

The special status of sad infant faces: age and valence differences in adults' cortical face processing

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Abstract

Understanding the relative and joint prioritization of age- and valence-related face characteristics in adults' cortical face processing remains elusive because these two characteristics have not been manipulated in a single study of neural face processing. We used electroencephalography to investigate adults' P1, N170, P2 and LPP responses to infant and adult faces with happy and sad facial expressions. Viewing infant *vs* adult faces was associated with significantly larger P1, N170, P2 and LPP responses, with hemisphere and/or participant gender moderating this effect in select cases. Sad faces were associated with significantly larger N170 responses than happy faces. Sad infant faces were associated with significantly larger N170 responses in the right hemisphere than all other combinations of face age and face valence characteristics. We discuss the relative and joint neural prioritization of infant face characteristics and negative facial affect, and their biological value as distinct caregiving and social cues.

Key words: face processing; infant; adult; face valence; electroencephalography

Evidence suggests that our brains differentially process faces depending on their age and emotional valence. Viewing infant *vs* adult faces (e.g., Kringelbach *et al.*, 2008; Proverbio *et al.*, 2011) and negative *vs* positive facial expressions (e.g. Blau *et al.*, 2007) is associated with greater neural activity in regions sensitive to face processing. From an evolutionary perspective, the adaptive value of rapidly detecting and attending to infants (Darwin, 1872; Lorenz, 1943, 1971) and negative affect (Lazarus, 1991; Tooby and Cosmides, 1990) may have led to their neural prioritization. However, the extent to which age- and valence-related face characteristics compete for cortical resources and/or interact to affect adults' cortical face processing remains elusive, as these two characteristics have not been manipulated in a single study of neural face processing. To address this gap, we used electroencephalography (EEG) to investigate adults' neural responses to infant and adult faces with happy and sad facial expressions. We aimed to clarify the individual and joint associations of age- and valence-related face characteristics

with neural processing, and thereby shed further light on the apparent value of these distinct caregiving and social cues.

Evolutionary theorists have argued that infant face characteristics and negative facial affect serve as important cues for adaptive behavior in adults. Lorenz (1943, 1971) proposed that 'Kindchenschema' (i.e. infant-specific features), such as large eyes and bulging cheeks, trigger innate releasing mechanisms for attention, affection and nurturing in caregivers. Others have argued that negative facial affect is an evolved signal of distress that may elicit prosocial or caregiving responses from those who recognize it (Tooby and Cosmides, 1990; Lazarus, 1991). These claims are supported by behavioral studies indicating the attention-grabbing nature of infant faces and negative affect. Adults show an attentional bias to infants with more pronounced infantile characteristics (e.g. Glocker *et al.*, 2009; Little, 2012), pay more attention to infant *vs* adult faces in a dot probe task (Brosch *et al.*, 2007), and find it harder to disengage their attention from infant *vs* adult faces (Pearson *et al.*, 2010). In a

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similar vein of work, faces expressing negative emotion have been shown to capture attention more readily (Öhman et al., 2001) and guide it more effectively (Eastwood et al., 2003) than faces expressing positive emotion. Furthermore, evidence that facial threat elicits rapid, deeply engrained responses at the unconscious level (Dimberg et al., 2000) is consistent with the purported evolutionary advantages of detecting negative affect. More recent studies suggest that adults are particularly sensitive to the combination of these biologically relevant face characteristics. One study found delayed disengagement from distressed compared with neutral and happy infant faces in a group of pregnant women (Pearson et al., 2010). In a series of studies, Thompson-Booth et al. (2014a,b) found that distressed infant faces significantly captured attention and thereby hampered performance on a visual search task, and garnered greater attention allocation than pre-adolescent, adolescent and adult faces of varying emotionality. The unique state of combined vulnerability signaled by infant characteristics and negative affect may explain their interactive effects on attention.

Brain imaging studies suggest a neural basis for adults' heightened attentional prioritization of infant faces and negative facial affect. Viewing infant vs adult faces has been associated with greater activity in the orbitofrontal cortex (OFC; implicated in reward behavior) and right fusiform face area (FFA; e.g. Kringelbach et al., 2008; Strathearn et al., 2008; Glocker et al., 2009). Viewing negative (e.g. fearful and sad) vs neutral and happy facial expressions has been associated with greater activity in the amygdala (implicated in emotion processing) and FFA (Morris et al., 1998; Vuilleumier et al., 2001; Adolphs, 2002). However, such studies have typically relied on functional magnetic resonance imaging (fMRI). Although the excellent spatial resolution of fMRI allows for the localization of neural regions involved in emotional face processing, its temporal resolution does not allow for the precise timing of such activation (see Liu et al., 2002). In contrast, EEG can track the intensity of neural activity in the millisecond range as it unfolds over time and reflects different stages of processing (Luck, 2014).

Early and late event-related potentials (ERPs)—which underlie distinct cognitive processes—have been linked to discrete and shared aspects of face processing (for a review, see Maupin et al., 2015). Early ERP components reflect sensory visual processing of low-level stimulus characteristics (e.g. P1, N170) and initial allocation of attention (e.g. P2), while late ERP components reflect deeper stages of stimulus processing driven by motivational salience (e.g. the late positive potential (LPP); Hajcak et al., 2010), such as sustained attention to visual stimuli, decision making, semantic categorization and initial memory storage of events (Eimer, 2000; Batty and Taylor, 2003; Ashley et al., 2004; Brosh et al., 2008). The N170 is uniquely sensitive to the processing of facial features (Rossion et al., 2000), although its status as face specific has been contested (see Itier and Taylor, 2004).

