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Brief Report

The developmental emergence of unconscious fear processing from eyes during infancy

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ABSTRACT

From early in life, emotion detection plays an important role during social interactions. Recently, 7-month-old infants have been shown to process facial signs of fear in others without conscious perception and solely on the basis of their eyes. However, it is not known whether unconscious fear processing from eyes is present before 7 months of age or only emerges at around 7 months. To investigate this question, we measured 5-month-old infants' event-related potentials (ERPs) in response to subliminally presented fearful and non-fearful eyes and compared these with 7-month-old infants' ERP responses from a previous study. Our ERP results revealed that only 7-month-olds, but not 5-month-olds, distinguished between fearful and non-fearful eyes. Specifically, 7-month-olds' processing of fearful eyes was reflected in early visual processes over occipital cortex and later attentional processes over frontal cortex. This suggests that, in line with prior work on the conscious detection of fearful faces, the brain processes associated with the unconscious processing of fearful eyes develop between 5 and 7 months of age. More generally, these findings support the notion that emotion perception and the underlying brain processes undergo critical change during the first year of life. Therefore, the current data provide further evidence for viewing infancy as a formative period in human socioemotional functioning.

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Introduction

Detecting emotional expressions in others provides a vital basis for coordinating and regulating behavior during social interactions in humans (Frith, 2009; Shariff & Tracy, 2011). The ability to perceive, process, and differentiate other people's emotions based on facial expressions undergoes rapid development during the first year of life (see Leppänen & Nelson, 2009). For example, by 7 months of age, infants begin to reliably discriminate between different emotional facial expressions, which they perceive consciously (Flom & Bahrick, 2007; Kobiella, Grossmann, Reid, & Striano, 2008; Peltola, Hietanen, Forssman, & Leppänen, 2013; Peltola, Leppänen, Mäki, & Hietanen, 2009). Specifically, at around this age, an increased sensitivity to fearful facial expressions emerges in infants, which is reflected in infants' allocation of increased attention to fearful expressions when compared with happy expressions (Peltola, Leppänen, Mäki, et al., 2009). The emergence of this increased sensitivity to fear can be traced in infants' behavioral responses (looking time) but also in infants' neural responses (event-related potentials, ERPs) (Peltola, Leppänen, Mäki, et al., 2009). This sensitivity emerges at a time in development when other important and potentially related developmental changes occur (Leppänen & Nelson, 2012). Namely, at around the same time, infants start to exhibit fear themselves as seen as an increasing fear of strangers (Braungart-Rieker, Hill-Soderlund, & Karrass, 2010) and also begin to locomote (crawl) and thereby encounter dangerous situations associated with the experience of fear and fearful expressions in their caregivers (Campos, Kermoian, & Zumbahlen, 1992).

In adults, it has been shown that the processing of fearful faces can occur without conscious perception of the face (Kiss & Eimer, 2008; Liddell, Williams, Rathjen, Shevrin, & Gordon, 2004; Smith, 2012). In particular, adults show differential ERP responses to emotional faces compared with neutral faces (Kiss & Eimer, 2008; Liddell et al., 2004; Smith, 2012) as well as between different emotional expressions (Smith, 2012). Typically, these unconscious (or subliminal) stimuli are presented for a very brief duration (< 20 ms), too short to be consciously perceived. On a behavioral level, therefore, adults perform at chance level when asked to classify the emotional expression just presented (Kiss & Eimer, 2008). Nevertheless, differences in brain activation can be observed.

A number of different adult ERP components have been investigated in relation to subliminal and supraliminal emotional face processing. One of the earliest stages at which emotion processing can be observed is the occipital cortex (P1), for which the amplitude tends to be larger for threatening facial expressions (Nomi, Frances, Nguyen, Bastidas, & Troup, 2013). The P1 is typically followed by an N2, which has been linked to orienting to a salient stimulus such as an emotional face. Typically, fearful facial expressions elicit a larger amplitude compared with neutral or positive facial expressions (Liddell et al., 2004). This effect can also be observed in the absence of conscious awareness.

Evidence regarding emotion differences at the level of the N170, a component involved in face processing (see Rossion, 2014), are mixed; whereas some adult studies show emotion effects at the N170, others do not (Vuilleumier & Pourtois, 2007). Findings are also mixed for subliminal processing, with some work reporting an emotion effect on the N170 (Pegna, Landis, & Khateb, 2008) and other work observing no difference for the N170 (Kiss & Eimer, 2008).

