



## Investigating the association between parity and the maternal neural response to infant cues

Angela N. Maupin, Helena J. V. Rutherford, Nicole Landi, Marc N. Potenza & Linda C. Mayes


To cite this article: Angela N. Maupin, Helena J. V. Rutherford, Nicole Landi, Marc N. Potenza & Linda C. Mayes (2018): Investigating the association between parity and the maternal neural response to infant cues, *Social Neuroscience*, DOI: [10.1080/17470919.2017.1422276](https://doi.org/10.1080/17470919.2017.1422276)

To link to this article: <https://doi.org/10.1080/17470919.2017.1422276>



Accepted author version posted online: 02 Jan 2018.  
Published online: 08 Jan 2018.



[Submit your article to this journal](#) 



Article views: 32



[View related articles](#) 



[View Crossmark data](#) 

ARTICLE



## Investigating the association between parity and the maternal neural response to infant cues

Angela N. Maupin<sup>a</sup>, Helena J. V. Rutherford<sup>a</sup>, Nicole Landi<sup>a,b,c</sup>, Marc N. Potenza<sup>a,d</sup> and Linda C. Mayes<sup>a</sup>

<sup>a</sup>Yale Child Study Center, Yale University School of Medicine, New Haven, CT, USA; <sup>b</sup>Haskins Laboratories, Yale University, New Haven, CT, USA; <sup>c</sup>Department of Psychology, University of Connecticut, New Haven, CT, USA; <sup>d</sup>Departments of Psychiatry and Neurobiology and CASAColumbia, Yale University School of Medicine, New Haven, CT, USA

### ABSTRACT

Understanding the maternal neural response to infant affective cues has important implications for parent-child relationships. The current study employed event-related potentials (ERPs) to examine patterns in mothers' responses to infant affective cues, and evaluated the influence of maternal experience, defined by parity (i.e., the number of children a mother has) on ERP responses. Eighty-three mothers, three months postpartum, viewed photographs of displays of infant emotional faces (sad or happy) and listened to infant cries of different distress levels and a control tone. Maternal neural response was modulated by the emotional content of the auditory stimulus, as indexed by the N100 amplitude and latency. However, response to infant faces was not modulated by the emotional content of the stimuli as indexed by the N170. Neither N100 nor N170 were affected by parity. Maternal engagement with auditory stimuli, as indexed by the P300, was modulated by the emotional content of the cry and was affected by parity. A similar parity effect was observed for the P300 response to infant faces. Results suggest that parity may play an important role at later stages of maternal infant cue perception.

### ARTICLE HISTORY

Received 8 June 2017  
Revised 30 October 2017  
Published online 9 January 2018

### KEYWORDS

Parity; mothers; parenting; EEG/ERPs; infant faces; infant cries

The transition to parenthood marks an important developmental period accompanied by significant neurobiological, hormonal, and psychological changes that facilitate critical maternal behavior necessary for infant survival and the emerging dyadic relationship (Barrett & Fleming, 2011; Gonzalez, Atkinson, & Fleming, 2009). Much of this research, however, has been limited to primiparous mothers – or mothers with only one child – overlooking the potential importance of multiple reproductive and caregiving experiences that may shape or reinforce changes at neurophysiological and psychological levels. Therefore, assessing relations between maternal experience and neural responses to infant cues is important for understanding mother-infant relationships and may have important translational implications in parenting research.

Caring for newborns requires sensitive and timely parental responses to affective cues and relies on parents' abilities to rapidly decode and respond to cues, such as emotional expressions (e.g., smiles, distress) and vocalizations (e.g., cries). Despite behavioral evidence of the intuitive nature of rapid parental response to infants' cues (Papoušek, 2000), little is known about the neural bases of these responses and how they differ based on parity.

Neuroimaging research is beginning to unpack the neural correlates of parent-child interactions to provide a deeper understanding of parental responses to infant affective cues. Much of this research relies on functional magnetic resonance imaging (fMRI), which provides information about the neural regions recruited when parents engage with infant cues, but has less temporal precision than electroencephalography (EEG) and event-related potentials (ERPs) (Maupin, Hayes, Mayes, & Rutherford, 2015). Understanding differences in very rapid brain responses to infant affective cues could inform the understanding of parent-infant relationships and may help promote interventions targeting positive styles of parenting. To our knowledge, no research has yet examined variability in neural responses to infant cues with respect to maternal parity (i.e., the number of children a mother has). Primiparous as compared to multiparous mothers may differ in the perception and processing of infant affective cues given the latter groups' prior experiences with their own infants. Therefore, in the current ERP study, we examined whether parity affected maternal neural responses elicited by emotional, both positive and negative, infant cues (cries and facial affect) in a large community sample of mothers with infants.

## **Parity as an indicator of prior reproductive experience**

Pre-clinical and clinical research suggests that prior reproductive and child rearing experience may contribute to short and long-term neurobiological and hormonal changes to support differential, and perhaps more efficient, expressions of maternal care (Bridges, 2015; Morgan, Watchus, Milgram, & Fleming, 1999); however, this research is still in its own infancy (Maupin, Roginiel, Rutherford, & Mayes, 2016). At a neurobiological level, structural and functional brain changes accompany the transition to motherhood, with the medial preoptic area (MPOA) of the hypothalamus and ventral bed nucleus of the stria terminalis (BNST) implicated in the initiation and maintenance of maternal behaviors in preclinical samples (e.g., rats; Numan, 2006). Notably, damage to these neural connections has consistently resulted in abolished caregiving behaviors such as pup retrieval and nest building, as well as diminished nursing behavior. Maternally experienced rats, as compared to postpartum inexperienced rats, show greater *fos* expression – a marker of neural activity – in the MPOA (Fleming & Korsmit, 1996) with lower *fos* expression in areas thought to inhibit maternal behaviors, such as the medial amygdala (Morgan et al., 1999), suggesting differential neurobiological profiles based on parity. Similarly, alterations in hormone release have been found, particularly in preclinical samples, based on prior reproductive experience (Bridges, 2015).

Behaviorally, multiparous mothers, as compared to primiparous mothers, appear to more efficiently and effectively respond to infant cues, differentiating distress cues from non-distress cues (Boukydis & Burgess, 1982), as well as applying individualized soothing techniques based on the qualitative nature and interpretation of infants' cries (Drummond, McBride, & Weibe, 1993). Moreover, multiparous mothers have been found to rate infants' cries as less piercing (Boukydis & Burgess, 1982), suggesting a decreased level of sensory arousal to cry stimuli in general – likely due to prior experience responding to and managing infant distress. These differential responses are, perhaps, supported by differential neural expressions critical to parental responses to infant emotional cues (Maupin et al., 2016). In the current study, we probed maternal neural responses by presenting mothers with infant affective stimuli and measuring their ERPs, and evaluating whether these responses differed based on parity.

## **Maternal neural responses to affective infant cues**

Recent ERP studies have begun to examine neurophysiological correlates of infant cue perception in parents. Neural sensitivity to infant cues has been evaluated,

using fMRI, through parental responses to infant vocalizations and photographs of infant emotional faces – given that these are both salient signals of communication from the infant (Squire & Stein, 1993). Few ERP studies to date have examined neural correlates of infant cry and face perception in adult and maternal samples (N100 and N170, respectively) as well as attentional engagement with infant stimuli (P300), and no known studies have evaluated whether ERP responses differ based on maternal parity (Maupin et al., 2015).

