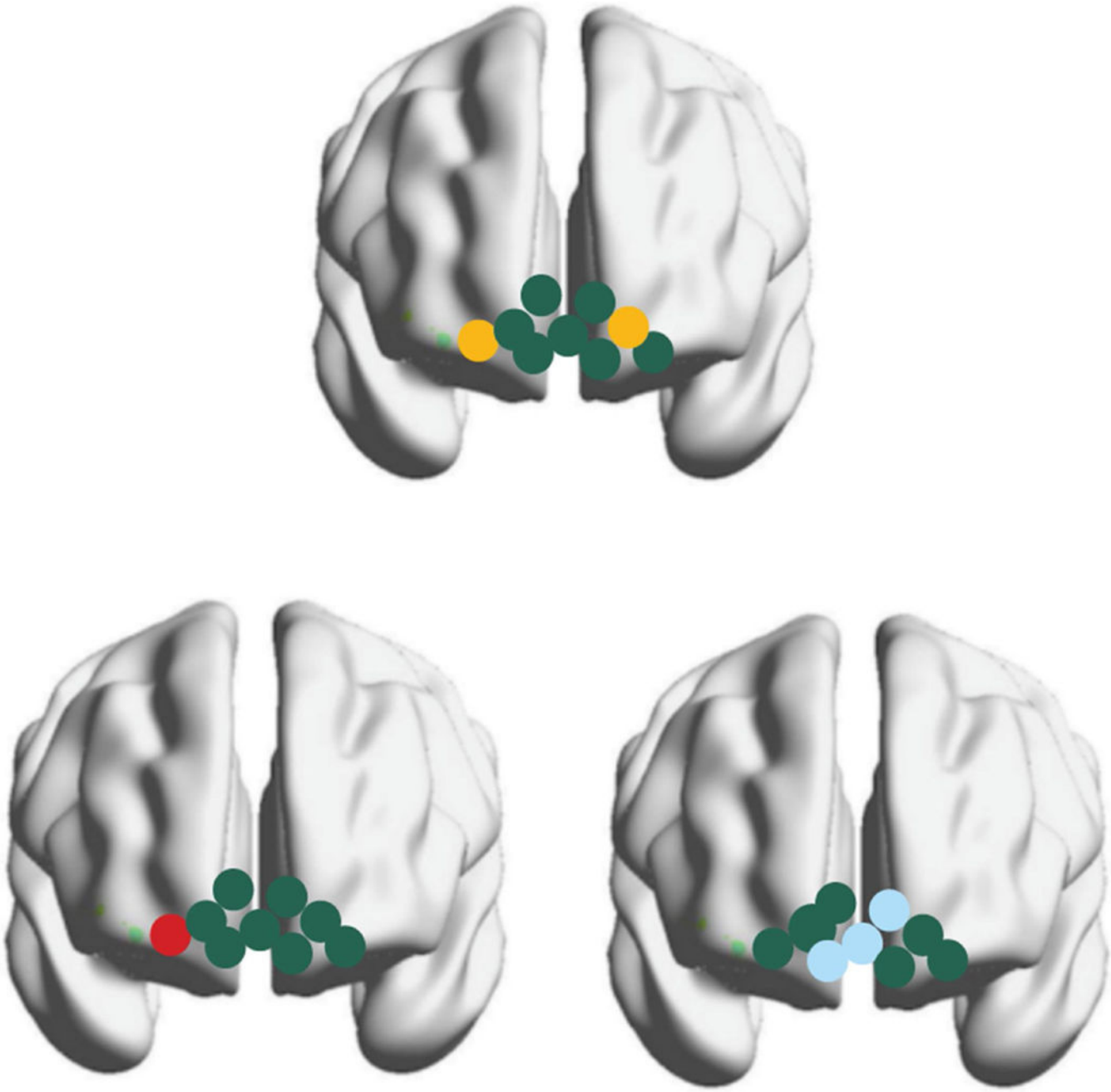

Fig. 3.

3D brain activity effects for significant HbO channels during the emotion faces task. Yellow = Happy face condition, Red = Angry face condition, Blue = Sad face condition. Green = > .05. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 1

Sample Characteristics (N = 16).

	%
Maternal education	
Associate's degree	7%
Vocational degree	7%
Some college	14 %
Bachelor's degree	43 %
Master's degree	22 %
Doctorate	7%
Marital status	
Married	94 %
Partnered	6%
Household income	
10,000–30,000	37%
30,000–60,000	6%
60,000–80,000	20.73%
90,000–100,000	25%
> 100,000	19%
Infant gender	56 % (male)
Infant Race/Ethnicity	
Black	6%
White	62 %
Latinx	13 %
Asian	6%
Multiracial	13 %

Table 2

Summary Table for One-Way Repeated Measures ANOVA Comparing Emotion Faces Conditions.

