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Research report

Neural signatures of conscious and unconscious emotional face processing in human infants

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ABSTRACT

Human adults can process emotional information both with and without conscious awareness, and it has been suggested that the two processes rely on partly distinct brain mechanisms. However, the developmental origins of these brain processes are unknown. In the present event-related brain potential (ERP) study, we examined the brain responses of 7-month-old infants in response to subliminally (50 and 100 msec) and supraliminally (500 msec) presented happy and fearful facial expressions. Our results revealed that infants' brain responses (Pb and Nc) over central electrodes distinguished between emotions irrespective of stimulus duration, whereas the discrimination between emotions at occipital electrodes (N290 and P400) only occurred when faces were presented supraliminally (above threshold). This suggests that early in development the human brain not only discriminates between happy and fearful facial expressions irrespective of conscious perception, but also that, similar to adults, supraliminal and subliminal emotion processing relies on distinct neural processes. Our data further suggest that the processing of emotional facial expressions differs across infants depending on their behaviorally shown perceptual sensitivity. The current ERP findings suggest that distinct brain processes underpinning conscious and unconscious emotion perception emerge early in ontogeny and can therefore be seen as a key feature of human social functioning.

1. Introduction

The ability to perceive and distinguish between emotional facial expressions of others is of critical importance for adaptive social behavior as it helps us predict others' actions and guide our own behavior during social interactions (Adolphs, 2002; Frith, 2009). Given the significance of this ability it is not surprising that it not only relies on the conscious perception of others' emotional states, by which inferences about inner state and future behavior of another person can be drawn, but that the detection of emotional expressions in others occurs independent of conscious awareness (Morris, Ohman, & Dolan, 1999; Tamietto & de Gelder, 2010).

From a neuroscience perspective, prior work examining event-related brain potentials (ERPs) in human adults suggests that the responding to emotional information relies on

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distinct brain processes that (a) depend on conscious perception (supraliminal processing) and (b) are independent of conscious perception (both supra- and subliminal processing). Specifically, the processing of perceptually unconscious emotional information is characterized by an enhanced N2 for negative facial expressions (Kiss & Eimer, 2008; Liddell, Williams, Rathjen, Shevrin, & Gordon, 2004; Williams et al., 2004). The adult human brain thus responds to evolutionarily significant stimuli such as negative facial expressions, even in the absence of conscious awareness (Cacioppo & Berntson, 1999; Liddell et al., 2004). On the contrary, conscious processing of emotional faces involves a more detailed structural analysis of faces, as indexed by emotion effects on the N170, which only occur when the correct emotion is successfully recognized (Japee, Crocker, Carver, Pessoa, & Ungerleider, 2009; Smith, 2012). Moreover, consciously perceived emotional expressions elicit enhanced P3 amplitudes in response to fearful facial expressions (Kiss & Eimer, 2008; Liddell et al., 2004). This suggests that the conscious perception of fearful expressions results in a controlled evaluation of the stimulus content, which is associated with deeper memory encoding (Polich, 2007). In addition, the processing of emotional faces independent of conscious perception also involves shared neural mechanisms. In response to both sub- and supraliminal facial expressions, an enhanced anterior positivity for negative compared to neutral facial expressions is elicited (Kiss & Eimer, 2008; Smith, 2012). This positivity originates in the prefrontal or anterior cingulate cortex and indicates the rapid detection of emotionally salient information (Eimer & Holmes, 2007). Taken together, emotional faces trigger a fast recruitment of attentional resources irrespective of conscious perception. However, only consciously perceived faces involve an additional, more elaborate structural analysis of the perceived facial information. While common and distinct brain processes in conscious emotion perception and emotion perception irrespective of conscious awareness have been identified in adults, it is not known whether comparable processes can be observed in infancy.

Prior work with infants has exclusively focused on the conscious processing of emotional facial expressions. Newborns show a basic preference for positive facial expressions (Farroni, Menon, Rigato, & Johnson, 2007). However, only from around 7 months of age, infants reliably distinguish between positive and negative emotions (Grossmann et al., 2011; Grossmann, Striano, & Friederici, 2007; Kobiella, Grossmann, Reid, & Striano, 2008; Leppänen, Moulson, Vogel-Farley, & Nelson, 2007; Peltola, Leppänen, Mäki, & Hietanen, 2009). In particular, previous infant ERP studies have revealed differences between emotional expressions for the negative component (Nc) (Grossmann et al., 2011; Hoehl & Striano, 2010; Leppänen et al., 2007; Nelson & de Haan, 1996). At 7 months, infants respond with a larger Nc to fearful compared to happy facial expressions and they look longer at fearful compared to happy facial expressions (Peltola et al., 2009). They also show differential responses to different negative facial expressions, as indicated by a larger Nc to angry compared to fearful facial expressions (Kobiella et al., 2008). These Nc differences suggest a differential allocation of attentional resources to emotional faces (Courchesne, Ganz, & Norcia, 1981; Richards, 2003; Webb, Long, & Nelson, 2005). In addition, differential responses to emotional faces can be observed for the N290/P400 complex (Hoehl & Striano, 2008; Kobiella et al., 2008; Leppänen et al., 2007). However, while some authors report a larger P400 for fearful facial compared to neutral facial expressions (Leppänen et al., 2007), others did not find any emotion effects at this component (Grossmann et al., 2007). Likewise for the N290, where some studies report differential responses to different emotional faces (Hoehl & Striano, 2008), while others did not observe emotion effects (Leppänen et al., 2007). Generally, both N290 and P400 have been link to the structural encoding and analysis of faces. In fact, the N290/P400 complex has been suggested as a precursor to the face-sensitive adult N170 (de Haan, Johnson, & Halit, 2003; de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003). Furthermore, differential processing of happy and fearful facial expressions has also been observed at the positivity before (Pb) (Nelson & de Haan, 1996; Grossmann et al., 2011). In sum, at around 7 months of age the brain processes that underlie the conscious perception of emotional facial expressions in infants are comparable to those in adults. Infants similarly display indices of increased attention as well as a more detailed structural analysis of the face in response to negative emotions, and in particular, fear. The lack of a fear bias in younger infants is thought to serve important adaptive functions related to bonding with a caregiver by increasing approach and reducing fear behaviors (Tottenham, 2012). Interestingly, the development of this fear bias also coincides with other crucial steps in development, including the emergence of stranger anxiety and locomotion (Campos, Kermoian, & Zumbahlen, 1992; Leppänen & Nelson, 2012). On a neural level, this development has been linked to a maturation of the amygdala and connected brain structures (see Tottenham, 2012, for a discussion). The question that remains is whether the brain processes underlying emotion processing can also be elicited when emotional faces are presented subliminally, and are therefore independent of conscious perception.

