Developmental changes in infants' processing of happy and angry facial expressions: A neurobehavioral study

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Abstract

Event-related brain potentials were measured in 7- and 12-month-old infants to examine the development of processing happy and angry facial expressions. In 7-month-olds a larger negativity to happy faces was observed at frontal, central, temporal and parietal sites (Experiment 1), whereas 12-month-olds showed a larger negativity to angry faces at occipital sites (Experiment 2). These data suggest that processing of these facial expressions undergoes development between 7 and 12 months: while 7-month-olds exhibit heightened sensitivity to happy faces, 12-month-olds resemble adults in their heightened sensitivity to angry faces. In Experiment 3 infants' visual preference was assessed behaviorally, revealing that the differences in ERPs observed at 7 and 12 months do not simply reflect differences in visual preference.
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1. Introduction

Facial expressions are an important way to communicate emotions in social interactions (Izard, 1991). Recognizing facial expressions permits us to detect another person's emotional state and provides cues on how to respond in these social situations. Facial expressions are central to non-verbal social exchange as markers of (a) internal states and (b) intentions (Schupp et al., 2004). For example, across cultures the internal state of anger is externally expressed as frowning brows, staring eyes, and a shut mouth with tense lips (Ekman & Friesen, 1975), which in turn signals readiness for physical or symbolic attack on an observer. Because angry faces signal potential negative consequences to the observer, they are regarded as threatening. This dual role of facial expressions also applies to happy expressions which are considered to be friendly faces. In the current

study the developmental course of processing happy (friendly) and angry (threatening) facial expressions was examined.

Previous research with adults has revealed that negative events generally evoke stronger and more rapid physiological, cognitive, emotional, and social responses than do neutral or positive events (Taylor, 1991). Consistent with these findings, adults detect angry schematic faces more readily than happy schematic faces (Öhmann, Lundqvist, & Esteves, 2001). Also, fear conditioning to angry faces is more resistant to extinction than fear conditioning to happy faces (Öhmann & Mineka, 2001). From an evolutionary perspective, it has been argued that because it is difficult to reverse the consequences of an injurious or fatal assault, the process of natural selection may have resulted in a propensity to react more strongly to negative than to positive stimuli (Cacioppo & Berntson, 1999). This heightened sensitivity to negative information, termed 'negativity bias,' is a reliable psychological phenomenon in adults (Cacioppo, Gardner, & Berntson, 1999).

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In accordance with the notion of a negativity bias, a recent event-related brain potential (ERP) study (Schupp et al., 2004) provides evidence that adults show an enhanced neural processing of angry facial expressions. In this study adults were shown angry, happy, and neutral faces. Angry faces compared to happy and neutral faces were found to elicit an Early Posterior Negativity (EPN) with a maximum over occipital sites peaking around 300 ms after stimulus onset. The EPN has been shown to appear uniformly to evolutionarily significant stimuli as a negative shift in the waveform, indicating emotional enhancement of sensory processing in the visual cortex (Junghöfer, Bradley, Elbert, & Lang, 2001; Schupp, Junghöfer, Weike, & Hamm, 2003). Similar ERP effects are observed when participants have to direct their attention selectively to particular features (e.g., color or orientation) of a visual stimulus (Michie et al., 1999). This has been taken as support for the hypothesis that sensory encoding of evolutionarily significant affective stimuli is enhanced by 'natural' selective attention (Lang, Bradley, & Cuthbert, 1997).

It has been suggested that the amygdala might be one particularly relevant structure of a distributed network that is devoted to determining the significance of external stimuli and regulating the enhancement processes at a sensory cortical level (Davis & Whalen, 2001; Pessoa, Kastner, & Ungerleider, 2002). Although amygdala activation has been most commonly reported in response to facial expressions of fear (Davis & Whalen, 2001) there is evidence suggesting that it is also responsive to facial expressions of anger (Adolphs, Tranel, Damasio, & Damasio, 1995; Morris, Öhmann, & Dolan, 1998; Whalen et al., 2001). The enhancement of sensory processing in the visual cortex by the amygdala might rely on direct projections, connections to anterior attention networks, or ascending neuromodulatory systems (Davis & Whalen, 2001). However, more direct evidence is needed to support any of these hypothesized mechanisms.

From a developmental perspective, it is well established that infants reliably discriminate a range of static facial expressions of emotion (e.g., Caron, Caron, & Myers, 1985; LaBabera, Izard, Vietze, & Parisi, 1976; Serrano, Iglesias, & Loeches, 1995; Striano, Brennan, & Vanman, 2002; Young-Browne, Rosenfeld, & Horowitz, 1997). For example, behavioral studies have shown that by 3 months of age, infants visually discriminate happy from angry facial expressions (Barrera & Maurer, 1981). Then, at 7 months of age, infants detect similarity of happy faces over changing identities and discriminate this category of happy expressions from angry expressions (Kestenbaum & Nelson, 1990). It is not until 10 months of age (Ludemann, 1991) that infants are able to categorize expressions more generally according to affective tone (positive versus negative). By 12 months of age, human infants use others' positive and negative facial expressions to disambiguate uncertain situations and to regulate their behavior accordingly (Baldwin & Moses, 1996; Sorce, Emde, Campos, & Klinnert, 1985).

While behavioral measures have revealed much about which emotions infants can discriminate, the processes underlying these abilities are much less understood. Researchers have begun to measure ERPs to provide information about the ongoing neurocognitive processes that occur while an infant is responding to an event rather than measuring only the final behavioral response.

