

Emotion in motion: Facial dynamics affect infants' neural processing of emotions

Ermanno Quadrelli^{1,2}  | Stefania Conte^{1,2} | Viola Macchi Cassia^{1,2} | Chiara Turati^{1,2}

¹Department of Psychology, University of Milano-Bicocca, Milano, Italy

²NeuroMI, Milan Center for Neuroscience, Milan, Italy

Correspondence

Ermanno Quadrelli, Department of Psychology, University of Milano-Bicocca, Milano, Italy.

Email: ermanno.quadrelli@unimib.it

Funding information

H2020 European Research Council, Grant/Award Number: 241176

Abstract

Research investigating the early development of emotional processing has focused mainly on infants' perception of static facial emotional expressions, likely restricting the amount and type of information available to infants. In particular, the question of whether dynamic information in emotional facial expressions modulates infants' neural responses has been rarely investigated. The present study aimed to fill this gap by recording 7-month-olds' event-related potentials to static (Study 1) and dynamic (Study 2) happy, angry, and neutral faces. In Study 1, happy faces evoked a faster right-lateralized negative central (Nc) component compared to angry faces. In Study 2, both happy and angry faces elicited a larger right-lateralized Nc compared to neutral faces. Irrespective of stimulus dynamicity, a larger P400 to angry faces was associated with higher scores on the Negative Affect temperamental dimension. Overall, results suggest that 7-month-olds are sensitive to facial dynamics, which might play a role in shaping the neural processing of facial emotional expressions. Results also suggest that the amount of attentional resources infants allocate to angry expressions is associated to their temperamental traits. These findings represent a promising avenue for future studies exploring the neurobiological processes involved in perceiving emotional expressions using dynamic stimuli.

KEYWORDS

attention, emotion, event-related potentials, motion, temperament

1 | INTRODUCTION

Social communication is a dynamic process in which rapidly changing visual inputs need to be quickly evaluated. In the context of social interactions, facial expressions provide an extraordinarily important source of information as they allow us to infer others' internal dispositions and mental states. This is especially true for preverbal infants, who cannot rely on linguistic cues to derive expectations about others' behavior. There is now a considerable amount of behavioral and electrophysiological studies detailing the ontogeny of the ability to recognize others' emotions (see reviews by Hoehl, 2014; Leppänen & Nelson, 2009). Nonetheless, despite the fact that emotional facial expressions are usually perceived as dynamic in everyday life, most of the existing research focused on infants' responses to static images.

In particular, only few studies have explored infants' neural processing of dynamic facial emotional expressions (Missana, Grigutsch, & Grossmann, 2014; Rotem-Kohavi, Oberlander, & Virji-Babul, 2017). To fill this gap in the literature, the current study examines infants' neural sensitivity to happiness and anger by comparing 7-month-olds' Event-Related Potential (ERP) responses evoked by statically and dynamically presented facial expressions of such emotions.

Research has shown that facial dynamics influence the perception of facial expressions in adults (e.g., Ambadar, Schooler, & Cohn, 2005; Biele & Grabowska, 2006; Kamachi et al., 2013), and that naturally moving faces provide more valid stimulus material, compared to static faces, for the investigation of the neural correlates of facial expression perception (e.g., Kilts, Egan, Gideon, Ely, & Hoffman, 2003). Indeed, neuroimaging and electrophysiological studies with

adults show enhanced activation in visual areas when participants evaluated dynamic in comparison to static facial expressions (Recio, Sommer, & Schacht, 2011), and a more distributed activation of connections between limbic and prefrontal structures (Kilts et al., 2003). These findings suggest augmented attentional orientation and more elaborative processing of emotional expressions under dynamic as opposed to static presentation condition (Fichtenholtz, Hopfinger, Graham, Detwiler, & LaBar, 2007; Recio, Schacht, & Sommer, 2014).

Although much progress has been made in understanding the neural processing of dynamic emotional expressions in adults, little is known about how dynamic information affects the processing of emotional faces in infants. Previous research supports the importance of motion in infants' perception across various domains, including face recognition (Bulf & Turati, 2010; Missana et al., 2014; Nelson & Russell, 2011; Otsuka et al., 2009; Rotem-Kohavi et al., 2017; Xiao et al., 2014). With regard to emotional faces, Missana and colleagues (2014) compared neural processing of dynamic expressions of pain and anger in 8-month-old infants and adults, and found opposite pattern of results for the two groups, with infants allocating more attention to angry faces and adults showing increased emotional arousal in response to pain. In a more recent study, Rotem-Kohavi and colleagues (2017) explored functional brain network connectivity in response to dynamic expressions of happiness and sadness in adults and 8- to 10-month-old infants. Their results suggest that, although, at the global level, the overall brain organization for the processing of emotional expressions is still immature in infants, at the regional level they share with adults a similar functional network organization, with frontal, parietal, and temporal nodes playing the major role in both groups.

Nonetheless, beyond a few exceptions, a common feature of the majority of studies investigating the neural correlates of infants' emotion perception is the use of static stimulus material, with facial emotions typically displayed at the time of their strongest expression. This approach raises important issues of ecological validity: on one hand side, static images provide diminished information and likely limit the intensity of the perceived emotion (Krumhuber, Kappas, & Manstead, 2013). This may cause relevant underestimation of infants' sensitivity and attentional response to emotional signals. On the other hand, it is also possible that presenting infants with static faces in which emotions are displayed at the peak of their expressed intensity leads to overestimation of infants' emotion recognition abilities.

Infant research has devoted great efforts to trace the developmental origins of the attentional bias to social signals of fear conveyed through facial expressions, showing that it is not until 7 months of age that infants prefer to attend to fearful faces, at least when they are contrasted to happy faces (Peltola, Leppänen, Maki, & Hietanen, 2009). Indeed, few-day-old infants prefer to look at happy over fearful facial expressions (Farroni, Menon, Rigato, & Johnson, 2007), and heightened sensitivity to happy faces has been shown to persist until at least 7 months (Vaish, Grossmann, & Woodward, 2008). At this age, infants begin to manifest a negativity bias, as their attention is preferentially attracted to fearful faces when these

are contrasted to happy faces (Kotsoni, de Haan, & Johnson, 2001; Nelson & Dolgin, 1985). Interestingly enough, evidence from recent studies using looking time measures suggests that the negativity bias to fearful faces might be apparent in infants even younger than 7 months (i.e., 5 months) when emotional expressions are posed by dynamic faces (Heck, Hock, White, Jubran, & Bhatt, 2016, 2017). These changes in attentional responses to emotional expressions are intended to result from the interplay between species-specific sensitivity to perceptual cues for aversive situations (Leppänen, 2011; Nelson, Morse, & Leavitt, 1979) and increased exposure to reactions of fear induced in caregivers by infants' improved locomotor skills (e.g., crawling) and the risk of harm that they pose (Campos et al., 2000; Leppänen et al., 2010).

The attentional bias toward fearful faces in infants has been investigated also by measuring electrocortical responses to emotional faces. Several ERP studies have consistently shown that, in 7-month-old infants, the Negative Central (Nc) component, a negative deflection occurring over fronto-central electrode sites reflecting allocation of attentional processing resources (Dennis, Malone, & Chen, 2009; de Haan, Johnson, & Halit, 2007), is enhanced in response to fearful faces as compared to happy ones (Leppänen, Moulson, Vogel-Farley, & Nelson, 2007; Nelson & de Haan, 1996). Existing studies have also shown that facial emotional expressions modulate occipito-temporal cortical responses at the level of the P400 (e.g., Leppanen et al., 2007; Vanderwert et al., 2015), a face-sensitive ERP component which, together with the N290, is thought to be the infant precursor to the adult N170 (see de Haan et al., 2007). The P400 was found to be larger for fearful faces compared to happy and neutral ones (Leppänen et al., 2007), and also compared to angry faces (Kobiella, Grossmann, Reid, & Striano, 2008). Unlike the P400, the N290 is less consistently affected by emotional facial expressions, as evidence is currently limited and mixed (e.g., Kobiella et al., 2008; Leppanen et al., 2007).

Of note, infants' neural sensitivity to emotional expressions is robustly associated with individual differences in temperamental traits (Martinis, Matheson, & de Haan, 2012; Ravicz, Perdue, Westerlund, Vanderwert, & Nelson, 2015; Taylor-Colls & Fearon, 2015). For example, de Haan and colleagues (2004) reported that being higher on fearfulness on the Infant Behavior Questionnaire (IBQ-R; Gartstein & Rothbart, 2003) at 7 months is related to a larger Nc to static fearful faces. A recent study using functional near-infrared spectroscopy (fNIRS) reported a negative correlation between brain activation triggered by smiling faces over the left prefrontal cortex and emotional distress, as assessed through the IBQ-R, at 7 months (Ravicz et al., 2015).

Although infants' behavioral and neural responses to fearful faces have been extensively investigated, infants' reactions to anger has remained almost unexplored, and the question of whether the negative bias toward fearful expressions generalizes to other emotions connoted by negative valence remains unanswered. In adults, heightened activation of the amygdala has traditionally been associated with increased reactivity to fearful expressions (e.g., Davis & Whalen, 2001), but there is also evidence for its responsiveness to

angry faces (e.g., Whalen et al., 2001). In accord with the idea that angry faces represent a source of potential threat, electrophysiological data collected from a wide range of age groups show that observing angry faces elicits reactions of fear (e.g., Beall, Moody, McIntosh, Hepburn, & Reed, 2008; Geangu, Quadrelli, Conte, Croci, & Turati, 2016; Moody, McIntosh, Mann, & Weisser, 2007). For example, Geangu and colleagues (2016) reported that observing pictures of angry facial expressions in children triggered an increased electromyographic activation of the frontalis muscle, which is typically involved in expressing fear. Behavioral and neuroimaging studies have also shown that neural sensitivity to facial expressions of anger emerges early in development (Ravicz et al., 2015; Vaish et al., 2008). Looking time measures showed that both 7- and 12-month-old infants prefer to look at happy over angry faces (Grossmann, Striano, & Friederici, 2007; Vaish et al., 2008), thus demonstrating of being able to discriminate facial expressions of the two emotions. However, the discriminative response is accompanied by an attentional bias in the opposite direction with respect to the one for fearful expressions, as infants show a negativity bias when happy faces are contrasted to fearful faces (Peltola et al., 2009), and a positivity bias when happy faces are contrasted to angry faces (Grossmann et al., 2007).