With respect to infant cry perception, new mothers compared to non-mothers, have evidenced a heightened detection and emotional response to infant cries, as well as a more general increased arousal to non-cry auditory stimuli (Purhonen, Kilpelainen-Lees et al., 2001; Purhonen, Valkonen-Korhonen, & Lehtonen, 2008). Specifically, new mothers (3 days postpartum) evidenced enhanced N100 amplitudes in response to their own infant's cries and neutral word stimuli compared to non-mothers (Purhonen, Kilpelainen-Lees et al., 2001). This early finding was replicated in a subsequent study; in new mothers as compared to non-mothers, N100 amplitudes in response to their own infant cries and tones were enhanced. However, no group differences were found for later ERP components (N200, P300), suggesting that the N100 may be uniquely situated to capture group differences in the initial detection of auditory stimuli, including infant cries (Purhonen et al., 2008). These past studies examined only one exemplar of infant cry and did not account for parity; whether the maternal N100 is related to varying intensities of infant cry (e.g., high-distress, low-distress) and maternal parity is unknown, but plausible given differential ratings of infant distress at the behavioral level (Boukydis & Burgess, 1982).

The transition to parenthood is also marked by an increased exposure to infant faces that provides critical cues to facilitate parental responses. Because the N170 component has been used extensively to examine the specificity of adult face perception (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion et al., 2000), recent studies have begun to explore infant face perception, as indexed by the N170. Similar to the adult face perception literature, there are mixed findings regarding whether the N170 is modulated by infant emotional expressions, with some studies showing N170 sensitivity, particularly in response to infant distress (Peltola et al., 2014; Proverbio, Brignone, Matarazzo, Del Zotto, & Zani, 2006; Rodrigo et al., 2011), and other studies evidencing no modulation of the N170 by infant emotional expression (Malak, Crowley, Mayes, & Rutherford, 2015; Noll, Mayes, & Rutherford, 2012). In contrast to the N170, the later-peaking P300, which is a marker of stimulus engagement and attentional processing (Luck, 2005), is sensitive to the emotional content of infant face stimuli. Both biological

and foster mothers have evidenced a greater P300 response when viewing their own infant faces compared to unfamiliar infant faces (Bick, Dozier, Bernard, Grasso, & Simons, 2013; Grasso, Moser, Dozier, & Simons, 2009); however, maternal responses to varying infant emotional expressions were not systematically evaluated in these studies. Proverbio and colleagues (2006) found the P300 was sensitive to emotional facial expression, with infant distress eliciting the greatest P300 response. Evaluating responses to emotional expressions may provide important information on how infant affect can elicit neural response patterns that may promote specific parenting behaviors.

While data support the notion of maternal neural sensitivity to infant affective cues, especially to distress-related cues, there are likely to be significant sources of variability that may influence these findings (Maupin et al., 2015). First, much work in this area is limited by small sample sizes and variability in infant ages. Further, most studies report primarily ERP amplitudes and have not considered latency, which may represent a better measure for exploring time courses of infant cue perception. Finally, these studies typically have limited assessment of maternal characteristics, such as maternal parity, that may affect the findings and inform interpretation. Therefore, it is important to understand how normative maternal factors (e.g., primiparous vs. multiparous maternal status) may contribute to the perception and processing of affective infant cues, which may have important implications for measuring these processes in clinical samples of mothers (including those with post-partum depression, anxiety disorders, and addiction), as well as informing the delivery of parenting programs.

### **The present study**

Utilizing a large community sample of new and experienced mothers at a comparable period postpartum, the current study sought to address previous methodological limitations by evaluating ERP amplitudes and latencies in response to unfamiliar infant affective cues and examining how maternal parity related to these responses. To our knowledge, this paper is the first to evaluate the association between parity and maternal neural responses to infant affective cues. Infant affective cues in this study included faces with varied infant emotional expressions (happy, sad, neutral) and vocalizations (high- and low-distress cries). Primary study aims were to evaluate maternal ERP responses to infant facial and auditory affective cues in a normative community sample and explore how maternal parity relates to these neural responses. Given previous work on the relationship between infant affective cues

and ERP response, we hypothesized affective modulation of the N100 (in response to cries) and P300 (to faces and cries). With respect to the N170 we did not have an *a priori* prediction given inconsistent findings on whether this component is modulated by the emotional content of face stimuli (Malak et al., 2015; Noll et al., 2012; Peltola et al., 2014; Proverbio et al., 2006; Rodrigo et al., 2011). For our second aim, we examined parity given longstanding interest in parity effects in human and preclinical parenting research (e.g., Ferber, 2004; Moltz, Robbins, & Parks, 1966). We hypothesized that ERP response to all infant affective cues would be greater in primiparous relative to multiparous mothers based on prior research indicating increased sensitivity in this population.

## **Method**

### **Participants**

The Human Investigations Committee at the Yale University School of Medicine approved all procedures prior to participant recruitment. Ninety-three mothers were recruited from the local and surrounding community as part of a larger program of research investigating maternal sensitivity to infant stimuli. All participants provided informed consent, and data were collected approximately 3 months postpartum ( $M = 1.70$ ;  $SD = 1.03$ , range = 0 to 5 months). Although this was a community sample, substance use has been reported in maternal samples recruited from this area (Landi et al., 2011); therefore, all women were screened and showed no evidence of substance use during pregnancy or the postpartum period (e.g., negative urine toxicology screening and no self-report of use). Ten mothers were excluded from analyses for not completing the paradigm or not having enough trials per condition, even after applying Ocular Artifact Removal (OAR; described below). In the remaining sample ( $n = 83$ ), mothers were on average 29 years old ( $SD = 6.04$ , range = 17 to 42). Mothers were primarily Caucasian ( $n = 41$ , 49%), African American ( $n = 25$ , 30%), Hispanic/Latina ( $n = 8$ , 10%), and Asian ( $n = 5$ , 6%). Twenty-eight mothers were single (35%) and fifty-one were married (64%). Fifty-three mothers (66%) were primiparous (first-time mothers) and twenty-seven (34%) were multiparous mothers (more than one child; number of children ranged from 2 to 6). There were no differences in age between primiparous and multiparous mothers ( $t(78) = -1.12$ ,  $p = .27$ ). Seventy-three (96%) mothers had completed high school. All demographic information was assessed by self-report measure during the EEG visit. Mothers were compensated \$50 dollars for their participation and infants received an age-appropriate toy.

### Apparatus and stimuli

All stimuli were presented on a Pentium-IV computer controlling a 51 cm color monitor (75Hz, 1024 by 768 resolution) running E-Prime 1.2 software (Schneider, Eschman, & Zuccolotto, 2002). Displays were viewed at a distance of approximately 70 cm in a sound-attenuated room with low ambient illumination. Continuous EEG was recorded using Net Station 4.2.1 with a sampling rate of 250 Hz and high impedance amplifiers (0.1 Hz high pass, 100 Hz low pass). A 128 Ag/AgCl electrode sensor net (Electrical Geodesics, Inc.) was placed on each participant's head and fitted according to manufacturer specifications. All electrodes were spaced evenly and symmetrically to cover the scalp from nasion to inion and from left to right ear. Prior to application, the net was soaked in a warm potassium chloride electrolyte solution to improve the signal detected at the scalp. We used a Cz electrode reference during EEG recording, and all electrode impedances were kept below 40 k $\Omega$ .