The P1 is an early, positive-going deflection that is most prominent in bilateral medial occipital regions (Desjardins and Segalowitz, 2013). It shows elevated amplitudes in response to happy (Dubal et al., 2011), sad (Chammat et al., 2010) and fearful faces (Rotshtein et al., 2010) in comparison to neutral faces, and fearful over happy faces (Pourtois et al., 2004, 2005), suggesting that emotional face processing has an early and rapid neural signature. The N170 is a pronounced, negative-going deflection around 170 ms (Rossion et al., 2000). It is typically right lateralized and maximal over occipital-temporal sites (Kanwisher et al., 1997; McCarthy, Puce et al., 1997). Growing evidence suggests that—beyond the structural coding of facial features—the

N170 is sensitive to higher-order, variable face characteristics. Larger (i.e. more negative) N170 amplitudes in adults have been found in response to infant vs adult faces (Proverbio et al., 2011), distressed vs neutral and smiling infant faces (Doi and Shinohara, 2012) and fearful vs neutral adult faces (Blau et al., 2007).

With peak activity detected in central-parietal regions, the positive-going P2 has also shown sensitivity to emotional and face-related stimuli. Negative emotional faces—depicting anger, fear, sadness and disgust—elicit larger P2 amplitudes than neutral or happy faces (Eger et al., 2003; Eimer et al., 2003; Jaworska et al., 2010; Smith et al., 2013; Peltola et al., 2014). Moreover, late ERP components, such as the LPP, become more positive in response to viewing both pleasant and unpleasant facial stimuli. Larger LPP amplitudes have been found for angry vs neutral or happy faces (Schupp et al., 2004; Holmes et al., 2008; Wangelin et al., 2012) and for self-relevant faces (i.e. family members, romantic partners; Guerra et al., 2012). Such modulations in LPP may reflect enhanced sensitivity to emotional expressions mediated by affect-sensitive neural regions, such as the amygdala, and may stem from top-down processes that control attentional engagement (Hajcak et al., 2010). The P2 and LPP have also been implicated in the preferential processing of infant vs adult faces. Hahn et al. (2016) found that both early (i.e. N170, P2) and late (i.e. LPP) stages of neural processing were enhanced for infant faces, suggesting that infants trigger attention more and hold greater motivational salience than adults. Finally, Rodrigo et al. (2011) found that the LPP was less pronounced in neglectful compared with non-neglectful mothers viewing sad infant faces, while Malak et al. (2015) found heightened LPP amplitudes to distressed vs neutral infant faces in recent mothers, with those high in state anxiety showing higher LPP amplitudes to neutral infant faces. Together, these studies highlight complex links between cortical processing, psychological variables and (mal)adaptive parenting.

In sum, behavioral, neuroimaging and electrophysiological studies suggest that we rapidly prioritize and attend to infant facial features and negative facial expressions. The notion that both face age and face valence have long competed for our attention by communicating valuable information for successful social interaction and survival (Darwin, 1872; Lorenz, 1943, 1971; Tooby and Cosmides, 1990; Lazarus, 1991; Öhman et al., 2000) may be reflected in the cortical prioritization of rapid neural processing. However, the relative and joint association(s) of these distinct face characteristics with adults' cortical face processing have not been fully investigated. Does the adult brain prioritize face age, face valence and/or some combination of the two? How does this prioritization—or lack thereof—manifest across different stages of stimulus processing reflected by distinct ERPs? In this study, we addressed these questions by investigating adults' neural responses to happy infant, sad infant, happy adult, and sad adult faces. In line with behavioral findings demonstrating the special status of infant distress (e.g. Thompson-Booth et al., 2014a,b) and electrophysiological studies demonstrating the sensitivity of our selected ERPs to face age and face valence, respectively (e.g. Proverbio et al., 2011; Hahn et al., 2016), we expected sad infants to elicit the strongest P1, N170, P2 and LPP responses. Although women, particularly mothers, have a special biological role in the upbringing of children that may imply a processing advantage in the current study, findings on gender differences in the attentional and neural prioritization of infant faces, as well as the processing of emotional faces, have yielded mixed results (e.g. Proverbio et al., 2006; Brosch et al., 2008; Thompson-Booth et al., 2014a,b). Thus,

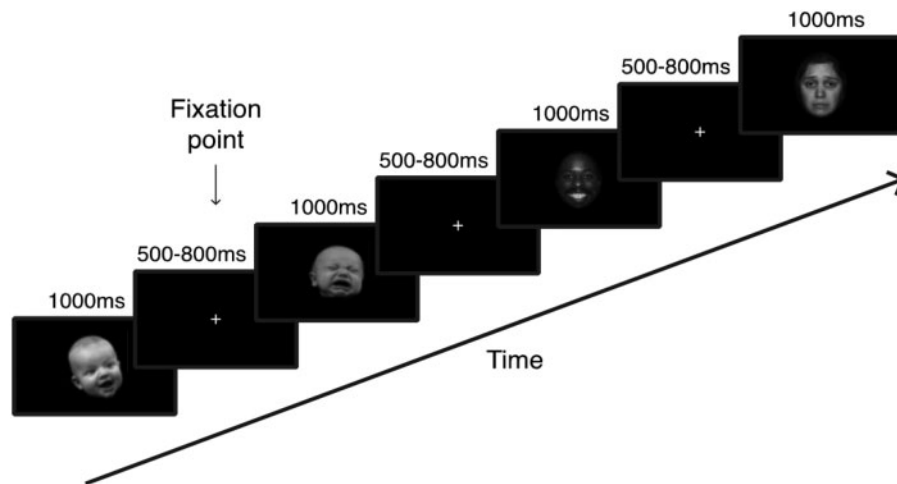


Fig. 1. Forty trials from each of the four conditions (happy infant, sad infant, happy adult and sad adult) were randomly administered for a total of 160 trials. Stimuli were presented for 1000 ms followed by inter-stimulus intervals that varied from 500 to 800 ms.

we chose a sample of female and male non-parents to comprehensively examine the breadth of a potential neural bias to infant and/or sad faces.