One crucial aspect in the investigation of unconscious emotion processing is to ensure that the emotional information is indeed subliminal, that is, not perceived consciously (see Wiens, 2006). Only recently have researchers begun to investigate the threshold for conscious perception in infants of different age groups. There is now behavioral evidence for such thresholds, suggesting that at 10 months of age, infants can only detect faces when presented for 150 msec or longer (Gelskov & Kouider, 2010). This indicates that the perceptual threshold for detecting faces in infants is approximately three times the duration in adults (e.g., Del Cul, Baillet, & Dehaene, 2007). This behavioral evidence is corroborated by ERP evidence identifying the late slow wave (LSW) as a neural marker for perceptual consciousness in infants (Kouider et al., 2013), which is evoked only when faces are presented above the perceptual threshold for a given age group. This work established that as a group, infants younger than 10 months of age do not consciously perceive information that is presented for less than 150 msec.

However, it has been shown in adults that the perceptual threshold for the detection of facial expressions varies considerably between individuals, which is an issue that has

been discussed in several recent studies on subliminal emotion perception (Kiss & Eimer, 2008; Pessoa, Japee, & Ungerleider, 2005). Therefore, it is plausible that the perceptual threshold in infants is also subject to individual differences. As individual perceptual thresholds are difficult to determine in infants experimentally, we decided to obtain a more general measure of the infants' ability to detect and behaviorally respond to slight changes in their environment by assessing their perceptual sensitivity as measured by the Infant Behavior Questionnaire (IBQ-R) (Gartstein & Rothbart, 2003).

In the current study, we examined perceptually conscious and unconscious emotion processing in infants by measuring ERPs in response to subliminally (50 and 100 msec) and supraliminally (500 msec) presented happy and fearful facial expressions in 7-month-old infants. More specifically, the current study concentrated on two main questions. First, does the human brain show evidence for emotional face processing irrespective of conscious awareness during infancy? Second, are the infant brain processes that underpin conscious emotion perception distinct from those that do not require conscious awareness? Third, are the brain processes involved comparable to the responses reported in adults? With respect to the first question, our hypothesis was that if infants process emotions independent of conscious awareness, we expected to find differences in the ERP response not only to supra- but also to subliminally presented facial expressions. With respect to the second and third question, our hypothesis was that if infants process emotional facial expressions similarly to adults then processing dependent on conscious perception and processing independent of conscious perception would be reflected in distinct neural processes. Namely, we hypothesized that only supraliminally presented emotional expressions would result in ERP differences for the N290 and P400 associated with the detailed structural analysis of faces. In contrast, subliminally and supraliminally presented facial expressions would elicit ERP differences for the Nc linked to the allocation of attention. Furthermore, similar to what has been shown in adults (Kiss & Eimer, 2008), we expected that infant brain responses vary as a function of perceptual sensitivity.

2. Material and methods

2.1. Participants

The final sample of participants included in the present study consisted of 21 7-month old infants (mean age: 212 days, range: 197–225 days, 11 female). An additional 28 infants had to be excluded because of crying ($N = 1$), equipment failure ($N = 1$), failure to contribute a minimum of 8 artifact-free trials per condition ($N = 19$), or because the parents did not return the questionnaire ($N = 7$). On average, each infant contributed 14.5 trials per condition [happy, 50 msec: 14.1 (SD = 4.3), fear, 50 msec: 14.3 (SD = 4.3), happy, 100 msec: 14.2 (SD = 5.5), fear, 100 msec: 14.8 (SD = 4.9), happy, 500 msec: 14.2 (SD = 5.2), fear, 500 msec: 15.5 (SD = 5.7)]. The number of trials did not differ between the conditions ($p > .1$). All infants were born full-term (between 38 and 42 weeks of gestation) with a birth-weight of at least 2800 g. The parents gave written informed consent, the study was approved by the local ethics committee, and conducted according to the declaration of Helsinki.

2.2. Stimuli

The stimuli consisted of color photographs of happy and fearful facial expressions taken from the FACES database (Ebner, Riediger, & Lindenberger, 2010). We selected photographs from 15 actresses (age 19 to 30, ID-numbers 22, 34, 48, 54, 63, 69, 71, 85, 90, 115, 125, 134, 150, 152, 173). We chose to include only pictures of women as it is a common procedure in infant studies and therefore increases comparability with previous studies (Grossmann et al., 2007; Kobiella et al., 2008; Leppänen et al., 2007). The photographs did not differ in luminance, and the respective emotion was recognized with an accuracy of at least 90% by a young rater group [52 adults between 20 and 31 years of age, 27 female, as described by Ebner et al. (2010)]. The photographs were cropped so that only the face and a minimum of hair were visible within an oval shape. In addition, we created mask stimuli by scrambling photographs showing a neutral facial expression of the same actress. Both faces and masks had a height of about 21 cm and a width of 15 cm.