In an ERP study examining infants' processing of pictures of facial expressions (Nelson & de Haan, 1996), 7-month-olds watched happy versus fearful faces in a first experiment. Results revealed that fearful faces elicited an enhanced negative component (Nc) peaking around 500 ms. The Nc has its maximum at frontal and central sites and has been thought of as an obligatory attentional response sensitive to stimulus familiarity (Courchesne, Ganz, & Norcia, 1981; Snyder, Webb, & Nelson, 2002). Dipole modeling has revealed that the cortical sources of the Nc can be localized in the anterior cingulate and other prefrontal regions (Reynolds & Richards, 2005). Therefore, it has been argued that 7-month-old infants in Nelson and de Haan's study allocated more attentional processing resources to the unfamiliar fearful than to the familiar happy expression as indicated by an enhanced Nc. In a second experiment Nelson and de Haan showed another group of 7-month-olds fearful versus angry faces and there was no difference in their ERP response. One possibility is that infants in Nelson and de Haan (1996) second experiment, although able to discriminate between the angry and fearful expressions, did not display different brain responses to the two expressions because they perceived the signal value of both expressions as "negative." Another plausible explanation is that infants perceived both expressions as equally unfamiliar and therefore the Nc, which is sensitive to the familiarity of a stimulus, did not differ between conditions.

In the current research, we attempted to extend Nelson and de Haan (1996) findings by comparing infants' responses to happy and angry faces. While behavioral research with infants points to an early ability to discriminate happy and angry facial expressions, only little is known about how the neural processing of these facial expressions as revealed by ERP might develop during infancy.

To examine the development of processing of happy and angry facial expressions, 7-month-old infants (Experiment 1) and 12-month-old infants (Experiment 2) were tested using ERP measures. The relation between the ERP response and infants' looking behavior is yet to be determined. Therefore, in a behavioral experiment (Experiment 3), 7- and 12-month-old infants' discrimination of happy and angry facial expressions was further examined using a preferential looking paradigm.

2. Experiment 1

In a first ERP study, we presented happy and angry facial expressions to 7-month-old infants. We wanted to examine whether infants at this age already show an enhanced sensory

processing of angry faces, indexed by an enhanced EPN (Schupp et al., 2003, 2004) to the angry face. Furthermore, in previous work with 7-month-olds, Nelson and de Haan (1996) assessed ERPs to fearful, angry, and happy facial expressions. They found that a fearful face elicited a larger Nc than a happy face whereas the Nc did not differ between angry and fearful expressions. Based on these findings, we hypothesized that the angry facial expression would also elicit an enhanced Nc as compared to the happy facial expression.

2.1. Method

2.1.1. Participants

The final sample consisted of 20 7-month-old infants (10 females, $M = 7;03$, $SD = 2$, range $= 6;26$ to $7;07$). An additional four 7-month-olds were tested but not included in the final sample due to fussiness. All infants were born full-term (37–42 weeks gestation) and with normal birthweight (>2500 g).

2.1.2. Stimuli

The stimuli were two color portrait photographs of the same woman posing either a happy or an angry facial expression (Fig. 1). The photographs were chosen on the basis of a survey in which 20 adults (10 females) were asked to rate a set of pictures of seven women posing various facial expressions (happy, angry, sad, surprised, fearful, and disgusted). Raters had to identify both the specific emotion displayed in the pictures as well as how arousing each emotion was. The pictures that were finally used as stimuli were correctly identified by 95% of the raters as either happy or angry. Both pictures were rated as equally arousing (happy: $M = 1.6$, $SD = 0.6$; angry: $M = 1.5$, $SD = 0.6$) on a scale from 1 (lightly arousing) to 4 (very strongly arousing).

In a previous ERP experiment (Striano & Grossmann, 2005), these same happy and angry facial expressions were presented to a group of 20 adults, who passively viewed the stimuli. Striano and Grossmann (2005) results replicated prior adult ERP studies (Schupp et al., 2004) that have shown an enhanced negativity to angry faces versus happy

faces, indicating an increased sensitivity to angry faces. The successful replication of prior findings using these stimuli ensured their experimental reliability, thus justifying their use in investigating facial expression processing in infants, especially since the experimental procedure used here with infants matched that used by Striano and Grossmann (2005) with adults.

2.1.3. Procedure

The infants were seated on their mother's lap in a dimly lit, sound-attenuated, and electrically shielded room. Happy and angry facial stimuli were presented randomly on the screen for 1000 ms with the constraint that each emotion was presented no more than twice in a row. Prior to each presentation of a facial expression, a pattern of randomly distributed white squares appeared at the centre of the screen for 500 ms to attract infants' attention. The inter-stimulus interval varied randomly between 800 and 1200 ms. All stimuli were projected in the centre of the screen on a black background, using a 70 Hz, 17 in. computer screen at a distance of 60 cm from the eyes. The image sizes were 27×22 cm and the vertical and horizontal visual angles were 12.12° and 10.07°, respectively. The stimuli were presented in random order. Mothers were instructed to look down at the infant rather than at the computer screen. The session continued until the infant had seen the maximum number of trials (200) or became fussy. A camera mounted above the screen recorded a close-up view of the infant's face and also received a signal sent by the stimulation computer when a face was presented in order to monitor infants' visual attention to the stimuli.

2.1.4. EEG measurement and data analysis

The EEG was recorded with Ag–AgCl electrodes from 19 scalp locations of the 10–20 system (Fig. 2), referenced

Fig. 1. Stimuli pictures of a woman posing either a happy (left) or an angry facial expression (right).
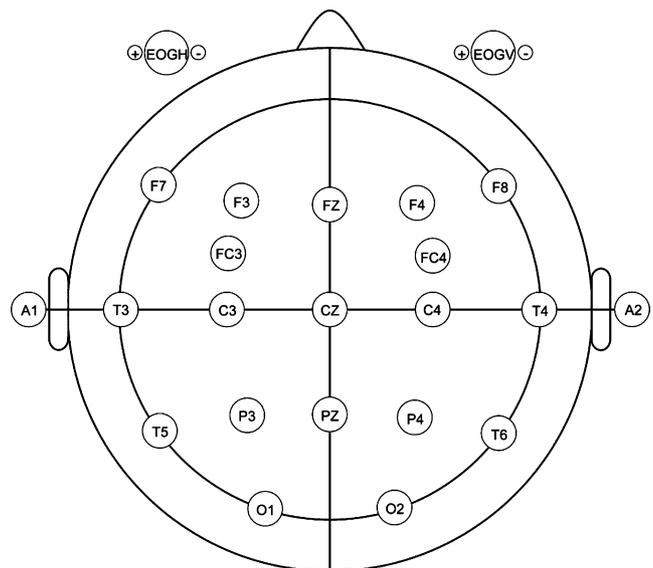

Fig. 2. Electrode positions used in the ERP experiments.

to CZ. Horizontal and Vertical EOGs were recorded bipolarly. Sampling rate was 250 Hz. EEG data was re-referenced to the algebraic mean of the left and the right mastoid electrodes, and band-pass filtered with 0.3 to 20 Hz (1501 points). Data were baseline corrected by subtracting the average voltage in the 200 ms baseline period from each post-stimulus data point.