Finally, emotional information also affects later stages of processing, especially when information is perceived consciously. One component of particular importance here is the P3, which has been linked to a higher order processing of emotional information (Kiss & Eimer, 2008).

In direct comparison between subliminal and supraliminal emotion processing, some ERP components appear to be specific to subliminal stimuli (e.g., an enhanced N2; Kiss & Eimer, 2008; Liddell et al., 2004), whereas others can be observed for both subliminal and supraliminal emotion processing (e.g., an enhanced frontal positivity; Smith, 2012). Therefore, subliminal emotion processing appears to rely on distinct mechanisms but also on mechanisms shared in common with supraliminal emotion processing.

Interestingly, the unconscious processing of fear can be seen not only in response to faces but even in response to minimal information from the eye whites (sclerae) (e.g., Whalen et al., 2004). Whalen and colleagues (2004) presented adults subliminally with only the sclerae of happy and fearful facial expression, and they observed an increased amygdala activation to fearful eyes, which is comparable to what had been reported previously for fearful faces (Morris et al., 1996). This is particularly

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interesting because there are a number of studies arguing for the relevance of eyes in the processing of (emotional) faces (see Itier & Batty, 2009, for a review on the role of eyes and eye gaze in social cognition). Eyes alone have also been found to elicit the classical face-sensitive N170, and this component is not seen when eyes are removed from facial stimuli (Itier, Alain, Sedore, & McIntosh, 2007; Itier, Van Roon, & Alain, 2011).

Recently, this line of work has been extended into infancy. Specifically, using ERPs, 7-month-old infants have been shown to process facial signs of fear in others without conscious perception (Jessen & Grossmann, 2015), comparable to what had previously been shown for conscious emotion processing (Peltola, Leppänen, Mäki, et al., 2009). Furthermore, similar to adults, eyes play a key role when 7-month-olds respond to fear in others because sensitive ERP responses can be seen to eye whites presented in isolation (Jessen & Grossmann, 2014). Infants have also been shown to exhibit an increased focus on the eye region already from birth (Farroni, Csibra, Simion, & Johnson, 2002; Rigato, Menon, Johnson, & Farroni, 2011).

As in adults, a number of different ERP components have been investigated in this context. The P1 is one of the earliest components at which emotional differences can be observed in adults, and the same holds true during development. Children between 4 and 7 years of age show a modulation of the P1 by emotional content (Batty & Taylor, 2006; Curtis & Cicchetti, 2011). Furthermore, a face sensitivity of the P1 can already be observed during infancy (de Haan, Johnson, & Halit, 2003).

More commonly, however, emotional differences have been investigated at the N290/P400 complex, commonly considered a precursor to the adult N170. Similar to adults, previous findings are mixed with respect to emotional differences at this processing level; whereas some studies report differences at the N290/P400 (Kobiella et al., 2008; Leppänen, Moulson, Vogel-Farley, & Nelson, 2007), others do not find any differences (Peltola, Leppänen, Mäki, et al., 2009). For subliminal processing, evidence from previous work is limited, but one study directly contrasting subliminal and supraliminal emotion processing in 7-month-old infants reported emotion effects at the N290/P400 complex only for supraliminally presented stimuli (Jessen & Grossmann, 2015).

The most commonly investigated ERP component in this context, however, is the frontal cortex (Nc), a frontocentral negativity between 400 and 800 ms that has been linked to the allocation of attention and/or the detection of novel events (Webb, Long, & Nelson, 2005). Furthermore, it shows robust differences between different (supraliminal) emotional expressions, starting at around 7 months of age (Kobiella et al., 2008; Peltola, Leppänen, Mäki, et al., 2009).

Interestingly, emotion differences at the Nc have been observed not only for supraliminal emotion expressions but also for subliminal emotion expressions (Jessen & Grossmann, 2015).

However, from a developmental perspective, it is not known when during infancy this unconscious fear processing from eyes emerges. More specifically, it is unclear whether it is present before 7 months of age or, similar to the conscious perception of fearful faces (Peltola, Leppänen, Mäki, et al., 2009), it only emerges at around 7 months. To test between these two possibilities, we measured 5-month-old infants' ERPs in response to subliminally presented fearful and non-fearful eyes and compared these with 7-month-old infants' ERP responses from a previous study (Jessen & Grossmann, 2014). Based on prior work on the conscious perception of fearful faces (Peltola, Leppänen, Mäki, et al., 2009) and other work demonstrating developmental changes in socioemotional responding toward the second half of the first year of life (Vaish, Grossmann, & Woodward, 2008), we predicted that 7-month-olds, but not 5-month-olds, would show evidence for the ability to discriminate between fearful and non-fearful eyes. Critically, similar to prior work (Farroni et al., 2005; Jessen & Grossmann, 2014; Whalen et al., 2004), we employed a control condition in which we presented polarity-inverted eye stimuli, which allowed us to assess the specificity of infants' responses to human sclerae.