Electrophysiological evidence of infants' sensitivity to anger is very scarce, and rather mixed. There is evidence that, by the end of the first year of life, infants can discriminate between facial expressions of anger and neutral facial expressions (Stahl, Parise, Hoehl, & Striano, 2010) and other negative emotions (Kobiella et al., 2008; Xie, McCormick, Westerlund, Bowman, & Nelson, 2018). Indeed, greater attention allocation, as indexed by larger Nc, was observed in response to angry facial expressions compared to expressions of fear (Kobiella et al., 2008) and pain (Missana et al., 2014). Evidence from an ERP study comparing neural responses to angry and happy faces in 7- and 12-month-old infants, showed that, while younger infants exhibit a larger Nc to happy as compared to angry faces, older infants manifest an enhanced posterior negativity in response to angry faces compared to happy ones (Grossmann et al., 2007). The authors interpreted these findings as evidence that infants younger than 12 months do not detect the threat conveyed by a static image of an angry face, and allocate more attentional resources to more familiar happy faces. Nonetheless, in contrast to this evidence, a recent study measuring skin conductance response showed that, already at the age of 3–4 months, the autonomic nervous system reacts with higher arousal in response to the subliminal and supraliminal presentation of angry faces compared to happy faces (Nava, Romano, Grassi, & Turati, 2016). These findings are taken as supporting the involvement of a subcortical pathway in detection of threatening stimuli, which is recruited early in life, well before the time—that is, 7 months—when infants first show behavioral evidence of discriminating between angry and happy facial expressions. Altogether, the developmental time-course of infants' ability to recognize different emotional expressions, and more specifically of angry faces, leaves many questions that need to be answered.

In the present study, we examined the hypothesis that, when emotional facial expressions are dynamically presented, the

attentional bias toward angry facial expressions is apparent at the neural level even before the age of 12 months (as in Grossmann et al., 2007). To this aim, in two different studies we explored electrocortical responses evoked by static (Study 1) and dynamic (Study 2) happy, neutral and angry faces in two groups of 7-month-old infants. In both studies, we measured the sensitivity of the Nc, N290, and P400 components to the positive versus negative valence of the emotional faces. Finally, in light of the few existing studies examining individual differences in infants' attentional responsiveness to emotional faces (Martinos et al., 2012; Taylor-Colls & Fearon, 2015), and capitalizing on the larger sample size obtained by merging the participants from Study 1 and 2, we explored the association between infants' temperamental traits and their neural response to happy and angry faces by performing statistical analyses across the two studies. Based on reports of infants' reactivity to fearful faces (e.g., Martinos et al., 2012), we hypothesized that infants scoring higher on the Negative Affect temperamental dimension, as measured through the IBQ-R (Gartstein & Rothbart, 2003), would show enhanced attentional response to angry faces. Moreover, we expected to observe greater activation in response to happy faces in infants scoring higher on the Surgency temperamental dimension (e.g., Ravicz et al., 2015).

2 | STUDY 1

2.1 | Methods

2.1.1 | Participants

The final sample consisted of 18 seven-month-old healthy infants (eight males, M age = 207 days, SD = 8.1 days, range = 196–233 days). All were born full-term (37–42 weeks' gestation) and had normal birth weight ($> 2,500$ g). Nine additional infants were tested but excluded from the final sample because of fussiness ($n = 4$), excessive artifacts ($n = 4$), or technical problems during data collection ($n = 1$); the attrition rate is in line with that of other infant ERP studies (e.g., de Haan et al., 2004). Infants needed to have at least 10 artifact-free trials per emotion to qualify for further data analysis. Infants who were excluded did not significantly differ from those included in the sample in terms of temperamental traits (all $ps > 0.21$).

The protocol was carried out in accordance with the ethical standards of the Declaration of Helsinki (BMJ 1991; 302:1194) and approved by the ethical committee of the University of Milano-Bicocca (Protocol number: 236). Participants were recruited via a written invitation that was sent to parents based on birth record provided by neighboring cities. The study was explained to the parents and their written consent was obtained. Data on infant temperament were collected by asking the mother or primary caregiver to complete the Infant Behavior Questionnaire-Revised in its very short form (IBQ-R VSF; Putnam, Helbig, Gartstein, Rothbart, & Leerkes, 2014). The questionnaire included queries aimed to assess the frequency of specific temperament-related behaviors observed within the last week. Since we were interested in data pertaining to negative and

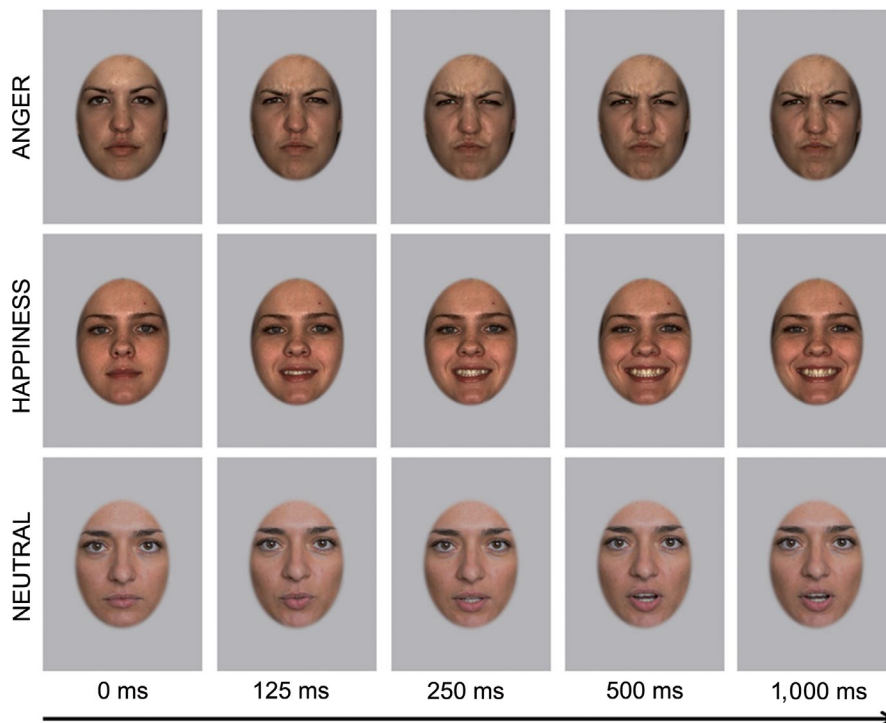


FIGURE 1 Examples of screenshots from videos used in the dynamic condition portraying the neutral (bottom), angry (top), and happy (central) facial expressions used as stimuli. The last picture for each emotion was used in the static condition

positive affect, two main temperamental dimensions were selected: Negative Affect (NA) and Surgency (SU). NA is analogous to the personality trait of Neuroticism, and refers to a difficulty being soothed and a predisposition to experience negative feelings; SU is analogous to the personality trait of Extraversion and refers to the tendency to act with impulsive and active behaviors.

2.1.2 | Stimuli

The stimuli consisted of color photographs of nine female Caucasian actresses posing angry, happy and neutral facial expressions while facing forward (Figure 1). Happy and angry faces were extracted from videos of the Binghamton University 4D Facial Expression database (BU-4DFE; Yin, Sun, Worm, & Reale, 2008); neutral faces were extracted from videos recorded at our laboratory. There was no overlap between the identities posing the three facial expressions as a different identity was used for each condition. Using the software Adobe Photoshop, all face images were cropped into an oval shape to remove hair and external features in order to emphasize and facilitate the processing of featural (i.e., features' shape) and configural (i.e., spatial distance and relation among the features) cues diagnostic of each emotion (Leitzke & Pollak, 2016; Richoz, Lao, Pascalis, & Caldara, 2018). Indeed, it is known that the external facial features greatly attract infants' attention (e.g., Leitzke & Pollak, 2016), and that masking the hair encourages the processing of the internal portion of the face (e.g., Mondloch, Geldart, Maurer, & Grand, 2003). Stimuli were also equalized for luminance, which did not differ between emotion categories, Kruskal-Wallis H test, $\chi^2(2) = 5.60$; $p = 0.08$; $\eta_p^2 = 0.60$. All faces subtended 15.3° of visual angle vertically and 10.5° of visual angle horizontally when viewed

from approximately 60 cm, and were pasted on a grey background. All stimuli were screened and selected for their emotional valence by asking 19 adult raters (13 females) to complete a survey in which they identified the specific emotion expressed by each face and assigned to the face a score ranging from -10 (i.e., angry) to 10 (i.e., happy) to describe the intensity of the expressed emotion, with 0 corresponding to absence of emotional expression (i.e., neutral). Happy, angry, and neutral expressions were correctly identified by respectively 100%, 86%, and 76% of the raters. Wilcoxon Signed-ranks tests performed for each emotion on the intensity scores indicated that both happy ($M = 7.20$; $SD = 0.81$, $Z = 3.84$; $p < 0.001$, $\eta^2 = 1.64$, and angry expressions ($M = -6.56$; $SD = 1.08$, $Z = -3.84$; $p < 0.001$, $\eta^2 = 1.64$, were perceived as equally different from neutral expressions, which instead were properly perceived as nonemotional ($M = 0.42$; $SD = 0.89$, $Z = 1.814$; $p = 0.07$, $\eta^2 = 0.38$).

2.1.3 | Procedure

The experiment took place in a dimly lit, audiometric, and electrically shielded cabin, where participants were seated on their mother's lap, at approximately 60 cm from a 24-inch monitor, in a behavioral state of quiet alertness. Stimuli were presented using E-Prime software v2.0 (Psychology Software Tools Inc., Pittsburgh, PA). Mothers were instructed to remain as still as possible and keep silence during the experimental session in order to avoid any acoustic interference. The whole experiment was recorded through an infrared video camera, hidden over the monitor, which fed into the data acquisition computer, located outside the testing cabin. The data acquisition computer displayed the live image of the infants' face and body to allow the experimenter to pause or terminate the session when

the infant became too fussy. Each infant was presented with all nine face identities, which were presented in a random order, with the only constraint that models expressing the same emotion could not occur more than three times in a row. The experimental session was

terminated when infants attended to the maximum number of trials ($N = 270$) or got tired of the experiment. A trial consisted of 1,000 ms stimulus presentation followed by an interstimulus interval which varied randomly between 900 and 1,100 ms. Whenever necessary