For elimination of artifacts caused by eye and body movements, EEG data for the whole trial were rejected off-line whenever the standard deviation within a 200-ms gliding window exceeded 80 μV for the vertical or horizontal electro-oculogram and 50 μV at any electrode. In addition, the infants' video recordings were examined, and all trials in which infants did not look at the screen were rejected from the EEG. The mean number of successful trials was 17.1 ($SD = 2.3$) for happy and 15.6 ($SD = 2.7$) for angry faces. The mean number of trials presented to the infant was 67 ($SD = 8.4$). For statistical analysis of mean amplitude effects, a time window of 400 to 600 ms was chosen around the amplitude peak of the difference wave (happy minus angry). ERPs were evaluated by computing the following regions of interest (ROIs): left frontal (F3), right frontal (F4), left central (C3), right central (C4), left temporal (T3), right temporal (T4), left parietal (P3), right parietal (P4), left occipital (O1), and right occipital (O2). Variances were analyzed by repeated measures ANOVAs. Analyzed factors were (1) facial expression (happy × angry), (2) lateralization (left × right), (3) distribution (frontal × central × temporal × parietal × occipital) and (4) gender (female × male). Peak latencies were determined and statistically evaluated for ERPs in response to happy and angry faces for the computed ROIs. Pair-wise *t*-tests were corrected for multiple comparisons using a modified Bonferroni procedure (Keppel, 1991).

2.2. Results

Seven-month-olds' ERPs to happy faces were more negative in their mean amplitude than ERPs elicited by angry
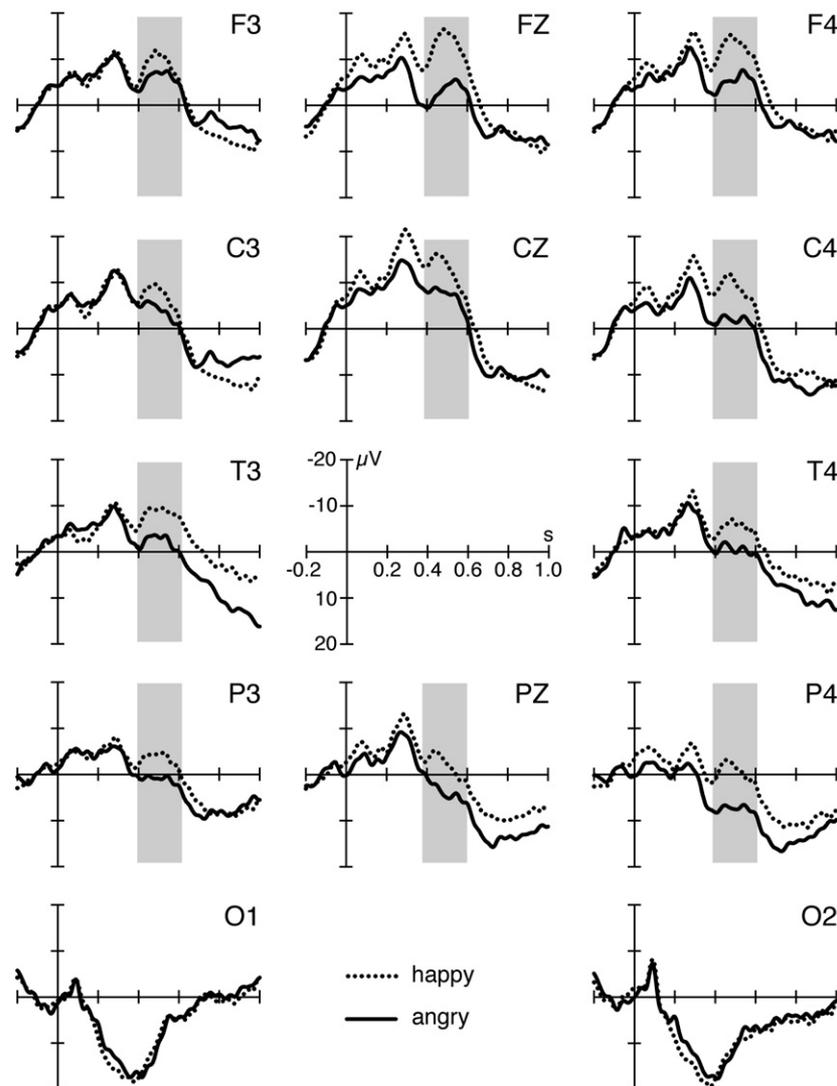

Fig. 3. ERPs in response to happy and angry facial expressions in 7-month-old infants. The Nc for which significant differences were observed between emotions at frontal, central, temporal, and parietal electrode sites is marked in grey.

faces as early as 400 ms after stimulus onset with a maximum at frontal and central electrode sites (see Fig. 3). This difference between facial expressions reached its peak amplitude around 480 ms, and was statistically significant in the 400–600 ms latency interval, $F(1, 19) = 6.09$, $p < .03$. Furthermore, the ANOVA revealed an interaction between facial expression and distribution, $F(1, 19) = 5.1$, $p < .04$. Subsequent *t*-tests for the same latency interval (400–600 ms) revealed that the mean amplitudes between happy and angry differed significantly (with happy more negative than angry) at frontal ($t = 2.57$, $p < .02$), central ($t = 2.54$, $p < .02$), temporal ($t = 2.26$, $p < .04$), parietal sites ($t = 2.24$, $p < .04$), but not at occipital sites ($t = 0.34$, $p > .74$) (see Fig. 4).