Method

Participants

A total of 23 5-month-old infants participated in the current study (11 girls, mean age = 154 days, range = 140–165). An additional nine infants were tested but not included in the final analysis because of continued crying ($n = 1$) or failure to contribute at least 10 artifact-free trials per condition ($n = 8$). Infants contributed an average of 25.9 ± 10.4 (mean ± *SD*) trials per condition (happy–original: 24.8 ± 9.7; happy–inverted: 25.5 ± 11.2; fear–original: 26.1 ± 11.1; fear–inverted: 27.1 ± 11.1). The number of trials did not differ between conditions ($p > .10$).

For comparison, published data from a group of 24 7-month-old infants (13 girls, mean age = 216 days, range = 209–225) undergoing the same experimental manipulation were used (Jessen & Grossmann, 2014). The experimental protocol was identical to the one described below. In this group, infants contributed an average of 31.6 ± 14.3 trials per condition (happy–original: 30.9 ± 13.4; happy–inverted: 31.2 ± 14.7; fear–original: 32.5 ± 13.5; fear–inverted: 31.8 ± 16.2). Again, the number of trials did not differ between conditions, and the number of trials also did not differ between the two age groups ($p > .10$).

All infants were born full-term (between 38 and 42 weeks of gestation) and had a birthweight of at least 2800 g. They were recruited from middle-class to upper middle-class families from the area of Leipzig, a medium-size German city. All infants were Caucasian with the exception of one infant of East Asian decent and one infant of South Asian decent (both in the 5-month group). The parents gave written informed consent. The study was conducted according to the Declaration of Helsinki and was approved by the local ethics committee.

Stimuli

The stimulus material was identical to that used by Whalen and colleagues (2004). It consisted of photographs of fearful and happy facial expressions from eight individuals (five females; Ekman & Friesen, 1976), from which all information except the sclera was removed. The rest of the photograph was colored in black (for examples, see Figs. 1 and 2 in Results). As control stimuli, we created a polarity-inverted version of these photographs showing a black "sclera" on a white background. In addition, neutral facial expressions of the same actors, which were edited to contain only black and white, were used as masks during the experiment. Stimuli and all details of stimulus presentation were identical to those in Jessen and Grossmann (2014).

Design

The experiment consisted of four conditions, resulting in a 2 × 2 design with the factors emotion (happy or fear) and polarity (original or inverted). A total of 80 stimuli were presented in each condition (10 per actor), leading to a total of 320 trials. The stimuli were presented in a pseudo-randomized order, with each participant receiving an individual randomization list. The list consisted of 10 blocks with 32 trials each (8 per condition), which were presented consecutively without interruption. It was ensured that the same condition was not repeated more than once.

At the beginning of each trial, a fixation star was presented for 500 ms, followed by the actual stimulus presented for 50 ms. The stimulus was followed by a mask presented for 750 ms. After an intertrial interval of 800 to 1200 ms, during which a gray screen was shown, the next trial followed.

Previous studies suggest that the threshold for consciously discriminating faces from non-faces in 5- and 10-month-olds lies between 100 and 150 ms (Gelskov & Kouider, 2010). Based on these values, a presentation duration of 50 ms can be assumed to be clearly below the perceptual threshold for the 5- and 7-month-olds tested in the current study.

Procedure

The EEG recording was prepared while the infant was sitting on a caregiver's lap. An elastic cap in which 27 Ag/AgCl electrodes were mounted according to the 10–20 system was used for recording. In addition, an electrode was attached below the infant's right eye to compute the electroocculogram. A PORTI-32/MREFA amplifier (Twente Medical Systems) was used for recording the electroencephalogram (EEG) signal with a sampling rate of 500 Hz.