2.3. Design

Photographs were presented in three different timing conditions: 50 msec, 100 msec, and 500 msec, resulting in a 2 × 3 design with the factor emotion (happy, fear) and duration (50, 100, 500). Each trial started with the presentation of a fixation star on a gray background for 500 msec, followed by the stimulus. The stimulus was directly succeeded by the mask of the same actress, which was presented for 150 msec. The following inter-trial interval varied randomly between 1500 and 2100 msec (see Fig. 1 for an example). For each participant, four randomization lists were created. Each list consisted of 90 trials, 15 in each condition (for each emotion, the picture of

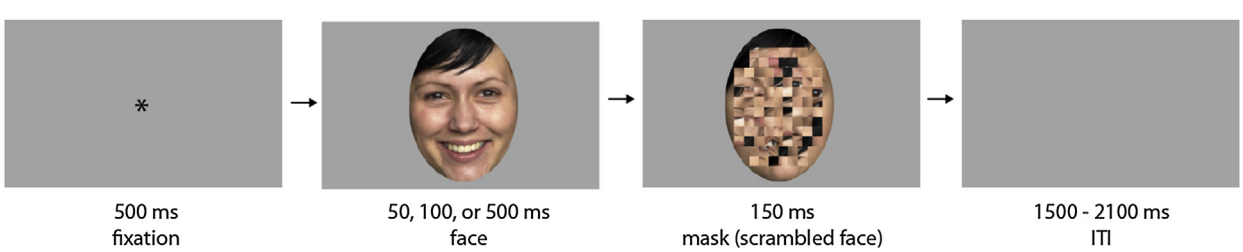

Fig. 1 – Stimulus Material. Example of one trial showing a happy facial expression. *ITI*, inter-trial interval.

each actress expressing the respective emotion was shown once in every duration condition). It was ensured that trials from the same condition did not occur more than twice in a row. The lists were presented consecutively without interruption, leading to a maximum of 360 trials. The experiment was programmed using the Presentation software package (Neurobehavioral Systems, Inc.).

2.4. Procedure

Upon arrival in the lab, parents were informed about the study, signed a consent form, and child and parents were given time to familiarize with the new environment. The EEG recording was then prepared while the infant was sitting on his/her caregiver's lap. For EEG measurement, an elastic cap was used in which 27 AgAgCl-electrodes were fixed according to the 10–20 system, using CZ as reference. In addition, a single electrode was attached below the right eye of the infant for recording the electrooculogram. The EEG signal was recorded with a sampling rate of 500 Hz using a PORTI-32/MREFA (Twente Medical Systems) amplifier. The experiment took place in a soundproof chamber, in which the mother was seated on a chair with the infant on her lap. The mother was instructed not to interact with the infant during the experiment. Stimuli were presented on a 1024 × 768 CRT-monitor with a 60 Hz refresh rate approximately 90 cm in front of the infant. Above the monitor, a small camera was mounted to monitor and record the infant's looking behavior during the experiment. If the infant did not attend to the screen, short video clips with abstract colorful shapes accompanied by ring tones were played in order to redirect the attention to the screen. The experiment continued until the infant became too fussy or the maximum number of trials was presented.

In addition to the EEG experiment, the parents were asked to fill in the German version of the IBQ-R (Gartstein & Rothbart, 2003; see Vonderlin, Ropeter, and Pauen (2012) for a validation of the German version). The IBQ-R is a measurement of infant temperament based on the parents' judgment on 191 items with a 7-point Likert scale. Based on these items, 14 scales can be computed. Our analysis was limited to the "Perceptual Sensitivity" scale of the IBQ-R because this appeared to be the most relevant with respect to gathering information regarding variation in infants' ability to detect small changes or objects in their environment that are difficult to perceive. Sample items contributing to the scale "Perceptual Sensitivity" included questions such as: "How often does the infant look up from playing when s/he heard voices in the next room?" or "How often did your baby notice a bird or squirrel up in a tree?" (1 = never, 7 = always, see supplementary material for a full list of all 12 questions). The questionnaires were filled in at home and returned to the laboratory soon after testing.

2.5. EEG analysis

The data analysis was done using Matlab (The MathWorks, Inc., Natick, Massachusetts, United States), the Matlab toolbox FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) and SPSS (IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp.). Data were re-referenced offline to the mean of TP9 and TP10 (see e.g., Grossmann et al., 2007, 2011; Kobiella et al., 2008), and bandpass filtered between .2 and 20 Hz. In three participants, one electrode was noisy and therefore interpolated using spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989). Data were segmented into epochs ranging from 150 msec before until 1450 msec after the onset of a picture. To detect trials containing artifacts, the standard deviation was computed in a sliding window of 200 msec within these epochs. If the standard deviation exceeded 100 mV at any electrode, the respective trial was rejected. In addition, the data was inspected visually for any remaining artifacts.