Methods

Participants

Fifty-three right-handed, non-parent undergraduate students ($M_{\text{age}} = 20 \pm 2.08$; 26 females, 27 males) participated for course credit. Their ethnic composition included Asian (43%), South Asian (38%), Caucasian (14%) and other (5%) origins. All had normal or corrected-to-normal vision and reported no history of mental illness and/or drug abuse.

Stimuli and behavioral ratings

Adult faces displaying happy and sad expressions were derived from the NimStim set ($n=20$ actors; 10 females, 10 males; 21–30-years old; 65% Caucasian, 25% African-American, and 10% Asian; Tottenham et al., 2009), while infant faces displaying happy and sad expressions were derived from Barrett et al. (2012; $n=20$; 3-months old; 95% Caucasian and 5% African-American). To equate the two sets of faces, they were cropped, re-sized (8.5×7 cm), adjusted for brightness and presented in grayscale behind a black outer foreground that concealed the neck and upper portion of the chest. After stimulus presentation, a questionnaire adapted from the Self-Assessment Manikin (Bradley and Lang, 1994) was issued to collect behavioral ratings of the faces on a seven-point scale ranging from 1 = 'extremely sad' to 7 = 'extremely happy'. Ratings of sad faces were reverse coded to compare all faces on the basis of expressivity. An ANOVA testing face age (infant, adult) and face valence (happy, sad) as within-subjects factors, and participant gender as a between-subjects factor revealed significant effects of face age, $F(1, 49) = 23.10$, $P < 0.001$, $\eta_p^2 = 0.32$, and face valence, $F(1, 49) = 5.13$, $P = 0.028$, $\eta_p^2 = 0.10$. Infant faces ($M = 5.27$) were rated as more expressive than adult faces ($M = 4.57$). Happy faces ($M = 5.07$) were rated as more expressive than sad faces ($M = 4.77$).

Procedure

After providing their informed consent, participants were seated comfortably in a dark, acoustically shielded room facing a computer screen ~ 50 cm from their eyes. They were instructed to fixate on a cross at the center of the screen and remain still and alert throughout a passive face-processing task. For this task, they viewed 40 faces from each of the four conditions (i.e. happy infant, sad infant, happy adult and sad adult), which were randomly presented for a total of 160 trials (see Figure 1). Specifically, 20 adult and 20 infant actors displaying happy and sad facial expressions (i.e. 80 faces with distinct facial expressions) were presented twice.

EEG recording, processing and analysis

EEG was recorded throughout the passive viewing task with a 128-electrode Hydrocel Geodesic Sensor Net (Electrical Geodesics, Inc.; Eugene, OR). The electrodes were evenly and symmetrically spaced from nasion toinion and left to right ear according to the 10-5 International System (Oostenveld and Praamstra, 2001). Data were sampled at 250 Hz with 0.1–100 Hz band-pass filters, a 60 Hz notch filter, 20K amplification, and no $>40 \Omega$ impedance. Prior to analyses, they were re-referenced from the vertex to the average. Data were segmented 100 ms pre-stimulus and 900 ms post-stimulus. Baseline correction was performed using the 100 ms pre-stimulus interval and pre-processing was conducted using Net Station 4.3.1 artifact detection tools. Segments with signals exceeding $150 \mu\text{V}$ were identified as bad channels, $140 \mu\text{V}$ as eye blinks, and $40 \mu\text{V}$ as excessive eye movements. Channels with artifacts in $>20\%$ of trials were deemed bad and segments with >10 bad channels were excluded from analyses. For each participant, artifact-free epochs were averaged by electrode and condition. Within the electrodes of interest, the rates of missing data were 11.7% in both the sad adult and happy infant conditions, 9.8% in the sad infant condition and 7.8% in the happy adult condition. Four participants were removed due to missing or rejected observations in more than half of the trials.

As depicted in Figure 2, the peak amplitude (μV ; i.e. the largest, positive-going deflection occurring between 55 and 155 ms post-stimulus onset) and latency (ms) to peak of the P1 were measured at occipital-temporal (left: 58, 64, 68, 59, 65, 69; right:

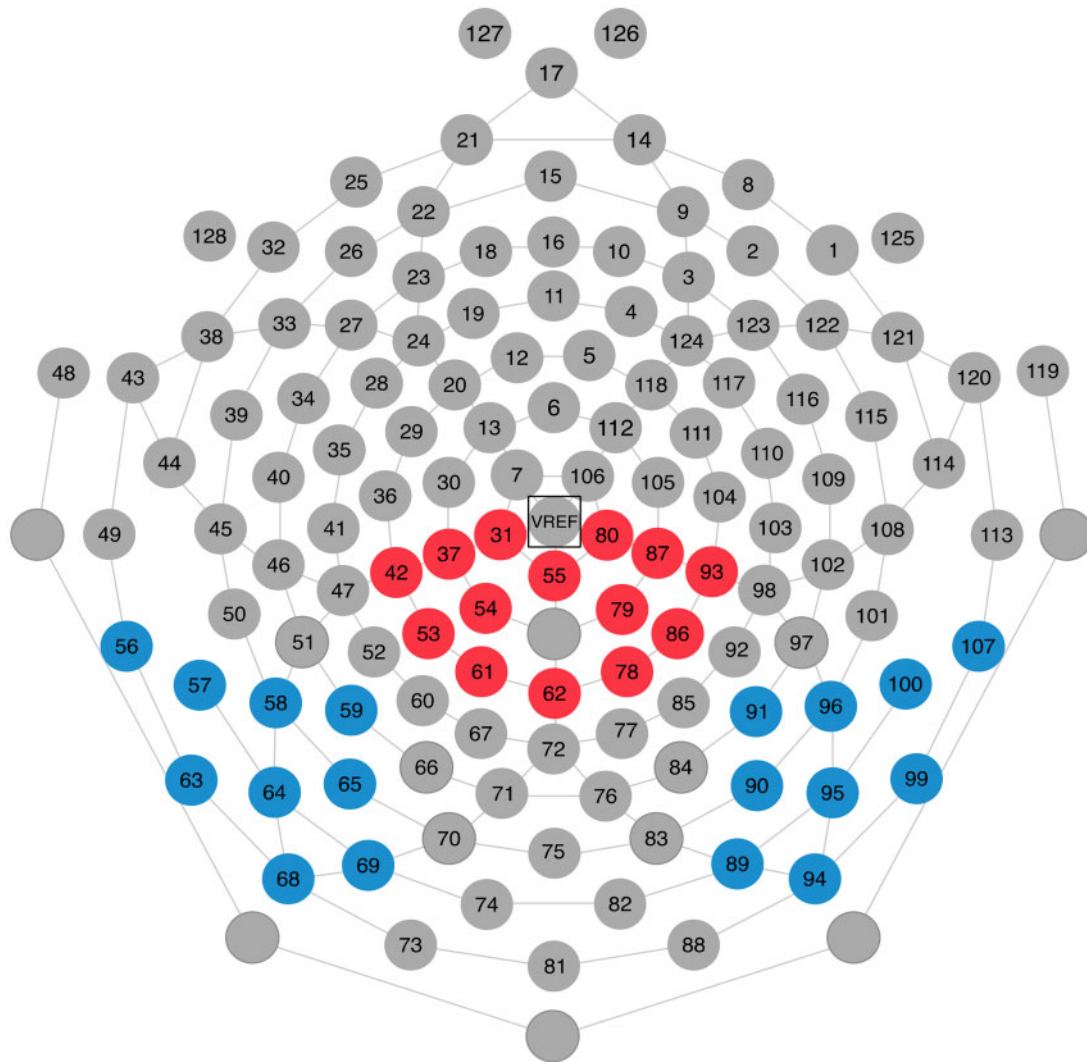


Fig. 2. Analyzed electrodes encompassed left and right occipital-temporal/temporal (blue; P1/N170) and central (red; P2/LPP) brain regions.

96, 95, 94, 91, 90, 89) and temporal (left: 56, 57, 63; right: 107, 100, 99) electrode sites. The peak amplitude (i.e., the largest, negative-going deflection occurring between 140 and 200 ms post-stimulus onset) and latency to peak of the N170 were measured at the same electrode sites as the P1. The peak amplitude (i.e. the largest, positive-going deflection occurring between 190–260 ms post-stimulus onset) and latency to peak of the P2 were measured at central (31, 55, 80, 37, 54, 79, 87, 42, 53, 61, 62, 78, 86, 93) electrode sites. The peak amplitude (i.e., the largest, positive-going deflection occurring between 500 and 800 ms post-stimulus onset) and latency to peak of the LPP were measured at the same electrode sites as the P2. These time windows and electrode sites overlap with dense-array ERP research on face processing (e.g. Blau et al., 2007; Noll et al., 2012; Malak et al., 2015).

Resulting P1, N170, P2 and LPP amplitudes and latencies were subject to a series of omnibus ANOVAs that each included face age (infant, adult) and face valence (happy, sad) as within-subjects factors, and participant gender as a between-subjects factor (ANOVAs for P1 and N170 amplitudes and latencies included hemisphere [left, right] and region [occipital-temporal, temporal] as additional within-subjects factors). Interactions

were probed with follow-up ANOVAs to isolate main effects. Only focal effects (i.e. those involving face age and/or face valence) are reported below.

Results

P1

For P1 amplitudes, the interaction of face age \times participant gender was significant, $F(1, 38) = 6.42$, $P = 0.016$, $\eta_p^2 = 0.14$. However, the interaction of face age \times participant gender \times hemisphere was also significant, $F(1, 38) = 6.04$, $P = 0.019$, $\eta_p^2 = 0.14$, revealing a face age \times participant gender interaction in the left, $F(1, 38) = 12.98$, $P = 0.001$, $\eta_p^2 = 0.26$, but not right, hemisphere. In the left hemisphere, females showed larger amplitudes in response to infant ($M = 2.76 \mu\text{V}$) than adult ($M = 2.22 \mu\text{V}$, $P = 0.042$) faces, whereas males showed larger amplitudes in response to adult ($M = 6.10 \mu\text{V}$) than infant ($M = 5.18 \mu\text{V}$, $P = 0.006$) faces (see Figure 3). For P1 latencies, the interaction of face age \times participant gender was significant, $F(1, 38) = 4.17$, $P = 0.048$, $\eta_p^2 = 0.10$, as latencies to peak in response to adults were significantly