The experiment took place in a soundproof, electrically shielded chamber. The parent was instructed not to interact with the child during the experiment. The stimuli were presented on a

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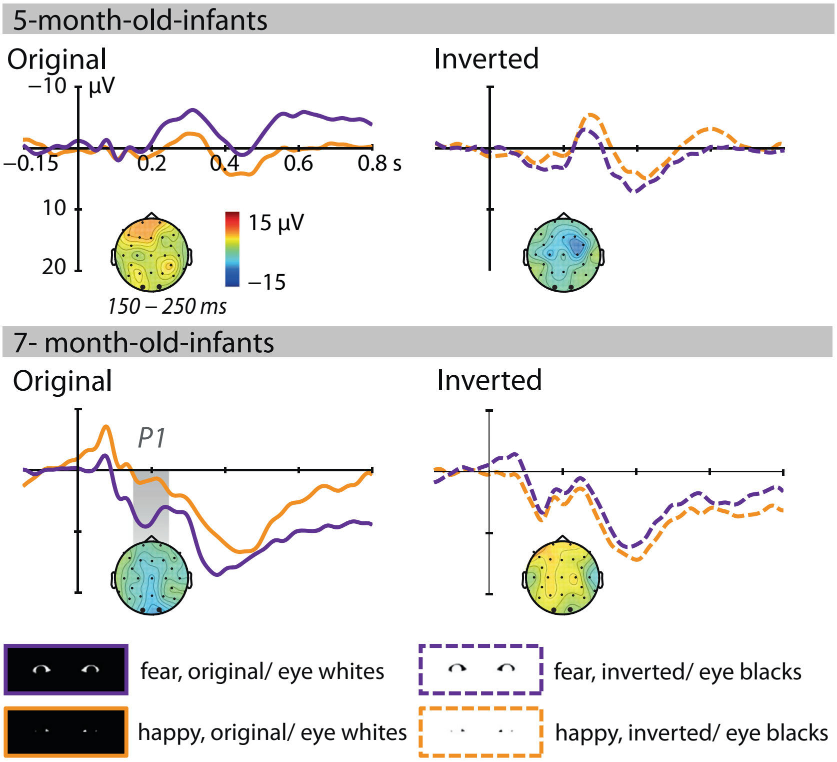

Fig. 1. ERP responses at occipital electrodes. The top row shows 5-month-old infants' ERP responses to fearful (purple) and happy (orange) sclerae, left in the original condition and right in the control condition. No significant differences were observed. In the bottom row, 7-month-old infants' ERP responses are shown. Between 150 and 250 ms (gray field), 7-month-olds showed a P1 that was significantly greater in response to original fearful sclerae compared with original happy sclerae. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

CRT monitor (resolution = 1024 × 786, refresh rate = 60 Hz) positioned approximately 90 cm in front of the infant. The infant's looking behavior during the experiment was recorded using a small camera mounted on top of the monitor. If the infant looked away from the screen, short video clips containing colorful moving abstract shapes accompanied by ring tones were presented to redirect the infant's attention to the screen. The experiment continued until the infant became too fussy or the maximum number of trials was presented.

EEG analysis

Data were re-referenced offline to the mean of TP9 and TP10 and were bandpass filtered between 0.2 and 20 Hz. Trials were segmented into 1-s epochs ranging from 200 ms before stimulus onset to 800 ms after stimulus onset. In one participant, one electrode was noisy and, therefore, was interpolated using spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989). To detect trials contaminated by artifacts, the standard deviation was computed in 200-ms sliding windows within the epochs. If the standard deviation exceeded 80 mV at any electrode, the trial was rejected from further analysis. In addition, the data were inspected visually for any remaining artifacts. All trials in which the infant did not attend to the screen were excluded.

Data were averaged for each condition and age group and were baseline corrected using the data segment 150 ms before stimulus onset. We analyzed ERPs in two regions of interest (ROIs): an occipital ROI consisting of O1 and O2 and a frontal ROI encompassing F7, F3, FZ, F4, and F8. We chose these