Data for each condition were averaged and a baseline correction was performed using a window of 150 msec before stimulus onset as baseline. Additionally, the video recording of the infant during the experiment was checked and only those trials in which the infant looked at the screen were considered for further analysis. We analyzed ERPs in two regions of interest (ROIs): an occipital ROI consisting of O1 and O2 (commonly used for analyzing the N290/P400 complex with the given electrode layout, see e.g., Hoehl & Striano, 2008), and a central ROI encompassing T7, C3, C4, and T8 (based on visual inspection of the topography as well as prior literature, e.g., Peltola et al., 2009). For both ROIs, time-windows for ERP analysis were defined based on visual inspection. All time-windows were defined relative to the face onset. In the occipital ROI, time-windows analyzed included 170–250 msec, 260–390 msec, and 800–1200 msec (corresponding to N290, P400, and LSW, respectively). For the central ROI, we chose time-windows from 250 to 350 msec (Pb), and 360 to 540 msec (Nc). For each time-window, the mean amplitude was computed and entered into a general linear model (GLM) with the factors Hemisphere (left, right), Duration (50 msec, 100 msec, 500 msec), and Emotion (fear, happy). We chose to include Hemisphere as a factor because the topography in the relevant time-windows suggested a right-lateralization of some of the ERP components. Furthermore, the score obtained on the IBQ-R scale perceptual sensitivity was centered by subtracting the mean value across participants (Delaney & Maxwell, 1981) and included as a covariate. A Greenhouse-Geisser correction was applied when necessary. To further investigate the influence of perceptual sensitivity, we computed the correlation between Perceptual Sensitivity (not centered) and ERP data whenever an interaction with Perceptual Sensitivity reached significance.

3. Results

3.1. ERP results in the occipital ROI

Between 170 and 250 msec (N290 time-window), we found a significant interaction between Duration, Emotion, and Perceptual Sensitivity [$F(1.76, 33.46) = 3.50$, $p = .047$, $\eta^2 = .16$, see Fig. 2]. Post-hoc tests showed no significant difference for 50 msec and 100 msec Duration ($p > .1$), while for the 500 msec-Duration condition, we found a more negative amplitude for happy compared to fearful faces [$F(1,19) = 4.66$, $p = .044$, $\eta^2 = .20$; happy: mean: 1.22 μV (SE = 3.30), fearful: mean: 1.91 μV (SE = 2.75)]. Investigating the effect of Perceptual Sensitivity, we found a positive correlation for the difference

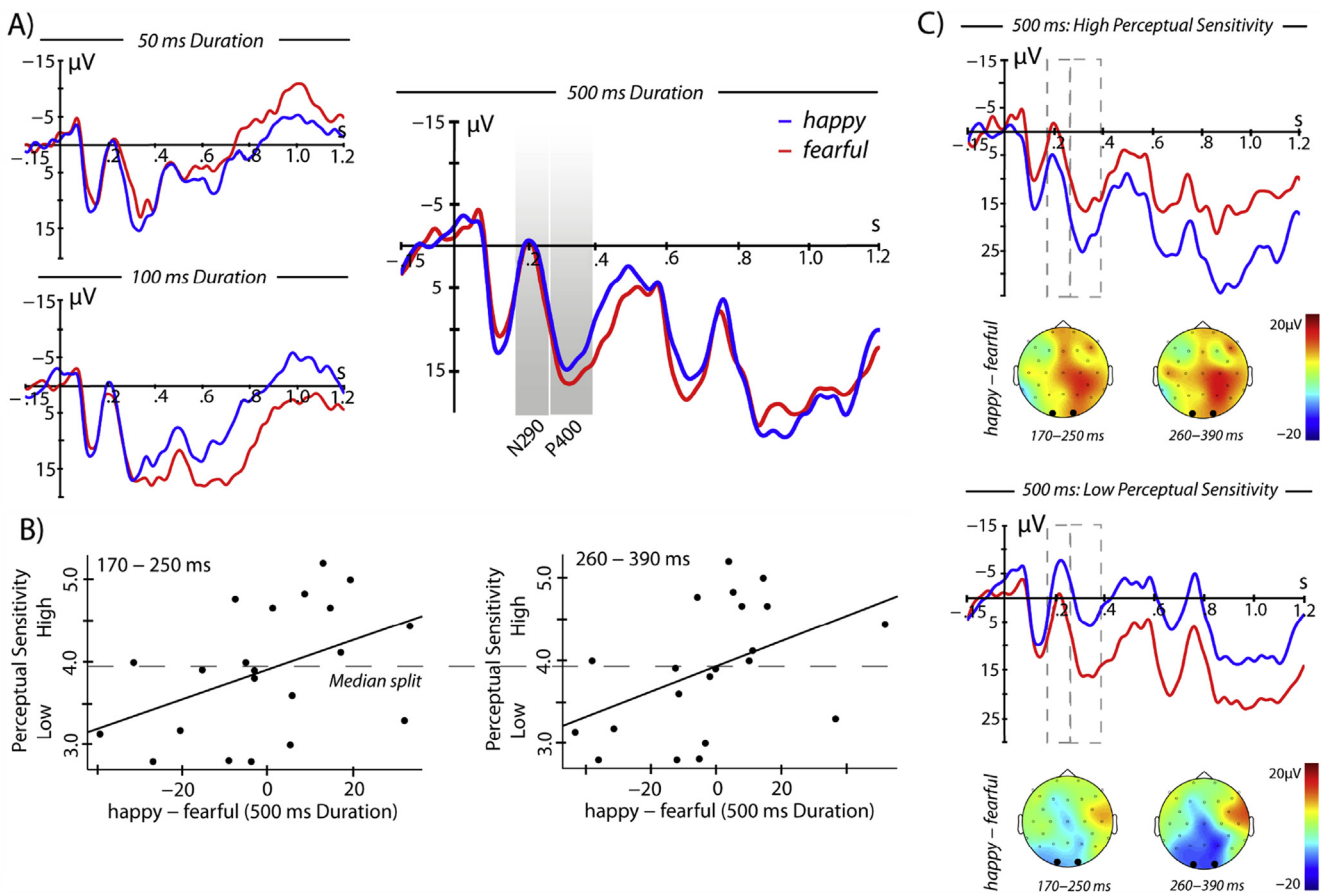

Fig. 2 – ERP responses at occipital electrodes. This figure shows the responses averaged across O1 and O2. In A), the ERP response is shown separately for the three duration conditions; gray boxes mark the time-windows in which the contrast between happy and fear reached significance. B) The correlation between the difference between happy and fear (in the 500 msec condition) and perceptual sensitivity is shown. A median split was used to separate the participants into a high perceptual sensitivity group (perceptual sensitivity > 3.91) and a low perceptual sensitivity group (perceptual sensitivity ≤ 3.91). In C), the ERP response for the high and low perceptual sensitivity groups are depicted separately, showing the difference between happy and fear in the 500 msec condition. The topographical representations show the distribution of the difference between happy and fear in the two time-windows of interest, which are marked by dashed lines.