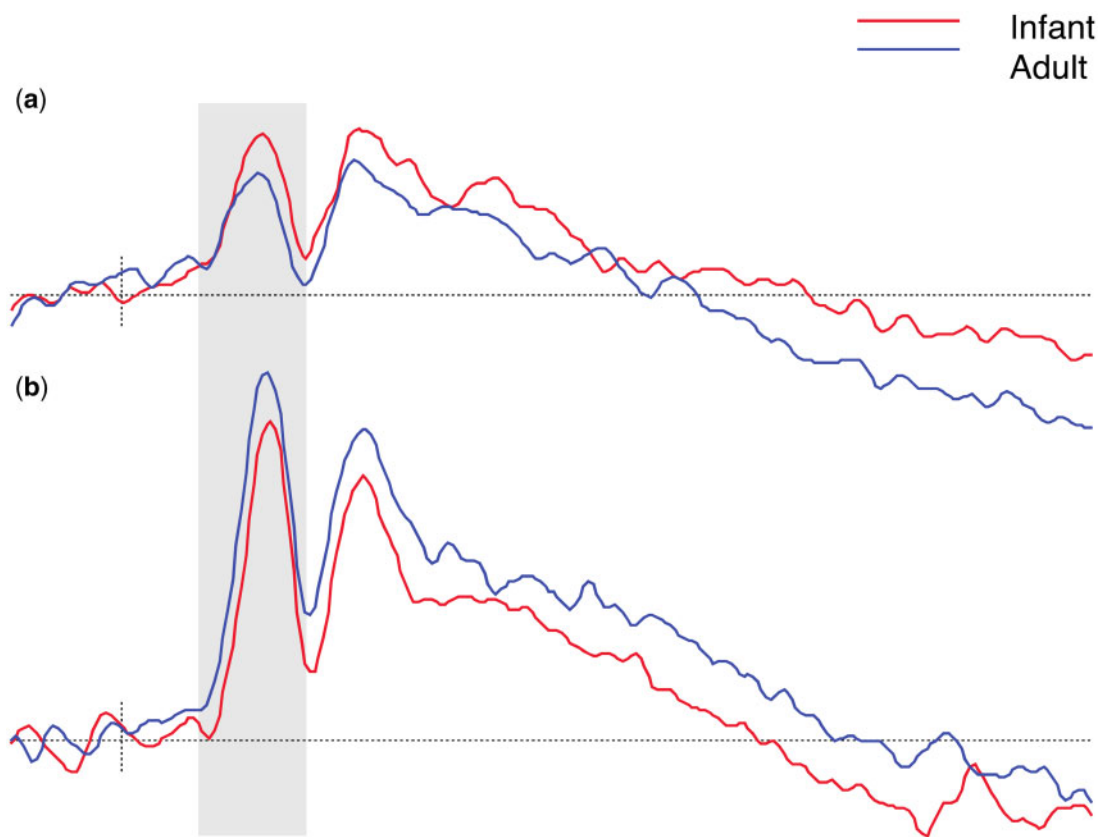


Fig. 3. Grand-averaged P1 response to infant vs adult face conditions in the left hemisphere (highlighted by transparent window) for (a) female and (b) male participants.

slower for males ($M = 147.85$ ms) than females ($M = 134.97$ ms, $P = 0.001$).

N170

For N170 amplitudes, the effect of face age was marginally significant, $F(1, 47) = 3.95$, $P = 0.053$, $\eta_p^2 = 0.08$. However, the interaction of face age \times hemisphere was significant, $F(1, 47) = 8.14$, $P = 0.006$, $\eta_p^2 = 0.15$, revealing a face age effect in the right, $F(1, 47) = 10.29$, $P = 0.002$, $\eta_p^2 = 0.18$, but not left, hemisphere. Amplitudes in the right hemisphere were larger in response to infant ($M = -3.08$ μV) than adult ($M = -2.75$ μV) faces. The effect of face valence was significant, $F(1, 47) = 9.31$, $P = 0.004$, $\eta_p^2 = 0.17$, revealing larger amplitudes in response to sad ($M = -3.11$ μV) than happy ($M = -2.89$ μV) faces. Of particular interest, the interaction of face age \times face valence \times hemisphere was marginally significant, $F(1, 47) = 2.73$, $P = 0.10$, $\eta_p^2 = 0.06$, as the interaction of face age \times face valence was marginally significant in the right, $F(1, 47) = 2.88$, $P = 0.096$, $\eta_p^2 = 0.06$, but not left, hemisphere. As depicted in Figure 4, amplitudes in the right hemisphere were larger in response to sad infants ($M = -3.27$ μV) than happy infants ($M = -2.88$ μV , $P = 0.022$), happy adults ($M = -2.72$ μV , $P < 0.001$), and sad adults ($M = -2.79$ μV , $P = 0.013$).