We included lateralization as a factor in the ANOVA because both face and emotion processing have been shown to be to a certain extent lateralized to the right hemisphere. Although visual inspection of 7-month-olds' Nc seems to suggest a lateralization of the effect to the right, there was no significant lateralization of the mean amplitude effect revealed in our statistical analysis. Analysis did not reveal any effect of facial expression on peak latencies.

Visual inspection of the waveforms suggests that time-locked activity occurred before stimulus onset, which requires explanation. Prior to each presentation of a facial expression, a pattern of randomly distributed white squares appeared at the centre of the screen for 500 ms to attract infants' attention. The deflections seen during baseline before the onset of the face were elicited by the attention getting stimulus. This explains the fact that baseline activity did not reflect an asymptote, thus contributing considerable noise. The size of the attention getting stimulus was relatively large (22×27 cm) especially in comparison to fixation crosses used in adult ERP studies. In addition, the contrast between a blank dark screen in a dimly lit room and the visual attention getting stimulus was very intense. This makes it very effective in drawing infants' attention to
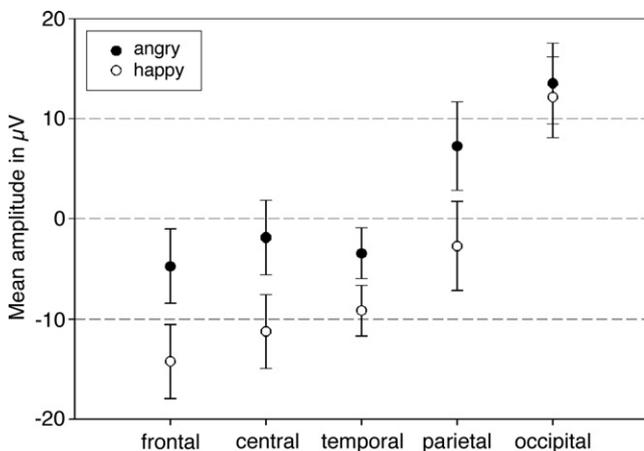

Fig. 4. Mean and standard error of amplitude scores in 7-month-old infants (400–600 ms) for the following regions of interest (ROIs): frontal (F3, F4), central (C3, C4), temporal (T3, T4), parietal (P3, P4), and occipital (O1, O2) electrodes.

the screen but it causes difficulties for extracting clean ERPs. We realize that the visual attention getter we used is not ideally suited and that there might have been carry over effects to the subsequently elicited components. However, since the attention getting stimulus was the same across conditions and the baseline activity and the early components of the ERP did not differ between facial expressions, it cannot account for the observed differential effects of later components of happy and angry facial expressions.

2.3. Discussion

ERPs revealed a significant effect of emotional expression, but contrary to our prediction based on Nelson and de Haan's study (1996), the amplitude of the Nc in 7-month-old infants' ERPs was larger for happy than for angry facial expressions. Under the assumption that an enhanced Nc reflects greater allocation of attentional resources to the stimulus (Courchesne et al., 1981; Reynolds & Richards, 2005), the current data indicate that infants at 7 months of age show greater attentional response to the happy facial expression.

This finding may be due to the ubiquity and familiarity of happy faces in infants' social interactions at this age. Previous work has shown that a familiar (mother's) face elicited larger negative amplitude than an unfamiliar (stranger's) face in 6-month-olds' ERPs (de Haan & Nelson, 1997). Presumably, at 7 months of age, happy facial expressions are more familiar than angry facial expressions. Thus, it is possible that the happy expression evoked a larger negative component in 7-month-olds' ERPs because it is more familiar. However, this interpretation is not consistent with previous findings showing a larger Nc to fearful as compared to happy expressions at 7 months of age (Nelson & de Haan, 1996), since fearful expressions are likely to be less familiar than happy expressions. This discrepancy concerning the Nc is not surprising given that the exact pattern of amplitude modulation by familiarity appears to vary across studies (Carver et al., 2003; de Haan & Nelson, 1997; Webb, Long, & Nelson, 2005).

Interestingly, there seems to be a context sensitivity of the revealed effect at 7 months such that if fearful expressions are presented with angry expressions, ERPs to the two do not differ (see Experiment 2, Nelson & de Haan, 1996). But if fearful faces are presented with happy faces, then there is a greater negative response to the fearful expression (see Experiment 1, Nelson & de Haan, 1996), and if angry faces are presented with happy faces as in the current study, then there is a greater negativity to the happy expression. According to Nelson and de Haan (1996), there is no difference in the Nc evoked by fearful and angry faces either because the signal value of the expressions is not perceived as different (e.g., both perceived as "negative") or because both expressions are perceived as equally unfamiliar. The current study shows a larger Nc to the happy face when compared to an angry face. One possible explanation for these discrepant results might be that 7-month-olds

perceive angry and fearful faces, at least in the context of happy faces, differently, and not simply as conveying negative valence. We therefore suggest that ERPs to facial expressions cannot be interpreted as context-independent events, but must be understood within the specific contexts in which the expressions are presented. Consistent with this notion, context effects have also been observed when comparing infants' behavioral responses to facial expressions (e.g., Striano & Liszkowski, 2005).