between happy and fearful faces (at 500 msec presentation time) and Perceptual Sensitivity ($r = .44$, $p = .044$) (see Fig. 2). This suggests that infants with a higher perceptual sensitivity showed a more negative amplitude for fearful faces, while infants with a low perceptual sensitivity showed a more negative amplitude for happy faces.

In the time-window 260–390 msec (P400 time-window), a similar pattern was observed. Namely, we found a significant interaction between Duration, Emotion, and Perceptual Sensitivity [$F(1.75, 33.39) = 4.16$, $p = .029$, $\eta^2 = .18$], and between Duration and Emotion [$F(1.75, 33.39) = 4.11$, $p = .030$, $\eta^2 = .18$] While no significant differences were found in the 50 msec- and the 100 msec-condition, a more positive amplitude for fearful compared to happy facial expressions was found in the 500 msec–condition [in interaction with Perceptual Sensitivity: $F(1,19) = 5.02$, $p = .037$, $\eta^2 = .21$; without Perceptual Sensitivity: $F(1,19) = 5.22$, $p = .034$, $\eta^2 = .22$] [happy: mean: 12.32 µV (SE = 5.18), fearful: mean: 14.40 µV (SE = 3.63)]. Correlating the difference between happy and fearful with Perceptual Sensitivity ($r = .46$, $p = .037$) revealed that infants with a higher perceptual sensitivity showed a more positive amplitude for happy faces, while infants with a low perceptual sensitivity showed a more positive amplitude for fearful faces.

Between 800 and 1200 msec after stimulus onset (LSW time-window), we observed a significant main effect of Duration [$F(1.35,24.38) = 15.38$, $p < .001$, $\eta^2 = .36$, see Fig. 3]. The response to a presentation duration of 500 msec differed significantly from the response to shorter durations [50 *vs* 500 msec: $F(1,18) = 16.85$, $p = .001$, $\eta^2 = .48$; 100 *vs* 500 msec: $F(1,18) = 42.22$, $p < .001$, $\eta^2 = .70$], revealing a larger amplitude for the 500-msec presentation duration [50 msec: mean: −4.82 µV (SE = 3.47), 100 msec: 1.10 µV (SE = 4.17), 500 msec: 19.30 µV (SE = 4.21)]. No significant difference was found between the 50- and the 100-msec presentation duration.

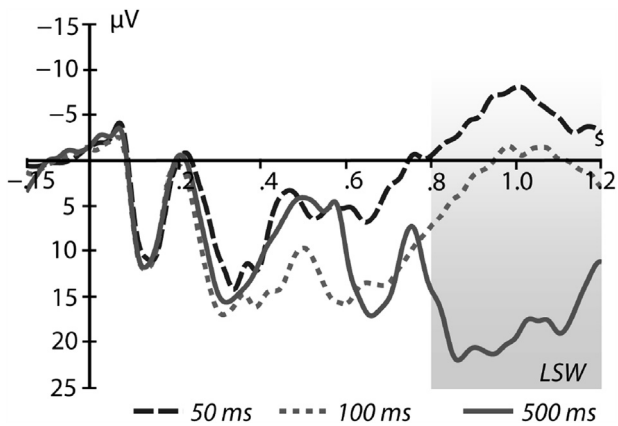

Fig. 3 – ERP response for different presentation durations at occipital electrodes. ERP responses at O1 and O2 in response to presentation durations of 50, 100, and 500 msec irrespective of emotional content are depicted. The gray box marks the time-window in which the difference between the subliminal presentation durations (50 and 100 msec) and the supraliminal presentation duration (500 msec) reached significance.

We did not observe an interaction with Hemisphere in any of the time-windows.

3.2. *ERP results in the central ROI*

Between 250 and 350 msec (Pb time-window), we observed a significant interaction between the factors Emotion and Perceptual Sensitivity [$F(1,19) = 5.18$, $p = .035$, $\eta^2 = .21$ see Fig. 4], revealing a more positive amplitude for happy compared to fearful facial expressions [happy: mean: −1.16 μV (SE = 1.93), fearful: mean: −3.79 μV (SE = 1.68)]. A correlation between the difference between happy and fear and Perceptual Sensitivity suggests that this effect increased with increasing perceptual sensitivity ($r = .46$, $p = .035$). We did not observe an interaction between Duration and Emotion [$F(1.87, 35.59) = 2.7$, $p = .08$, $\eta^2 = .12$], or between Duration, Emotion, and Perceptual Sensitivity [$F(1.87,35,59) = 2.07$, $p = .14$, $\eta^2 = .10$]. Furthermore, we did not find any interaction with the factor Hemisphere.