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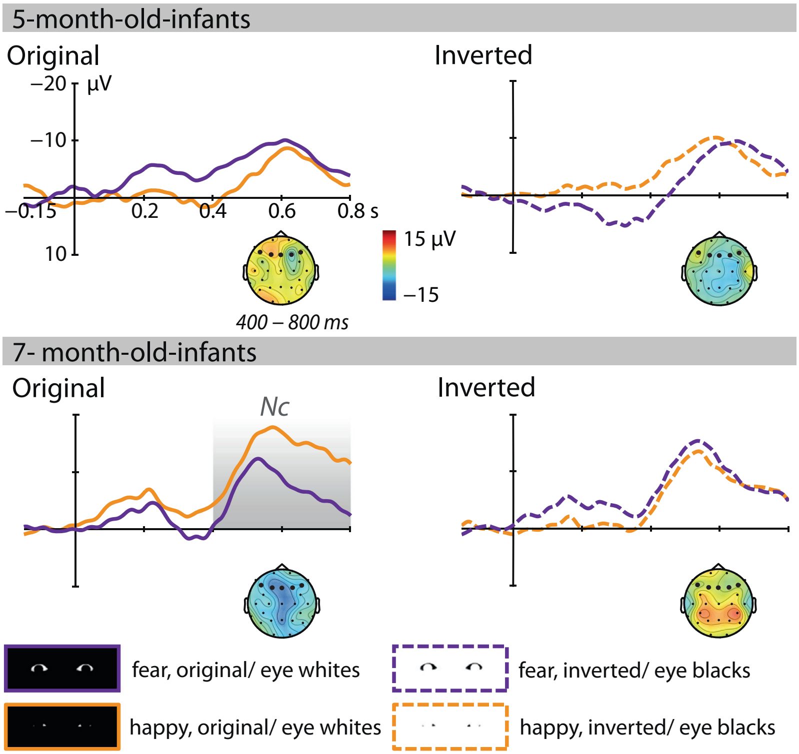

Fig. 2. ERP responses at frontal electrodes. The top row shows 5-month-old infants' ERP responses to fearful (purple) and happy (orange) sclerae, left in the original condition and right in the control condition. No significant differences were observed. In the bottom row, 7-month-old infants' ERP responses are shown. Between 400 and 800 ms (gray field), 7-month-olds showed a negative component (Nc) that was significantly greater in response to original happy sclerae compared with original fearful sclerae. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

electrodes based on visual inspection as well as prior studies (P1: Batty & Taylor, 2006; Nomi et al., 2013; Nc: Hoehl & Striano, 2010). In the occipital ROI, data were analyzed in a time window of 150 to 250 ms (P1). Because prior studies directly comparing conscious and unconscious emotion processing showed significant effects only on the N290/P400 complex for conscious emotional stimuli, we did not focus on the analysis of these components in the current study (which used only unconscious stimuli). In the frontal ROI, a time window of 400 to 800 ms (Nc) was analyzed (see Jessen & Grossmann, 2014). The mean amplitude across the respective electrodes for each time window was entered into a repeated measures analysis of variance (ANOVA) with the within-participant factors emotion (fearful or non-fearful) and polarity (original or inverted) and the between-participant factor age (5 months or 7 months). Student's *t*-tests were computed to further analyze interaction effects. Effect sizes are reported as partial eta-square (η^2) for ANOVAs and *r* for *t*-tests.

Results

Early occipital brain responses – P1

We observed a significant interaction among emotion, polarity, and age in the time window of 150 to 250 ms at occipital electrodes, $F(1,45) = 6.24$, $p = .016$, $\eta^2 = .12$ (see Fig. 1 and online supplementary material). Although we did not find any effects for 5-month-olds, for 7-month-olds we observed an interaction between emotion and polarity, $F(1,23) = 5.88$, $p = .024$, $\eta^2 = .20$. Specifically, only for original stimuli, fearful eyes elicited a more positive amplitude than non-fearful eyes, $t(23) = -3.00$, $p = .006$, $r = .53$ (fearful: 7.68 ± 2.57 μV; non-fearful: 1.93 ± 2.59 μV).

Later frontal brain responses – Nc

We observed a significant interaction among emotion, polarity, and age between 400 and 800 ms at frontal electrodes, $F(1,45) = 4.12$, $p = .048$, $\eta^2 = .08$ (see Fig. 2). In 7-month-olds, our analysis revealed an interaction between emotion and polarity, $F(1,23) = 4.96$, $p = .036$, $\eta^2 = .18$. Specifically, original non-fearful eyes elicited a more negative amplitude compared with original fearful eyes, $t(23) = -3.00$, $p = .006$, $r = .53$ (fearful: −6.89 ± 2.05 μV; non-fearful: −13.35 ± 1.44 μV). No differences were observed in 5-month-olds.

Discussion

In this study, we tested whether unconscious fear processing from eyes is present before 7 months of age or only emerges at around 7 months. Our ERP results show that only 7-month-old infants, but not 5-month-old infants, discriminated between fearful and non-fearful eyes. Specifically, 7-month-olds' processing of fearful eyes was reflected in early visual processes over occipital cortex and later attentional processes over frontal cortex. This suggests that the brain processes involved in the unconscious processing of fearful eyes develop between 5 and 7 months of age. This finding is consistent with previous work on the conscious perception of fearful facial expressions (Peltola, Leppänen, Mäki, et al., 2009) and also agrees with the general notion that infant responding to emotional information undergoes changes toward the second half of the first year of life (Vaish et al., 2008).

