Individual differences in infants' neural responses to their peers' cry and laughter

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ABSTRACT

Infants' ability to process others' emotional expressions is fundamental for their social development. While infants' processing of emotions expressed by faces and speech has been more extensively investigated, less is known about how infants process non-verbal vocalizations of emotions. Here, we recorded frontal N100, P200, and LPC event-related potentials (ERPs) from 8-month-old infants listening to sounds of other infants crying, laughing, and coughing. Infants' temperament was measured via parental report. Results showed that processing of emotional information from non-verbal vocalizations was associated with more negative N100 and greater LPC amplitudes for peer's crying sounds relative to positive and neutral sounds. Temperament was further related to the N100, P200, and LPC difference scores between conditions. One important finding was that infants with improved ability to regulate arousal exhibited increased sustained processing of peers' cry sounds compared to both laughter and cough sounds. These results emphasize the relevance of considering the temperamental characteristics in understanding the development of infant emotion information processing, as well as for formulating comprehensive theoretical models of typical and atypical social development.

1. Introduction

Nonverbal vocalizations of emotions such as laughter and crying are human universals, providing unambiguous and genuine information about our emotions (Barr, Hopkins, & Green, 2000; Dunbar, Baron, & Frangou, 2012; Paulmann & Kotz, 2008; Provine, 2004, 2016; Sauter, Eisner, Ekman, & Scott, 2010; Scherer, 1986, 1995). Both the production and the accurate interpretation of these social signals are thought to play crucial roles in communication, social bonding and elicitation of prosocial behaviors, and may be early precursors to empathy development (Decety, 2015; Decety & Howard, 2013; Geangu, 2015; Hoffman, 2000). Evidence suggests that nonverbal vocalizations of emotions may be important for our early social lives (e.g., Barr et al., 2000; Ostwald & Murry, 1985; Ross, Owren, & Zimmermann, 2009). For example, the presence of adults' laughter during adult-infant encounters is important for generating humorous situations which promote social closeness and interaction, potentially contributing to the development of mental state understanding (Ishijima & Negayama, 2017; Mireault, Sparrow, Poutre, Perdue, & Macke, 2012; Mireault, Poutre et al., 2012). Both the atypical sensitivity to others' nonverbal vocalizations of emotions and their production have been associated

with risk for developmental disorders characterized by impaired social functioning, such as autism (Blasi et al., 2015; Esposito, Nakazawa, Venuti, & Bornstein, 2013; Esposito, Venuti, & Bornstein, 2011; Reddy, Williams, & Vaughan, 2002). Despite their significance, the processing and use of nonverbal vocalizations of emotions, particularly during early development, remains understudied (Dunbar et al., 2012; Geangu, 2015; Pell et al., 2015; Provine, 1996).

Infancy is a crucial time period for tuning and optimising the brain circuitry for processing stimuli with socio-emotional relevance and emotional responsivity, setting the stage for both the refinement of the early acquired social skills and the emergence of new and more complex ones later in life (Johnson, 2011; Karmiloff-Smith, 1998). Both typical and atypical social developmental outcomes are the result of complex interactions between the developing social brain and the child's environment. While some of the outcomes are the direct consequence of the initial genetic or environmental characteristics, some reflect secondary 'cascading' effects of the genes-environment interactions at different points during ontogeny (Johnson, Gliga, Jones, & Charman, 2015). For example, it has been shown that 7-month-old infants with reduced attentional biases towards threat cues (e.g., facial expressions of fear) are more likely to develop disorganized patterns of

attachment with their caregivers, compared to infants with normative manifestations of such emotional biases (Peltola, Forssman, Puura, van IJzendoorn, & Leppänen, 2015). The development within this disorganized relational environment may further shape representational, physiological, and behavioural responses to emotional information, contributing to atypical social outcomes such as externalizing behaviours and poor social competence with peers (Groh et al., 2014). At the manifestation stage of atypical developmental outcomes, access to the early mechanisms precipitating their emergence is lost (Johnson et al., 2015; Morales, Fu, & Pérez-Edgar, 2016). From this perspective, the investigation of the neurocognitive mechanisms underlying emotional information processing and potential individual variations during infancy is essential for understanding typical and atypical social development, as well as for identifying methods for early detection and intervention (e.g., Bunford, Kujawa, Swain et al., 2017; Johnson et al., 2015; Morales et al., 2016). Towards this aim, the current study investigates infants' neural responses to their peers' nonverbal vocalizations of emotions and temperamental variations in such responses by using event-related potentials (ERPs).

Within a few hours after birth infants already manifest distress vocalizations when they hear the sound of another infant crying (Dondi, Simion & Caltran, 1999; Field, Diego, Hernandez-Reif, & Fernandez, 2007; Geangu, Benga, Stahl & Striano, 2010; Martin & Clark, 1982; Sagi & Hoffman, 1976; Simner, 1971). Such distress responses are more intense when neonates hear a human infant cry rather than an infant chimpanzee cry (Martin & Clark, 1982), while artificial noise does not elicit such responses (Sagi & Hoffman, 1976; Simner, 1971). Neonates also have the capacity to perceptually discriminate between their own cry and the cry of another same age infant (Dondi et al., 1999; Martin & Clark, 1982). Throughout the first year of life, infants continue to respond with facial and vocal distress to the crying sounds of their peers (Geangu et al., 2010), and this increase in arousal persists throughout toddlerhood, although with lesser intensity (Nichols, Svetlova, & Brownell, 2009; Nichols, Svetlova, & Brownell, 2015). When jointly presented with the corresponding facial expressions, the overt responses elicited by peer emotional vocalizations are accompanied by autonomic arousal changes. In 6-, 12-, and 15-month-old infants (Geangu, Hauf, Bhardwaj, & Bentz, 2011; Upshaw, Kaiser, & Sommerville, 2015), observation of audio-video recordings of a peer crying or laughing elicited an increase in pupil diameter reflecting autonomic sympathetic activation (Bradley, Miccoli, Escrig, & Lang, 2008). The valence of the stimuli, however, moderated the latency of pupil response with crying eliciting an early response already present at 6-months, while laughter had a delayed pupil response at 6-months, it shared a similar latency as crying by 12-months (Geangu et al., 2011). Overall, observing crying peers elicited greater arousal compared to observing laughter (Geangu et al., 2011; Upshaw et al., 2015). Taken together, these early signs of affect sharing suggest that infants' ability to detect and process non-verbal vocalizations of emotions is present from birth and continues to develop throughout infancy. However, it is unclear whether these behavioral and physiological responses reflect developments in the sensory encoding of the stimuli and/or perceptual and cognitive processing.

Measuring neural responses via event-related potentials (ERPs) can provide further information in this respect. One important characteristic of this method is its unique temporal resolution, allowing millisecond precision in detecting the change of the electrical activity of the brain locked to the stimulus onset and associated with different sensory and cognitive processes (Luck, 2015). This method is also suitable and accessible for studying individuals across the entire lifespan starting with birth (unlike some neuroimaging methods – e.g., functional magnetic resonance imaging [fMRI]), which facilitates the understanding of sensory and cognitive development in relation to brain maturation (de Haan & Johnson, 2005). Moreover, these features also facilitate the study of individual variability across ontogeny which is not otherwise observable by using behavioural methods alone (Bunford,

Kujawa, Fitzgerald et al., 2017).