### Auditory stimuli

All stimuli were unfamiliar to the participant. Cry stimuli were two-second segments extracted from longer recordings used by Gustafson and Green (1989). These cries were recorded from healthy infants who ranged in age from 27–32 days. Cries were recorded in the infants' homes before the infants were fed, with no additional external stimulation. Detailed information about the recording procedure has been reported elsewhere (Gustafson & Green, 1989). For the current study, we chose four two-second segments of cries from two infants that we determined to be either of high- or low-distress, resulting in both a high- and low-distress exemplar from each infant. We chose to use multiple exemplars for each level of distress in order to avoid measuring differences associated with the particular physical properties of any one cry. Distress level was verified by an independent group of ten nulliparous participants (aged 19–24 years), as reported previously in Landi et al. (2011). Specifically, participants rated each cry on a scale of 1 (calm) to 10 (distressed). High-distress cries were rated as significantly more distressed ( $M = 8.06$ ,  $SD = 1.3$ ) than low-distress cries ( $M = 3.54$ ,  $SD = 0.82$ ) [ $t = 11.52$ ,  $p < .001$ ]. In addition to cries, participants also heard a "neutral" stimulus. The neutral stimulus was a 220-hz pure tone. Additional information on the acoustic properties of the cries and neutral stimulus is contained in the Appendix.

### Visual stimuli

All infant stimuli were unfamiliar to the participants. Digital photographs of infant faces between the ages of five and ten months were adapted from previous work (Strathearn & McClure, 2002). Twenty-one images from

each of the six infants, resulting in a total of 126 color images, were equally balanced for both gender and race (Caucasian and African American). We chose images of Caucasian and African American infants in order to be consistent with the racial identity of the participating moms. The infant face images displayed affect states of happy, neutral, and sad. Infant face images were on average 7.63° by 8.07° (9.32 cm by 9.88 cm) in size and were presented on a black background. As reported in Landi et al. (2011), all face stimuli were pre-rated by an independent group of 11 nulliparous participants, who were members of the research community and had no explicit knowledge of the study goals, on a scale of 1 (happy) to 10 (distressed) to assess the perceived affect level. A repeated measures ANOVA of the infant face ratings on the three emotions (happy, neutral, sad) was significant [ $F(2, 20) = 146.43$ ,  $p < 0.001$ ]. Pairwise comparisons showed that happy faces ( $M = 2.19$ ,  $SD = 0.24$ ) were rated as significantly less distressed (Mean difference =  $-1.55$ ,  $SD = 0.37$ ,  $p = 0.006$ ) than neutral faces ( $M = 3.74$ ,  $SD = 0.43$ ). Neutral faces were rated as significantly less distressed (Mean difference =  $-4.16$ ,  $SD = 0.41$ ,  $p < 0.001$ ) than sad faces ( $M = 7.90$ ,  $SD = 0.11$ ).

### Design

Trials consisted of a centrally presented fixation cross, followed by the stimulus (cry/tone or face), and then a blank screen. The inter-trial interval, which was jittered randomly and varied during both the fixation cross and blank screen, ranged between 1400–2000 ms to avoid expectancy effects of stimulus onset. Face stimuli were presented for 500 ms and auditory stimuli were presented for 2000 ms. In the visual condition, there were 42 trials representing each of the happy, neutral, and sad conditions. In the auditory condition, there were 42 trials for high-distress cries, 44 trials for low-distress cries, and 40 trials for the neutral tone. The experiment consisted of 7 blocks of 42 trials, each block containing infant face presentations, auditory presentations (cries or tone), and catch trials (described below), that were quasi-randomly presented, resulting in a total of 294 trials. A total of 252 experimental trials were used in the current study (catch trials were excluded from analyses). This order of presentation was kept constant across participants.

Across the course of the experiment, a one-back memory task was included to ensure participants maintained their attention to stimulus presentation. In these trials, which occurred infrequently (14%), a question mark replaced the fixation cross to indicate a behavioral response was required. Participants were asked to indicate whether the proceeding stimulus was the same or different. Participants used a button box to make their



response and these catch trials were not included in the analysis. The ratio of same and different catch trials was 50/50 and this resulted in an additional 42 trials in the experiment. Mean accuracy on this task was 93% ( $SD = .06$ ) for faces, and 93% ( $SD = .10$ ) for cries. The catch trials were not included in the ERP analyses. These experimental trials were preceded by 8 practice trials to familiarize the participant with the procedure. The experiment took approximately 30 minutes to complete.

## Data analysis

### Preprocessing

EEG data were pre-processed and prepared for statistical analysis using Net Station 4.5. Prior to segmentation, each file was digitally filtered with a 0.1 Hz first-order high-pass filter and a 30-Hz low-pass filter. EEG signal was segmented into epochs of one second, beginning 100 ms before and ending 900 ms after stimulus onset. Net Station artifact detection was set to 200  $\mu$ V for bad channels, 150  $\mu$ V for eye blinks, and 150  $\mu$ V for eye movements. Channels with artifacts in more than 40% of trials were marked as bad channels and replaced through spline interpolation. Following artifact detection procedures, data were re-referenced to the average reference of all electrodes. The data were then baseline corrected to the 100-ms interval prior to stimulus onset. Data were then averaged for each individual across the stimuli conditions. Ocular Artifact Removal (OAR; Gratton, Coles, & Donchin, 1983), using a blink slope threshold = 14  $\mu$ V/ms, was applied where there were fewer than 21 blink and other artifact free trials per condition in the averaged file without using OAR. OAR was applied to data from 59 participants (69%). At completion of preprocessing, there were on average 36 trials per condition across all participants ( $SD = 4$ ).

### Statistical analysis

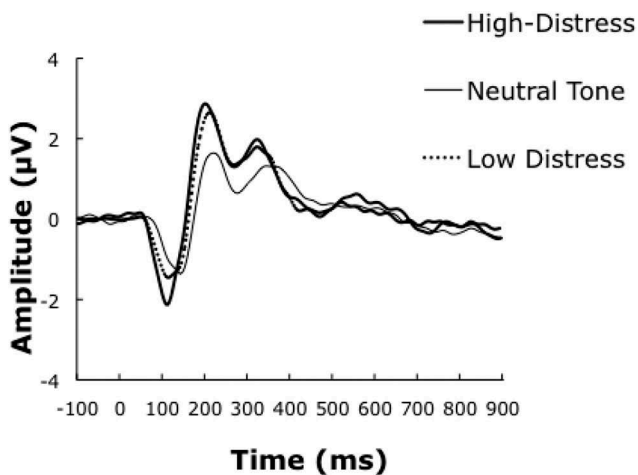
For the analysis of face-processing data, N170 ERPs were assessed at 6 electrodes over the left (58, 59, 64, 65, 69, 70) and right (90, 91, 92, 95, 96, 97) posterior scalp sites. These sites overlap with the 10/20 low-dense array EEG electrode sites T5 and T6 (Bentin et al., 1996; Eimer, 2000) as well as high-dense array EEG electrode sites (McPartland, Dawson, Webb, Panagiotides, & Carver, 2004) that have been used to quantify the N170. The N100 was examined at 16 central electrode sites (CZ, 6, 7, 13, 31, 32, 38, 54, 55, 62, 80, 81, 88, 106, 107, 113). These electrode sites were based on visual inspection of the grand averaged data and existing literature on the N100 in cry perception (Purhonen, Kilpeläinen-Lees et al., 2001; Purhonen, Pääkkönen, Yppäriä, Lehtonen, & Karhu, 2001). The P300 was examined for both faces and

cries and were assessed at six electrode sites (54, 61, 62, 68, 79, 80) that clustered around Pz, consistent with prior research (Bornstein, Arterberry, & Mash, 2013; Grasso et al., 2009; Proverbio et al., 2006).