In combination with prior work, our results further indicate that responding to both unconscious and conscious fear signals relies on shared brain mechanisms that undergo development between 5 and 7 months of age (see Jessen & Grossmann, 2015, for a discussion of how the neural correlates of conscious and unconscious emotional face perception differ). Based on work in adults, it is thought that regardless of whether processed consciously or unconsciously, the discrimination of threat-relevant stimuli, including fearful facial signals, relies on subcortical brain structures such as the amygdala (Adolphs, 2002; Vuilleumier & Pourtois, 2007; Whalen et al., 2004). Therefore, it is possible that the developmental pattern observed in the current study is related to the development of amygdala function (see Leppänen & Nelson, 2009). However, our ERP data do not provide direct evidence for this claim because the ERP components assessed do not directly reflect amygdala activation. Considering this, one major limitation of our study is that we cannot rule out that subcortical brain regions may show sensitive responses to fearful eyes even in 5-month-olds. Nevertheless, previous ERP studies using source localization provide some evidence about the origin of the P1 and Nc. In an emotional face processing task in adults, the P1 has been localized to the extrastriate cortex (Pourtois, Grandjean, Sander, & Vuilleumier, 2004). The Nc, in contrast, has been localized in infants using a familiarization procedure with abstract patterns in which an increased Nc was observed in response to novel stimuli (Reynolds & Richards, 2005). These data suggest the anterior cingulate and prefrontal cortex as the origin of the Nc.

Both extrastriate cortex and anterior cingulate cortex are assumed to receive direct input from the amygdala (Amaral, Behniea, & Kelly, 2003; Kim et al., 2011), and emotional information has been shown to systematically modulate activity in these brain regions (Etkin, Egner, & Kalisch, 2011; Pourtois et al., 2004). Thus, it is plausible that the ERP effects observed here represent further cortical processing steps as a result of initial subcortical (amygdala) involvement. With respect to the developmental pattern seen, this might suggest that what develops is the functional interaction between amygdala and connected cortical brain regions (see Leppänen & Nelson, 2009).

Another point for discussion is that, in contrast to previous studies on conscious emotion perception (Leppanen et al., 2007; Peltola, Leppänen, Mäki, et al., 2009), we observed an increased Nc in response to happy eyes compared with fearful eyes in 7-month-old infants. Previous studies on conscious emotion processing from faces, however, typically reported an enhanced Nc amplitude

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(Peltola, Leppänen, Mäki, et al., 2009) or P400 amplitude (Leppänen et al., 2007) for fearful faces compared with neutral or happy faces. This suggests that 7-month-olds in our study allocated greater attention, as indexed by an enhanced Nc, to happy eyes. Although there are a number of conceptual factors related to the infants' predisposition or environment that have been shown to affect the exact modulation of the Nc in response to fearful faces (Grossmann et al., 2011; Krol, Rajhans, Missana, & Grossmann, 2015), the inconsistencies between current and prior studies are most likely related to methodological differences. Our study differed methodologically from previous studies in a number of aspects: (a) eyes versus faces as stimuli and (b) subliminal versus supraliminal presentation. Specifically, fearful eyes alone might not be sufficient to elicit enhanced attention to fear in 7-month-olds (see below). Furthermore, subliminal emotion processing may rely on different pathways compared with supraliminal emotion processing, and although both seem to affect the Nc amplitude, preceding processes may differ between subliminal and supraliminal processing. Regardless of this issue, our ERP data provide evidence that 7-month-olds do discriminate between fearful and non-fearful eyes irrespective of conscious awareness, and this effect is seen only in response to eye whites and not in response to polarity-inverted control stimuli.

Interestingly, the role of eyes in the processing of fear during infancy was investigated previously by Peltola, Leppänen, Vogel-Farley, Hietanen, and Nelson (2009), who reported that fearful eyes alone are not sufficient to elicit the fear bias commonly observed in 7-month-old infants. However, their study differed from the current study in two main aspects. First, Peltola and colleagues investigated behavioral responses (attentional disengagement in an eye-tracking paradigm), whereas in the current study we compared ERP responses. Therefore, although information from eyes might not be sufficient to elicit behavioral difference, it might still lead to differential cortical processing. Second, Peltola and colleagues did not present eyes in isolation but rather put fearful eyes onto neutral faces. Thereby, they created a mismatch between two visual sources of emotional information, namely the eyes versus the rest of the face. Thus, it is possible that resolving such a mismatch may elicit different processes compared with the processing of eye information alone. Future studies are necessary to assess the possible reasons for this discrepancy.