Based on electrophysiological evidence from adults, Schirmer and Kotz (2006) proposed a three-stage model for processing emotional vocalizations. At the first stage of processing, the brain shows sensitivity to the embedded emotional information as early as 100–200 ms after stimulus onset; indexed by the emergence of an N100 and P200 (Jessen & Kotz, 2011; Liu et al., 2012; Pell et al., 2015; Paulmann, Bleichner, & Kotz, 2013; Schirmer, Kotz, & Friederici, 2005). The N100, a negative deflection in the ERP waveform occurring around 100 ms, is considered to be an index of early sensory encoding of the physical properties of the sound (Näätänen & Picton, 1987) and the effort associated with the allocation of processing resources to form and maintain a sensory memory trace (Obleser & Kotz, 2011). Recently, evidence suggests that the amplitude of the N100 is modulated by the emotional valence of auditory stimuli (Jessen & Kotz, 2011; Liu et al., 2012). The positive component observed around 200 ms (P200) is proposed to reflect the processing of the semantically-relevant acoustic parameters involved in the early meaning detection or general stimulus categorization at the second stage of the model (García-Larrea, Lukaszewicz, & Mauguiére, 1992; Pell et al., 2015). The P200 is modulated by the motivational saliency of the acoustic signal as indicated by both the discrete emotional qualities of the stimulus and the associated arousal (Paulmann et al., 2013). The latency of both the N100 and the P200 shows that nonverbal vocalizations of emotions are processed much faster than emotional speech prosody, emphasizing the heightened relevance afforded by these crude means of expressing genuine emotions (Pell et al., 2015). More advanced analysis of the emotional meaning expressed by human emotional vocalizations are associated with the third stage of processing evidenced by neural components with longer latencies such as the late positive complex (LPC) (Jessen & Kotz, 2011; Kotz & Paulmann, 2011; Paulmann & Pell, 2010; Schirmer & Kotz, 2003, 2006; Schirmer, Chen, Ching, Tan, & Hong, 2013). For example, the amplitude of the LPC has been found to vary as a function of stimulus level of arousal and emotional expression, with increased amplitude for cues of threat (e.g., anger) compared to non-threat (e.g., sadness, happiness) or for expressions with higher versus lower levels of arousal (Paulmann et al., 2013; Pell et al., 2015). Such differences may reflect the evaluation of the stimulus meaning as related to the representations stored in an individual's memory; with preferential allocation of processing resources to the stimuli highly relevant for the individual (Hinojosa, Carretié, Valcárcel, Méndez-Bértolo, & Pozo, 2009; Kanske & Kotz, 2007; Paulmann et al., 2013; Pell et al., 2015). The emotional modulations of the LPC are also more pronounced and faster for nonverbal vocalizations of emotions compared to emotional prosody embedded in speech (Pell et al., 2015), suggesting that the emotional meaning of nonverbal vocalizations maintain prioritised processing continuing into adulthood.

Although studies exist to suggest that socially salient auditory information, including emotionally loaded human vocalizations, modulate infant neural responses, the findings have been mixed. The infant brain seems to differentiate between emotional prosody embedded in speech soon after birth (Cheng, Lee, Chen, Wang, & Decety, 2012; Zhang et al., 2014), probably relying on automatic discrimination processes related to the activity of primary and non-primary auditory areas in the temporal cortex (Näätänen, Paavilainen, Rinne, & Alho, 2007). While there is limited evidence to make such claims, auditory processing of emotion prosody in infancy seems to resemble adult-like processing demonstrating sensitivity to emotional content both at early processing stages (Grossmann et al., 2013) and at later ones (Grossmann, Striano, & Friederici, 2005). Recent evidence suggests that 8-month-olds' ERP responses may also be sensitive to peers' nonverbal vocalizations of emotions. Missana, Alvater-Mackensen, and Grossman (2017) presented infants with the sounds of peers' cry and laughter, as well as the neutral humming of an adult. While the early positive and negative components responded selectively to either peer crying or laughter, no differentiation between emotions was reported at later

stages of processing. On the contrary, a recent fMRI study with infants showed that the insula and the orbitofrontal cortex – brain areas known to be related to emotion information processing (Blasi et al., 2011; Grossmann, Oberecker, Koch, & Friderici, 2010; Lloyd-Fox, Blasi, Mercure, Elwell, & Johnson, 2012) – were more active in response to the sounds of adult crying compared to both adult laughter and neutral non-verbal vocalizations like coughs and sighs (Blasi et al., 2011).

The disparate results reported by these studies may be explained by the differences in the temporal resolution of the methods used (EEG/ERP vs. fMRI) and the fact that they may reflect different stages of processing, or they may be due to differences in the stimuli. While Blasi et al. (2011) compared hemodynamic responses to nonverbal vocalizations produced by adults, Missana et al. (2017) contrasted ERPs to peer emotional nonverbal vocalizations with adult neutral vocalizations. As reported above, behavioural studies have demonstrated infants' sensitivity to the age of the voice expressing nonverbal vocalizations of emotions (Martin & Clark, 1982). Further, the effect of familiarity, a well-known effect in the processing of visual information (e.g., faces – Kahana-Kalman & Walker-Andrews, 2001; de Haan, Johnson, & Halit, 2003), may have driven the reported ERP findings, not by the emotional content, but by the degree of familiarity of adult versus peer voices (Kooijmann, Hagoort, & Cutler, 2005; Thierry, Vihman, & Roberts, 2003). Contrasting 8-month-old infants' ERP responses to emotional and neutral nonverbal vocalizations which both belong to their peers is essential for providing a clear picture of the neurocognitive mechanisms involved in processing this type of emotional expressions.

Despite the universal relevance of emotions, humans vary greatly in how they respond to emotional cues (e.g., Wieser & Brosch, 2012). For example, some individuals are faster at detecting stimuli with emotionally negative content and dwell more on them than others (e.g., Bishop, Duncan, Brett, & Lawrence, 2004; McNaughton & Gray, 2000). Conversely, some individuals show attenuated neural responses to emotional expressions of happiness (Bunford, Kujawa, Swain et al., 2017). Individuals also vary greatly in terms of how intensely they react to emotional information (Hamann & Canli, 2004; Wheaton, Fitzgerald, Phan, & Klumpp, 2014). These differences are present starting with early infancy (Fox et al., 2005) and have been associated with individual temperamental characteristics (e.g., Jarcho et al., 2014). Variations in temperamental reactivity and self-regulation are thought to stem from a person's enduring biological make-up, shaped by the interplay between heredity, maturation, and experience (Rothbart & Derryberry, 1981). Infants' and young children's temperamental characteristics manifest stable influences on an individual's emotional life (Jarcho et al., 2014) and are significantly linked to adult personality traits (Fox et al., 2005; Kagan, Reznick, Clarke, Snidman, & Garcia-Coll, 1984). Importantly, these early individual differences in emotional reactivity, regulation, and in processing emotional information are important predictors for several socio-emotional development outcomes (Bunford, Kujawa, Fitzgerald et al., 2017; Bunford, Kujawa, Swain et al., 2017; Frick & Morris, 2004; Morales et al., 2016; Olson, Sameroff, Kerr, Lopez, & Wellman, 2005; Pérez-Edgar & Fox, 2005). Understanding how temperamental differences in emotional reactivity and regulation relate to the processing of emotional cues beginning in infancy is crucial for early detection and intervention of those individuals more likely to manifest atypical patterns of development.