3. Experiment 2

Previous adult ERP work indicated enhanced sensory processing of angry facial expressions as indexed in an EPN (Schupp et al., 2004). In contrast, 7-month-olds in Experiment 1 did not show enhanced sensory processing of the angry, but an increased allocation of attention to the happy facial expression. Thus, the question arises: when during development does the human brain begin to exhibit an adult-like response? It is known from behavioral studies that at the end of the first year, infants' social cognitive abilities undergo significant changes (Elman et al., 1996; Ruff & Rothbart, 1996; Tomasello, Carpenter, Call, Behne, & Moll, 2005; Walden & Ogan, 1988). Furthermore, with the onset of self-produced locomotion around 10 months (Illingworth, 1983), caregivers' expression of anger toward their infant increases (Campos et al., 2000). These developmental changes at the end of the first year may affect infants' processing of socially relevant stimuli such as happy and angry facial expressions. Therefore, we hypothesized that at this age infants would show an enhanced sensory processing of angry facial expressions as reflected in an enhanced posterior (occipital) negativity to the angry expression. In order to test this hypothesis a second ERP experiment was conducted in which 12-month-olds' processing of happy and angry expressions was examined.

3.1. Method

3.1.1. Participants

The final sample consisted of 20 12-month-old infants (10 females, $M = 12;02$, $SD = 4$, range $= 11;23$ to $12;07$). An additional 20 12-month-olds were tested but not included in the final sample due to fussiness. All infants were born full-term (37–42 weeks gestation) and with normal birthweight (>2500 g). The stimuli, procedure, EEG measurement, and data analyses were exactly the same as in Experiment 2. The mean number of successful trials was 23.3 ($SD = 3.3$) for happy and 21.5 ($SD = 4.1$) for angry faces. The mean number of trials presented to the infant was 63 ($SD = 6.2$).

3.2. Results

As shown in Fig. 5, angry faces as compared to happy faces elicited a relative negative shift in 12-month-old infants' ERP at occipital sites. This effect reached its peak amplitude around 410 ms (as determined by the difference

wave obtained by subtracting happy from angry). An ANOVA revealed an interaction between facial expression and distribution, $F(1,19) = 4.51$, $p < .05$. Subsequently employed t-tests for the latency interval from 400 to 600 ms revealed that the angry face elicited a significantly larger negative amplitude than the happy face only at occipital sites ($t = 3.12$, $p < .03$), but not at frontal ($t = 0.21$, $p > .83$), central ($t = -0.67$, $p > .51$), temporal ($t = 0.02$, $p > .98$), and parietal ($t = -0.17$, $p > .86$) sites (see Fig. 6). Analysis did not reveal any effect of facial expression on peak latencies.

As in Experiment 1, visual inspection of the waveforms suggests that time-locked activity occurred before stimulus onset, which can be explained by the attention getting stimulus we used in both experiments.

3.3. Discussion

Consistent with our hypothesis, 12-month-old infants showed enhanced posterior negativity to the angry facial expression at occipital electrode sites, indicating an adult-like enhanced visual processing of this expression (Schupp et al., 2004). Similar to the effect shown in the adult ERP work (Schupp et al., 2003, 2004), the enhanced posterior negativity seen here occurred as a relative negative shift at occipital sites in the infant ERP waveform. The observed latency of the effect around 400 ms is about 100 ms later than observed in adults (Schupp et al., 2004). This is in accordance with the time difference seen when comparing adult with the corresponding infant ERP components (e.g., de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003). The corresponding timing and topography of the posterior negativity seen in adults in prior work and in 12-month-olds in the current study supports the interpretation of similar underlying visual enhancement mechanisms. The finding of an enhanced sensory processing of angry faces differs from what was observed in 7-month-olds (Experiment 1), and suggests that processing of happy and angry facial expressions undergoes development between 7 and 12 months of age.

Research has shown that 7-month-olds discriminate between facial expressions based on feature information rather than on affective meaning (Caron et al., 1985; Kestenbaum & Nelson, 1990; Ludemann, 1991). On the other hand, older infants (10 months) are able to identify common affect among facial expressions and discriminate them from novel expressions (Caron et al., 1985; Ludemann, 1991). Additionally, it was shown that infants can use others' angry and happy facial cues to disambiguate uncertain situations and regulate their behavior accordingly (e.g., Sorce et al., 1985). This developmentally important shift from 'feature-sensitivity' to 'affect-sensitivity' might also relate to the developmental difference between 7 and 12 months revealed in the current study, as the former processes may deal with aspects of familiarity, whereas the latter allow for the detection of affective signals.

More specifically, the finding of enhanced sensory processing of angry faces in 12-month-olds is consistent with a scenario suggested by Öhmann and Mineka (2001) in which
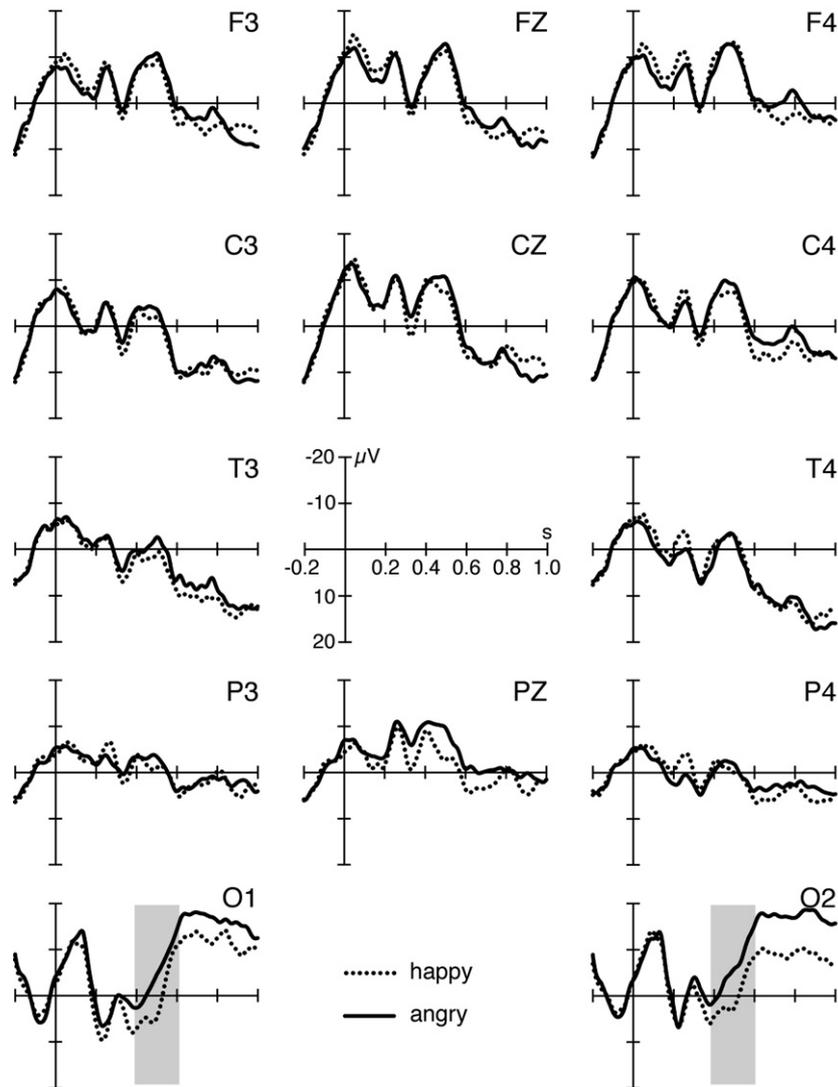
Fig. 5. ERPs in response to happy and angry facial expressions in 12-month-old infants. The posterior negativity for which significant differences between emotions were observed at occipital electrode sites is marked in grey.