Finally, we cannot completely rule out the possibility that the two age groups differ in some unknown additional factor besides age. Both groups are matched in terms of size, male/female ratio, and trial number included in the final analyses, and infants are from the same population (see "Participants" section). Future studies, therefore, will need to confirm that our results also hold true in other samples.

To conclude, the current study demonstrates that the cortical brain processes associated with infants' unconscious processing of fearful eyes emerge between 5 and 7 months of age. This development appears to occur in concert with other critical developmental milestones related to infants' responding to and experience of fear. Therefore, the current ERP findings provide further evidence for the notion that infancy is an important and formative period in socioemotional development.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jecp.2015.09.009.

References

Adolphs, R. (2002). Recognizing emotion from facial expressions: Psychological and neurological mechanisms. *Behavioral and Cognitive Neuroscience Reviews, 1*, 21–62.

Amaral, D. G., Behniea, H., & Kelly, J. L. (2003). Topographic organization of projections from the amygdala to the visual cortex in the macaque monkey. *Neuroscience, 118*, 1099–1120.

Batty, M., & Taylor, M. J. (2006). The development of emotional face processing during childhood. *Developmental Science, 9*, 207–220.

Braungart-Rieker, J. M., Hill-Soderlund, A. L., & Karrass, J. (2010). Fear and anger reactivity trajectories from 4 to 16 months: The roles of temperament, regulation, and maternal sensitivity. *Developmental Psychology, 46*, 791–804.

Campos, J. J., Kermoian, R., & Zumbahlen, M. R. (1992). Socioemotional transformations in the family system following infant crawling onset. In N. Eisenberg & R. A. Fabes (Eds.), *Emotion and its regulation in early development* (pp. 25–40). San Francisco: Jossey-Bass.

Curtis, W. J., & Cicchetti, D. (2011). Affective facial expression processing in young children who have experienced maltreatment during the first year of life: An event-related potential study. *Development and Psychopathology, 23*, 373–395.

de Haan, M., Johnson, M. H., & Halit, H. (2003). Development of face-sensitive event-related potentials during infancy: A review. *International Journal of Psychophysiology, 51*, 45–58.

Ekman, P., & Friesen, V. (1976). *Pictures of facial affect [database]*. Palo Alto, CA: Consulting Psychologists Press.

Etkin, A., Egner, T., & Kalisch, R. (2011). Emotional processing in anterior cingulate and medial prefrontal cortex. *Trends in Cognitive Science, 15*, 85–93.

Farroni, T., Csibra, G., Simion, F., & Johnson, M. H. (2002). Eye contact detection in humans from birth. *Proceedings of the National academy of Sciences of the United States of America, 99*, 9602–9605.

Farroni, T., Johnson, M. H., Menon, E., Zulian, L., Faraguna, D., & Csibra, G. (2005). Newborns' preference for face-relevant stimuli: Effects of contrast polarity. *Proceedings of the National academy of Sciences of the United States of America, 102*, 17245–17250.

Flom, R., & Bahrick, L. E. (2007). The development of infant discrimination of affect in multimodal and unimodal stimulation: The role of intersensory redundancy. *Developmental Psychology, 43*, 238–252.

Frith, C. (2009). Role of facial expressions in social interactions. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 364*, 3453–3458.

Gelskov, S. V., & Kouider, S. (2010). Psychophysical thresholds of face visibility during infancy. *Cognition, 114*, 285–292.

Grossmann, T., Johnson, M. H., Vaish, A., Hughes, D. A., Quinque, D., Stoneking, M., et al (2011). Genetic and neural dissociation of individual responses to emotional expressions in human infants. *Developmental Cognitive Neuroscience, 1*, 57–66.

Hoehl, S., & Striano, T. (2010). Infants' neural processing of positive emotion and eye gaze. *Social Neuroscience, 5*, 30–39.

Itier, R. J., Alain, C., Sedore, K., & McIntosh, A. R. (2007). Early face processing specificity: It's in the eyes! *Journal of Cognitive Neuroscience, 19*, 1815–1826.

Itier, R. J., & Batty, M. (2009). Neural bases of eye and gaze processing: The core of social cognition. *Neuroscience and Biobehavioral Reviews, 33*, 843–863.