A similar effect was found between 360 and 540 msec (Nc time-window). We observed a significant interaction between Emotion and Perceptual Sensitivity [$F(1,19) = 5.65$, $p = .028$, $\eta^2 = .23$], revealing a more negative amplitude for fearful compared to happy facial expressions [happy: mean: −12.57 μV (SE = 2.16), fearful: mean: −14.24 μV (SE = 1.67)]. We again computed a correlation between the difference between happy and fear and perceptual sensitivity ($r = .48$, $p = .028$). Again, we did not find an interaction between Duration and Emotion [$F(1.84,35.0) = .93$, $p = .40$, $\eta^2 = .05$], or between Duration, Emotion, and Perceptual Sensitivity [$F(1.84,35.0) = .98$, $p = .38$, $\eta^2 = .05$], and we did not find any interaction with Hemisphere.

The observed effect suggests that the difference in response between happy and fearful faces becomes larger with increasing perceptual sensitivity.

4. Discussion

The present study investigated whether infants discriminate between fearful and happy facial expressions irrespective of conscious perception, and whether emotion processing dependent and independent of conscious perception relies on distinct neural processes. Our ERP data revealed that infants at 7 months of age show differential brain responses (Pb and Nc) to fearful and happy facial expressions irrespective of conscious perception, suggesting that they can indeed detect differences between emotional expressions when presented subliminally. Moreover, our results show that there are brain responses (N290 and P400) that are specific to the conscious processing of emotional facial expressions, as they were only elicited when faces were presented supraliminally. Critically, our data provide evidence for the notion that both, processes that depend on conscious perception and processes that are independent of conscious perception, are modulated by infants' behaviorally expressed perceptual sensitivity. This suggests that infants show a similar distinction as adults between the processing of emotional facial expressions that are consciously perceived and processes independent of conscious awareness, including marked individual differences.

4.1. *ERP evidence for distinct neural mechanisms*

We observed a modulation of the central positivity before (Pb) and Nc components by emotional expression regardless of conscious perception. While the Pb amplitude decreased for fearful expressions, the Nc amplitude was larger in response to fearful than to happy faces. In line with previous studies on consciously perceived emotions, fearful facial expressions elicited a more negative-going ERP response than happy expressions (Grossmann et al., 2011; Leppänen et al., 2007; Nelson & de Haan, 1996). This pattern reflects an increased allocation of attention to the negative expression (Vaish, Grossmann, & Woodward, 2008). Our data therefore critically extend prior work by showing that these attentional mechanisms operate independent of conscious perception of fearful faces. This is in agreement with the notion that, due to its adaptive significance, the detection of evolutionarily relevant stimuli such as emotional facial expressions in others can occur even in the absence of any conscious awareness (Tamietto & de Gelder, 2010). In contrast, we did not find evidence for a modulation of the face-sensitive N290/P400 complex by subliminally presented facial expressions. Only consciously perceived faces resulted in differences for these ERP components. Specifically, fearful facial expressions elicited a more negative-going ERP response at occipital electrodes compared to happy facial expressions, as shown in an increased N290 and decreased P400 amplitude. This indicates that, in line with prior findings, emotional information only affects the detailed structural analysis of faces if perceived consciously (Hoehl & Striano, 2008; Kobiella et al., 2008; Leppänen et al., 2007).

It may seem counterintuitive that ERP differences specific to conscious emotional face processing (N290) occur earlier in time than the ERP differences observed independent of

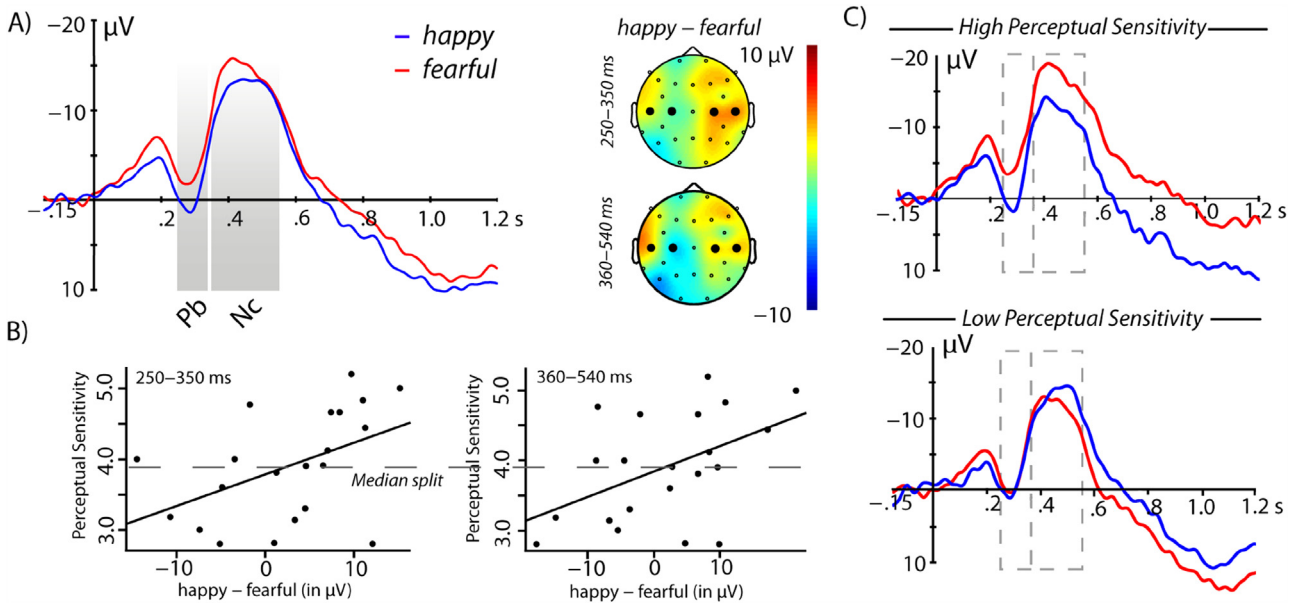

Fig. 4 – ERP responses at central electrodes. The ERP response is shown averaged across all three duration conditions and across T7, C3, C4, and T8. A) The ERP response is shown without taking perceptual sensitivity into account; significant differences in the response to happy and fearful faces were observed during the time-windows marked in gray. The topographical representations show the distribution of the difference between happy and fear in the two time-windows which reached significance. B) The results of the correlation between the difference between happy and fear and perceptual sensitivity for the two significant time-windows are shown.