For N170 latencies, there was a significant main effect of face age, $F(1, 45) = 14.97$, $P < 0.001$, $\eta_p^2 = 0.25$. However, the interaction of face age \times region was significant, $F(1, 45) = 4.96$, $P = 0.031$, $\eta_p^2 = 0.10$, with stronger face age effects in the temporal, $F(1, 45) = 19.72$, $P < 0.001$, $\eta_p^2 = 0.31$, than occipital-temporal, $F(1, 45) = 8.60$, $P = 0.005$, $\eta_p^2 = 0.16$, regions. Latencies

to peak in the temporal regions were slower in response to infant ($M = 182.36$ ms) than adult ($M = 181.11$ ms) faces. The main effect of face valence was marginally significant, $F(1, 45) = 3.65$, $P = 0.062$, $\eta_p^2 = 0.08$, although the face age \times face valence interaction was significant, $F(1, 47) = 10.29$, $P = 0.002$, $\eta_p^2 = 0.18$, as latencies to peak were slower in response to sad infants ($M = 182.95$ ms) than happy infants ($M = 181.32$ ms, $P = 0.002$), happy adults ($M = 181.34$ ms, $P = 0.001$), and sad adults ($M = 180.83$ ms, $P < 0.001$).

P2

For P2 amplitudes, the significant effect of face age, $F(1, 38) = 4.53$, $P = 0.04$, $\eta_p^2 = 0.11$, revealed larger amplitudes in response to infant ($M = 1.61$ μV) than adult ($M = 1.40$ μV) faces (see Figure 5). For P2 latencies, the effect of face age was also significant, $F(1, 38) = 4.52$, $P = 0.04$, $\eta_p^2 = 0.11$, revealing slower latencies to peak in response to infant ($M = 212.20$ ms) vs adult ($M = 205.57$ ms) faces.

LPP

For LPP amplitudes, the significant interaction of face age \times participant gender, $F(1, 38) = 5.30$, $P = 0.027$, $\eta_p^2 = 0.12$, revealed larger amplitudes in response to infant ($M = 1.51$ μV) than adult ($M = 1.07$ μV , $P = 0.043$) faces for females, but not males (see Figure 5). There were no significant main effects or interactions for LPP latencies.

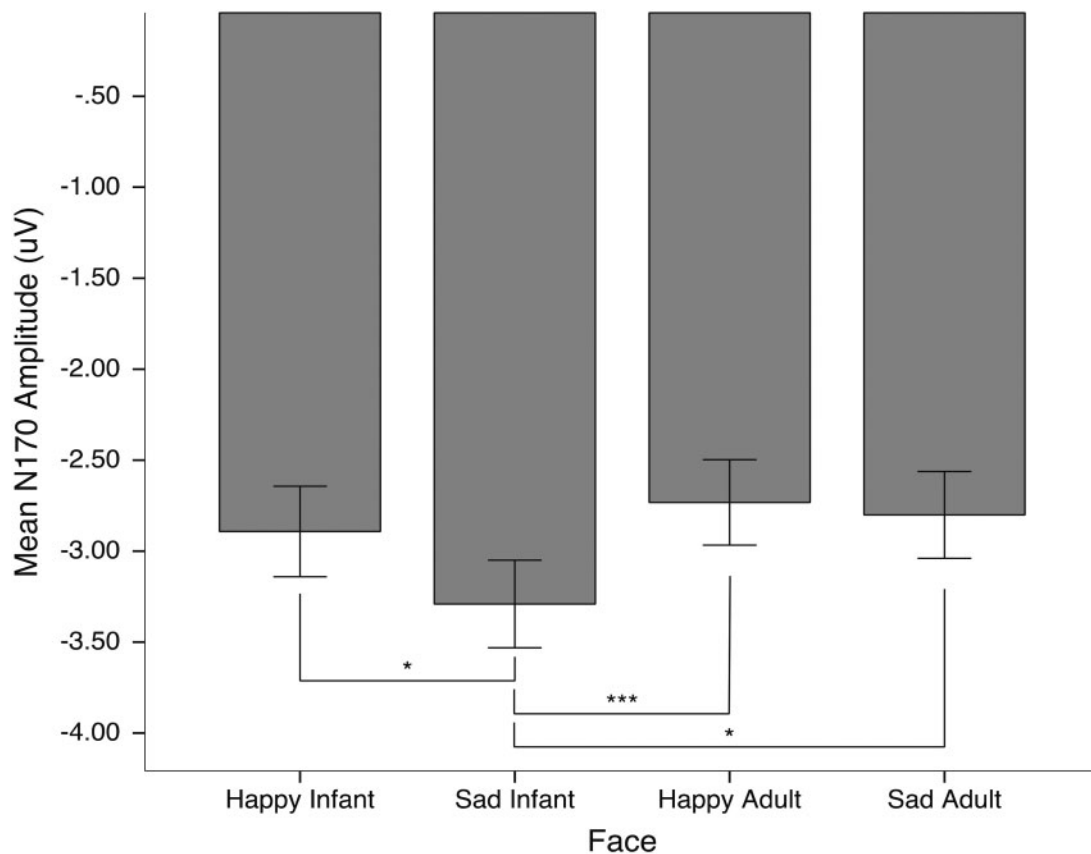


Fig. 4. Grand-averaged N170 response to sad infant vs happy infant, happy adult and sad adult face conditions in the right hemisphere.

Relations between behavioral ratings and ERPs

It was important for us to ensure—at least in part—that the above patterns of neural responding stemmed from differences in face age and/or face valence, rather than differences in the perceived expressivity of our stimuli indicated by behavioral ratings. We therefore ran a series of correlations between difference scores in behavioral ratings (e.g. between infant vs adult faces) and difference scores in P1/N170/P2/LPP responses (e.g. between amplitudes/latencies in response to infant vs adult faces). None of the focal difference scores in participants' behavioral ratings were significantly related to their corresponding difference scores in P1/N170/P2/LPP amplitudes/latencies (P s ranged from 0.14 to 0.76). In other words, whether participants rated certain face characteristics or combinations thereof as more or less expressive than others did not appear to be driving underlying differences in their neural responding to such characteristics.