Recent studies have shown that infants' neural responses to visual cues of others' emotions are significantly related to their temperamental characteristics (Martinos, Matheson, & de Haan, 2012; Missana, Grigutsch, & Grossmann, 2014; Rajhans, Missana, Krol, & Grossmann, 2015; Ravicz, Perdue, Westerlund, Vanderwert, & Nelson, 2015). In particular, infants with a disposition to express negative emotions during everyday life are more likely to manifest increased attention allocation to positive facial expressions (Martinos et al., 2012). In contrast, infants lower on negative emotionality are more likely to allocate their attention to processing negative emotional expressions

(Rajhans et al., 2015). Infants' with better emotion regulation abilities also seem to allocate more attention to processing fearful emotional facial expressions (Martinos et al., 2012). The specific ability to recover from peak arousal is particularly related to the degree of attentional engagement in processing angry facial expressions, suggesting that those infants who are better able to control their own state, are more likely to focus on processing facial cues of threat (Missana et al., 2014). Further, both infants' regulatory abilities and aspects of their negative emotionality are significantly associated with their behavioural emotional responses to peer cry sounds (Geangu et al., 2011). Taken together, this suggests that temperament may be related to the individual differences in the processing of emotional vocalizations, and that these may be detectable at the neural level of processing. This is the first study to systematically investigate temperamental variance in infants' neural responses to their peers' nonverbal vocalizations of emotions.

The aim of our study was two-fold: to test whether infants' neural processing of peers' nonverbal emotional vocalizations is sensitive to the valence of the conveyed emotion; and whether these neural responses can be modulated by the infants' temperamental characteristics. Towards these aims, we measured 8-month-old infants' ERPs in response to audio recordings of emotional (negative/crying and positive/laughing) and non-emotional (i.e., coughing) nonverbal vocalizations. Crucially, all these nonverbal vocalizations were produced by infants. On the basis of previous studies on emotion perception from voice in both infants (Cheng et al., 2012; Grossmann et al., 2005; Missana et al., 2017; Zhang et al., 2014) and adults (Jessen & Kotz, 2011; Liu et al., 2012; Paulmann et al., 2013; Pell et al., 2015; Schirmer et al., 2005), we examined differences between affective and neutral auditory stimuli at the level of the early ERP components, in particular those corresponding to the N100 and the P200. Given the sensitivity of the N100 and P200 amplitude to emotional information (e.g., Missana et al., 2017; Paulmann et al., 2013; Pell et al., 2015), we hypothesized that emotional nonverbal vocalizations would evoke larger N100 and P200 amplitudes relative to neutral vocalizations. In addition, we hypothesized that the emotional sounds would have sustained processing in comparison to the neutral condition, as reflected by the LPC (Missana et al., 2017; Pell et al., 2015). In terms of the temperamental characteristics, we predicted a significant relation between aspects of infants' negative emotionality and their ERP responses to their peers' nonverbal vocalizations of emotions since this relation has been more systematically reported in previous studies (Martinos et al., 2012; Missana et al., 2014; Rajhans et al., 2015).

2. Methods

2.1. Participants

Thirty 8-month-old infants (13 females, M_{age} = 291.90 days, SD_{age} = 110.49 days) were included in the final EEG data analysis. An additional 12 infants were tested but not included in the final sample due to excessive artifacts and insufficient number of trials (N = 10) or missing IBQ-R data (N = 2). All participants were recruited from a small urban area in North West England, did not suffer from any neurological or other medical condition, and were observed to have a normal audition for their age.

Prior to the experiment, all parents were informed that at the end of the experiment they would receive £10 in order to cover traveling expenses and that the infant will be rewarded with a book for their participation. Informed consent was obtained from all parents. All data were collected in accordance with the ethical principles of the Declaration of Helsinki (BMJ 1991; 302: 1194) and the study was approved by the Lancaster University Faculty Ethics Committee.

2.2. Stimuli

A sample of 12 nonverbal emotional vocalizations produced by pre-

Table 1
Authenticity and arousal ratings for the non-verbal emotional stimuli.

	Arousal 1 extremely weak to 7 extremely strong	Authenticity 1 extremely false to 7 extremely authentic
Cry	6.19 (0.43)	5.83 (0.16)
Laughter	6.25 (0.40)	5.49 (0.28)
Cough	3.74 (1.09)[a]	5.21 (0.31)

Note: Mean (and SD) ratings from n = 20 adults.

[a] Cough sounds were rated significantly less arousing than cry ($p < 0.001$) or laughter ($p < 0.001$).

verbal infants was gathered from sound library sources. The stimuli consisted of 4 positive (i.e., laughter), 4 negative (i.e., cry), and 4 neutral (i.e., cough) non-speech sounds. Each vocalization was produced by a different individual. The use of coughing sounds as neutral nonverbal vocalizations is in line with previous investigations of auditory emotion processing as an emotionally neutral contrast to emotionally loaded vocalizations (Armony, Chochol, Fecteau, & Belin, 2007; Blasi et al., 2011; Fecteau, Belin, Joanette, & Armony, 2007). The sound recordings were edited to a 1.4 s length and rated by a group of 20 university students (10 females; M_{age} = 26 years; SD = 2.82 years) with respect to perceived arousal and authenticity of the emotion by using a 7-point Likert scale (Table 1).

Separate one-way analyses of variance (ANOVA) with emotion (laughter/positive, cry/negative, and cough/neutral) as a factor were performed on the arousal and authenticity ratings for the nonverbal stimuli. No significant differences between affective stimuli were found on authenticity ($F(2, 59)$ = 1.693; p = 0.193), while a main effect of emotion was obtained for the arousal ratings ($F(2, 59)$ = 80.244; $p < 0.001$). Post-hoc comparisons revealed that cough sounds were rated as less arousing than both cry ($p < 0.001$) and laughter vocalizations ($p < 0.001$).

In addition, participants were asked to indicate the valence of the stimuli (positive, negative or neutral). On average, crying sounds were judged as "negative" by 97% of participants, laughing sounds were rated as "positive" by 99% of participants, and neutral sounds were rated as "neutral" by 75% of participants. These ratings are similar to those reported in previous studies using vocal emotional expressions (e.g., Belin et al., 2008; Pell et al., 2015). Basic acoustic properties of the stimuli are presented in Fig. 1. The nonverbal vocalizations were edited so that all audio stimuli had an average root mean square intensity of 40 dB, after edge smoothing (linear rise/fall times of 20 ms) by applying cosine-squared ramps to the onset and offset. All sounds were bandpass filtered from 1 to 10,000 Hz with a digital finite impulse

response filter in order to remove any potential background noise.