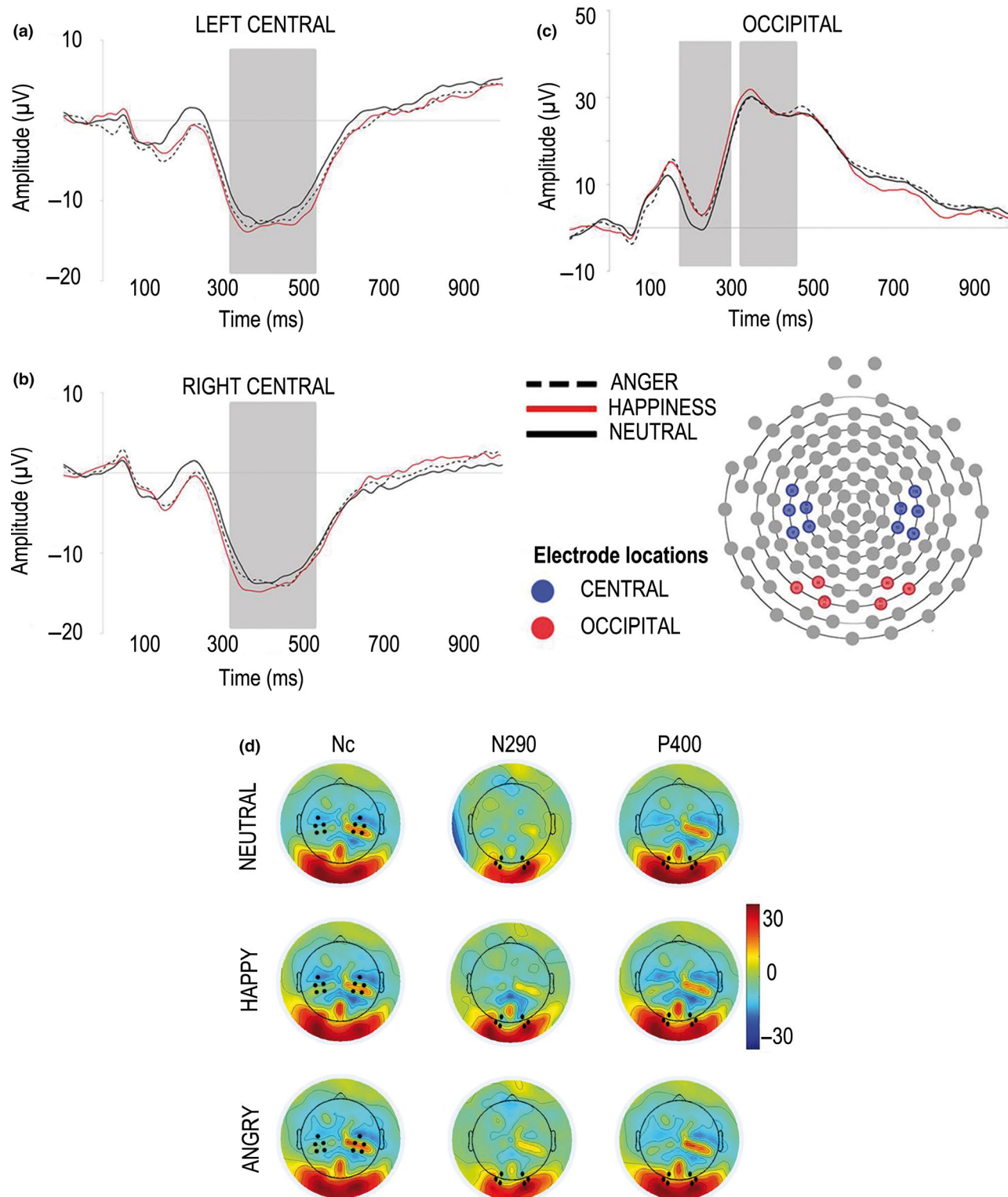


FIGURE 2 Topographic scalp maps in the time range of the components of interest (Nc: 330–530 ms, N290: 200–300 ms, P400: 320–460 ms) (d) and waveform plots depicting grand-average ERPs for the Nc (a; b), N290 and P400 (c) components in response to happy (solid red line), angry (dashed black line), and neutral (solid black line) expressions at selected electrode locations in the static condition (Study 1). Note that negative values are plotted downward and the head in the scalp map is for orientation purposes only and not to scale

the experimenter presented a looming fixation point between trials to reorient the infant's attention to the monitor. The caregivers were instructed to keep attention to the screen ahead without distracting their child by pointing or vocalizing.

2.1.4 | EEG recording and processing

The electroencephalogram (EEG) was recorded with a 128-electrode HydroCel Geodesic Sensor Net (Electrical Geodesic Inc., Eugene, OR). EEG was recorded continuously and referenced to the vertex electrode (Cz). The signals were amplified using an EGI NetAmps 300 amplifier with a sampling rate of 500 Hz and an online band-pass filter of 0.1–100 Hz. Impedances were checked online prior to the beginning of the session and considered acceptable if lower than 50 K Ω . EEG data were processed offline using NetStation v4.6.4 (Eugene, OR). The continuous signals were subsequently band-pass filtered with 0.3–30 Hz, segmented into epochs centered on stimulus onset with a 100 ms baseline and comprising 1,000 ms of stimulus presentation, and re-referenced to the algebraic mean of all the channels. To eliminate artifacts, individual channels were automatically rejected whenever the signal exceeded ± 200 μ V in a sliding window of 80 ms on the segmented data and then hand-edited for any remaining artifacts. If more than 15% of the channels ($N \geq 18$) were marked as bad, the whole trial was excluded from further analysis (e.g., Halit, de Haan, & Johnson, 2003). Of the remaining trials, individually excluded channels were replaced using spherical spline interpolation. Across participants, the mean number of trials contributing to the average ERP and statistical analyses was 19.5 for happy, 18.3 for angry, and 18.3 for neutral faces. Inspection of the grand-averaged waveforms revealed a well-defined Nc component over fronto-central electrode sites. One cluster of electrodes was selected for each hemisphere where the Nc was more clearly visible (left: 35, 36, 41, 42, 47; right: 93, 98, 103, 104, 110; see Figure 2). These electrode clusters correspond to those in which the Nc has been recorded in previous studies (Taylor-Colls & Fearon, 2015). A time-window of 330–530 ms was chosen based on previous infant ERP reports of this component, and on visual examination of the component's peak for each participant. Inspection of the grand-averaged waveforms also revealed well-defined N290 and P400 face sensitive components at medial occipital channels, that were analyzed by averaging electrodes within occipital–temporal regions of the left (65, 66, 70) and right (83, 84, 90) hemispheres. As in previous infant ERP reports of these components (e.g., Leppänen et al., 2007), time windows for analyses were, respectively 200–300 ms, and 320–460 ms. For each of the three components, peak latency (ms) and mean and peak amplitude (μ V) values were extracted and entered in the statistical analyses (Martinot et al., 2012). For all components, analyses on peak amplitude confirmed the results obtained on mean amplitude values, and they are, therefore, not reported in the following sections. Moreover, visual inspection of waveforms revealed that amplitude differences at the level of the P400 might

be driven by differences at the preceding N290 component. In order to take into account the effect of the N290 on the P400, we decided to obtain a peak-to-trough measure, defined as the difference between the maximum value of the P400 and the minimum value of the N290.

2.1.5 | Data analysis

The analyses were conducted using IBM SPSS 24.0 (IBM Corporation, Armonk, NY, USA). Peak latency and mean amplitude of the Nc, N290, and P400 were analyzed through a 3×2 repeated measures Analysis of Variance (ANOVA) including two within-subjects factors: emotion (angry, happy, neutral) and hemisphere (left and right). All statistical tests were conducted on a 0.05 level of significance (two-tailed); when the ANOVAs yielded significant effects, pairwise comparisons including ≤ 3 means which were performed by applying *t* tests and the Fisher's least significant difference procedure (Howell, 2009; after Leppänen et al., 2007).

3 | RESULTS

3.1 | Negative Central (Nc)

Latency. Analysis performed on the Nc peak latency values revealed a significant emotion \times hemisphere interaction, $F(2,34) = 3.53$, $p = 0.04$, $\eta_p^2 = 0.17$. Latency of the Nc was significantly faster in response to happy faces ($M = 402.07$ ms, $SD = 46.48$) than to angry faces ($M = 421.84$ ms, $SD = 38.87$) over the right hemisphere, $t(17) = 2.34$, $p = 0.03$, $d = 0.45$, and showed a trend toward being faster in response to happy faces than to neutral faces ($M = 419.28$ ms, $SD = 51.03$) over the right hemisphere, $t(17) = -2.02$, $p = 0.06$, $d = 0.35$ (Figure 2). On the other hand, there were no significant differences in Nc latency over the left hemisphere (all $ps > 0.17$).

Amplitude. The ANOVA performed on the Nc mean amplitude revealed no significant effects (all $ps > 0.18$).

3.2 | N290

Latency. Analysis performed on the N290 peak latency values revealed a significant main effect of hemisphere, $F(1,17) = 7.67$; $p = 0.013$, $\eta_p^2 = 0.31$, with the N290 peaking earlier over the right ($M = 218.23$ ms, $SD = 16.47$) than the left ($M = 226.99$ ms, $SD = 16.85$) recording sites. No other main effects or interactions attained significance (all $ps > 0.22$).

Amplitude. Analysis on the amplitude of the N290 revealed a significant emotion main effect, $F(2,34) = 3.66$; $p = 0.03$, $\eta_p^2 = 0.18$, with neutral faces ($M = -3.09$ μ V; $SD = 13.59$) evoking larger response ($p = 0.04$) compared to angry ($M = 0.97$ μ V; $SD = 12.24$), but not happy faces ($M = -0.85$ μ V; $SD = 12.41$; $p = 0.09$). No difference emerged between happy and angry faces ($p = 0.20$). There were no effects involving the factor hemisphere (all $ps > 0.32$).

3.3 | P400

Latency. The analysis on the P400 peak latency values revealed no significant main effects or interactions (all $ps > 0.22$).

Amplitude. As for the amplitude values, the analysis showed an emotion \times hemisphere interaction, $F(2,34) = 3.522$; $p = 0.04$, $\eta_p^2 = 0.17$. This interaction, however, proved spurious as no significant differences were found between facial expressions at the electrodes of interest (all $ps > 0.21$). Moreover, no hemispheric asymmetries or main effect of emotion were observed in P400 responses (all $ps > 0.27$). The same analysis was repeated on the peak-to-trough amplitude values (i.e., P400 - N290), and did not reveal significant main effects or interactions (all $ps > 0.10$).

4 | DISCUSSION

Our results show that happy facial expressions elicit a faster Nc compared to angry faces over the right hemisphere, thus implying faster orienting of attentional resources to signals of positive affect in 7-month-old infants. Happy faces also tended to elicit faster response compared to neutral faces, but this comparison did not attain full statistical significance. These findings parallel those obtained by earlier studies showing enhanced sensitivity to static facial expressions of happiness compared to expressions of anger (Grossmann et al., 2007) and indicate that the attentional bias toward happy emotional expression is rather stable at 7 months.

For what concerns the N290 and the P400 components, while speaking in favor of a differentiation between emotion and neutral expressions, our results also highlighted the absence of neural modulation between emotional expressions. To date, evidence supporting the effects of emotional expressions on the amplitude and latency of the N290 and P400 is limited and varying results have been reported (e.g., Kobiella et al., 2008; Leppänen et al., 2007; Vanderwert et al., 2015; Xie et al., 2018). Some researchers observed that the amplitude of the N290 and P400 varied in response to angry and fearful expressions (Kobiella et al., 2008). Further studies examining the N290 found it to be larger in response to fearful compared to angry faces (Hoehl & Striano, 2008) and happy faces (van den Boomen, Munsters, & Kemner, 2017). Additionally, differential processing of emotional faces was also found in a recent cross-sectional study comparing the amplitude of the N290 and P400 components and determining their specific cortical sources in 5-, 7-, and 12-month-old infants while they were viewing angry, fearful, and happy faces (Xie et al., 2018). Indeed, regardless of infants' age, N290 responses were greater to fearful and happy faces compared to angry expressions, and while P400 responses were found to be greater in response to angry than happy and fearful faces. The incongruence between our results and those obtained by previous studies might be due to an important methodological aspect. Indeed, previous electrophysiological investigations typically used a maximum of two identities to represent each emotional expression. Similarly to Vanderwert

and colleagues (2015), who reported a lack of modulation of latency and amplitude values at the level of the N290 and P400, the use of multiple identities expressing the emotions might have increased task demands, rendering difficult for 7-month-old infants to fully categorize the three different facial expressions.