threatening stimuli are already tagged for further processing during sensory encoding. In this scenario, based on pre-existing knowledge about the world, automatic routines (e.g., sensory tagging/enhancement) might be used to detect significant cues in the environment. The current data suggest that development between 7 and 12 months equips the infant with the ability to detect threat as a significant cue.

The developmental difference observed could also be, at least in part, due to a perceptual switch such that 7-month-olds focus less on different perceptual features in the face than do 12-month-olds. Accordingly, in one study, 4-, 6-, and 8-month-old infants detected an identity change of the eyes following habituation to a face, whereas only the oldest infants (8 months) were found to detect an identity change of the mouth (Zauner & Schwarzer, 2003). Furthermore, when 6-month-old infants were familiarized to a surprised face and then tested with a face in which either the eyes or the mouth changed to show fear, they detected the change only when it occurred for the eyes (Nelson & Horowitz, 1980; cited in de Haan & Nelson, 1998). It has also been argued that attending

to the mouth region is important for the identification of an angry facial expression (Boucher & Ekman, 1975). Under the assumption that the 7-month-olds in Experiment 1 of the current study, like 6-month-olds in prior studies (Nelson & Horowitz, 1980; Zauner & Schwarzer, 2003), focused on the eye region, whereas the older infants in Experiment 2 focused on both eyes and mouth, it is possible that this perceptual difference between the age groups contributed to the developmental difference observed in their ERPs in response to happy and angry faces.

4. Experiment 3

The ERP results of Experiment 1 and 2 suggest that 7-month-olds' processing of happy and angry facial expressions differs from that of 12-month-olds. The relation between the ERP response and infants' looking behavior, however, is yet to be determined. It is possible that the facial expression that elicits larger Nc in infants' ERP is also the one that infants look longer at. Accordingly, past
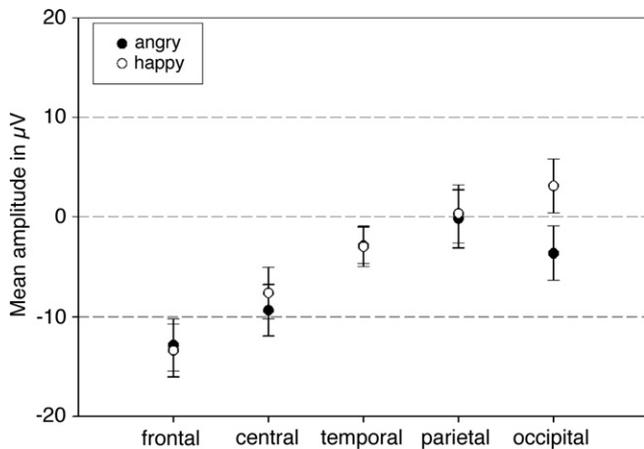
Fig. 6. Mean and standard error of amplitude scores in 12-month-old infants (400–600 ms) for the following regions of interest (ROIs): frontal (F3, F4), central (C3, C4), temporal (T3, T4), parietal (P3, P4), and occipital (O1, O2) electrodes.

work has shown that 7-month-olds look longer at fearful than at happy faces (Nelson & Dolgin, 1985), and their ERPs show a larger negative amplitude to fearful than to happy faces (Nelson & de Haan, 1996).

Interestingly, and related to the current findings, visual preference studies have shown that 4- to 6-month-olds look longer at happy than at angry facial expressions (LaBabera et al., 1976). If a larger Nc actually indicates a spontaneous visual preference for one over the other facial expression, then, based on the findings in Experiment 1 and 2, 7-month-olds should look longer at happy than at angry expressions, whereas 12-month-olds should not differ in their looking to angry and happy expressions because their Nc did not differ between emotions. To date, 7- and 12-month-olds' looking patterns have never been investigated in this context. In order to gain better insight into the meaning of the ERP effects in the previous studies, a third experiment was conducted in which both facial expressions were presented simultaneously and looking times to each expression were measured in 7- and 12-month-old infants.

4.1. Method

4.1.1. Participants

The final sample consisted of 20 7-month-old infants (10 females, $M = 6;29$, $SD = 5$, range = 6;22 to 7;06) and 20 12-month-old infants (10 females, $M = 12$, $SD = 6$, range = 11;17 to 12;09). An additional two 12-month-olds were tested but not included in the final sample due to fussiness. All infants were born full-term (37–42 weeks gestation) and with normal birthweight (>2500 g).