Discussion

We assessed the individual and joint association(s) of age- and valence-related face characteristics with adult non-parents' cortical processing. As expected and in line with previous findings (e.g. Proverbio et al., 2011; Hahn et al., 2016), the P1, N170, P2 and LPP each evidenced a bias to infant over adult faces. Unlike in previous studies, these results were demonstrated while considering the effect of emotional facial expression (happy vs sad), which suggests that—even in the presence of other salient facial cues—the adult brain rapidly processes and prioritizes

infant face characteristics. The modulation of both early and late ERP components may indicate that infant faces garner heightened initial and sustained attentional resources that serve to facilitate an adaptive caregiving response (see Maupin et al., 2015). However, whereas Hahn et al. (2016) found that early and late ERP components were modulated by infant faces regardless of participant gender, we found that this preference was gender-specific for select ERPs. Specifically, P1 and LPP amplitudes were larger in response to infant than adult faces for females only, suggesting a unique advantage for women in the early processing of infant faces and sustained attention thereof. This relative cortical bias may reflect the special biological role of women in the upbringing of children. Further research on gender differences and potential differences in mothers vs non-mothers in such processing is warranted.

In line with its face-sensitive status (Rossion et al., 2000), the N170 was particularly sensitive to age- and valence-related face characteristics, regardless of viewer gender. Specifically, infant faces elicited larger N170 responses than adult faces in the right hemisphere. Proverbio et al. (2011) reported a similar age-graded N170 effect in non-parents, albeit bilateral in women and right lateralized in men. However, this subtle gender difference may have stemmed from task-related effects, as the authors instructed their participants to ignore the faces presented. With a similar passive viewing paradigm to the one used in the current study, Noll et al. (2012) found right lateralization of the N170 in non-mothers responding to infant faces only. Corroborating and extending this finding, the N170 responses of males and females in the current study were lateralized to the right

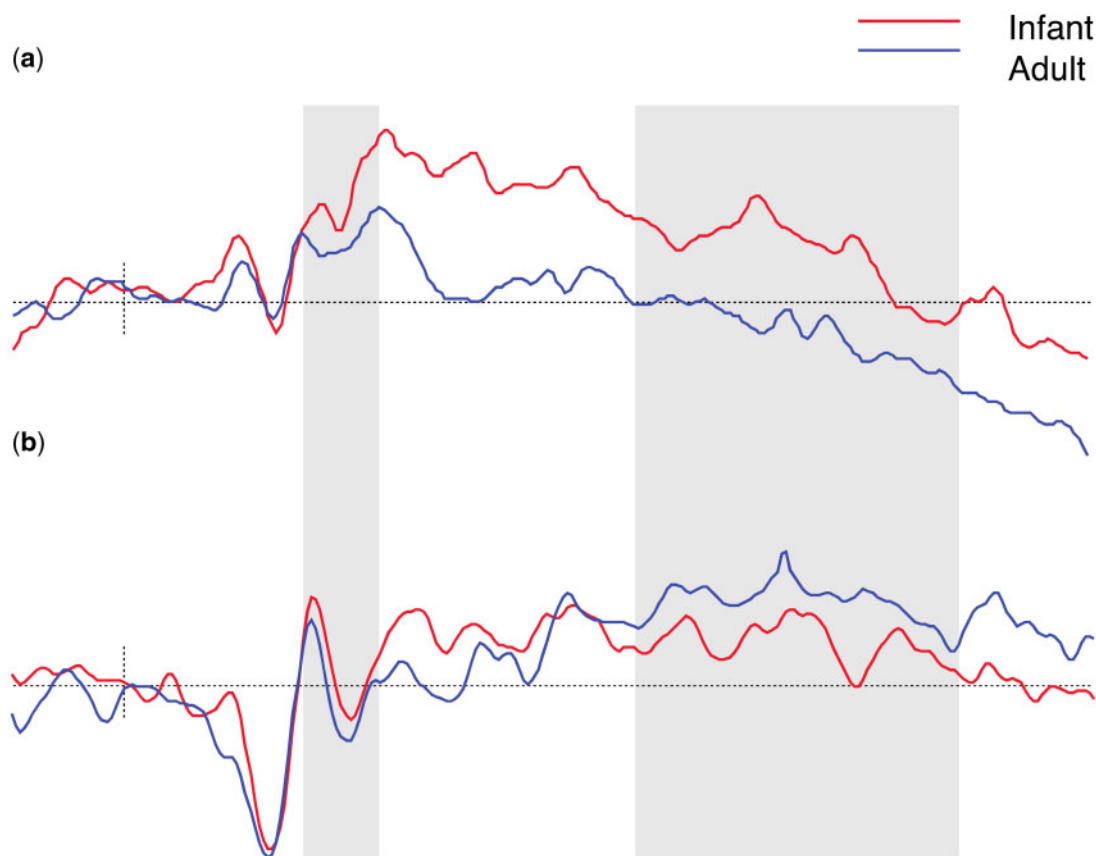


Fig. 5. Grand-averaged P2 and LPP responses to infant vs adult face conditions (denoted by transparent windows) for (a) female and (b) male participants.

hemisphere and sensitive to infant rather than adult faces. Grasso *et al.* (2009) also manipulated face age in a passive viewing paradigm, but found no relation to the N170. Notably, their younger faces ranged from infancy to childhood (i.e. ~5 years of age), which—considering the biological importance of infant-specific facial features (Darwin, 1872; Lorenz, 1943, 1971; Thompson-Booth *et al.*, 2014b)—may have diluted a potential age effect.