Our statistical analysis of ERP components mirrored previous work in this area (Proverbio et al., 2006). The time windows for the peak mean N170 ( $M = 126.71$  ms –  $M = 197.65$  ms) and N100 ( $M = 83.67$  ms –  $M = 170.86$  ms) were derived and customized for each individual participant using the Net Station user-defined event function that enables statistical extraction of each component to be representative of the variability in waveforms. Consistent with Proverbio and colleagues (2006), we examined the mean amplitude within the time windows of 200 to 600 following stimulus presentation in our examination of the P300.

Our first analysis focused on replicating and extending the modulation of maternal neural responses to infant cues by affective content. Statistical analysis was conducted separately for each component (N170, N100, P300) on amplitude measures, and separately for latency measures (N170, N100) for each experimental condition using a repeated measures analysis of variance (ANOVA). The N170 data were averaged from electrode sites within the left hemisphere and right hemisphere and were analyzed using a 3 (emotional expression: happy, neutral, sad) by 2 (hemisphere: left, right) within-subjects ANOVA. For the N100, auditory stimuli were averaged together within the central electrode sites and analyzed using a one-way repeated measures ANOVA specifying emotional content (high-distress cry, low-distress cry, neutral tone) as the within-subjects factor. The P300 data were averaged together and analyzed using a one-way repeated measures ANOVA specifying emotional content (either faces: happy, neutral, sad; or cries: high-distress cry, low-distress cry, neutral) as the within-subject factor. Faces and cries were analyzed in separate analyses.

In our second analysis to investigate the influence of parity on maternal neural responses, parity was first correlated with individual ERP components (N100, N170, & P300). Parity was dichotomized to reflect whether a mother was primiparous (first-time mother) or multiparous (more than one child). Next, if a significant association was observed, a mixed between-/within-subjects ANOVA was used to assess the impact of parity, specifying parity as the between-group factor. Effect size is presented as partial eta-squared ( $\eta^2_{\text{partial}}$ ), where .01 represents a small effect size, .06 represents a medium effect size, and .14 represents a large effect size (Cohen, 1988). Greenhouse-Geisser corrections were used when sphericity assumptions were violated.



**Figure 1.** Grand averaged ERP waveforms representing the response to infant cries (N100) in recent mothers ( $n = 82$ ).

## Results

### Infant cry perception

Grand averaged data averaged across the central electrode sites for auditory stimuli (cries and tone) for the N100 are presented in Figure 1.

### N100 amplitude

One participant was removed from analyses due to her outlying neural responses (neutral tone). The N100 amplitude was modulated by the emotional content of the auditory stimulus [ $F(1.70, 137.44) = 14.20, p < .001; \eta^2_{\text{partial}} = .15$ ]. To understand this main effect further, paired t-tests were conducted to compare the amplitude between stimulus conditions. The N100 amplitude was greatest for high-distress cries ( $M = -3.38 \mu\text{V}; SD = 1.80$ ) compared to low-distress cries ( $M = -2.85 \mu\text{V}; SD = 1.65$ ),  $t(81) = -4.92, p < .001; \eta^2 = .23$ , and the neutral tone ( $-2.70 \mu\text{V}; SD = 1.61$ ),

$t(81) = 4.33, p < .001, \eta^2 = .19$ . There was not a statistically significant difference in amplitude response between low-distress cries and the neutral tone,  $t(81) = -1.13, p = .26$ .

Correlations between the N100 amplitude for each stimulus (high-distress cry, low-distress cry, and tone) and parity were then assessed. Parity was not significantly related to maternal neural response to high- ( $r = .09, p = .45$ ) or low-distress cries ( $r = .05, p = .66$ ) or the neutral tone ( $r = .06, p = .63$ ).

### N100 latency

The N100 latency was modulated by the emotional content of the auditory stimulus [ $F(1.62, 132.50) = 87.44, p < .001; \eta^2_{\text{partial}} = .52$ ]. To understand this main effect further, paired t-tests were conducted to compare the

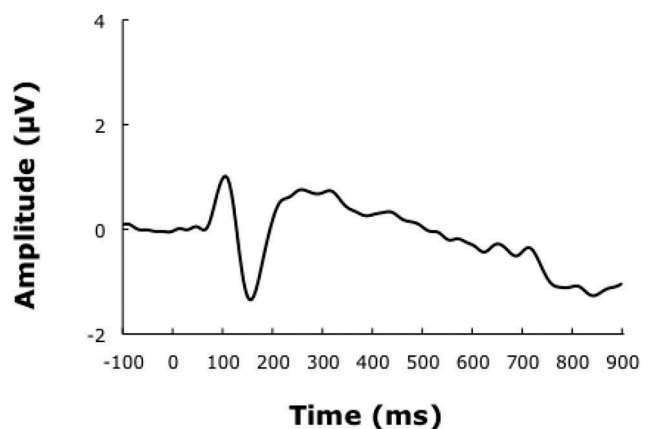
latency between stimulus conditions. The N100 latency was earliest for high-distress cries ( $M = 113.68 \text{ ms}; SD = 13.84$ ) compared to low-distress cries ( $M = 122.59 \text{ ms}; SD = 16.25$ ),  $t(82) = -7.93, p < .001; \eta^2 = .44$ , and the neutral tone ( $M = 134.37 \text{ ms}; SD = 16.82$ ),  $t(82) = -11.74, p < .001, \eta^2 = .63$ . The N100 latency differences between the low-distress cry and neutral tone also differed,  $t(82) = -6.78, p < .001, \eta^2 = .36$ . There were no associations found between N100 emotional content and parity, ( $r = .05, .01, \& .11, p > .30$ ) for high-distress cry, low-distress cry, and neutral tone, respectively. Taken together, these findings suggest that N100 amplitude and latency are both modulated by the emotional content of the stimulus, but are not affected by maternal experience linked to parity.

### Infant face perception

Grand averaged data for visual stimuli (infant faces) averaged across left and right hemisphere electrodes for the N170 are presented in Figure 2.

### N170 amplitude

One participant was removed from analyses due to her outlying neural responses (right hemisphere; sad face). There was no main effect of hemisphere [ $F(1, 81) = 1.42, p = .28; \eta^2_{\text{partial}} = .02$ ] or emotional expression [ $F(2, 166) = .04, p = .96; \eta^2_{\text{partial}} = .00$ ], and no hemisphere and emotional expression interaction was found [ $F(2, 166) = 1.03, p = .36; \eta^2_{\text{partial}} = .01$ ]. Therefore, we averaged across conditions to obtain a single measure of N170 amplitude. Parity was not correlated with N170 amplitude ( $r = -.13, p = .26$ ). Taken together, results suggest that the N170 is not modulated by the



**Figure 2.** Grand averaged ERP waveform representing the early response to infant faces (N170) in recent mothers ( $n = 82$ ). Data are averaged across the three infant emotional expressions and right and left hemisphere.

emotional expressions of the stimuli and is not affected by parity-related maternal experience.