2.3. Temperament measure: Infant Behaviour Questionnaire – Revised (IBQ-R)

Parental reports of infant temperament were obtained using the Infant Behaviour Questionnaire – Revised (IBQ-R, Gartstein & Rothbart, 2003) that characterises temperament along 3 scales and 14 subscales from a total of 191 items. This instrument is widely used and is typically reported to have satisfactory reliability and validity (Gartstein & Rothbart, 2003). For the current study, we focused on the temperamental dimension *Negative Emotionality* and its subscales since this dimension had been previously related to differences in infant ERP responses to emotional information conveyed by facial and body expressions (Martinos et al., 2012; Missana et al., 2014; Rajhans et al., 2015). *Negative Emotionality* (α = 0.757) refers to the tendency to show various forms of negative affect such as generalised distress, fear, and anger, and it is defined by four subscales: *Sadness* (lowered mood and activity related to personal suffering, physical state, object loss, or inability to perform a desired action; general low mood; α = 0.763); *Distress to Limitations* (fussing, crying or showing distress while in a confining place or position; in caretaking activities; or when unable to perform a desired action; α = 0.810); *Fear* (startle or distress to sudden changes in stimulation, novel physical objects or social stimuli; inhibited approach to novelty; α = 0.902); and *Falling Reactivity* (rate of recovery from peak distress, excitement, or general arousal; ease of falling asleep – typically regarded to reflect infants' ability to regulate their own state; α = 0.883).

2.4. Procedure

ERPs were recorded while infants sat on their parent's lap at a distance of approximately 70 cm from a 17-inch monitor in a dimly lit room. The auditory stimuli were randomly presented using MATLAB software (MathWorks, Natick, MA), over two hidden speakers placed to the left and right of the monitor. No more than two sounds of the same emotional category were presented consecutively. A trial consisted of 1400 ms sound stimulus followed by a silent interstimulus interval, which varied randomly in duration between 1200 ms and 2000 ms. A black fixation cross on a grey background was displayed on the monitor during the entire procedure. The procedure continued until a maximum of 138 trials were presented (46 per category) or until the infant showed signs of boredom and unrest. In order to minimize infants' movements and maintain their interest, an experimenter was present to quietly blow soap bubbles throughout the whole procedure. Both the parent and the experimenter avoided visual contact and any attempt for

Waveforms and spectrograms of exemplary non-verbal vocalizations

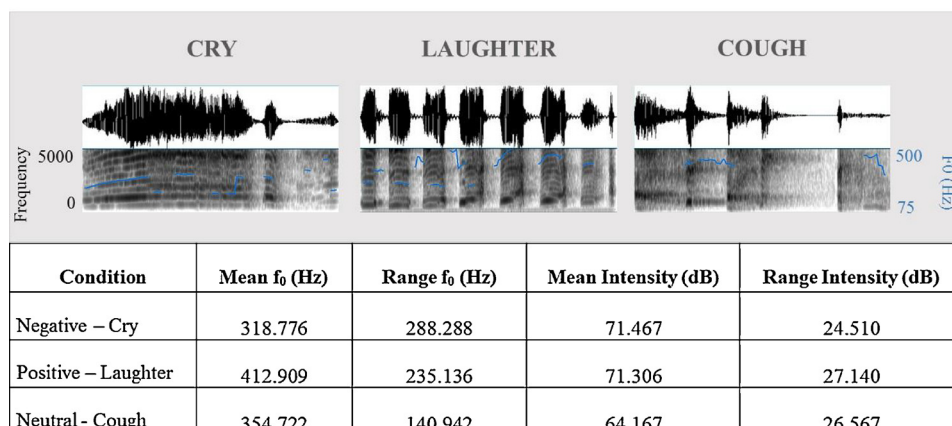| Condition	Mean f_0 (Hz)	Range f_0 (Hz)	Mean Intensity (dB)	Range Intensity (dB)
Negative – Cry	318.776	288.288	71.467	24.510
Positive – Laughter	412.909	235.136	71.306	27.140
Neutral - Cough	354.722	140.942	64.167	26.567

Fig. 1. Waveforms and spectrograms of exemplary non-verbal vocalizations included in the study and the average acoustic features for each affective category. The fundamental frequency (f_0) or pitch is measured in Hertz (Hz), while the intensity in decibels (dB). The values represent the averages across all exemplars within a category, calculated for the entire stimulus duration. The range for f_0 and intensity is calculated by subtracting the minimum from the maximum value recorded for each stimulus and then averaged across all exemplars.

social interaction with the infant. The procedure lasted approximately 8 min. After stimulus presentation, parents completed the IBQ-R questionnaire.

2.5. Electroencephalogram recording and data analysis

The EEG was recorded continuously using a 128-electrode HydroCel Geodesic Sensor Net (Electrical Geodesic Inc., Eugene, OR) and amplified using an EGI NetAmps 300 amplifier. The signal was referenced online to the vertex electrode (Cz), a bandpass filter of 0.1–100 Hz was applied, and the data were sampled at 500 Hz. Impedances were checked prior to the beginning of the recording and considered acceptable if lower than 50 kΩ (Ferree, Luu, Russell, & Tucker, 2001), which is a conservative threshold for infants and in accordance with the methodological recommendations for this age group (Johnson et al., 2001). EEG data were further processed offline using NetStation v4.6.4 (Eugene, OR). The signal was band-pass filtered (0.3–30 Hz), and the ERP trials were segmented with a 200 ms baseline and 1400 ms following stimulus onset. Data were corrected to the average voltage during baseline and re-referenced to the algebraic mean of channels. To eliminate artifacts, trials were automatically rejected whenever the signal exceeded ± 200 μV at any electrode for more than eighteen channels. Data were further checked through visual inspection for any artifacts not detected by the automated algorithm, such as those due to eye-movements, eye-blinks and body movements. Of the remaining trials, individual bad channels were replaced using spherical spline interpolation. Individual subject averages were computed separately for each channel across all trials within each condition and then data re-referenced to the average reference. For each participant, a minimum of 9 trials/condition was required in order to be further included in the analysis. Across participants, the mean number of trials contributing to the average ERP was 18 per condition (Coughing: $M = 18.41$, $SD = 6.49$; Crying: $M = 17.19$, $SD = 5.67$; Laughing: $M = 18.53$, $SD = 5.88$).

On the basis of visual inspection of ERP waveforms and previous adult and infant auditory ERP studies (Kushnerenko, Ceponiene, Balan, Fellman, & Näätänen, 2002; Kushnerenko et al., 2007; Little, Thomas, & Letterman, 1999; Ohlrich & Barnet, 1972; Shucard, Shucard, Cummins, & Campos, 1981; Shucard, Shucard, & Thomas, 1987; Paulmann et al., 2013; Pell et al., 2015; Wunderlich & Cone-Wesson, 2006), mean amplitudes were analysed at three time-windows at frontal locations: 50–150 ms (N100), 150–200 ms (P200), and 550–950 ms (LPC). Unlike previous studies with adults (Paulmann et al., 2013; Pell et al., 2015) and infants (Missana et al., 2017) the morphology of the waveform at central locations did not indicate the presence of an LPC (Fig. 2), thus the mean amplitude effects were only assessed for the time window of 150–200 ms (P200). These differences in the topography of the LPC may be due to age and methodological differences (e.g., the use of an average reference more typical to high density systems vs. the linked-

Table 2
Correlations between the mean amplitude difference scores of the P200 (corrected) and LPC between affective conditions at frontal locations and temperament.