Overall, results of Study 1 provide further evidence that, when statically presented, happy faces are differentiated from angry expressions at the attentional stage of processing. To test for the hypothesis that, when emotional expressions are presented as developing dynamically over time, even 7-month-old infants might show enhanced attentional response to angry facial expressions, in Study 2 we compared ERP responses to short videos depicting dynamic neutral, happy, and angry facial expressions. We predicted that, if dynamic stimulus presentation boosts infants' neural sensitivity to emotional facial expressions (Heck, Hock, White, Jubran, & Bhatt, 2016, 2017), we may observe an enhanced response to angry faces compared to happy faces, and possibly even to neutral faces, already in infants aged 7 months, that is before the time when the negativity bias toward angry emotional expressions has been observed in studies using static faces as stimuli (Grossmann et al., 2007).

5 | STUDY 2

5.1 | Methods

5.1.1 | Participants

The final sample consisted of 18 seven-month-old healthy infants (six male infants, $M = 209$ days, $SD = 11.1$ days, range = 195–225 days). All infants were born full-term (37–42 weeks' gestation) and with normal birth weight ($> 2,500$ g). Eight additional infants were tested but excluded from the final sample because of fussiness ($n = 5$), excessive artifacts ($n = 3$). The IBQ-R VSF (Putnam et al., 2014) was administered to infants' parents. As in Study 1, infants who were excluded did not significantly differ from those included in the sample in terms of temperamental traits (all $ps > 0.19$).

5.1.2 | Stimuli

Stimuli consisted of short 1,000 ms videos of the same nine identities used in Study 1, each posing angry, happy, and neutral facial expressions. Videos were extracted from the same sources used to create the stimuli presented in Study 1. The unfolding of each emotional expression (i.e., neutral to 100% intensity) lasted 500 ms, and the full expression remained on the screen until the end of the video (i.e., for another 500 ms). Stimuli depicting a neutral expression were recorded at our laboratory and represented three actresses posing a neutral expression and then silently moving their mouth. Like in Study 1, all faces were oval-cropped, shown against a grey background, and there was no overlap between the facial identities posing the three expressions. Similar to the static condition, preliminary analysis on potential differences in low-level features between emotion conditions did not show any significant variation in luminance

between the stimuli, Kruskal–Wallis H test, $\chi^2(2) = 5.60$; $p = 0.08$, $\eta^2 = 0.57$. Moreover, a comparison between the overall amount of motion displayed in the videos depicting the three dynamic facial expressions did not reveal any difference in the amount of motion between angry, happy, and neutral expressions, Kruskal–Wallis H test, $\chi^2(2) = 3.60$; $p = 0.16$, $\eta^2 = 0.28$. The analysis of the motion content of the stimuli was performed through an established procedure described in Grossmann and Jessen (2017; see also Pichon, de Gelder, & Grèzes, 2009), which starts from the conversion of each individual frame of the video to a grayscale image. Mean change in luminance from one frame to the next were then calculated for all consecutive pairs of frames over the entire duration of the video, and the overall average per video was computed from these values. All videos were screened and selected for their emotional valence by asking 19 adult raters (14 females) to complete a survey in which they identified the specific emotion expressed by each face and assigned to the face a score ranging from -10 (i.e., angry) to 10 (i.e., happy) to describe the intensity of the expressed emotion, with 0 corresponding to absence of emotional expression (i.e., neutral). Happy, angry, and neutral expressions were correctly identified by respectively 97%, 91%, and 97% of the raters. Wilcoxon Signed-ranks tests performed for each emotion on the intensity scores indicated that both happy ($M = 7.16$; $SD = 0.84$), $Z = 3.83$; $p < 0.001$, $\eta^2 = 1.63$, and angry expressions ($M = -6.89$; $SD = 1.31$), $Z = -3.83$; $p < 0.001$, $\eta^2 = 1.63$, were perceived as equally different from neutral expressions, which instead were properly perceived as nonemotional ($M = 0.42$; $SD = 0.89$), $Z = 1.83$; $p = 0.07$, $\eta^2 = 0.37$.

5.1.3 | Procedure, EEG recording, and analysis

Procedure, EEG acquisition, and processing were the same as in Study 1. Across participants, the mean number of trials contributing to the average ERP and statistical analyses was 18.5 for happy, 16.8 for anger, and 16.8 for neutral. A similar number of trials for each emotion contributed to the final analysis in Study 2 (all $ps > 0.15$). As in Study 1, ERPs were time-locked to the onset of the stimuli, the same time windows were applied to extract peak latency and mean amplitude values of the Nc (330–530 ms), N290 (200–300 ms), and P400 (320–460 ms) in the dynamic condition and data were analyzed through a 3×2 repeated-measures ANOVA including two within-subjects factors: emotion (angry, happy, neutral) and hemisphere (left and right). Similar to Study 1, visual inspection of waveforms revealed that amplitude differences at the level of the P400 might be driven by differences at the preceding N290 component. Thus, in order to control for the possible effect of the N290 on the P400, we decided to obtain a peak-to-trough measure, defined as the difference between the maximum value of the P400 and the minimum value of the N290.

Furthermore, we performed a $2 \times 3 \times 2$ repeated measures ANOVA including stimulus presentation condition (dynamic and static) as between-subjects factor, and emotion (angry, happy, neutral) and hemisphere (left and right) as within-subjects factors in order to directly compare activation elicited by dynamic and static facial expressions in the two experimental conditions. Lastly, to verify the

documented effects of infants' temperament in modulating neural response to emotions (e.g., de Haan et al., 2004; Martinos et al., 2012; Taylor-Colls & Fearon, 2015), we capitalized on the larger sample size obtained by merging the participant samples from Study 1 and 2 to include Surgency and Negative Affect temperamental traits as continuous covariates in an additional $2 \times 3 \times 2$ repeated-measures ANCOVA including stimulus presentation condition (dynamic and static) as between-subjects factor, and emotion (angry, happy, neutral) and hemisphere (left and right) as within-subjects factors. In light of previous reports of individual differences in infants' responses to fearful faces (e.g., Martinos et al., 2012), we hypothesized that infants scoring higher on Negative Affect (i.e., predisposition to experience negative feelings) would show greater or faster attention allocation to angry faces. Moreover, we expected that infants scoring higher on Surgency (i.e., predisposition to show active and impulsive behaviors) would show greater activation in response to happy faces (e.g., Ravicz et al., 2015). After Taylor-Colls and Fearon (2015), each temperament effect was followed up by correlational analyses between temperament and ERP difference scores computed by subtracting peak latencies values or mean amplitudes values for neutral faces from those recorded for angry (i.e., angry–neutral) and for happy (i.e., happy–neutral) faces. Like in Study 1, results of the analyses on peak amplitude values confirmed those obtained on mean amplitude values, therefore, only results for mean amplitude are reported below.

6 | RESULTS

6.1 | Negative Central (Nc)

Latency. Analyses performed on the Nc peak latency values did not yield significant main effects or interactions (all $ps > 0.32$; anger left: $M = 422.31$ ms, $SD = 47.53$; anger right: $M = 437.18$ ms, $SD = 49.52$; happy left: $M = 417.53$ ms, $SD = 43.47$; happy right: $M = 434.27$ ms, $SD = 49.93$; neutral left: $M = 436.27$ ms, $SD = 55.96$; neutral right: $M = 433.27$ ms, $SD = 54.24$).

Amplitude. The ANOVA performed on the Nc mean amplitude revealed a significant emotion \times hemisphere interaction $F(2,34) = 6.21$; $p = 0.005$, $\eta_p^2 = 0.27$. Post hoc t -tests applied within each hemisphere revealed that both happy ($M = -15.39$ μ V, $SD = 3.96$) and angry ($M = -13.33$ μ V, $SD = 4.06$) expressions elicited a larger Nc compared to neutral ($M = -11.27$ μ V, $SD = 4.68$) expressions over the right hemisphere (happy versus neutral: $t(17) = -4.16$, $p = 0.001$, $d = 0.95$; angry versus neutral: $t(17) = -2.29$, $p = 0.047$, $d = 0.47$) (Figure 3), while no significant differences were found over the left hemisphere, and no hemispheric asymmetries were observed in Nc responses to any emotional expression (all $ps > 0.49$).

6.2 | N290

Latency. Analyses performed on the N290 peak latency values did not yield significant main effects or interactions (all $ps > 0.11$; anger left: $M = 247.55$ ms, $SD = 20.19$; anger right: $M = 241.74$ ms, $SD = 26.50$; happy left: $M = 239.78$ ms, $SD = 22.57$; happy right:

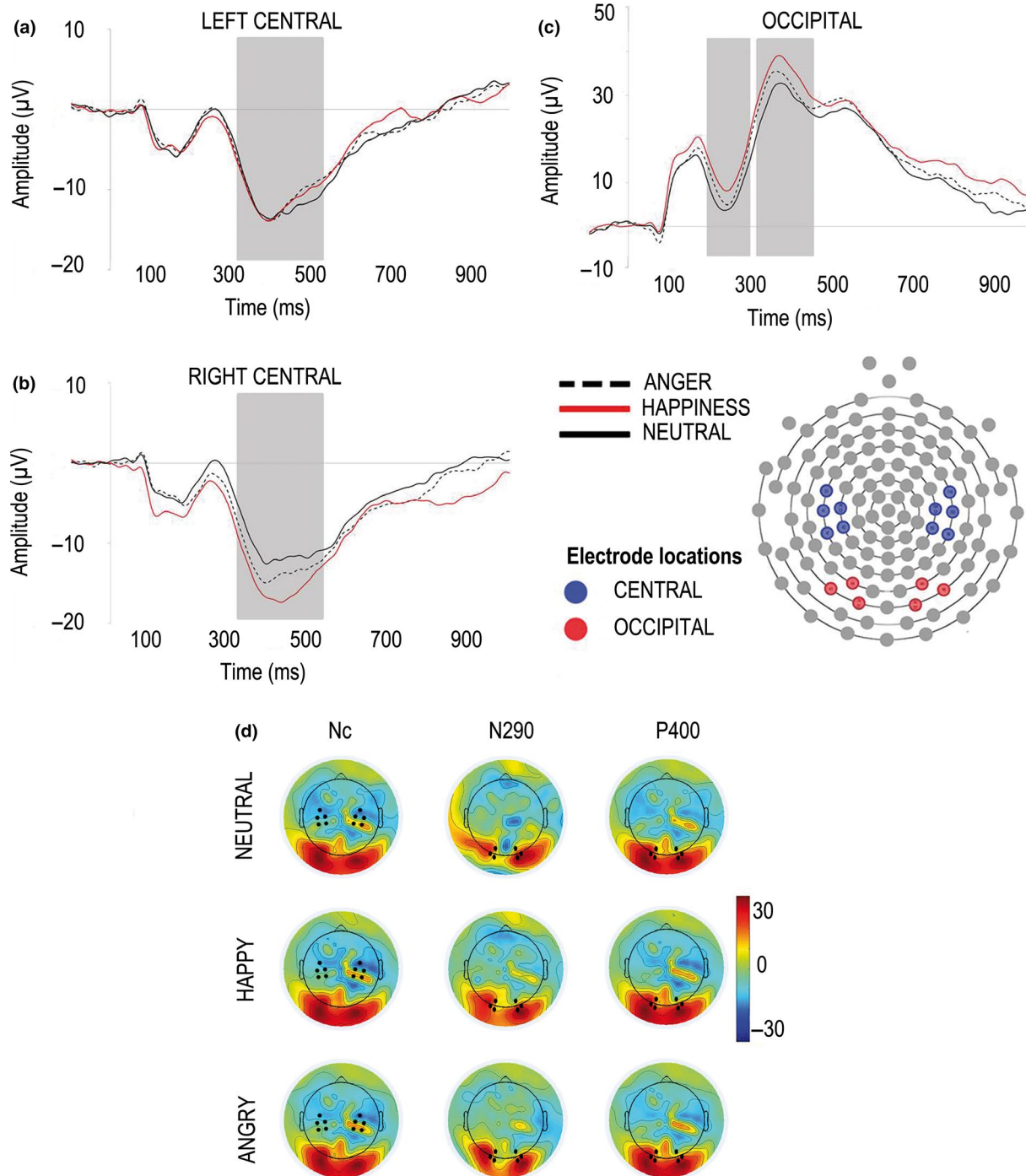


FIGURE 3 Topographic scalp maps in the time range of the components of interest (Nc: 330–530 ms, N290: 200–300 ms, P400: 320–460 ms) (d) and waveform plots depicting grand-average ERPs for the Nc (a; b), N290 and P400 (c) components in response to happy (solid red line), angry (dashed black line), and neutral (solid black line) expressions at selected electrode locations in the dynamic condition (Study 2). Note that negative values are plotted downward and the head in the scalp map is for orientation purposes only and not to scale

$M = 242.48$ ms, $SD = 24.69$; neutral left: $M = 239.78$ ms, $SD = 23.38$; neutral right: $M = 240.07$ ms, $SD = 25.43$).

Amplitude. The ANOVA performed on the N290 mean amplitude values yielded a marginally significant main effect of emotion, $F(2,34) = 3.11$; $p = 0.058$, $\eta_p^2 = 0.15$, with a trend toward larger negative

response to neutral faces ($M = 6.68$ μV; $SD = 10.29$) compared to happy ($M = 11.70$ μV; $SD = 9.23$), but not angry faces ($M = 9.12$ μV; $SD = 11.27$; $p = 0.30$). No difference emerged between happy and angry faces ($p = 0.20$). No other main effect or interaction attained significance (all $ps > 0.41$).

6.3 | P400

Latency. Analysis performed on the P400 peak latency values did not yield significant main effects or interactions (all $ps > 0.13$; anger left: $M = 378.47$ ms, $SD = 25.34$; anger right: $M = 374.83$ ms, $SD = 23.89$; happy left: $M = 379.78$ ms, $SD = 21.58$; happy right: $M = 381.44$ ms, $SD = 20.59$; neutral left: $M = 381.22$ ms, $SD = 28.23$; neutral right: $M = 389.89$ ms, $SD = 27.46$).

Amplitude. The ANOVA performed on the P400 mean amplitude values revealed a significant main effect of emotion, $F(2,34) = 5.56$, $p = 0.008$, $\eta_p^2 = 0.25$ (Figure 3); post hoc comparisons revealed larger activation in response to happy faces ($M = 34.34$ μV , $SD = 7.37$) compared to neutral faces ($M = 28.43$ μV , $SD = 7.02$), $t(17) = 3.91$, $p = 0.001$, $d = 0.82$. No difference emerged between angry faces ($M = 31.02$ μV , $SD = 9.64$) and neutral or happy facial expressions (all $ps > 0.12$). However, when repeating the same analysis on the of the peak-to-trough amplitude values (P400–N290), no significant main effects or interactions were highlighted (all $ps > 0.49$).

6.4 | Static versus Dynamic stimulus presentation comparison

To directly compare the neural responses elicited by static (Study 1) and dynamic (Study 2) facial expressions, we performed three 2 (presentation condition) \times 3 (emotion) \times 2 (hemisphere) ANOVAs for each of the three analyzed ERP components, one for each dependent variable (i.e., peak latency and mean amplitude).

6.5 | Negative Central (Nc)

Latency. The ANOVA performed on the Nc latency revealed a significant three-way presentation condition \times emotion \times hemisphere interaction, $F(2,68) = 3.21$, $p = 0.047$, $\eta_p^2 = 0.09$. The presence of this interaction confirms that the static (Study 1) and dynamic (Study 2) stimulus presentation conditions differently affect neural sensitivity to emotional facial expressions. The presence of such differential sensitivity is further corroborated by results emerged from the separate 3 (emotion) \times 2 (hemisphere) ANOVAs performed for each of the two conditions (see results from Study 1 and Study 2). Between subjects post hoc comparisons directly contrasting infants' responses to static and dynamic presentation conditions were nonsignificant for all the three emotions (all $ps > 0.08$). No other main effect or interaction attained significance (all $ps > 0.35$).

Amplitude. The ANOVA performed on the Nc peak amplitude values revealed significant main effects of emotion, $F(2,34) = 3.13$ $p = 0.049$, $\eta_p^2 = 0.08$, and hemisphere, $F(1,34) = 4.34$ $p = 0.04$, $\eta_p^2 = 0.11$. These main effects were qualified by a significant three-way interaction between presentation condition, emotion, and hemisphere, $F(2,68) = 2.01$, $p = 0.049$, $\eta_p^2 = 0.06$. Again, this confirms that neural sensitivity to emotional expressions is modulated by the static (Study 1) versus dynamic (Study 2) presentation of the stimuli, as shown by the results of the 3 (emotion) \times 2 (hemisphere) ANOVAs performed separately for each presentation conditions. Between subjects post

hoc comparisons directly contrasting infants' responses to static and dynamic presentation conditions were nonsignificant for all the three emotions (all $ps > 0.23$). No other main effect or interaction attained significance (all $ps > 0.14$).

6.6 | N290

Latency. Analysis performed on the N290 peak latency values revealed a significant emotion \times hemisphere interaction, $F(2,68) = 3.47$, $p = 0.04$, $\eta_p^2 = 0.09$, with happy ($M = 233.33$ ms; $SD = 19.45$) and neutral ($M = 231.55$ ms; $SD = 22.37$) faces eliciting faster peaks compared to angry expressions ($M = 239.15$ ms; $SD = 20.96$) selectively over the left hemisphere, (happy versus angry: $t(35) = 2.44$, $p = 0.02$, $d = 0.30$; neutral versus angry: $t(35) = 2.44$, $p = 0.02$, $d = 0.37$). No other main effect or interaction attained significance for the N290 latency values (all $ps > 0.32$).

Amplitude. The ANOVA performed on the amplitude values of the N290 highlighted a significant main effect of emotion, $F(2,68) = 5.04$, $p = 0.009$, $\eta_p^2 = 0.13$, with neutral faces ($M = 1.79$ μV ; $SD = 11.43$) eliciting a greater negative deflection as compared to both happy ($M = 5.42$ μV ; $SD = 10.80$) and angry ($M = 5.05$ μV ; $SD = 10.98$) expressions. No other main effect or interaction attained significance for the N290 amplitude values (all $ps > 0.11$).

6.7 | P400

Latency. The ANOVA performed on the P400 peak latency values revealed the presence of the critical presentation condition \times emotion \times hemisphere interaction, $F(2,68) = 3.29$, $p = 0.043$, $\eta_p^2 = 0.09$, confirming that the static (Study 1) and dynamic (Study 2) stimulus presentation conditions elicited different patterns of activation also at the level of the P400, as shown by the separate 3 (emotion) \times 2 (hemisphere) ANOVAs performed for each of the two presentation conditions. Between subjects post hoc comparisons directly contrasting infants' responses to static and dynamic presentation conditions were nonsignificant for all the three emotions (all $ps > 0.32$). No other main effect or interaction attained significance for the P400 latency values (all $ps > 0.21$).

Amplitude. The ANOVA performed on the P400 amplitude values revealed a significant emotion \times presentation condition interaction, $F(2,68) = 4.48$, $p = 0.01$, $\eta_p^2 = 0.12$, with happy faces eliciting a marginally significant greater activation in the dynamic ($M = 34.34$ μV ; $SD = 7.37$) compared to the static ($M = 28.35$ μV ; $SD = 10.46$) condition, $t(34) = -1.99$, $p = 0.06$, $d = 0.66$ (all other $ps > 0.72$). No other main effect or interaction attained significance for the P400 amplitude values (all $ps > 0.18$).

6.8 | Temperament effects

The association between infants' temperamental traits (i.e., Negative Affect and Surgency) and their neural response to happy and angry faces was explored in the larger sample size obtained by merging the participants from Study 1 and 2 by means of three 2 (presentation

condition) \times 3 (emotion) \times 2 (hemisphere) ANCOVAs for each of the three analyzed ERP components, one for each dependent variable (i.e., peak latency and mean amplitude).

6.9 | Negative central (Nc)

The three-way presentation condition \times emotion \times hemisphere interaction remained significant for both latency, $F(2,64) = 3.39$, $p = 0.040$, $\eta_p^2 = 0.10$, and amplitude, $F(2,64) = 3.24$, $p = 0.046$, $\eta_p^2 = 0.09$, when Negative Affect and Surgency were entered as continuous covariates. Additionally, for latency, there was also a significant emotion \times hemisphere \times Surgency interaction, $F(2,64) = 3.17$, $p = 0.049$, $\eta_p^2 = 0.09$. However, there were no significant correlations between Surgency scores and Nc latency difference scores (all $ps > 0.12$). No other main effect or interaction attained significance for both latency and amplitude values of the Nc (all $ps > 0.11$).

6.10 | N290

The emotion \times hemisphere interaction on latency values of the N290 remained significant also when Negative Affect and Surgency were entered as covariates, $F(2,64) = 5.45$; $p = 0.007$, $\eta_p^2 = 0.15$. Moreover, there was also a significant emotion \times hemisphere \times Negative Affect interaction, $F(2,64) = 5.329$; $p = 0.007$, $\eta_p^2 = 0.15$, but there were no significant correlations between Negative Affect and the N290 latency scores (all $ps > 0.1$). No other main effect or interaction attained significance for both latency and amplitude values at the level of the N290 (all $ps > 0.10$).

6.11 | P400

The ANCOVA on the amplitude of the P400 showed a significant emotion \times Negative Affect interaction, $F(2,64) = 4.11$, $p = 0.02$, $\eta_p^2 = 0.11$. Correlational analysis showed a significant positive association between P400 amplitude values evoked by angry expressions and Negative Affect, $r(34) = 0.42$, $p = 0.01$, $d = 0.92$, with infants scoring higher on Negative Affect showing larger P400 amplitudes to angry relative to neutral faces (Figure 4). No other main effects or interactions attained significance for latency nor amplitude of the P400 (all $ps > 0.13$).