### N170 latency

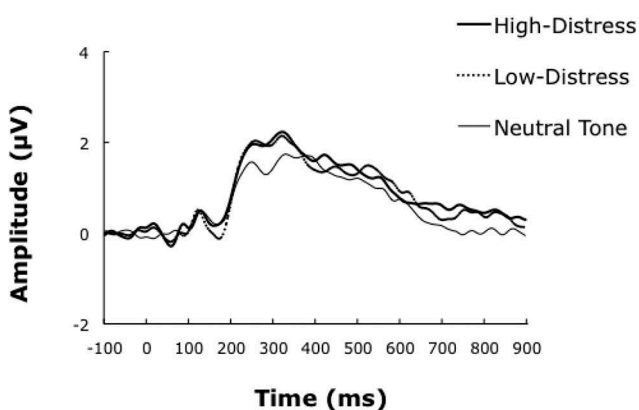
One participant was removed from analyses due to her outlying neural responses (left hemisphere; happy face). As with N170 amplitude analysis, there was no main effect of hemisphere [ $F(1, 81) = 1.37, p = .25; \eta^2_{\text{partial}} = .02$ ], emotional expression [ $F(2, 162) = 2.46, p = .09; \eta^2_{\text{partial}} = .03$ ], or their interaction [ $F(2, 162) = .39, p = .68; \eta^2_{\text{partial}} = .01$ ]. There were no significant associations between each emotional expression condition for each hemisphere and parity. Therefore, we averaged across all conditions to obtain a mean N170 latency measure ( $M = 157.83$  ms;  $SD = 12.90$  ms). No statistically significant associations were found between N170 latency and parity ( $r = -.03, p = .77$ ).

### Late ERP responses

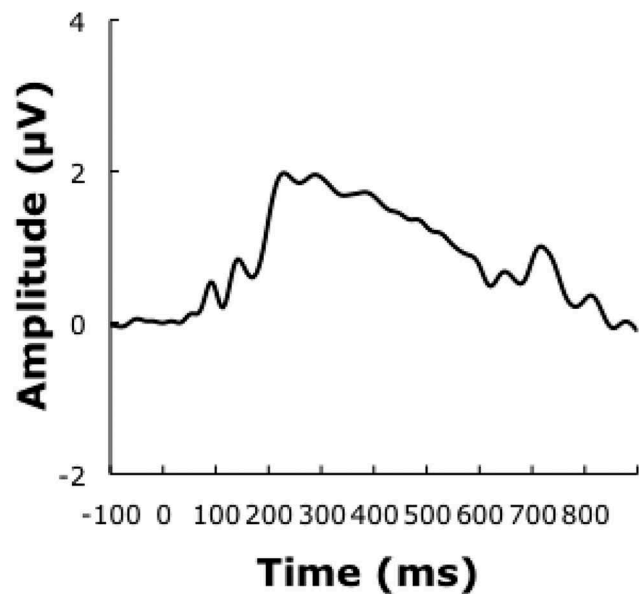
Grand averaged data for auditory stimuli (cries and tone) and visual stimuli (infant faces) for the P300 are presented in Figures 3 and 4, respectively.

### P300 cries

The P300 amplitude was modulated by the emotional content of the auditory stimulus [ $F(2, 164) = 3.14, p < .05; \eta^2_{\text{partial}} = .04$ ]. To understand this main effect further, paired t-tests were conducted to compare the amplitude response between stimulus conditions. The P300 amplitude was greatest for high- ( $M = 1.60$   $\mu\text{V}$ ;  $SD = 1.29$ ) and low-distress cries ( $M = 1.57$   $\mu\text{V}$ ;  $SD = 1.56$ ). Maternal response to high-distress cries was significantly different from their response to a neutral tone ( $M = 1.31$   $\mu\text{V}$ ;  $SD = 1.11$ ),  $t(82) = -2.62, p < .05; \eta^2 = .08$ . The difference between low-distress cries ( $M = 1.57$   $\mu\text{V}$ ;  $SD = 1.56$ ) and the neutral tone followed a



**Figure 3.** Grand averaged ERP waveforms representing the P300 response to infant cries in recent mothers ( $n = 83$ ).



**Figure 4.** Grand averaged ERP waveforms representing the P300 response to infant faces in recent mothers ( $n = 83$ ). Data are averaged across the three infant emotional expressions.

similar trend and approached statistical significance,  $t(82) = 1.86, p = .067$ . There were no statistically significant differences between the neural responses to high- and low-distress cries,  $t(82) = .227, p = .82$ .

Correlations between P300 emotional content (high-distress cry, low-distress cry, and tone) and parity were next assessed. There was a negative correlation between P300 mean amplitude to the neutral sound and parity ( $r = -.35, p < .001$ ), with greater P300 responses to a neutral tone in primiparous mothers. An independent samples t-test confirmed this difference between primiparous and multiparous mothers in their P300 responses to the neutral tone,  $t(79) = 2.73, p < .01$ . Next, a mixed between-within subjects ANOVA was conducted with parity included as the between-subject factor. There was a main effect for emotional content [ $F(1.85, 144.27) = 3.56, p = .03; \eta^2_{\text{partial}} = .04$ ], but emotional content did not interact with parity [ $F(1.85, 144.27) = 1.05, p = .35; \eta^2_{\text{partial}} = .01$ ]. However, the main effect of parity approached statistical significance [ $F(1, 78) = 11.82, p = .09; \eta^2_{\text{partial}} = .04$ ].

### P300 faces

The average P300 amplitude response was 1.57  $\mu\text{V}$  ( $SD = 1.25$ ) to happy faces, 1.54  $\mu\text{V}$  ( $SD = 1.45$ ) to sad faces, and 1.43  $\mu\text{V}$  ( $SD = 1.23$ ) to neutral faces. The P300 amplitude was not modulated by the emotional expression of the visual stimulus [ $F(1.86, 152.81) = .82, p = .44; \eta^2_{\text{partial}} = .01$ ].



Correlations between P300 emotional expression (happy, sad, and neutral) and parity were then examined. Larger responses to neutral faces ( $r = -.23$ ,  $p < .05$ ), and approaching statistical significance for happy faces ( $r = -.20$ ,  $p = .07$ ), were associated with parity. These results suggest a larger response to infant faces in primiparous mothers. An independent samples t-test revealed significant differences between primiparous and multiparous mothers in response to neutral faces,  $t(69.63) = 2.36$ ,  $p = .02$ . With parity included as the between-subject factor, there was no main effect for emotional expression [ $F(2, 156) = .99$ ,  $p = .37$ ;  $\eta^2_{\text{partial}} = .01$ ], and emotional expression did not interact with parity [ $F(2, 156) = .08$ ,  $p = .93$ ;  $\eta^2_{\text{partial}} = .00$ ]. However, there was a main effect of parity [ $F(1, 78) = 4.45$ ,  $p < .05$ ;  $\eta^2_{\text{partial}} = .05$ ].

## Discussion

In a large community sample of mothers with newborn infants, the current study investigated whether parity was associated with maternal neural responses to infant affective cues using ERPs. With respect to infant cry perception, results suggest that the N100 and P300 were both modulated by the emotional content of the auditory stimuli, and the P300 was affected by parity. With respect to infant face perception, we did not find that the N170 and P300 were modulated by the emotional content of the visual stimuli. However, the face-specific P300 was related to maternal parity. To our knowledge, this is the first empirical study to suggest that maternal neural responses to infant affective cues are modulated by maternal parity in a large community sample.