Temperament	P200 (150–250 ms)			LPC (550–950 ms)		
	Lg–Cr	Lg–Cg	Cr–Cg	Lg–Cr	Lg–Cg	Cr–Cg
Negative Emotionality	− 0.289	− 0.400*	− 0.092	0.283	0.076	− 0.193
Distress	− 0.279	− 0.262	0.037	0.208	0.196	− 0.044
Fear	− 0.281	− 0.161	0.140	− 0.197	− 0.272	− 0.019
Sadness	− 0.248	− 0.182	0.083	0.243	0.462**	0.112
Falling Reactivity	0.033	0.513**	0.481**	− 0.527**	0.143	0.558**

*$p < 0.05$, **$p < 0.01$; Lg = Laughter, Cr = Cry, Cg = Cough.

mastoid reference – Liu et al., 2012). The regions of interest (ROIs) were: frontal (left – 23, 24, 27, 28; right – 3, 117, 123, 124) and central (left – 36, 41, 42, 47; right – 93, 96, 103, 104) (Fig. 2). Separate 3 (emotion: positive, negative, neutral) × 2 (hemisphere: left, right) repeated-measures ANOVAs were conducted for each of these time windows at their respective regions of interest. All ERP statistical tests were conducted at 0.05 level of significance (two-tailed) and the significant main effects or interactions were followed up by planned comparisons. Pearson correlations (two tailed, $p < 0.05$) were computed to examine the relations between infants' general score on the *Negative Emotionality scale*, as well as the scores for its subscales (i.e., Sadness, Distress to Limitations, Fear, and Falling Reactivity), and the mean amplitude difference scores of the N100, P200 corrected and LPC between affective conditions (i.e., laughter *vs.* cry, cry *vs.* coughing, laughter *vs.* coughing; Table 2). For each time window the mean amplitude obtained in response to coughing sounds was subtracted from the mean amplitude recorded in response to laughter sounds (i.e. Laughter [Lg] – Coughing [Cg]: $N100_{Lg-Cg}$, $P200_{Lg-Cg}$, LPC_{Lg-Cg}) and crying sounds (i.e. Crying [Cr] – Coughing [Cg]: $N100_{Cr-Cg}$, $P200_{Cr-Cg}$, LPC_{Cr-Cg}). In addition, for each component the mean amplitude elicited by crying sounds was subtracted from the mean amplitude elicited by laughter sounds (i.e. Laughter [Lg] – Crying [Cr]: $N100_{Lg-Cr}$, $P200_{Lg-Cr}$, LPC_{Lg-Cr}).

3. Results

The grand averages for all conditions at different scalp locations are presented in Fig. 2. A more detailed illustration of the scalp topographies for the frontal components is included in Fig. 3.
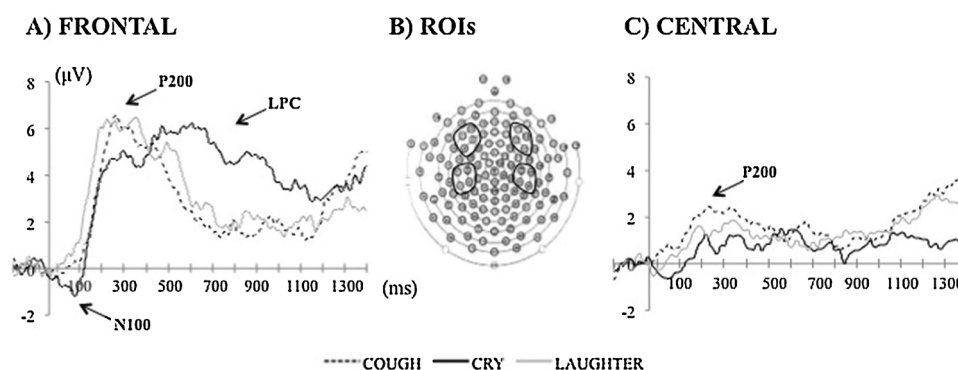

Fig. 2. Grand average ERPs for the cry (dark solid line), laughter (light gray solid line) and cough (dotted line) sounds over frontal (A), and central (C) locations. The location of the analyzed ROIs is indicated in (B).
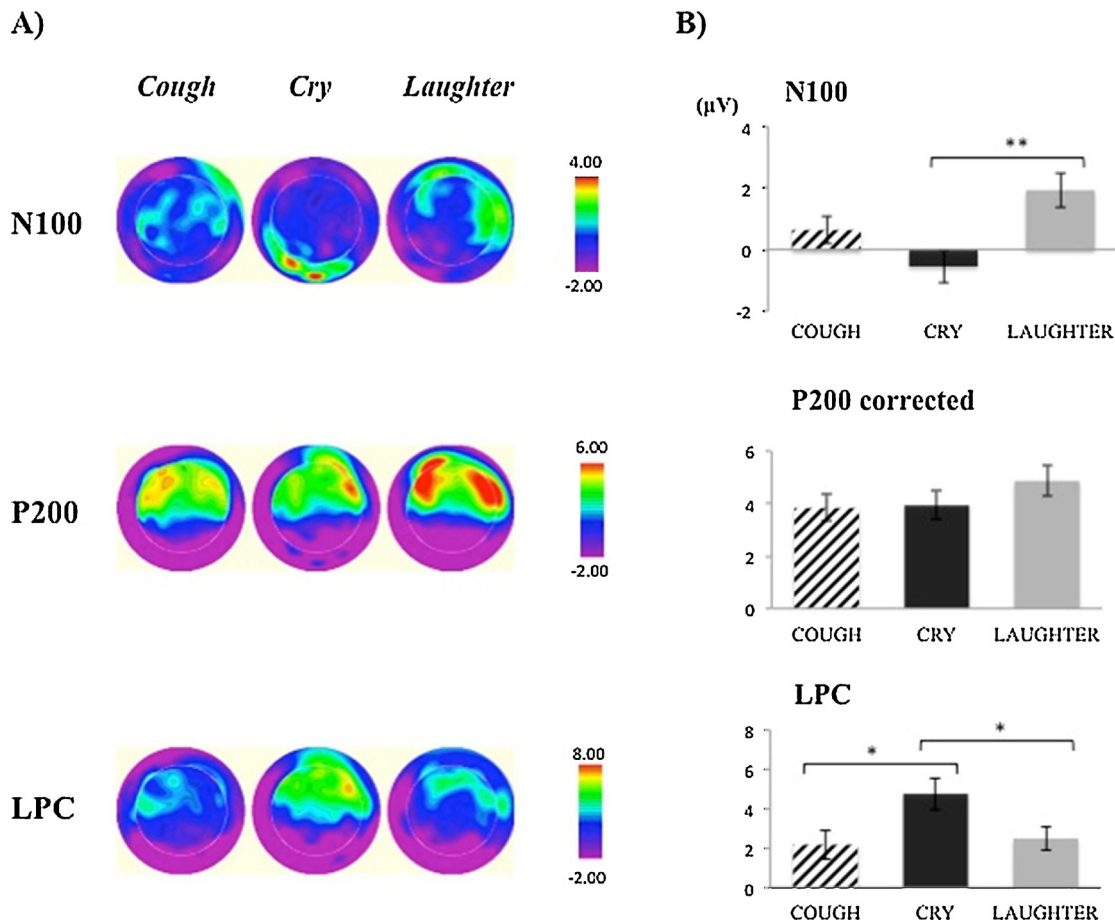
Fig. 3. Scalp topographies for the frontal ERP components. (A) Voltage topographies of the frontal ERP components over the scalp for Cough (first column), Cry (middle column) and Laughter (last column) sounds. (B) Bar graphs showing the mean amplitude values (plus standard errors of the mean) per experimental condition for the frontal ERP components. The mean amplitude values for P200 are controlled for N100 variations. *p < 0.05, **p < 0.01.