7 | GENERAL DISCUSSION

The present study aimed at investigating the electrocortical responses evoked in 7-month-old infants by static and dynamic faces displaying neutral, positive (i.e., happy), and negative (i.e., angry) emotional expressions. Our results provide evidence of a differential modulation of latency and amplitude of the attentional Nc in response to static and dynamic emotional expressions at 7 months of age. Consistent with evidence from earlier studies using static emotional faces as stimuli (e.g., Grossmann et al., 2007; Vaish et al., 2008),

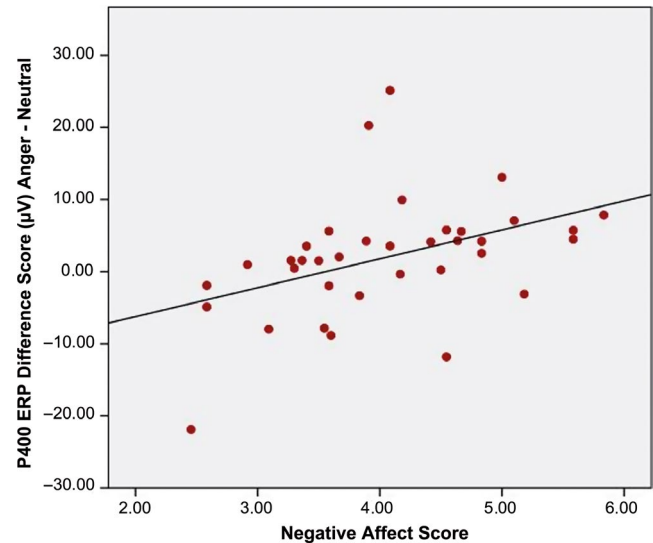


FIGURE 4 Scatterplot depicting the positive correlation between the Negative Affect temperament scores and the P400 amplitude evoked by angry expressions expressed through the angry minus neutral differential scores

our results showed that the Nc peaked faster over the right hemisphere in response to happy faces than to angry faces, and the same trend was marginally significant for happy compared to neutral faces. Under the assumption that an earlier Nc reflects faster allocation of attentional resources to the considered stimulus (Martinis et al., 2012), and that larger amplitude of the Nc reflects greater allocation of attention to the stimulus, these findings suggest that 7-month-old infants are more sensitive and respond faster to happy facial expressions than to angry expressions, when faces are static. As such, our results are in line with earlier reports of longer looking times to static happy faces compared to angry faces in 7- and 12-month-old infants (Grossmann et al., 2007), and of larger Nc response to happy static faces than to angry faces at 7 months of age (Grossmann et al., 2007; Schupp et al., 2004). Indeed, our results add to earlier EEG evidence indicating that at 7 months of age infants do not process the threat conveyed by static angry faces, thus allocating more attentional resources to the more familiar happy facial expression (Grossmann et al., 2007). On the other hand, our study differs from previous ones on an important aspect. Early ERP studies typically used a quite limited number of identities (i.e., one or two; Hoehl & Striano, 2008; Kobiella et al., 2008) to represent each emotional expression. This may increase the likelihood of idiosyncratic responses to specific facial features, making it difficult to understand whether observed results reflect true categorization of emotional expressions or more simple visual discrimination between facial expressions (see Grossmann et al., 2007 for a similar argument). In the current study, the use of a large number of identities (i.e., nine), and the absence of identity overlap across emotional conditions, provided a more rigorous test of infants' neural sensitivity to emotional expressions, as their ability to process and differentiate among emotional expressions is tested over perceptual differences linked to identity variation. At the same time, though, this methodological choice might have increased task

demands, and thus prevent infants to fully categorize the three different emotions (see Vanderwert et al., 2015 for a similar argument). This methodological difference may have contributed to the inconsistencies between current and previous results.

A common feature of the results obtained for the Nc component under both static (Study 1) and dynamic (Study 2) stimulus presentation conditions is the hemispheric asymmetry in the observed effect of emotional expression, which is right-lateralized. Indeed, neuroimaging studies in adults indicate that attention to facial expressions elicits greater activation in the right superior temporal sulcus (rSTS; Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001). Most crucially, right lateralization of frontotemporal brain responses to faces has been observed also in infants using Near Infrared Spectroscopy (i.e., NIRS; Carlsson, Lagercrantz, Olson, Printz, & Bartocci, 2008; Kobayashi, Macchi Cassia, Kanazawa, Yamaguchi, & Kakigi, 2016). Our findings add to this earlier evidence showing that right-lateralization of neural responses to facial expressions emerges early in the first year of life (Nakato, Otsuka, Kanazawa, Yamaguchi, & Kakigi, 2011; Nelson & de Haan, 1996).

We found no evidence that the static versus dynamic nature of stimulus presentation affected 7-month-olds' neural responses to emotional faces, as indicated by the lack of a significant main effect of presentation condition in the omnibus ANOVA and in post hoc tests directly comparing infants' neural responses to static versus dynamic presentation conditions for each of the three emotions. This points to the overall ecological validity of existing research on infants' emotional discrimination using static stimulus material. Critically, though, our results show differential modulations of ERP responses to different emotional expressions under static (Study 1) and dynamic (Study 2) stimulus presentation conditions. Indeed, the amplitude of the Nc did not differentiate between static facial expressions, while it did differentiate between neutral and emotional expressions when the faces were dynamically presented. In particular, both happy and angry dynamic faces evoked a larger Nc compared to neutral faces over the right-central scalp region. This finding is in line with earlier demonstrations of selective/enhanced neural processing of emotionally meaningful facial expressions compared to neutral expressions by both cortical and subcortical brain structures (Kilts et al., 2003; Leppänen et al., 2007). Therefore, our results converge to indicate that, in the dynamic condition only, emotional faces elicited enhanced neural processing compared to neutral faces, triggering emotion-selective neural processing in infants.

While Study 1 and earlier studies (e.g. Vaish et al., 2008) using static stimuli showed faster or greater attention allocation in response to happy compared to angry faces in 7-month-olds, results from Study 2, in which emotional expressions were dynamically presented, paint a somewhat different picture. Specifically, the difference in neural response to emotional (i.e., angry and happy) and neutral dynamic faces observed in Study 2, together with the lack of differentiation between happy and angry faces, might suggest that when emotional faces are presented under more ecologically valid conditions—that is, dynamic rather than static—they hold greater attention at 7 months of age. This specific pattern for the Nc, while providing evidence for differential

attention allocation to emotional faces compared to neutral ones, is difficult to interpret. One possibility is that the transition from the positivity bias to the negativity bias for angry faces gradually unfolds between 5 and 12 months of age, thus undergoing through a time when both positive and negative facial expressions are perceived as equally salient. It is also possible that the difference in neural activation elicited by neutral and emotional faces is a by-product of the different level of prototypicality of the two face types, with neutral faces being perceived as more prototypical than emotional faces. Within this view, both positive and/or negative deviations in the expressed facial emotion would elicit similarly enhanced brain responses, in the same way as faces expressing low levels and high levels of trustworthiness elicit similar brain responses at the level of the P400 and the Nc in 7-month-old infants (Jessen & Grossmann, 2017).

Another aspect of the current findings that further extends earlier demonstration of neural sensitivity to emotional expressions in 7-month-old infants relates to the N290 and P400 recorded at semi-medial occipital sites, which also showed differential sensitivity to variations in emotional expressions under static versus dynamic stimulus presentation condition. In particular, when faces were presented in the static condition (i.e., Study 1), neutral expressions elicited a larger N290 compared to angry expressions; however, under dynamic presentation conditions (i.e., Study 2), neutral expressions elicited a larger N290 compared to happy faces. Moreover, we also observed a marginally larger P400 response to happy than neutral dynamic expressions, and no difference between happy and angry dynamic expressions. Notably, effects observed at the P400 component in the dynamic condition disappeared when corrected for the preceding N290 component. These findings are not consistent with existing literature (e.g., Hoehl & Striano, 2008) showing an enhanced P400 response to angry faces compared to happy expressions, and point to the importance of extending research on the development of the ability to process emotional expressions beyond the study of attentional responses evoked by static emotional expressions. Indeed, both the N290 and the P400 might serve as markers of perceptual discrimination between dynamic emotion categories, as the N290 is thought to mediate the structural encoding of the physical properties of the face (de Haan et al., 2007), while the P400 is seen as related to the extraction of the communicative and affective significance from facial features (Tager-Flusberg, 2010).

Current findings may have been limited by the fact that emotional faces gradually appeared and reached the peak expression 500 ms later in the dynamic condition compared to the static one. This may have had an impact on the timing of the observed effects in the two conditions, especially for the attentional-related Nc component, whose time window captures the time when the full-blown emotion becomes visible in the dynamic condition. However, no differences in latencies were observed overall in the static and dynamic conditions for the considered ERP components, thus indicating the presence of a similar neural sensitivity to different emotion intensities in our stimuli. Indeed, there is ample evidence that, by the age of 5 months, infants can recognize emotional facial expressions across intensity variations (e.g., Bornstein & Arterberry, 2003; Ludemann &

Nelson, 1988). It is, therefore, possible that, as in real-life situations, the decoding of emotional expressions in our 7-month-old infants was not an all-or-nothing event, and that few dynamic changes in the unfolding facial expression might have been sufficient to trigger the neural processing of the observed emotion. This possibility could be addressed in future investigations measuring oscillatory brain responses to dynamic emotional expressions, which would allow to track ongoing changes in brain responses without requiring a direct-time locking to stimulus onset.

Our findings highlight the presence of individual differences in the processing of emotional facial expressions: infants with a stronger tendency to experience negative feelings (i.e., higher Negative Affect scores) had heightened P400 amplitudes to angry faces relative to neutral faces. These results add to earlier observations of an association between individual differences in infants' temperamental traits and neural sensitivity to emotional expressions (e.g., Taylor-Colls & Fearon, 2015). They further suggest that the development of attentional biases toward emotional facial expressions might be influenced by individual differences in temperamental traits potentially influencing the maturation and development of cortical networks (e.g., Leppänen & Nelson, 2009). The finding that infants who scored high on Negative Affect showed a larger P400 response to angry expressions in comparison to those who scored low on the same scale suggests more effortful perceptual processing of angry faces in the former than the latter group. This resonates well with recent evidence showing that high levels of Negative Affect in infancy are related to a decrease in the hemodynamic response to social dynamic (i.e., moving actors) compared to nonsocial dynamic (i.e., moving toys and machinery) stimuli (van der Kant, Biro, Levelt, & Huijbregts, 2018), and to happy facial expressions (Ravicz et al., 2015). Similarly, our result suggests that high levels of withdrawal or distress in response to limitations might heighten infants' responsiveness to angry facial expressions already in the earliest stages of perceptual processing, suggesting that infant's temperament shapes the way in which the brain responds to emotional information.