Regardless of hemisphere, region, face age and participant gender, sad faces elicited larger N170 responses than happy faces. This finding corroborates a series of studies demonstrating larger N170 responses to distressed vs non-distressed infant faces (Rodrigo *et al.*, 2011; Doi and Shinohara, 2012) and distressed vs non-distressed adult faces (Blau *et al.*, 2007; Hendriks *et al.*, 2007) at bilateral occipital-temporal electrode sites. Interestingly, sad infant faces elicited larger N170 responses in the right hemisphere than happy infant faces, happy adult faces and sad adult faces. Although previous studies have demonstrated the neural prioritization of distressed vs non-distressed infants (Doi and Shinohara, 2012) and distressed vs non-distressed adults (Blau *et al.*, 2007), this is the first evidence for the relative cortical prioritization of sad infant faces over other combinations of age- and valence-related face characteristics. These cortical findings nicely mirror behavioral findings indicating an attentional bias to distressed infants (e.g. Thompson-Booth *et al.*, 2014a,b). The high degree of vulnerability signaled by infant face characteristics—perhaps in lieu of their verbal communication abilities—is likely amplified by sadness, further signaling reduced capability (see Hareli *et al.*, 2009) and thereby recruiting the most cortical resources of all face age and face

valence combinations. Furthermore, the specificity of this response belies a two-stage model of face processing (i.e. that the N170 is strictly linked to the structural encoding of faces; e.g. Liu *et al.*, 2002) and supports a parallel, distributed model that recruits several brain regions to simultaneously encode both structural and variable facial features (Haxby *et al.*, 2000; Öhman *et al.*, 2000).

Some limitations and future directions of the current study should be considered. First, we tested a sample of non-parents, much like the broader literature on the perceptual processing of emotional facial stimuli. Studies with parents have extended this work by comparing the brain activity of mothers vs non-mothers while viewing or listening to infant-related stimuli. In doing so, they have uncovered maternal-specific regions of interest and heightened activity in mothers vs non-mothers, especially in response to their own vs other infants. The prefrontal cortex, medial preoptic area, hypothalamus, amygdala, anterior cingulate cortex, nucleus accumbens, OFC, dorsolateral substantia nigra and insula of mothers are consistently activated in response to infant-related stimuli, supporting the role of these brain areas in parenting (Rutherford and Mayes, 2011; Swain, 2011; Lambert and Kinsley, 2012). Individual differences in maternal neural responses to infant-related stimuli have also been associated with aspects of sensitive parenting (Atzil *et al.*, 2011; Kim *et al.*, 2011; Musser *et al.*, 2012; Noriuchi *et al.*, 2008). A longitudinal study revealed that mothers who showed greater attentional bias to faces depicting infant distress during their third trimester of pregnancy reported greater maternal sensitivity to their own infants at 3–6 months postpartum (Pearson *et al.*, 2011). Future studies should examine

the extent to which the current findings manifest in parents vs non-parents, or based on alloparenting experience (e.g. babysitting younger siblings and/or relatives).

Second, our passive experimental paradigm prevented us from making more specific mechanistic claims related to parenting. Although passive viewing paradigms offer insight into the neural responses reflecting enhanced attention to facial stimuli, investigating the relations between neural biases to emotional infant vs adult faces and higher-order cognitive processes (e.g. executive functioning, theory of mind) can shed light on the role of sad infant faces in related decision making. For example, Pearson et al. (2010) found that infant face valence modulated cognitive performance: parents took longer to respond to a go/no-go task when there was a photograph of a distressed vs non-distressed infant in the background.

Third, we did not account for psychological conditions, such as depression and anxiety, which may modulate neurophysiological responsiveness to emotional infant vs adult cues. Noll et al. (2012) investigated the effect of depressive symptoms on the early visual processing of infant faces in a non-clinical sample of mothers. A positive correlation was observed between depressive symptom severity and N170 amplitudes, suggesting that mild depressive symptomology may actually heighten sensitivity to distressed infant faces. Malak et al. (2015) found a positive link between recent mothers' state anxiety and LPP amplitudes when viewing neutral infant faces, further suggesting that psychological symptoms exacerbate neurophysiological responsiveness to infants, although contrary related findings have also emerged (Rodrigo et al., 2011). Finally, the races of the participants and facial stimuli were not matched in this study. Given that race of a model has been shown to impact face processing—both behaviorally and neurophysiologically (e.g. Elfenbein and Ambady, 2002; Lieberman et al., 2005; Herrmann et al., 2007)—the potential for race effects to exacerbate or mitigate neural biases to emotion- and/or age-based face characteristics should be considered.

To conclude, our results extend previous work by providing novel, comprehensive evidence for the role of infant faces in modulating both early (N170, P1, P2) and late (LPP) stages of face processing, and for the sensitivity of the N170 to sad infant faces over other combinations of face age and face valence characteristics. In line with the theorizing of Darwin (1872) and Lorenz (1943, 1971), preferential responses to infants in need, much like preferential responses to fearful or threatening affective stimuli (Tooby and Cosmides, 1990; Lazarus, 1991), likely serve an adaptive function. A cortical face processing bias to distressed infants may reflect an instinctual attunement with such cues. This select neural activation may equip parents (and future parents in this case) with the capacity to attune and respond as early and often as possible to infants' affective distress signals.

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