3.1. ERP analysis

3.1.1. Frontal

3.1.1.1. N100 (50–150 ms). A main effect of emotion was found for the N100 mean amplitude at frontal leads, $F(2,58) = 5.847$; $p = 0.005$; $\eta^2 = 0.168$. Pairwise comparisons revealed that the N100 was significantly more negative for cry ($M = -0.547 \mu V$; $SE = 0.527$) than for laughter sounds ($M = 1.931 \mu V$; $SE = 0.571$; $p = 0.007$; $d = 0.45$; 95% CI [-4.215, -0.740]). No significant differences were observed between the neutral and emotional sounds ($p > 0.067$). No other main effects or interaction were found ($p > 0.262$).

3.1.1.2. P200 (150–200 ms). At frontal locations, the analysis of P200 mean amplitude revealed a significant main effect of emotion, $F(2,58) = 4.481$; $p = 0.016$; $\eta^2 = 0.134$. Pairwise comparisons revealed that laughter sounds elicited more positive P200 amplitudes ($M = 6.241 \mu V$; $SE = 0.848$) than cry vocalizations ($M = 3.510 \mu V$; $SE = 0.745$; $p = 0.012$; $d = 0.419$; 95% CI [0.647, 4.816]), and marginally more positive amplitudes than cough sounds ($M = 4.645 \mu V$; $SE = 0.713$; $p = 0.057$; $d = 0.329$; 95% CI [-0.052, 3.243]). No differences were observed between cry and cough vocalizations ($p > 0.223$; $d = -0.197$; 95% CI [-3.003, 0.731]). Similar mean amplitudes were recorded for both hemispheres, $F(1,29) = 0.476$; $p = 0.496$; $\eta^2 = 0.016$. No significant emotion x hemisphere interaction was found, $F(2,58) = 0.449$; $p = 0.640$; $\eta^2 = 0.015$.

Given the temporal proximity between this component and the N100 at frontal locations, it is possible that variations in the N100

parameters may have affected the P200 component differently across conditions. Thus, complementary peak-to-peak measurement and analysis were performed to control for N100 variations. The same statistical analyses as described above were performed on the mean amplitude difference between the peak of the P200 and the N100 (i.e., P200 – N100). These analyses revealed no significant main effects or interactions (all $ps > 0.606$). Therefore, when accounting for peak-to-peak amplitude differences, the main effect of emotion disappears.

3.1.1.3. LPC (550–950 ms). For this late time window at frontal locations, a main effect of emotion was found for the mean amplitude, $F(2,58) = 4.161$; $p = 0.020$; $\eta^2 = 0.125$. Planned comparisons revealed that LPC amplitudes were more positive for cry ($M = 4.754 \mu V$; $SE = 0.812$) than laughter ($M = 2.480 \mu V$; $SE = 0.603$; $p = 0.028$; $d = 0.333$; 95% CI [0.259, 4.289]) and cough sounds ($M = 2.163 \mu V$; $SE = 0.726$; $p = 0.030$; $d = 0.346$; 95% CI [0.274, 4.909]). No difference was observed between laughter and cough sounds ($p = 0.691$; $d = 0.058$; 95% CI [-1.302, 1.936]). No other main effects or interactions were found (all $ps > 0.341$).

3.1.2. Central

3.1.2.1. P200 (150–250 ms). A similar mean amplitude was elicited by all conditions, $F(2,58) = 2.114$; $p = 0.130$; $\eta^2 = 0.068$. No main effect of hemisphere, $F(1,29) = 0.150$; $p = 0.702$; $\eta^2 = 0.005$, or interaction between emotion and hemisphere was identified, $F(2,58) = 2.768$; $p = 0.071$; $\eta^2 = 0.087$.
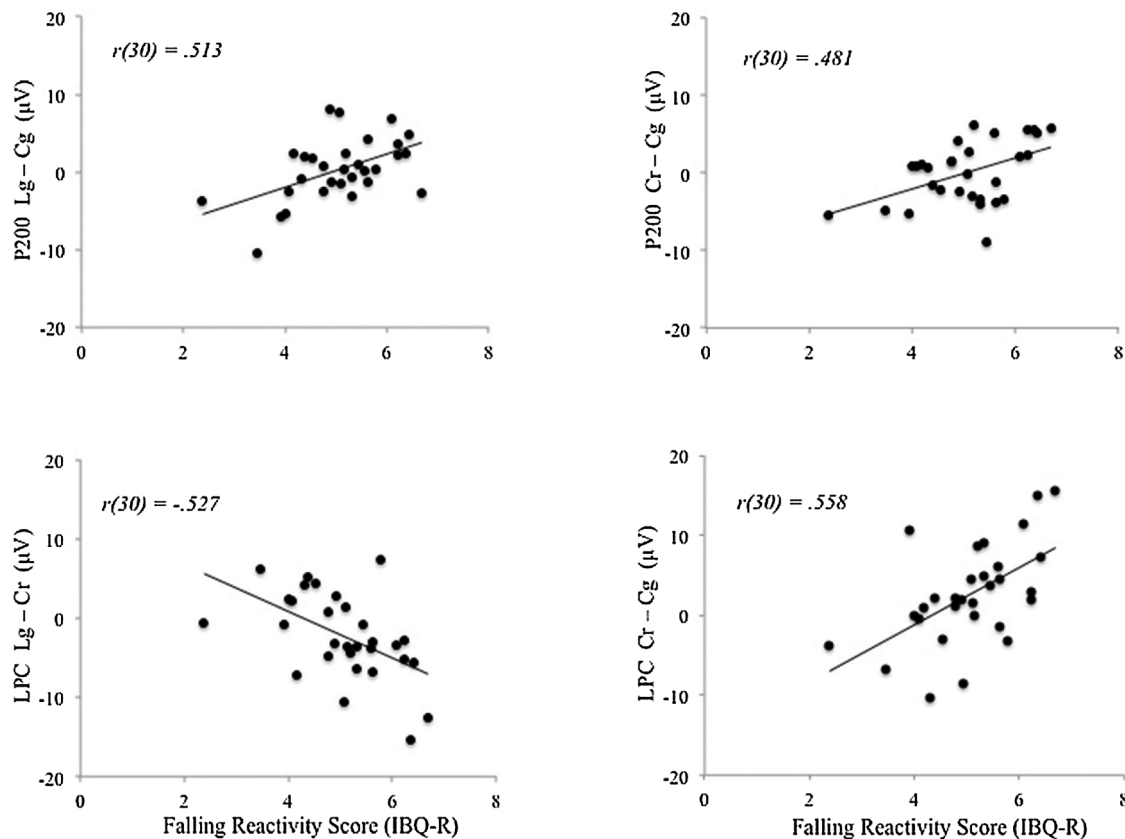
Fig. 4. Correlations between infant ERP difference scores and Falling Reactivity scores (IBQ-R). Scatterplots representing the significant correlations (all $ps < 0.01$) between the mean amplitude difference scores of the frontal P200 corrected (top) and frontal LPC (bottom) and infants' scores on IBQ-R Falling Reactivity. Lg = Laughter, Cr = Cry, Cg = Cough.