4.1.2. Stimuli

The stimuli were the same two color portrait photographs used in Experiments 1 and 2 of a woman posing a happy or an angry facial expression. From the infants' viewpoint, the visual angle for each photograph was kept the same as in Experiments 1 and 2.

4.1.3. Procedure

The procedure closely matched that of Nelson and Dolgin (1985). Infants were seated on their mother's lap. The stimuli were presented on a 20-in. computer monitor located in the front-wall of a darkened chamber, about 50 cm in front of the infants. Mothers were instructed to look down at their infant rather than at the computer screen. Infants' faces were recorded with a video camera located on top of the computer monitor. A mini-VCR and a computer used to display the stimuli were located outside the testing chamber, and were connected to the video camera. During the test session, the only source of light was the computer monitor. Each infant was presented with two 45-s trials, and each trial consisted of simultaneously presented happy and angry facial expressions. The positions of the emotion were counterbalanced across infants, and the positions were reversed between trials. Looking time was coded from video using a computer coding system (Interact, Mangold Software). On the basis of gaze direction, a coder who was blind to experimental conditions determined for how long (duration) and how many times (frequency) the infant looked at each of the stimuli in both trials. To establish reliability, a second coder, also blind to the experimental conditions, coded infant looking for a random 20% of the infants (i.e., four in each age group). Cohen's Kappa between the two coders was .77 for 7-month-olds and .85 for 12-month-olds.

4.2. Results

4.2.1. Duration of looks

Looking time (cumulative duration of looks, averaged across the trials) was analyzed as dependent variable using a 2 (facial expression: happy, angry) × 2 (age: 7 months, 12 months) repeated measures ANOVA. This analysis revealed a significant main effect of facial expression on infants' looking time ($F(1, 38) = 5.00$, $p < .04$). As shown in Fig. 7, infants of both ages looked longer at happy facial expressions (7-month-olds: $M = 18.04$, $SD = 3.78$; 12-month-olds: $M = 15.09$, $SD = 4.81$) than at angry facial
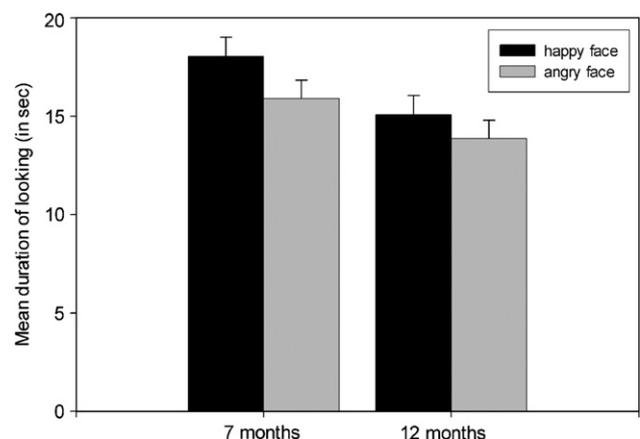

Fig. 7. Mean duration and standard error of looking towards the happy and angry facial expression in 7- and 12-month-old infants.

expressions (7-month-olds: $M = 15.9$, $SD = 4.14$; 12-month-olds: $M = 13.9$, $SD = 4.11$). Furthermore, this analysis also revealed a main effect of age on infants' looking time ($F(1, 38) = 5.10$, $p < .03$). Overall, 7-month-old infants ($M = 33.96$, $SD = 6.26$) looked significantly longer at the facial expressions than did 12-month-old infants ($M = 28.95$, $SD = 7.67$).

4.2.2. Frequency of looks

Frequency of looks (number of looks during one trial) was analyzed as dependent variable using a 2 (facial expression: happy, angry) × 2 (age: 7 months, 12 months) repeated measures ANOVA. This analysis did not reveal a significant interaction, nor any significant main effects.

4.3. Discussion

The current data revealed that both 7- and 12-month-old infants looked significantly longer at happy than at angry faces, which extends previous work with 4- to 6-month-old infants (LaBabera et al., 1976). Longer looking at one expression than another is taken as evidence for discrimination between the two expressions (de Haan & Nelson, 1998) which suggests that infants at both ages discriminated between happy and angry expressions. More importantly, the preferential looking method is thought to be especially sensitive to infants' spontaneous reactions to facial expressions (de Haan & Nelson, 1998). This suggests that infants at both ages show a spontaneous preference for happy expressions over angry expressions, perhaps because happy expressions are more familiar and can provide and facilitate rewarding and self-enhancing experiences for the infant (LaBabera et al., 1976).

It was hypothesized that if a larger Nc actually indicates a visual preference for one over the other facial expression, then, according to the findings in Experiment 1 and 2, 7-month-olds should look longer at happy than at angry expressions, whereas 12-month-olds' looking should not differ between expressions. The current finding of an age-independent visual preference for happy faces does not seem to support this link between visual preference and the Nc. However, it is still possible, but unlikely, that Nc amplitude correlates with visual preference at 7 months of age and only dissociates at the age of 12 months. Since the amplitude differences in the negative component in Experiment 1 and 2 cannot simply be explained by visual preference, it is especially important to employ the ERP method to further our understanding of the development of facial expression processing.

One factor that might have contributed to the discrepancy between ERP and looking time measures is differences in the way the faces were presented. During Experiment 3, faces were presented simultaneously for 45 s, whereas during ERP testing, both faces were presented repeatedly for 1000 ms. These procedural differences may have affected the way infants visually explored these faces.

Another possibility is that the behavior observed at 7 and 12 months of age is the result of different underlying neurocognitive processes as suggested by the findings from Experiment 1 and 2. Different neurocognitive processes can results in similar overt behavior. It is possible, for instance, that 7-month-olds showed a visual preference for the familiar happy face whereas 12-month-olds avoided looking at the angry face because they perceived it as threatening and might even have been comforted by looking at the happy face. This scenario would result in longer looking to the happy expression at both ages but possibly different ERP effects reflecting the different underlying neurocognitive processes. This interpretation is consistent with the ERP findings reported in Experiment 1 and 2 which show that 7-month-olds allocate more attentional resources to the happy face whereas 12-month-olds detect threat, at least at a sensory level.