	Condition						
	Angry	Sad	Happy				
Variable	M(SE)	M(SE)	M(SE)	df	F	η_p^2	*P*
HbO	−165107.94(471224.80)	−176503.79(464334.16)	−234168.50(535257.93)	2	2.26	.13	.12
HbR	62316.36(439497.44)	35365.95(448151.26)	29751.99(473698.50)	2	1.43	.09	.26

Table 3

Pearson Correlations Between Total HbO and HbR per Condition, Infant Temperament, and Maternal Stress.

Scale	Happy HbO	Happy HbR	Sad HbO	Sad HbR	Angry HbO	Angry HbR	Surgency/ Extraversion	Negative Emotionality	Orienting/ Regulating	Total Stress	Difficult Child	Parent-Child Dysfunction	Parental Distress
Surgency/ Extraversion	−.145	.319	−.223	.246	−.184	.260							
Negative Emotionality	−.582 *	.698 **	−.627 *	.673 **	−.638 **	.663 *	.590 *						
Orienting/ Regulating	.043	.188	−.028	.167	−.012	.156	.256	−.118					
Total Stress	.177	.512	.271	.697 *	.468	.707 *	−.009	−.280	.594				
Difficult Child	.231	.435	−.002	.414	.039	.340	.104	−.317	.641	.828 **			
Parent-Child Dysfunction	.488	.680 *	.246	.558	.085	.494	−.153	−.368	.651	.751 *	.840 **		
Parental Distress	−.268	−.014	.298	.420	.723 *	.555	−.003	.080	−.045	.417	−.114	−.214	
M	−234168.50	29751.99	−176503.79	35365.95	−165107.94	62316.36	5.08	3.62	4.92	141.11	46.44	54.22	40.44
SD	535257.93	473698.50	464334.16	448151.26	471224.80	439497.44	0.64	0.75	0.47	14.68	7.95	6.14	8.35

Note.

* $p < .05$.

** $p < .01$.

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Table 4

Multiple Regression Analysis of Total Maternal Stress and Negative Emotionality Predicting Happy, Sad, and Angry Face HbR Activation.

HbR	Predictor Variables	*B*	*SE(B)*	*β*	R^2	*F*
Happy	Total Stress	4183.83	2652.71	.51	.26	2.49
	Negative Emotionality	96892.57	60497.32	.65	.48	2.80
	Total Stress x Negative Emotionality	−4987.37	5643.49	−3.66	.55	2.06
Sad	Total Stress	47990.75	15269.18	4.79	.49	6.60*
	Negative Emotionality	1677089.79	604034.36	6.91	.60	4.56
	Total Stress x Negative Emotionality	−11132.03	4215.46	−6.67	.83	8.38*
Angry	Total Stress	44094.64	5730.56	5.91	.50	6.98*
	Negative Emotionality	1571793.38	226695.71	8.69	.58	4.10
	Total Stress x Negative Emotionality	−10631.89	1582.07	−8.55	.96	3.93*

Note.

*$p < .05$.

**$p < .01$.

Table 5

Multiple Regression Analysis of Parent-Child Dysfunctional Interaction and Negative Emotionality Predicting Happy, Sad, and Angry Face HbR Activation.

HbR	Predictor Variables	*B*	*SE(B)*	*β*	R^2	*F*
Happy	Parent-Child Dysfunction	17929.34	3609.93	.92	.46	6.03*
	Negative Emotionality	127683.42	36555.85	.65	.82	13.94**
	Parent-Child Dysfunction x Negative Emotionality	9303.38	20648.76	2.77	.85	9.43
Sad	Parent-Child Dysfunction	−42422.54	822.42.76	−1.77	.31	3.17
	Negative Emotionality	−887275.49	1359349.55	−3.66	.45	2.40
	Parent-Child Dysfunction x Negative Emotionality	17577.94	24276.39	−3.66	.49	1.65
Angry	Parent-Child Dysfunction	−20621.47	69953.21	−1.16	.24	2.26
	Negative Emotionality	−467096.39	1156221.73	−2.58	.32	1.40
	Parent-Child Dysfunction x Negative Emotionality	9303.37	20648.76	2.77	.35	.88

Note.

*$p < .05$.

**$p < .01$.