3.2. Correlation analysis

For the N100, there was no apparent relation between Negative Emotionality scores and the amplitude difference scores ($p > 0.647$).

For the P200 corrected, the factor Negative Emotionality was negatively associated with the P200$_{Lg-Cg}$ amplitude difference score, $r(30) = -0.400$, $p = 0.028$. Infants lower on Negative Emotionality were more likely to record larger P200 amplitudes for laughter compared to coughing. Similarly, our analysis revealed a significant positive correlation between infant's ability to recover from distress (IBQ-R Falling Reactivity scale) and the mean amplitude scores for P200$_{Lg-Cg}$ ($r(30) = 0.513$, $p = 0.004$) and P200$_{Cr-Cg}$ scores $(r(30) = 0.481$, $p = 0.007$) (Fig. 4). In this case, the higher parents rated their infants' ability to recover form peak arousal, the more positive the amplitude of the P200 for emotional vocalizations (crying and laughter) relative to neutral nonverbal vocalizations (coughing).

For the LPC difference scores, no association was observed with the main factor Negative Emotionality ($p > 0.129$). Nonetheless, a closer inspection of the subscales revealed a significant negative correlation between infants' ability to recover from distress (IBQ-R Falling Reactivity scale) and the LPC$_{Lg-Cr}$ score, $r(30) = -0.527$, $p = 0.003$ (Fig. 4). In particular, the higher parents rated their infants' ability to regulate and recover from peak arousal, the more positive the amplitude of the LPC for cry as opposed to laughter. In the same line, our results showed a significant positive correlation between infant's Falling Reactivity and the LPC$_{Cr-Cg}$ amplitude difference score, $r(30) = 0.558$, $p = 0.001$ (Fig. 4). Specifically, the higher infant's ability to regulate and recover from peak arousal, the more positive the amplitude of the LPC for cry as opposed to cough. Finally, our analysis revealed a positive correlation between infants' general low mood (IBQ-R Sadness score) and the mean amplitude of LPC$_{Lg-Cg}$, such that the

higher parents rated their infants' tendency to show low mood, the more positive the amplitude of the LPC for laughter compared to cough ($r(30) = 0.462$, $p = 0.010$).

4. Discussion

In this study, we aimed to investigate 8-month-old infants' ERP responses to their peers' non-verbal vocalizations of emotions and whether these are modulated by temperament. Sounds of infants crying and laughing were presented alongside neutral nonverbal vocalizations (i.e., coughing) and parents reported on their infants' temperamental characteristics. Results showed that the processing of emotional information from nonverbal vocalizations at the age of 8 months was associated with differential ERP activity at frontal locations, indexed by the N100, P200, and LPC components. Importantly, the differentiation in response between emotional and non-emotional stimuli was significantly related to temperamental differences in negative emotionality.

In line with several previous studies reporting a sensitivity to emotional vocalizations within the early stages of auditory processing (Missana et al., 2017; Pell et al., 2015; Schirmer & Kotz, 2006), our results showed that 8-month-old infants responded with a more negative N100 amplitude to their peers' cry sounds than to their peer's positive nonverbal emotional vocalizations. The N100 is considered to be at least partially generated by the processing of the acoustic input in the auditory cortex (Eggermont & Ponton, 2003; Näätänen & Picton, 1987). Empirical evidence from infants suggests the N100 is less likely to be influenced by the novelty of the sound, and much more likely to be modulated by other auditory properties such as spectral richness (Csibra, Kushnerenko, & Grossmann, 2008; Kushnerenko et al., 2007), as well as the sound onset features which determine the amount of

acoustic energy entering the auditory system (e.g., slope, amplitude of sounds rise/fall) (Čeponienė, Aku, Westerfield, Torki, & Townsend, 2005; Čeponienė, Torki, Alku, Koyama, & Townsend, 2008). The early processing of auditory cues contributes to the extraction of the emotional salience (Jessen & Kotz, 2011; Schirmer & Kotz, 2006) and may explain the differences observed in our study, with crying and laughing sounds being the most distinct in relation to each other.

The variations in infants' tendencies to respond with negative emotionality during everyday life events was not related to the differences in N100 amplitude between conditions. One possible explanation is that at such an early stage of processing, infants are primarily extracting the sensory properties of the stimuli, operations that are not related to individual differences in emotional responsivity. It is also possible that these relations become more obvious once these individual differences manifest with higher intensity and in a more stable manner later in ontogeny since adults who tend to be highly anxious show increased N100 amplitude for emotional non-verbal vocalizations (Pell et al., 2015).

Presenting 8-month-old infants with their peers' nonverbal vocalizations also elicited an early P200 at frontal and central locations. Previous studies reported that the mother's voice (Purhonen, Kilpeläinen-Lees, Valkonen-Korhonen, Karthu, & Lehtonen, 2004; Purhonen, Kilpeläinen-Lees, Valkonen-Korhonen, Karthu, & Lehtonen, 2005) and the sound of infant's own name (Parise, Friederici, & Striano, 2010) trigger in infants early positive components with higher and faster amplitude at anterior scalp locations compared to a stranger's voice and name, respectively. These effects may be partially due to stimulus social salience, given the relevance of the mother's voice and own name for social interaction and survival. In our study, all nonverbal vocalization evoked a P200 of similar amplitude, suggesting that they were perceived to have similar saliency. Although laughter appeared to record a larger amplitude compared to the sound of cry and cough, this effect did not hold when correcting for the N100 amplitude differences. As it is typically reported for faces (e.g., Lee, Kang, Park, Kim, & An, 2008; Wieser & Brosch, 2012), the neutral non-verbal vocalizations of emotions included in this study were not as unambiguously perceived as such by the adult raters. This ambiguity may have influenced infants' early ERP responses, potentially explaining some of the lack of differentiation between the emotional and neutral conditions. Interestingly however, temperament *was* related to differentiation in P200 amplitude between the emotional (both positive and negative) and the neutral nonverbal vocalizations in our sample. Infants who were rated by their mothers as having greater self-regulation (Falling Reactivity) had a larger P200 to both laughter and crying compared to those infants rated as having poor self-regulation. These results expand previous findings by showing that infants' temperamental variations in the ability to regulate arousal are not only related to ERP responses to emotional facial expressions (Missana et al., 2014; Martinos et al., 2012), but also to their ability to preferentially attend to their peers' nonverbal vocalizations of emotions; a skill that may be a precursor to developing empathy (Geangu, 2015).