5. General discussion

In the current series of experiments the development of processing facial expressions of emotion was examined. The ERP data of Experiment 1 and 2 revealed that infants' ERPs at 7 and 12 months differ significantly when they look at happy versus angry faces, suggesting the following developmental course. At 7 months of age, infants show a larger Nc to the happy than to the angry face observed at frontal, central, temporal, and parietal sites (Experiment 1). This effect changes in its direction and topography at 12 months of age, when infants' ERPs show a larger posterior negativity to angry as compared to happy faces at occipital sites (Experiment 2).

This difference in topography suggests that different brain systems are involved in processing of the same stimuli depending on the age of the infant. More specifically, by 7 months, a larger Nc is elicited, indicating a greater allocation of attentional resources, to happy faces. In previous work with infants, it has been shown that cortical activity related to the Nc can be localized in the prefrontal cortex (Reynolds & Richards, 2005). This suggests that prefrontal regions allocate different processing resources to happy and angry expressions at 7 months of age. Our data suggest that this difference in prefrontal involvement in processing happy and angry faces is either no longer present in the older infants or is no longer demonstrated in the ERP. By 12 months, enhanced posterior negativity to an angry face at occipital sites might indicate greater sensitivity to angry faces during sensory processing in the visual cortices. In support of this interpretation, ERP findings show that angry compared to happy and neutral facial expressions elicit a larger EPN at occipital sites in adults (Schupp et al., 2004). This negative ERP component is thought to indicate enhanced sensory processing of emotional cues and appears uniformly also in other experimental designs and with other stimulus materials (Schupp et al., 2003). Furthermore a recent fMRI study in adults revealed increased activation of occipital regions for angry versus other facial expressions (Kesler-West et al., 2001).

Immediate and appropriate responses to emotionally salient (e.g., threat-related) cues in the environment are of obvious adaptive value for the survival of individuals of our species. To this end, the detection of emotionally significant stimuli should be rapid and accurate. In this context, the enhancement at an early stage of sensory processing to angry facial expression observed in 12-month-old infants appears to be a highly adaptive response. This effect might not be threat-specific but rather rely on a more general mechanism because it has been shown that sensory enhancement can be elicited by a variety of emotionally significant cues (e.g., Schupp et al., 2003). The amygdala is hypothesized to be part of a distributed network that helps determine the significance of external stimuli and might also mediate facilitatory sensory cortical processes (Davis & Whalen, 2001; Pessoa et al., 2002). However, this assumption can only be speculative since the current ERP data do not provide direct evidence for the involvement of limbic structures.

One possible developmental account is that although infants can discriminate between both facial expressions at 7 months of age and younger (Barrera & Maurer, 1981), they still have not had sufficient exposure to angry faces to learn the signal value (threat) that an angry expression conveys (Campos et al., 2000). With increased exposure to angry faces towards the end of the first year, infants begin to detect the angry face as a signal of threat that signifies potential negative consequences. In support of this interpretation, following the onset of self-produced locomotion around 10 months of age (Illingworth, 1983), the frequency and quality of emotional communications from the adult to the infant changes. Specifically, self-produced locomotion increases the number of opportunities for caregivers to regulate infant's explorations facially and vocally. Indeed, mothers of locomoting as compared to prelocomoting infants reported a sharp increase in their expression of anger toward their infants (Campos et al., 2000; Campos, Kermoian, & Zumbahlen, 1992).

One potential avenue for future research could therefore be to assess inter-individual differences in facial expression processing as a function of locomotion or affective experience. Along these lines, processing of facial expressions has been studied as a function of particular experiences such as physical abuse (Pollak, Cicchetti, Klorman, & Brumaghim, 1997; Pollak, Klorman, Thatcher, & Cicchetti, 2001), early institutional rearing (Parker et al., 2005) and maternal personality (de Haan, Belsky, Reid, Volein, & Johnson, 2004). In general, these various studies suggest that experiential factors influence the ways that infants and children process facial expressions. It is important to note that the reverse may also be true, i.e., that neural development occurring at the end of the first year (Diamond, 1991, 2000; Johnson, 2001, 2005) may impact infant behavior and subsequently infants' experiences with others.

Longitudinal investigations could be one way to assess the bi-directional impact of maturation and experience. In addition, in future research, it would be useful to assess the relation between behavioral responsiveness and ERPs among the same infants, and to assess a wider range of expressions and actors across modalities (i.e., such as voice). Such an approach could be helpful in determining the various mechanisms that give rise to processing of emotional information, and in assessing how these processes may change as a function of development. Additionally, future research should try to overcome the limitations of the current study and Nelson and de Haan's study (1996) by using more than one model and by varying the intensity of the expressions. This would allow us to investigate the neural correlates of infants' abilities to categorize facial expressions, which would also provide a more rigorous test of their understanding of emotional expressions.

Results from Experiment 3 indicated that looking time to the two facial expressions did not differ between 7- and 12-month-olds, which indicates that looking time and ERP measures might sometimes dissociate. Dissociation between behavioral results and ERP findings has previously been reported by de Haan and Nelson (1997). In their study, 6-month-old infants showed no evidence of recognizing the mother's face when compared to a stranger's face in a behavioral visual preference test; however, ERPs differed significantly between the two faces. The authors concluded that ERPs are a more sensitive measure than is looking time. The dissociation revealed in the current experiment provides further support for this notion.

In sum, the results of the current experiments provide insight into the neurodevelopmental trajectory of the processing of happy and angry facial expressions. In addition, the study highlights the importance of an interdisciplinary approach in understanding the development of facial expression processing. Clearly, the combination of behavioral and ERP findings provided valuable clues about the processing of facial expressions that one or the other method in isolation could not.

Acknowledgments

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