conscious emotional face processing (Pb). This might be explained by the fact that the rapid unconscious emotion detection (especially for fear) takes place in subcortical brain regions such as the amygdala (Whalen et al., 2004), whose response profile cannot be directly observed in the ERP signal. Thus, the modulations of the Pb and Nc likely reflect subsequent processing steps that follow this initial detection in subcortical structures. In contrast, conscious extraction of emotional information, as indicated by the N290, is assumed to involve cortical structures such as the superior temporal sulcus and the fusiform gyrus (Johnson, 2005) and is therefore directly reflected in the ERPs. This distinction is in line with the assumed differentiation between a subcortical and a cortical route for emotion processing (LeDoux, 1996; Ohman, 2005). Intriguingly, the observed distinction between processing dependent on and processing independent of conscious awareness closely resembles the pattern described in adults. Namely, in adults, an increased frontal positivity in response to negative facial expressions can be observed irrespective of conscious perception, and an increased face-sensitive N170 occurs only for consciously perceived negative expressions (Japee et al., 2009; Kiss & Eimer, 2008; Smith, 2012). It is important to note that the brain responses observed in prior work with adults and in the current study with infants show similarities not only at the functional level, but also with respect to the previously identified neural generators for the ERP components. Particularly, in source localization studies, the adult frontal positivity as well as the infant Nc have been shown to be generated in the prefrontal cortex and anterior cingulate cortex (adult positivity: Eimer & Holmes, 2007; infant Nc: Reynolds & Richards, 2005). Similarly, the neural sources of the adult N170 and the infant N290 have been localized to the fusiform gyrus and the superior temporal sulcus (adult N170: Itier & Taylor, 2002, 2004; infant N290: Johnson et al., 2005).

Taken together, the current evidence shows that early in development the human brain not only discriminates between unconsciously presented happy and fearful facial expressions, but also that, similar to adults, emotion processing dependent on and independent of conscious perception relies on distinct neural processes. This demonstrates that distinct processing mechanisms involved in the analysis of facial expressions emerge early in development, supporting accounts that emphasize the early maturation (during the first year) of sensitive responding to emotions in others (see Davidov, Zahn-Waxler, Roth-Hanania, & Knafo, 2013). The current findings must also be discussed with respect to recent theories concerning the neural bases of perceptually unconscious emotion processing. In particular, subcortical structures, especially the amygdala and the superior colliculus, are thought to play a key role in subliminal emotion processing (Tamietto & de Gelder, 2010). These subcortical regions are strongly interconnected with the anterior cingulate cortex and prefrontal cortex (Aggleton, Burton, & Passingham, 1980; Field, Johnston, Gati, Menon, & Everling, 2008; Kim et al., 2011). Given that the ERP effect (Nc) observed independent of conscious perception in the current study is assumed to originate from the anterior cingulate cortex and prefrontal cortex (Reynolds & Richards, 2005), this may (indirectly) support the account put forward

by Tamietto and de Gelder (Tamietto & de Gelder, 2010). Furthermore, subcortical structures are thought to be among the first brain structures to be functional in human infants and it has been proposed that subcortical structures (amygdala and superior colliculus) drive face preferences in neonates (Johnson, 2005). Reciprocal connections between the amygdala and the frontal cortex might contribute to an early emotion discrimination (Leppänen & Nelson, 2009). Thus, the brain structures assumed to underlie subliminal emotion perception in adults may be similar to those associated with neonates' face preferences, suggesting that this brain system might be in place from birth. It might thus be possible that evidence for subliminal emotion processing can be found in infants before they can consciously discriminate between facial expressions. Clearly, future work is needed to further specify the developmental trajectory of subliminal emotion processing.

Another important point is to ensure that in the subliminal conditions infants did indeed not perceive the faces. This is because otherwise the observed effects may have been driven by conscious processing of information rather than by true subliminal processing (see Kiss & Eimer, 2008; Pessoa et al., 2005 for a discussion regarding prior work with adults). However, this possibility is highly unlikely because infant face visibility thresholds at both 5 and 10 months of age lie between 100 and 150 msec presentation time (Gelskov & Kouider, 2010). The infants in the current study were 7 months of age, and the subliminal presentation times (50 and 100 msec) were well below the perceptual threshold determined for younger as well as older infants.

4.2. *Perceptual sensitivity – the role of individual differences*

Our data further revealed that behaviorally expressed perceptual sensitivity as rated by the infants' caregiver was associated with an increased neural sensitivity, as indexed by the ERP responses (Nc and Pb) to emotional facial expressions.

Thus, infants' emotion processes are subject to individual differences, irrespective of whether they depend on conscious perception or not. This is in line with prior work with adults (Kiss & Eimer, 2008; Pessoa et al., 2005), suggesting that individual differences may impact emotion processing throughout the life-span. In research on subliminal emotion processing in adults, the term perceptual sensitivity is commonly used to refer to the perceptual thresholds for detecting a specific facial expression (usually fear) behaviorally in an experimental setting (Kiss & Eimer, 2008). The perceptual threshold varies between participants, and to properly investigate subliminal processing, it appears essential to ensure that the presented stimuli are indeed subliminal for all participants (Kiss & Eimer, 2008). While the current infant data together with prior work with adults concur in that perceptual sensitivity impacts emotion processing, it is not clear (1) whether the concept of perceptual sensitivity is comparable between infants and adults and (2) whether it has a comparable influence on the observed brain responses. Perceptual sensitivity as measured in infants by the IBQ-R (Gartstein & Rothbart, 2003) is a general aspect of infant temperament judged by the infant's caregiver, rather than an experimentally determined perceptual threshold. Nevertheless, high perceptual sensitivity in an infant may be associated with reduced perceptual thresholds in detecting faces and facial expressions. Whether such a link exists should be examined in future studies that directly compare behavioral responses in an experimental setting with general perceptual sensitivity as judged by the infant's caregiver.