To conclude, current evidence suggests that static emotional faces appear to be able to convey important clues for infants' processing of emotions, as documented by existing research on infants' processing of facial emotional expressions using static stimuli in infancy, as well as by the results reported in our Study 1. Our findings are consistent with previous research showing enhanced attentional responses to happiness at 7 months of age when stimuli are static (Grossmann et al., 2007; Vaish et al., 2008). Nonetheless, results reported in the current study extend previous evidence by showing that stimulus dynamicity modulates the attentional response to emotional faces. Indeed, in the dynamic condition we observed no ERP differentiation between happy and angry faces, while both emotional expressions were differentiated from the neutral expression. These data suggest that a similar amount of attentional resources is devoted to angry and happy facial expressions when emotional information is conveyed under dynamic and more ecologically valid conditions. These results and those provided by few existing studies measuring infants' behavioral responses to dynamic emotional

faces (Heck, Hock, White, Jubran, & Bhatt, 2016, 2017) suggest that further investigations are needed to explore infants' processing of dynamic emotional expressions. It will be important to test whether the current results would hold under even more ecological conditions, in which uncropped faces are used as stimuli and external features, such as hair and ears, are preserved. This might provide additional insight into our understanding of the development of emotion processing abilities in early infancy. Moreover, future studies might explore the associations between neural responses evoked by dynamic emotional faces and the attentional sampling of specific dynamic facial features (e.g., eye and mouth regions) by tracking infants' eye movements whilst ERPs are recorded. Tracking infants' eye movements would provide critical information about which facial features are more extensively explored while emotions are unfolding. Furthermore, the current research focused on ERP responses to dynamic and static emotional expressions. Future EEG investigations could explore the effects of dynamic positive and negative emotional faces in eliciting specific patterns of frontal alpha asymmetry responses. Indeed, these stimulus-related neural oscillations are known to reflect motivational processes linked to approach and avoidance responses evoked by emotional expressions in the case of static faces (Missana et al., 2014). Lastly, there is now increasing interest in the role of sensorimotor brain regions in the processing of dynamic and static facial expressions in adults, but research is still needed to investigate the extent to which these parietal-premotor regions are recruited during the observation of facial emotions in the first years of life (e.g., Rayson, Bonaiuto, Ferrari, & Murray, 2017).

DATA AVAILABILITY STATEMENT

Data cannot be made publicly available as the dataset contains sensitive and identifying information. The authors confirm that the data and experimental stimuli will be made available upon request. Requests may be sent to the corresponding author.

ACKNOWLEDGMENTS

This work was supported by a European Research Council Starting Grant to Prof. Chiara Turati on a project entitled "The origins and development of the human mirror neuron system" – ODMIR No. 241176.

CONFLICT OF INTEREST

The authors whose names are listed above certify that there are no affiliations with or involvement in any organization or entity with a direct financial interest in the subject matter or materials discussed in the manuscript (e.g., employment, consultancies, stock ownership, honoraria, and/or expert testimony).

ORCID

Ermanno Quadrelli  <https://orcid.org/0000-0002-6834-0912>

REFERENCES

- Ambadar, Z., Schooler, J. W., & Cohn, J. F. (2005). Deciphering the enigmatic face: The importance of facial dynamics in interpreting subtle facial expressions. *Psychological Science*, 16(5), 403–410. <https://doi.org/10.1111/j.0956-7976.2005.01548.x>
- Beall, P. M., Moody, E. J., McIntosh, D. N., Hepburn, S. L., & Reed, C. L. (2008). Rapid facial reactions to emotional facial expressions in typically developing children and children with autism spectrum disorder. *Journal of Experimental Child Psychology*, 101(3), 206–223. <https://doi.org/10.1016/j.jecp.2008.04.004>
- Biele, C., & Grabowska, A. (2006). Sex differences in perception of emotion intensity in dynamic and static facial expressions. *Experimental Brain Research*, 171(1), 1–6. <https://doi.org/10.1007/s00221-005-0254-0>
- Bornstein, M. H., & Arterberry, M. E. (2003). Recognition, discrimination and categorization of smiling by 5-month-old infants. *Developmental Science*, 6(5), 585–599. <https://doi.org/10.1111/1467-7687.00314>
- Bulf, H., & Turati, C. (2010). The role of rigid motion in newborns' face recognition. *Visual Cognition*, 18(4), 504–512. <https://doi.org/10.1080/13506280903272037>
- Campos, J. J., Anderson, D. I., Barbu-Roth, M. A., Hubbard, E. M., Hertenstein, M. J., & Witherington, D. (2000). Travel broadens the mind. *Infancy*, 1(2), 149–219. https://doi.org/10.1207/S15327078IN0102_1
- Carlsson, J., Lagercrantz, H., Olson, L., Printz, G., & Bartocci, M. (2008). Activation of the right fronto-temporal cortex during maternal facial recognition in young infants. *Acta Paediatrica*, 97(9), 1221–1225. <https://doi.org/10.1111/j.1651-2227.2008.00886.x>
- Davis, M., & Whalen, P. J. (2001). The amygdala: Vigilance and emotion. *Molecular Psychiatry*, 6(1), 13–34. <https://doi.org/10.1038/sj.mp.4000812>
- de Haan, M., Belsky, J., Reid, V., Volein, A., & Johnson, M. H. (2004). Maternal personality and infants' neural and visual responsivity to facial expressions of emotion. *Journal of Child Psychology and Psychiatry*, 45(7), 1209–1218. <https://doi.org/10.1111/j.1469-7610.2004.00320.x>
- de Haan, M., Johnson, M. H., & Halit, H. (2007). Development of face-sensitive event-related potentials during infancy. In M. de Haan (Ed.), *Infant EEG and event-related potentials* (pp. 78–99). New York, NY: Psychology Press.
- Dennis, T. A., Malone, M. M., & Chen, C. C. (2009). Emotional face processing and emotion regulation in children: An ERP study. *Developmental Neuropsychology*, 34(1), 85–102. <https://doi.org/10.1080/87565640802564887>
- Farroni, T., Menon, E., Rigato, S., & Johnson, M. H. (2007). The perception of facial expressions in newborns. *European Journal of Developmental Psychology*, 4(1), 2–13. <https://doi.org/10.1080/17405620601046832>
- Fichtenholtz, H. M., Hopfinger, J. B., Graham, R., Detwiler, J. M., & LaBar, K. S. (2007). Happy and fearful emotion in cues and targets modulate event-related potential indices of gaze-directed attentional orienting. *Social Cognitive and Affective Neuroscience*, 2(4), 323–333. <https://doi.org/10.1093/scan/nsm026>
- Gartstein, M. A., & Rothbart, M. K. (2003). Studying infant temperament via the revised infant behavior questionnaire. *Infant Behavior and Development*, 26(1), 64–86. [https://doi.org/10.1016/S0163-6383\(02\)00169-8](https://doi.org/10.1016/S0163-6383(02)00169-8)
- Geangu, E., Quadrelli, E., Conte, S., Croci, E., & Turati, C. (2016). Three-year-olds' rapid facial electromyographic responses to emotional facial expressions and body postures. *Journal of Experimental Child Psychology*, 144, 1–14. <https://doi.org/10.1016/j.jecp.2015.11.001>
- Grossmann, T., & Jessen, S. (2017). When in infancy does the “fear bias” develop? *Journal of Experimental Child Psychology*, 153, 149–154. <https://doi.org/10.1016/j.jecp.2016.06.018>
- Grossmann, T., Striano, T., & Friederici, A. D. (2007). Developmental changes in infants' processing of happy and angry facial expressions: A neurobehavioral study. *Brain and Cognition*, 64(1), 30–41. <https://doi.org/10.1016/j.bandc.2006.10.002>
- Halit, H., De Haan, M., & Johnson, M. H. (2003). Cortical specialisation for face processing: Face-sensitive event-related potential components in 3- and 12-month-old infants. *NeuroImage*, 19(3), 1180–1193. [https://doi.org/10.1016/S1053-8119\(03\)00076-4](https://doi.org/10.1016/S1053-8119(03)00076-4)
- Heck, A., Hock, A., White, H., Jubran, R., & Bhatt, R. S. (2016). The development of attention to dynamic facial emotions. *Journal of Experimental Child Psychology*, 147, 100–110. <https://doi.org/10.1016/j.jecp.2016.03.005>
- Heck, A., Hock, A., White, H., Jubran, R., & Bhatt, R. S. (2017). Further evidence of early development of attention to dynamic facial emotions: Reply to Grossmann and Jessen. *Journal of Experimental Child Psychology*, 153, 155–162. <https://doi.org/10.1016/j.jecp.2016.08.006>
- Hoehl, S. (2014). Emotion processing in infancy. In K. H. Lagattuta (Ed.), *Children and emotion. New insights into developmental affective sciences* (pp. 1–12). Basel: Karger. <https://doi.org/10.1159/000354346>
- Hoehl, S., & Striano, T. (2008). Neural processing of eye gaze and threat-related emotional facial expressions in infancy. *Child Development*, 79(6), 1752–1760. <https://doi.org/10.1111/j.1467-8624.2008.01223.x>
- Howell, D. C. (2009). *Statistical methods for psychology*. Belmont, CA: Cengage Learning.
- Jessen, S., & Grossmann, T. (2016). Neural and behavioral evidence for infants' sensitivity to the trustworthiness of faces. *Journal of cognitive neuroscience*, 28(11), 1728–1736. https://doi.org/10.1162/jocn_a_00999
- Kamachi, M., Bruce, V., Mukaida, S., Gyoba, J., Yoshikawa, S., & Akamatsu, S. (2013). Dynamic properties influence the perception of facial expressions. *Perception*, 42(11), 1266–1278. <https://doi.org/10.1068/p3131n>
- Kilts, C. D., Egan, G., Gideon, D. A., Ely, T. D., & Hoffman, J. M. (2003). Dissociable neural pathways are involved in the recognition of emotion in static and dynamic facial expressions. *NeuroImage*, 18(1), 156–168. <https://doi.org/10.1006/nimg.2002.1323>
- Kobayashi, M., Macchi Cassia, V., Kanazawa, S., Yamaguchi, M. K., & Kakigi, R. (2016). Perceptual narrowing towards adult faces is a cross-cultural phenomenon in infancy: A behavioral and near-infrared spectroscopy study with Japanese infants. *Developmental Science*, <https://doi.org/10.1111/desc.12498>
- Kobiella, A., Grossmann, T., Reid, V. M., & Striano, T. (2008). The discrimination of angry and fearful facial expressions in 7-month-old infants: An event-related potential study. *Cognition and Emotion*, 22(1), 134–146. <https://doi.org/10.1080/02699930701394256>
- Kotsoni, E., de Haan, M., & Johnson, M. H. (2001). Categorical perception of facial expressions by 7-month-old infants. *Perception*, 30(9), 1115–1125. <https://doi.org/10.1068/p3155>
- Krumhuber, E. G., Kappas, A., & Manstead, A. S. (2013). Effects of dynamic aspects of facial expressions: A review. *Emotion Review*, 5(1), 41–46. <https://doi.org/10.1177/1754073912451349>
- Leitzke, B. T., & Pollak, S. D. (2016). Developmental changes in the primacy of facial cues for emotion recognition. *Developmental Psychology*, 52(4), 572. <https://doi.org/10.1037/a0040067>
- Leppänen, J. M. (2011). Neural and developmental bases of the ability to recognize social signals of emotions. *Emotion Review*, 3(2), 179–188. <https://doi.org/10.1177/1754073910387942>
- Leppänen, J. M., Moulson, M. C., Vogel-Farley, V. K., & Nelson, C. A. (2007). An ERP study of emotional face processing in the adult and infant brain. *Child Development*, 78(1), 232–245. <https://doi.org/10.1111/j.1467-8624.2007.00994.x>
- Leppänen, J. M., & Nelson, C. A. (2009). Tuning the developing brain to social signals of emotions. *Nature Reviews Neuroscience*, 10(1), 37–47. <https://doi.org/10.1038/nrn2554>
- Leppänen, J., Peltola, M. J., Mäntymaa, M., Koivuluoma, M., Salminen, A., & Puura, K. (2010). Cardiac and behavioral evidence for emotional