Itier, R. J., Van Roon, P., & Alain, C. (2011). Species sensitivity of early face and eye processing. *NeuroImage, 54*, 705–713.

Jessen, S., & Grossmann, T. (2014). Unconscious discrimination of social cues from eye whites in infants. *Proceedings of the National academy of Sciences of the United States of America, 111*, 16208–16213.

Jessen, S., & Grossmann, T. (2015). Neural signatures of conscious and unconscious emotional face processing in human infants. *Cortex, 64*, 260–270.

Kim, M. J., Loucks, R. A., Palmer, A. L., Brown, A. C., Solomon, K. M., Marchante, A. N., et al (2011). The structural and functional connectivity of the amygdala: From normal emotion to pathological anxiety. *Behavioural Brain Research, 223*, 403–410.

Kiss, M., & Eimer, M. (2008). ERPs reveal subliminal processing of fearful faces. *Psychophysiology, 45*, 318–326.

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*, 134–146.

Krol, K. M., Rajhans, P., Missana, M., & Grossmann, T. (2015). Duration of exclusive breastfeeding is associated with differences in infants' brain responses to emotional body expressions. *Frontiers in Behavioral Neuroscience, 8*. http://dx.doi.org/10.3389/fnbeh.2014.00459.

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*, 232–245.

Leppänen, J. M., & Nelson, C. A. (2009). Tuning the developing brain to social signals of emotions. *Nature Reviews Neuroscience, 10*, 37–47.

Leppänen, J. M., & Nelson, C. A. (2012). Early development of fear processing. *Current Directions in Psychological Science, 21*, 200–204.

Liddell, B. J., Williams, L. M., Rathjen, J., Shevrin, H., & Gordon, E. (2004). A temporal dissociation of subliminal versus supraliminal fear perception: An event-related potential study. *Journal of Cognitive Neuroscience, 16*, 479–486.

Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J., et al (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature, 383*, 812–815.

Nomi, J. S., Frances, C., Nguyen, M. T., Bastidas, S., & Troup, L. J. (2013). Interaction of threat expressions and eye gaze: An event-related potential study. *NeuroReport, 24*, 813–817.

Pegna, A., Landis, T., & Khateb, A. (2008). Electrophysiological evidence for early non-conscious processing of fearful facial expressions. *International Journal of Psychophysiology, 70*, 127–136.

Peltola, M. J., Hietanen, J. K., Forssman, L., & Leppänen, J. M. (2013). The emergence and stability of the attentional bias to fearful faces in infancy. *Infancy, 18*, 905–926.

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*, 134–142.

Peltola, M. J., Leppänen, J. M., Vogel-Farley, V. K., Hietanen, J. K., & Nelson, C. A. (2009). Fearful faces but not fearful eyes alone delay attention disengagement in 7-month-old infants. *Emotion, 9*, 560–565.

Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology, 72*, 184–187.

Pourtois, G., Grandjean, D., Sander, D., & Vuilleumier, P. (2004). Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex, 14*, 619–633.

Reynolds, G. D., & Richards, J. E. (2005). Familiarization, attention, and recognition memory in infancy: An event-related potential and cortical source localization study. *Developmental Psychology, 41*, 598–615.

Rigato, S., Menon, E., Johnson, M. H., & Farroni, T. (2011). The interaction between gaze direction and facial expressions in newborns. *European Journal of Developmental Psychology, 8*, 624–636.

Rossion, B. (2014). Understanding face perception by means of human electrophysiology. *Trends in Cognitive Science, 18*, 310–318.

Shariff, A. F., & Tracy, J. L. (2011). What are emotion expressions for? *Current Directions in Psychological Science, 20*, 395–399.

Smith, M. L. (2012). Rapid processing of emotional expressions without conscious awareness. *Cerebral Cortex, 22*, 1748–1760.

Vaish, A., Grossmann, T., & Woodward, A. (2008). Not all emotions are created equal: The negativity bias in social–emotional development. *Psychological Bulletin, 134*, 383–403.

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Vuilleumier, P., & Pourtois, G. (2007). Distributed and interactive brain mechanisms during emotion face perception: Evidence from functional neuroimaging. *Neuropsychologia, 45*, 174–194.

Webb, S. J., Long, J. D., & Nelson, C. A. (2005). A longitudinal investigation of visual event-related potentials in the first year of life. *Developmental Science, 8*, 605–616.

Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., ... Johnstone, T. (2004). Human amygdala responsivity to masked fearful eye whites. *Science, 306*, 2061.

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