Based on the current data, the impact of perceptual sensitivity on the ERP responses may be explained by different factors. One possibility is that the general ability of infants with a higher perceptual sensitivity to detect slight environmental changes carries over to their sensory processing below the perceptual threshold. In this scenario, supraliminal sensory processing may have operated particularly efficiently and sensitively, so that subliminal processing was improved. Relatedly, certain aspects of the experimental procedure might in part explain the observed effect of perceptual sensitivity. Specifically, for 7-month-old infants to complete an ERP experiment that consists of six conditions is a rather demanding task. Thus, perhaps only the infants generally prone to attend to small details (i.e., having a high perceptual sensitivity) managed to process the subliminal stimuli sufficiently, while infants with a lower perceptual sensitivity might not have been able to do so under such challenging circumstances. To rule out that these task characteristics played a role in this context, future studies could employ a simpler design with fewer conditions.

Another possibility is that, for infants with a high perceptual sensitivity, the stimuli intended to be subliminal might in fact have been supraliminal. As outlined above, the threshold for this age group is expected to lie between 100 and 150 msec (Gelskov & Kouider, 2010). It seems therefore unlikely that perceptual thresholds in infants vary to such a large degree that 7-month-olds outperform 5- and 10-month-olds by 100 msec (the data reported by Gelskov and Kouider (2010) support this assumption because distributional information (standard errors) for presentation times of 50 and 100 msec (in 5- and 10-month-olds) clearly show that infants perform at chance levels). Nonetheless, to completely exclude this possibility it would be necessary to empirically determine the infant's individual perceptual threshold to ensure presented stimuli are indeed subliminal.

Another finding from our analysis examining the role of perceptual sensitivity in infants' emotion processing is an effect on the N290 and P400 components in response to supraliminally presented stimuli. We found a more negative-going ERP for fearful faces when compared to happy faces in infants scoring high on perceptual sensitivity, whereas infants scoring low on perceptual sensitivity showed the reverse pattern. While the effect of perceptual sensitivity on the processing of supraliminal emotions was not the main focus of our study, this finding may provide an explanation for the inconsistent pattern of results observed in previous studies. Specifically, some studies have found effects of emotional facial expressions on the N290 and P400 (e.g., Hoehl & Striano, 2008; Kobiella et al., 2008; Leppänen et al., 2007), while others did not obtain such emotion effects on face-sensitive ERP components (e.g., Grossmann et al., 2011, 2007). As none of these studies controlled for perceptual sensitivity, different distributions of infants scoring high and

low on perceptual sensitivity in the respective samples may have lead to different overall results. Clearly, at this stage this is only a speculation and future studies are needed to examine the effects of perceptual sensitivity more systematically.

4.3. *LSW difference – the marker of perceptual consciousness?*

It has recently been proposed that the LSW is a marker for perceptual consciousness in infants, since it was shown to only occur when face stimuli were consciously detected (Kouider et al., 2013). Although we do find a difference between subliminal and supraliminal stimuli in the current study, the polarity of the LSW effect was opposite to the polarity observed previously (Kouider et al., 2013), exhibiting a positive amplitude for supraliminally and a negative amplitude for subliminally presented facial expressions. It is likely that this discrepancy can be explained by methodological differences across studies. The mask following the facial expression was only presented for 150 msec in our study, irrespective of how long the facial expression was presented, leading to a varying total duration of the stimulus plus mask (200, 250, and 650 msec, in the three different conditions). In contrast, Kouider et al. (2013) presented a mask for different durations, leading to fixed presentation time for face stimulus plus mask of 1500 msec. Since the LSW only starts around 800 msec after face onset, the LSW in the present study may have been obscured by a simultaneously occurring offset response to the mask, as can be seen by the negative-going peak in the 500-msec-condition at approximately 750 msec after face onset (see Fig. 3). Therefore, in order to compare between studies more directly, it would have been necessary to present the mask for a longer time, as Kouider et al. (2013) did. However, as the main focus of the current study was on the investigation of emotion processing and the study was not specifically designed to look at LSW effects, we employed a design closely matched to prior adult studies on subliminal emotion processing (Eimer, Kiss, & Holmes, 2008; Kiss & Eimer, 2008; Smith, 2012).

4.4. *Conclusions*

In summary, the current study provides novel insights into the brain processes that underpin emotion perception in infancy. Our ERP findings demonstrate that the responding to emotional information in 7-month-old infants relies on distinct brain processes which (a) depend on conscious perception as reflected in the N290 and P400 and (b) are independent of conscious perception as reflected in the Pb and Nc. This shows that the human infant brain not only discriminates between happy and fearful facial expressions irrespective of conscious perception but also that, similar to adults, subliminal and supraliminal emotion processing is associated with distinct neural correlates. Importantly, our data also suggest that the neural processing of emotional facial expressions generally differs across infants depending on their behaviorally shown perceptual sensitivity. These findings critically inform and extend accounts of emotion perception as they illuminate the neurodevelopmental origins of this crucial social capacity.

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2014.11.007.

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