Our study also revealed late effects of emotion, with the sounds of crying peers eliciting higher amplitude of the frontal LPC compared to both laughter and coughing. Modulations of the LPC by the valence of verbal and nonverbal emotion vocalizations have been systematically reported in adults and it is proposed to reflect the sustained cognitive processing of these social cues (e.g., Jessen & Kotz, 2011; Kotz & Paulmann, 2011; Paulmann et al., 2013; Schirmer et al., 2013; Schirmer & Kotz, 2006; Wildgruber, Ethofer, Grandjean, & Kreifelts, 2009). In infants, differentiation at the level of similar positive slow waves has been suggested to reflect the updating of existing memory representations (Nelson, Thomas, de Haan, & Wewerka, 1998). Our results show that although 8-month-olds perceived both cry and laughter as similarly salient social cues, they engaged in the sustained processing of only the cry sounds. These findings are in line with previous reports that listening to adult crying compared to laughter and neutral nonverbal

vocalizations leads 3- to 7-month-old infants to increased activation of the orbitofrontal cortex and the insula (Blasi et al., 2011), areas known to be involved in the automatic appraisal of the emotional stimuli outside awareness and the generation of emotional experiences (see Koelsch et al., 2015 for a review). Our findings are in contrast to those recently reported by Missana et al. (2017), who found no difference in LPC amplitude between cry and laughter, however, this may be due to differences in our methodology. In our study we used positive, negative, and neutral vocalizations from other infants which have greater salience in meaning to infants (Dondi et al., 1999; Martin & Clark, 1982) whereas Missana et al. (2017) included adults humming as a neutral stimulus. It is thus possible that the lack of LPC differentiation between the emotional conditions reported by Missana et al. (2017) was driven by the contrast between infant and adult voices.

Threat-related emotions are hypothesized to carry greater informational value than positive ones, and to require greater attention and cognitive processing (e.g., Cacioppo & Berntson, 1999; Peeters & Czapinski, 1990; Vuilleumier, 2005; Williams, 2006). In line with a rich body of literature showing that from around the age of 7-months infants increasingly manifest a negativity bias in their processing and use of emotional expressions (e.g., Leppänen, Kauppinen, Peltola, & Hietanen, 2007; Peltola, Leppänen, Mäki, & Hietanen, 2009; Vaish, Grossmann, & Woodward, 2008), our study showed that such bias may extend to peers' non-verbal vocalizations of emotions. The effect of the negative emotional condition on both the early N100 and the later LPC suggest that the emerging negativity bias may not be specific to viewing negative expressions but more broadly tuned to negative emotions in the infant's environment. Moreover, infants' temperament may moderate this effect, such that infants with improved ability to regulate their state of peak arousal also showed increasing attention allocation in response to their peers' cry compared to peer's laughter or neutral vocalizations. Although the correlational analysis does not allow the formulation of causal interpretations, our results add to existing evidence suggesting that early regulatory abilities are relevant for understanding infant emotion information processing and the emerging negativity bias. It is possible that the ability to regulate the high arousal elicited by negative emotional cues allow further engagement with the stimuli rather than avoidance. This in turn could lead to richer representations and more accurate appraisal of the threat cues, with potential further implications for emotion regulation and affective learning development (Britton, Lissek, Grillon, Norcross, & Pine, 2011; Morales et al., 2016). The longitudinal investigation of the complex relations between temperamental characteristics and emotional information processing beginning with infancy is thus essential for understanding typical and atypical social development.

Like cry, laughter is a pervasive non-verbal expression of emotion, which is universally recognized. Although it can reflect genuine positive emotional experiences, laughter is also frequently used for structuring social interactions and conversations, and to regulate others' responses (Scott, Lavan, Chen, & McGettigan, 2014). Importantly, laughter production and perception is to a great extent dependent on the visual presence of others (Provine, 2004; Scott et al., 2014). Towards the end of the first year, infants also show increased understanding of those social situations where laughter is more common, like humor (Mireault et al., 2014; Reddy, 2001, 2008). It is thus possible that compared to crying, the development of laughter processing is more protracted and dependent on the presence of other emotional social cues (e.g., face and body posture), and also related to the emergence of more advanced social cognition and communicative abilities. Adding to previous evidence suggesting that infants with higher negative emotionality are more sensitive to facial expressions of happiness (Martinos et al., 2012), in our study, infants characterized by increased tendencies to respond with sadness to negative life events tended to engage in increased sustained processing of laughter compared to emotionally neutral vocalizations. This pattern of responsivity could suggest an increased sensitivity to emotional cues, as previously

suggested, but may also reflect a reduced ability to differentiate between positive and negative emotional auditory cues in infants with high levels of negative emotionality. These results add to the literature showing individual variability in late ERP responses to visual cues of happiness and their relation to social problems in childhood (Bunford, Kujawa, Swain et al., 2017). Further research is needed to clarify any potential links between positive emotion processing during infancy and social outcomes in later childhood.

The sample size included in this study could be regarded as relatively small in comparison to other investigations of temperamental variations in infants social and emotional development; although similar to those reported in other studies relating infant temperamental characteristics to their ERP responses to facial and bodily expressions of emotions (Martinos et al., 2012; Missana et al., 2014; Rajhans et al., 2015). We have confidence that our findings are not due to a small sample size. First, the effects we observed range between moderate to large. Second and importantly, we found a consistent pattern across the correlations between ERP components and infant temperament that are also in line with previous reports. Nevertheless, future studies could use power analyses in order to inform decisions about the sample size based on the previously reported results in the literature. Furthermore, it could be argued that infants' ERP responses to recordings of non-verbal vocalizations of emotions have weaker ecological validity than responses to live productions. However, it is important to highlight that the stimuli used in the current study are based on recordings of spontaneous, naturally occurring infant non-verbal vocalizations. Thus, the fundamental acoustic properties are similar to those encountered in live productions. From this perspective one would expect some degree of generalizability of the current findings to live productions of non-verbal vocalizations of emotions.

To summarize, 8-month-old infants' ERP responses to nonverbal vocalizations suggest that they discriminate between emotionally valenced and neutral conditions even when they are presented with the more difficult task of processing infant only voices. The sensitivity of the ERP components to peers' emotional nonverbal vocalizations suggest the presence of a multistep process of social attention in infancy which deserves further investigation in order to clarify the ontogenetic links with the one described in adults (Pell et al., 2015; Schirmer and Kotz, 2006). Although 8-month-old infants appeared to perceive all nonverbal vocalizations as salient, they engaged in the sustained processing only of their peers' cry sounds. Temperamental negative emotionality, in particular the ability to regulate high states of arousal, was significantly related to the preferential processing of crying at later stages. This is particularly important given the high relevance of the individual variability in reactivity and regulation for different typical and atypical social development outcomes (e.g., Frick & Morris, 2004; Olson et al., 2005; Pérez-Edgar & Fox, 2005). Our findings add novel information to an increasing body of knowledge suggesting important links between infant temperament and the development of emotion information processing, with potential implications for understanding the ontogeny of complex social skills, such as empathy.

Acknowledgements

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