### Early ERP responses to cry and face stimuli

Building on existing research evidencing an increase in arousal and alertness to auditory stimuli in mothers compared to non-mothers (Purhonen, Kilpelainen-Lees et al., 2001; Purhonen, Paakkonen et al., 2001; Purhonen et al., 2008), we examined whether the N100 would be altered by stimulus content and associated with parity. We found that maternal parity did not modulate the amplitude or latency of the N100, consistent with findings that this component is a fairly robust response to infant cry stimuli (Purhonen, Kilpelainen-Lees et al., 2001; Purhonen et al., 2008). However, we extend earlier N100 findings to report that the N100 was modulated by the emotional content – indexed by intensity – of the infant cry. Specifically, the N100 amplitude was largest and peaked earliest in response to high-distress cries, compared to both low-distress cries and the neutral tone. Thus, recent mothers processed high-distress cries more intensely and efficiently relative to the other stimulus conditions.

Although there were no differences in amplitude between low-distress cries and the neutral tone, there was a latency difference such that mothers responded more quickly to low-distress cries compared to the neutral tone. Consequently, N100 latency measures may provide increased sensitivity, relative to N100 amplitudes, in differentiating neural responses to specific cry stimuli. Taken together, these findings suggest that high-distress infant cries are highly salient auditory stimuli that are processed efficiently by recent mothers, regardless of maternal parity. The functional significance of more rapid and larger neural response to high-distress cries may be through facilitating sensitive responding to promote infant well-being (Papoušek, 2000), which is an important component of the emerging dyadic relationship, irrespective of prior reproductive experience.

Parity did not modulate the amplitude or latency of the N170, and we did not find that the N170 amplitude and latency were affected by the emotional content of the infant faces. Due to the inconsistencies in prior research, the inclusion of the N170 in the current study was exploratory. While this finding contradicts some earlier research that has reported modulation of the N170 by infant emotional expression (Peltola et al., 2014; Proverbio et al., 2006; Rodrigo et al., 2011), it is consistent with the null results of previous studies that also utilized a passive viewing paradigm, similar to the one used in the current study (Malak et al., 2015; Noll et al., 2012). To understand this potential discrepancy, it is important to note that previous studies reporting N170 modulation by infant emotional expression engaged participants in an emotion-recognition task, requiring participants to actively categorize infant emotion during each trial. In contrast, in the current study and prior work (Malak et al., 2015; Noll et al., 2012) where no N170 and emotion expression effects were found, participants were not required to report on the emotional content of the stimulus presented. Therefore, it is possible that directing attention to the emotional content of the stimulus could account for the N170 differences between studies. Consequently, future research should investigate how task design influences maternal processing of face stimuli. Nevertheless, we interpret our findings in the context of research that describes the N170 as an early perceptual component that reflects the pre-categorical structural encoding of faces (Eimer, 2000), which is unaffected by maternal parity and infant emotional expression.

### Late ERP responses to cry and face stimuli

In terms of the later stages of processing, we examined the P300, which reflects both the cognitive evaluation of, and attentional engagement with, stimuli (Luck, 2005) and as such, has been modulated by both infant distress

and familiarity (Bick et al., 2013; Doi & Shinohara, 2012; Grasso et al., 2009). We found that the P300 to auditory stimuli was modulated by parity and stimulus content. Specifically, a larger P300 response was observed in response to infant cries compared to the neutral tone. However, there was no difference in the P300 elicited by high-distress and low-distress cries, suggesting an enhanced response to salient infant signals of distress more generally in this maternal sample. That is, the P300 is unaffected by cry intensity but differentiates cry from non-cry stimuli. While very recent mothers ( $M = 2.85$  days postpartum) have been found to be more generally sensitive to auditory stimuli that are not infant-specific during the earliest stages of stimulus detection (Purhonen et al., 2008), our study found that during later stages of engagement, mothers may actually begin to differentiate infant distress signals from non-distress signals (though not the intensity of the distress signal). Furthermore, we found this differentiation to be associated with parity. Specifically, primiparous mothers evidenced an enhanced neural response to the neutral tone compared to multiparous mothers, suggesting heightened sensitivity to non-infant specific auditory stimuli in first-time mothers. This preliminary finding suggests that reproductive experience may influence how women encode and respond to auditory stimuli, with a general state of alertness in primiparous mothers to non-cry stimuli – a response that perhaps helps them differentiate distress cues from non-distress cues over time facilitating attunement to their infant's needs as compared to multiparous mothers. The current study did not take into account mothers' interpretation of distress cues, making it difficult to conclude the meaning of the neutral tone and why it elicited a greater response in primiparous mothers. Parity differences in physiological and affective response (i.e., heart rate) to type of infant distress signal have previously been documented, with multiparous mothers evidencing greater differences in their sympathy responses to pain versus hunger cries when compared to primiparous mothers (Stallings, Fleming, Corter, Worthman, & Steiner, 2001). However, maternal response to type of infant distress has not been examined using ERPs. Thus, the association between parity and the neutral tone requires further investigation as this is the first study to report on this association and it remains unclear as to whether this is a general relationship between parity and all non-infant distress auditory stimuli, or whether there is an element of the neutral tone that may make it vary in salience dependent upon parity.

No differences in response to infant cries relative to parity were observed in the current study; the P300 elicited by low- and high-distress cries was comparable

across maternal groups. Perhaps infant cries are such a salient and compelling distress signal that prior maternal experience does not shape this neural response. This may be adaptive in facilitating sensitivity to infant distress cues irrespective of past parenting experiences. Consistent with this notion, Kaitz and colleagues (2000) found recent mothers (2–3 days postpartum), regardless of prior experience, to effectively eliminate their newborn infant cries through various soothing techniques, suggesting that primiparous mothers are equipped early on to effectively respond to infant cries, without taking into account the meaning of the cry.

Parity influenced the P300 elicited by infant faces. Specifically, first-time mothers had greater neural responses to infant facial expressions than mothers with more than one child. Our finding suggests that parity likely plays an important role in infant face perception. It is possible that infant facial cues may be more salient to first-time mothers and therefore more engaging, contributing to the generally enhanced neural responses to infant emotional expression seen in the current study. Given that parity effects were not observed for the N170, it is likely that these findings reflect sustained processing and engagement with these facial cues rather than merely the detection of a face and a parity effect on a more basic level of visual processing.

In contrast to the cry-specific P300, we found no modulation by infant emotional expression for the face-specific P300. This finding contradicts earlier studies that have found infant distress to influence later ERP components. Specifically, Proverbio and colleagues (2006) found that the P300 was sensitive to various facial expressions in unfamiliar infants in both mothers and fathers, with the emotional expression of distress eliciting the greatest P300 response in central and occipital electrode sites. The absence of P300 modulation by infant emotional expression in this study may reflect examination of the P300 at parietal electrode sites here, as well as differences in the intensity of negative emotional expressions employed across the two studies – with Proverbio and colleagues (2006) employing mildly and strongly distressed infant faces, the latter category eliciting the greatest P300. Future research should include other electrode configurations across scalp locations, which could contribute to differences or similarities seen in other studies (e.g., Proverbio et al., 2006).

Finally, previous research has also found the P300 to be affected by infant familiarity, with larger neural responses found in mothers when viewing their own infant crying (Doi & Shinohara, 2012) and in biological and foster mothers in response to images of their own child compared to an unfamiliar child, and familiar and unfamiliar

adults (Grasso et al., 2009). Thus, while the P300 may be uniquely situated to reflect higher-order cognitive processes and may be affected by infant familiarity and distress, it is possible that we did not detect modulation of infant emotional expression due to the participant's unfamiliarity with the stimuli (c.f., Proverbio et al., 2006). Future studies using familiar infant stimuli, expressing varying distress levels, are needed to better understand these processes in mothers.