- influences on attention in 7-month-old infants. *International Journal of Behavioral Development*, 34(6), 547–553. <https://doi.org/10.1177/0165025410365804>
- Ludemann, P. M., & Nelson, C. A. (1988). Categorical representation of facial expressions by 7-month-old infants. *Developmental Psychology*, 24(4), 492–501. <https://doi.org/10.1037//0012-1649.24.4.492>
- Martinos, M., Matheson, A., & de Haan, M. (2012). Links between infant temperament and neurophysiological measures of attention to happy and fearful faces. *Journal of Child Psychology and Psychiatry*, 53(11), 1118–1127. <https://doi.org/10.1111/j.1469-7610.2012.02599.x>
- Missana, M., Grigutsch, M., & Grossmann, T. (2014). Developmental and individual differences in the neural processing of dynamic expressions of pain and anger. *PLoS ONE*, 9(4), e93728. <https://doi.org/10.1371/journal.pone.0093728>
- Mondloch, C. J., Geldart, S., Maurer, D., & Le Grand, R. (2003). Developmental changes in face processing skills. *Journal of Experimental Child Psychology*, 86(1), 67–84. [https://doi.org/10.1016/S0022-0965\(03\)00102-4](https://doi.org/10.1016/S0022-0965(03)00102-4)
- Moody, E. J., McIntosh, D. N., Mann, L. J., & Weisser, K. R. (2007). More than mere mimicry? The influence of emotion on rapid facial reactions to faces. *Emotion*, 7(2), 447–457. <https://doi.org/10.1037/1528-3542.7.2.447>
- Nakato, E., Otsuka, Y., Kanazawa, S., Yamaguchi, M. K., & Kakigi, R. (2011). Distinct differences in the pattern of hemodynamic response to happy and angry facial expressions in infants—A near-infrared spectroscopic study. *NeuroImage*, 54(2), 1600–1606. <https://doi.org/10.1016/j.neuroimage.2010.09.021>
- Narumoto, J., Okada, T., Sadato, N., Fukui, K., & Yonekura, Y. (2001). Attention to emotion modulates fMRI activity in human right superior temporal sulcus. *Cognitive Brain Research*, 12(2), 225–231. [https://doi.org/10.1016/S0926-6410\(01\)00053-2](https://doi.org/10.1016/S0926-6410(01)00053-2)
- Nava, E., Romano, D., Grassi, M., & Turati, C. (2016). Skin conductance reveals the early development of the unconscious processing of emotions. *Cortex*, 84, 124–131. <https://doi.org/10.1016/j.cortex.2016.07.011>
- Nelson, C. A., & De Haan, M. (1996). Neural correlates of infants' visual responsiveness to facial expressions of emotion. *Developmental Psychobiology*, 29(7), 577–595. [https://doi.org/10.1002/\(SICI\)1098-2302\(199611\)29:7<577:AID-DEV3>3.0.CO;2-R](https://doi.org/10.1002/(SICI)1098-2302(199611)29:7<577:AID-DEV3>3.0.CO;2-R)
- Nelson, C. A., & Dolgin, K. G. (1985). The generalized discrimination of facial expressions by seven-month-old infants. *Child Development*, 56(1), 58–61. <https://doi.org/10.2307/1130173>
- Nelson, C. A., Morse, P. A., & Leavitt, L. A. (1979). Recognition of facial expressions by seven-month-old infants. *Child Development*, 50(4), 1239–1242. <https://doi.org/10.2307/1129358>
- Nelson, N. L., & Russell, J. A. (2011). Preschoolers' use of dynamic facial, bodily, and vocal cues to emotion. *Journal of Experimental Child Psychology*, 110(1), 52–61. <https://doi.org/10.1016/j.jecp.2011.03.014>
- Otsuka, Y., Konishi, Y., Kanazawa, S., Yamaguchi, M. K., Abdi, H., & O'Toole, A. J. (2009). Recognition of moving and static faces by young infants. *Child Development*, 80(4), 1259–1271. <https://doi.org/10.1111/j.1467-8624.2009.01330.x>
- Peltola, M. J., Leppänen, J. M., Mäki, S., & Hietanen, J. K. (2009). Emergence of enhanced attention to fearful faces between 5 and 7 months of age. *Social Cognitive and Affective Neuroscience*, 4(2), 134–142. <https://doi.org/10.1093/scan/nsn046>
- Pichon, S., de Gelder, B., & Grèzes, J. (2009). Two different faces of threat. Comparing the neural systems for recognizing fear and anger in dynamic body expressions. *NeuroImage*, 47(4), 1873–1883. <https://doi.org/10.1016/j.neuroimage.2009.03.084>
- Putnam, S. P., Helbig, A. L., Gartstein, M. A., Rothbart, M. K., & Leerkes, E. (2014). Development and assessment of short and very short forms of the Infant Behavior Questionnaire-Revised. *Journal of Personality Assessment*, 96(4), 445–458. <https://doi.org/10.1080/00223891.2013.841171>
- Ravicz, M. M., Perdue, K. L., Westerlund, A., Vanderwert, R. E., & Nelson, C. A. (2015). Infants' neural responses to facial emotion in the prefrontal cortex are correlated with temperament: A functional near-infrared spectroscopy study. *Frontiers in Psychology*, 6. <https://doi.org/10.3389/fpsyg.2015.00922>
- Rayson, H., Bonaiuto, J. J., Ferrari, P. F., & Murray, L. (2017). Early maternal mirroring predicts infant motor system activation during facial expression observation. *Scientific Reports*, 7(1). <https://doi.org/10.1038/s41598-017-12097-w>
- Recio, G., Schacht, A., & Sommer, W. (2014). Recognizing dynamic facial expressions of emotion: Specificity and intensity effects in event-related brain potentials. *Biological Psychology*, 96, 111–125. <https://doi.org/10.1016/j.biopsycho.2013.12.003>
- Recio, G., Sommer, W., & Schacht, A. (2011). Electrophysiological correlates of perceiving and evaluating static and dynamic facial emotional expressions. *Brain Research*, 1376, 66–75. <https://doi.org/10.1016/j.brainres.2010.12.041>
- Richoz, A. R., Lao, J., Pascalis, O., & Caldara, R. (2018). Tracking the recognition of static and dynamic facial expressions of emotion across the life span. *Journal of Vision*, 18(9), 5. <https://doi.org/10.1167/18.9.5>
- Rotem-Kohavi, N., Oberlander, T. F., & Virji-Babul, N. (2017). Infants and adults have similar regional functional brain organization for the perception of emotions. *Neuroscience Letters*, 650, 118–125. <https://doi.org/10.1016/j.neulet.2017.04.031>
- Schupp, H. T., Öhman, A., Junghöfer, M., Weike, A. I., Stockburger, J., & Hamm, A. O. (2004). The facilitated processing of threatening faces: An ERP analysis. *Emotion*, 4(2), 189–200. <https://doi.org/10.1037/1528-3542.4.2.189>
- Stahl, D., Parise, E., Hoehl, S., & Striano, T. (2010). Eye contact and emotional face processing in 6-month-old infants: Advanced statistical methods applied to event-related potentials. *Brain and Development*, 32(4), 305–317. <https://doi.org/10.1016/j.braindev.2009.04.001>
- Tager-Flusberg, H. (2010). The origins of social impairments in autism spectrum disorder: Studies of infants at risk. *Neural Networks*, 23(8–9), 1072–1076. <https://doi.org/10.1016/j.neunet.2010.07.008>
- Taylor-Colls, S., & Fearon, R. M. P. (2015). The effects of parental behavior on infants' neural processing of emotion expressions. *Child Development*, 86(3), 877–888. <https://doi.org/10.1111/cdev.12348>
- Vaish, A., Grossmann, T., & Woodward, A. (2008). Not all emotions are created equal: The negativity bias in social-emotional development. *Psychological Bulletin*, 134(3), 383. <https://doi.org/10.1037/0033-2909.134.3.383>
- van den Boomen, C., Munsters, N. M., & Kemner, C. (2017). Emotion processing in the infant brain: The importance of local information. *Neuropsychologia*, 126, 62–68. <https://doi.org/10.1016/j.neuropsychologia.2017.09.006>
- van der Kant, A., Biro, S., Levelt, C., & Huijbregts, S. (2018). Negative affect is related to reduced differential neural responses to social and non-social stimuli in 5-to-8-month-old infants: A functional near-infrared spectroscopy-study. *Developmental Cognitive Neuroscience*, 30, 23–30. <https://doi.org/10.1016/j.dcn.2017.12.003>
- Vanderwert, R. E., Westerlund, A., Montoya, L., McCormick, S. A., Miguel, H. O., & Nelson, C. A. (2015). Looking to the eyes influences the processing of emotion on face-sensitive event-related potentials in 7-month-old infants. *Developmental Neurobiology*, 75(10), 1154–1163. <https://doi.org/10.1002/dneu.22204>
- Whalen, P. J., Shin, L. M., McInerney, S. C., Fischer, H., Wright, C. I., & Rauch, S. L. (2001). A functional MRI study of human amygdala responses to facial expressions of fear versus anger. *Emotion*, 1(1), 70–83. <https://doi.org/10.1037/1528-3542.1.1.70>
- Xiao, N. G., Perrotta, S., Quinn, P. C., Wang, Z., Sun, Y. H. P., & Lee, K. (2014). On the facilitative effects of face motion on face recognition

and its development. *Frontiers in Psychology*, 5, 633. <https://doi.org/10.3389/fpsyg.2014.00633>

- Xie, W., McCormick, S. A., Westerlund, A., Bowman, L. C., & Nelson, C. A. (2018). Neural correlates of facial emotion processing in infancy. *Developmental Science*, e12758. <https://doi.org/10.1111/desc.12758>
- Yin, L., Chen, X., Sun, Y., Worm, T., & Reale, M. (2008). A high-resolution 3D dynamic facial expression database. In *Automatic face & gesture recognition, 2008. FG'08. 8th IEEE International Conference on Automatic Face & Gesture Recognition* (pp. 1–6). Hoboken, NJ: IEEE. <https://doi.org/10.1109/AFGR.2008.4813324>

How to cite this article: Quadrelli E, Conte S, Macchi Cassia V, Turati C. Emotion in motion: Facial dynamics affect infants' neural processing of emotions. *Developmental Psychobiology*. 2019;61:843–858. <https://doi.org/10.1002/dev.21860>