### **Limitations**

It is important to consider these findings in light of several limitations and directions for future research. While this is one of the first ERP studies to explore how maternal experience may influence the neural sensitivity to infant cues, additional normative factors that influence maternal sensitivity at the behavioral level were not modeled and may be informative in understanding the relationship between neurophysiological measures of infant cue sensitivity and down-stream parenting behavior. Future research should include factors, such as level of anxiety associated with parturition, perceived stress, social support, breastfeeding, delivery method, and hours of sleep, to answer such questions. Although this study provides important information regarding neural responses to infant cues in recent mothers, it remains unknown how these other normative maternal factors influence the visual and auditory processing of familiar infant cues. Mother's own infant cues may be more salient and potentially less sensitive to associations with participant demographic factors, as prior research has shown mothers to identify the type of cry (i.e., pain) accurately in their own infant compared to unknown infant and evidence greater electrodermal responses to own infant cries (Wiesenfeld, Malatesta, & DeLoach, 1981). With respect to ERPs, the P300 has previously been found to be affected by infant familiarity (Doi & Shinohara, 2012; Grasso et al., 2009). However, parity was not included as a measure in these studies, and warrants an important area for future research. Examination of other early and late ERP components, including the early posterior negativity and late positive potential, would allow the opportunity to further examine the impact of parity on infant cue processing.

Finally, while we were able to measure parity and begin to initially understand how experience may differentially influence neural response to infant cues, our measure was limited to the number of children a mother had and did not account for additional factors that comprise maternal experience, such as the amount of time spent with their children and with other children (e.g., caregiving relationships), as well as overall enjoyment in the caregiving relationship. Also, the extent to which

parity effects may be present in mothers who have not had prior reproductive experience, but care for multiple children, such as kinship and foster caregivers, warrants consideration, as pre-clinical research suggests that experience alone may be enough to induce maternal behavior (Stolzenberg & Champagne, 2016). Future research should also expand the definition of parity to include additional measures of experience, moving beyond the use of parity as a single marker of such processes. Finally, while the results provide preliminary evidence that parity plays a role in infant cue perception, it is unclear how these findings translate to maternal responses to infant cues at the behavioral level – an important next step for future research to understand the translational nature of ERP research.

### **Conclusion**

The current study examined ERP responses to infant affective cues, faces and cries, in both primiparous and multiparous mothers. We found that while the N100 and P300 were both modulated by the emotional content of the infant cry, the face-specific N170 and P300 were not modulated by infant emotional expression. We also found parity was associated with later stages of processing, as indexed by the P300. Primiparous mothers evidenced enhanced neural responses to auditory and visual stimuli suggesting increased attentional engagement with perceived emotional stimuli compared to multiparous mothers, who may more efficiently and effectively differentiate and respond to infant emotional cues. Findings suggest the importance of controlling for influences of maternal experience to help better understand the neural correlates of infant cue processing.

### **Acknowledgments**

The authors wish to thank Marion Mayes, Max Greger-Moser, Jasmine Coleman, and Amanda Ng for their help with data collection.

### **Disclosure statement**

The authors report that they have no financial conflicts of interest with respect to the content of this manuscript. Over the past 3 years, Dr. Potenza has received financial support or compensation for the following: Dr. Potenza has consulted for and advised Ironwood, Lundbeck, Shire, Rivermend Health, Lakelight Therapeutics/Opiant, and Jazz Pharmaceuticals; has received research support from the Mohegan Sun Casino, the National Center for Responsible Gaming; has participated in surveys, mailings or telephone consultations related to drug addiction, impulse control disorders or other health topics; has consulted for legal and gambling entities on issues related to impulse control disorders and addictions; provides

clinical care in the Connecticut Department of Mental Health and Addiction Services Problem Gambling Services Program; has performed grant reviews for the NIH and other agencies; has edited journals and journal sections; has given academic lectures in grand rounds, CME events and other clinical or scientific venues; and has generated books or book chapters for publishers of mental health texts. The other authors reported no biomedical financial interests or other conflicts of interest.

## Funding

This work was supported by the NIH (NIDA) grants [P01 DA022446; R01 DA026437], as well as the Anna Freud Centre (UK), the Connecticut Mental Health Center, the National Alliance for Medical Image Computing (NA-MIC) [U54 EB005149], and a NIMH T32 postdoctoral fellowship [MH018268]. This publication was also made possible by CTSA [Grant Number UL1 RR024139], from the National Center for Research Resources, a component of the NIH, and NIH roadmap for Medical Research. Its contents are solely the responsibility of the authors and do not necessarily represent the official view of any of the funding agencies.

## References

- Barrett, J., & Fleming, A. S. (2011). Annual research review: All mothers are not created equal: Neural and psychobiological perspectives on mothering and the importance of individual differences. *Journal of Child Psychology and Psychiatry*, 52(4), 368–397.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8(6), 551–565.
- Bick, J., Dozier, M., Bernard, K., Grasso, D., & Simons, R. (2013). Foster mother–infant bonding: Associations between foster mothers' oxytocin production, electrophysiological brain activity, feelings of commitment, and caregiving quality. *Child Development*, 84(3), 826–840.
- Bornstein, M. H., Arterberry, M. E., & Mash, C. (2013). Differentiated brain activity in response to faces of "Own" Versus "Unfamiliar" babies in primipara mothers: An electrophysiological study. *Developmental Neuropsychology*, 38(6), 365–385.
- Boukydis, Z. C. F., & Burgess, R. L. (1982). Adult physiological response to infant cries: effects of temperament of infant, parental status and gender. *Child Development*, 53(5), 1291–1298.
- Bridges, R. S. (2015). Neuroendocrine regulation of maternal behavior. *Frontiers in Neuroendocrinology*, 36, 178–196. doi:10.1016/j.yfrne.2014.11.007
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Doi, H., & Shinohara, K. (2012). Event-related potentials elicited in mothers by their own and unfamiliar infants' faces with crying and smiling expression. *Neuropsychologia*, 50, 1297–1307.
- Drummond, J. E., McBride, M. L., & Wiebe, C. F. (1993). The development of mothers' understanding of infant crying. *Clinical Nursing Research*, 2, 396–413. doi:10.1177/105477389300200403
- Drummond, J. E., McBride, M. L., & Wiebe, C. F. (1993). The development of mothers' understanding of infant crying. *Clinical Nursing Research*, 2, 396–413. doi:10.1177/105477389300200403
- Eimer, M. (2000). The face-specific N170 component reflects late stages in the structural encoding of faces. *Neuroreport*, 11(10), 2319–2324.
- Ferber, S. G. (2004). The nature of touch in mothers experiencing maternity blues: The contribution of parity. *Early Human Development*, 79(1), 65–75.
- Fleming, A. S., & Korsmit, M. (1996). Plasticity in the maternal circuit: effects of maternal experience on fos-lir in hypothalamic, limbic, and cortical structures in the postpartum rat. *Behavioral Neuroscience*, 110, 567–582. doi:10.1037/0735-7044.110.3.567
- Gonzalez, A., Atkinson, L., & Fleming, A. S. (2009). Attachment and the comparative psychobiology of mothering. In M. De Haan & M. R. Gunnar (Eds.), *Handbook of developmental social neuroscience* (pp. 225–245). New York, NY: Guilford Press.
- Grasso, D. J., Moser, J. S., Dozier, M., & Simons, R. (2009). ERP correlates of attention allocation in mothers processing faces of their children. *Biological Psychology*, 81(2), 95–102.
- Gratton, G., & Coles, M. G., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, 55(4), 468–484. doi:10.1016/0013-4694(83)90135-9
- Gustafson, G. E., & Green, J. A. (1989). On the importance of fundamental frequency and other acoustic features in cry perception and infant development. *Child Development*, 60(4), 772–780.
- Kaitz, M., Chriki, M., Bear-scharf, L., Nir, T., & Eidelman, A. I. (2000). Effectiveness of primiparae and multiparae at soothing their newborn infants. *The Journal of Genetic Psychology*, 161(2), 203–215. doi:10.1080/00221320009596706
- Landi, N., Montoya, J., Kober, H., Rutherford, H. J. V., Mencl, E., Worhunsky, P., ... Mayes, L. C. (2011). Maternal neural responses to infant cries and faces: Relationships with substance use. *Frontiers in Psychiatry*, 2(32). doi:10.3389/fpsy.2011.00032
- Luck, S. J. (2005). *An introduction to the event-related potential technique*. Cambridge, MA: MIT Press.
- Malak, S. M., Crowley, M. J., Mayes, L., & Rutherford, H. J. V. (2015). Maternal anxiety and neural responses to infant faces. *Journal of Affective Disorders*, 172, 324–330.
- Maupin, A. N., Hayes, N. J., Mayes, L. C., & Rutherford, H. J. V. (2015). The application of electroencephalography to investigate the neural basis of parenting. *Parenting: Science and Practice*, 15(1), 9–23.
- Maupin, A. N., Roginiel, A. C., Rutherford, H. J. V., & Mayes, L. C. (2016). A preliminary review of whether prior reproductive experience influences caregiving. *New Directions for Child and Adolescent Development*, 2016(153), 73–86. doi:10.1002/cad.20169
- McPartland, J., Dawson, G., Webb, S. J., Panagiotides, H., & Carver, L. J. (2004). Event-related brain potentials reveal anomalies in temporal processing of faces in autism spectrum disorder. *Journal of Child Psychology and Psychiatry*, 45(7), 1235–1245.



- Moltz, H., Robbins, D., & Parks, M. (1966). Cesarean delivery and maternal behavior of primiparous and multiparous rats. *Journal of Comparative and Physiological Psychology*, 61(3), 455.
- Morgan, H. D., Watchus, J. A., Milgram, N. W., & Fleming, A. S. (1999). The long lasting effects of electrical stimulation of the medial preoptic area and medial amygdala on maternal behavior in female rats. *Behavioural Brain Research*, 99, 61–73. doi: 10.1016/S0166-4328(98)00070-9
- Noll, L. K., Mayes, L. C., & Rutherford, H. J. V. (2012). Investigating the impact of parental status and depression symptoms on the early perceptual coding of infant faces: An event-related potential study. *Social Neuroscience*, 1–12. doi:10.1080/17470919.2012.672457
- Numan, M. (2006). Motivational systems and the neural circuitry of maternal behavior in the rat. *Developmental Psychobiology*, 49, 12–21. doi: 10.1002/dev.20198
- Papoušek, H. (Ed.). (2000). *Intuitive parenting* (Vol. 3). New York: John Wiley & Sons, Inc.
- Peltola, M. J., Yrttiaho, S., Puura, K., Proverbio, A. M., Mononen, N., Lehtimäki, T., & Leppänen, J. M. (2014). Motherhood and oxytocin receptor genetic variation are associated with selective changes in electrocortical responses to infant facial expressions. *Emotion*, 14(3), 469–477.
- Proverbio, A. M., Brignone, V., Matarazzo, S., Del Zotto, M., & Zani, A. (2006). Gender and parental status affect the visual cortical response to infant facial expression. *Neuropsychologia*, 44(14), 2987–2999.
- Purhonen, M., Kilpeläinen-Lees, R., Pääkkönen, A., Yppäriä, H., Lehtonen, J., & Karhu, J. (2001). Effects of maternity on auditory event-related potentials to human sound. *Neuroreport*, 12(13), 2975–2979.
- Purhonen, M., Pääkkönen, A., Yppäriä, H., Lehtonen, J., & Karhu, J. (2001). Dynamic behavior of the auditory N100 elicited by a baby's cry. *International Journal of Psychophysiology*, 41(3), 271–278.
- Purhonen, M., Valkonen-Korhonen, M., & Lehtonen, J. (2008). The impact of stimulus type and early motherhood on attentional processing. *Developmental psychobiology*, 50(6), 600–607.
- Rodrigo, M. J., León, I., Quiñones, I., Lage, A., Byrne, S., & Bobes, M. A. (2011). Brain and personality bases of insensitivity to infant cues in neglectful mothers: An event-related potential study. *Development and Psychopathology*, 23(01), 163–176.
- Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., & Crommelinck, M. (2000). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: An electrophysiological account of face-specific processes in the human brain. *Neuroreport*, 11(1), 69–74.
- Schneider, W., Eschman, A., & Zuccolotto, A. (2002). *E-prime user's guide*. Pittsburg: Psychology Software Tools Inc.
- Stallings, J., Fleming, A. S., Corter, C., Worthman, C., & Steiner, M. (2001). The effects of infant cries and odors on sympathy cortisol, and autonomic responses in new mothers and nonpostpartum women. *Parenting: Science and Practice*, 1 (1–2), 71–100.
- Stolzenberg, D. S., & Champagne, F. A. (2016). Hormonal and non-hormonal bases of maternal behavior: The role of experience and epigenetic mechanisms. *Hormones and Behavior*, 77, 204–210. doi: 10.1016/j.yhbeh.2015.07.005
- Strathearn, L., & McClure, S. M. (2002, November). *A functional MRI study of maternal responses of infant facial cues*. Paper presented at the Annual Scientific Meeting of the Society for Neuroscience, Washington, DC.
- Wiesenfeld, A. R., Malatesta, C. Z., & DeLoach, L. L. (1981). Differential parental response to familiar and unfamiliar infant distress signals. *Infant Behavior and Development*, 4, 281–295.

## Appendix

### Cry acoustic properties

Although cries were not selected based on acoustic properties, we report properties that have been observed to correlate with perceived distress including pitch, number of bouts, duration of bouts, number of inter-bout pauses and duration of inter-bout pauses. All cries had sampling frequencies of 44,100 Hz and ranged from 1.9–2.12 seconds. All cries were normalized to the same relative peak intensity using Praat software <http://www.fon.hum.uva.nl/praat/>. Presentation volume was occasionally adjusted for participant comfort. **High-distress cry 1:** minimum pitch 129.53 Hz; maximum pitch 433.6; mean pitch 351.27 Hz; number of bouts 2; mean bout length .97; mean pause length 0.09 seconds. **High-distress cry 2:** minimum pitch 209.68 Hz; maximum pitch 461.32; mean pitch 317.17 Hz; number of bouts 1; mean bout length 2.1 seconds; mean pause length 0 seconds. **Low-distress cry 1:** minimum pitch 297.548; maximum pitch 470.003 Hz; mean pitch 348.77 Hz; number of bouts 3; mean bout length .47 seconds; number of pauses 3; mean pause length .75 seconds. **Low-distress cry 2:** maximum pitch 469.824; mean pitch 351.40 Hz; number of bouts 9; mean bout duration .11 seconds; number of pauses 4; mean pause length .1 seconds. For the **220-hz pure tone** the sampling rate was 441,000 Hz; duration was 2 seconds; average pitch was 220 Hz. The pure tone had a 2 ms ramp up at the beginning and the end of the token.