

Infants' Emerging Sensitivity to Emotional Body Expressions: Insights From Asymmetrical Frontal Brain Activity

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Sensitive responding to others' emotional body expressions is an essential social skill in humans. Using event-related brain potentials, it has recently been shown that the ability to discriminate between emotional body expressions develops between 4 and 8 months of age. However, it is not clear whether the perception of emotional body expressions in others evokes sensitive brain responses linked to motivational processes in infants. We therefore examined frontal EEG alpha asymmetry in response to dynamic happy and fearful body expressions presented to 4- and 8-month-old infants in 2 orientations (upright and inverted). Our results revealed that only 8-month-olds but not 4-month-olds showed significant differences in their frontal asymmetry responses between emotional expressions when presented in an upright orientation. Specifically, 8-month-old infants showed a greater lateralization to the left hemisphere in response to happy expression, indexing a greater tendency to approach, whereas they showed a greater lateralization to the right hemisphere in response to fearful expressions, indexing a greater tendency to withdraw. These findings provide further support for the notion that infants' perception of emotion undergoes a developmental tuning during this period in development. Critically, the results suggest that the infant brain becomes sensitive to the motivational significance conveyed by the emotional body expressions.

Keywords: body expressions, development, emotion, frontal cortex, infants

Understanding others' emotional expressions is a vital skill that helps us predict others' actions and guide our own behavior during social interactions (Frith, 2009). Emotional communication is inherently multidimensional and multisensory in nature as emotional information can be gleaned from various sources such as the face, the voice, and the body posture and motion of a person (Heberlein & Atkinson, 2009). The bulk of research investigating emotion expression perception has focused on facial and vocal expressions (Belin, Campanella, & Ethofer, 2012). Much less work has been dedicated to understanding the perception of emotional body expressions, even though body expressions may be the most evolutionarily preserved and immediate means of conveying emotional information (de Gelder, 2006). The work on emotional body expressions has revealed that adults are readily able to detect and recognize various emotions from body expressions (Atkinson, 2013; de Gelder, 2009). This ability to recognize emotions from body expressions relies on specific brain processes localized principally in the right hemisphere, including superior temporal, somatosensory, and premotor cortices (Atkinson, 2013; de Gelder,

2006; Grèzes, Pichon, & de Gelder, 2007; Heberlein, Adolphs, Tranel, & Damasio, 2004; Heberlein & Saxe, 2005).

From a developmental perspective it has been shown that already during the first year of life infants' brains become sensitive to various facial and vocal expressions (for review, see Grossmann, 2013a). Despite the progress that has been made in understanding the ontogeny of emotion perception from face and voice by studying its neural correlates using event-related brain potentials (ERPs), how the ability to perceive and respond to others' emotional body expressions develops during infancy has only recently been investigated. Namely, Missana, Atkinson, and Grossmann (2014) examined ERPs in response to dynamic happy and fearful body expressions in 4- and 8-month-old infants using point-light displays (PLDs; Atkinson, Vuong, & Smithson, 2012) presented in an upright and inverted orientation. The ERP results of this study revealed that 8-month-olds but not 4-month-olds showed an emotion-sensitive responding as reflected in an increased positive component (Pc) from 700 to 1100 ms to happy relative to fearful expressions when presented in an upright orientation (Missana, Atkinson, and Grossmann, 2014). The Pc is taken to reflect recognition memory processes and a greater (more positive) Pc indexes the recognition of an item or event (Grossmann, Striano, & Friederici, 2006; Nelson & de Haan, 1996; Nelson, Thomas, de Haan, & Wewerka, 1998; Webb, Long, & Nelson, 2005). The ERP results from this study therefore suggest that (a) the infant brain becomes tuned to emotional body expressions between 4 and 8 months of age and (b) that at 8 months of age infants recognize positive body expressions. This is in line with work demonstrating that infants' perception of facial and vocal

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expressions of emotion undergoes similar developmental tuning during this period (Grossmann, Striano, & Friederici, 2005; Pelto, Leppänen, Mäki, & Hietanen, 2009).

Critically, the developmental emergence of infants' ability to detect fear in others and discriminate it from happy expressions occurs at a time in development when infants begin to express fear themselves (Campos, Kermoian, & Zumbahlen, 1992). For example, it has been shown that at 8 months of age, but not at 4 months of age, infants show increased anxiety toward strangers (Braungart-Rieker, Hill-Soderlund, & Karrass, 2010). This developmental change in infants' emotional responding has been linked to a sensitive period in infants' socioemotional development related to the onset of independent locomotion (Campos et al., 2000) and maturation of the amygdala and connected brain structures (see Tottenham, 2012, for a discussion). The occurrence of such developmental changes in early socioemotional development related to fear responding has been extensively studied in other altricial species such as rodents (Moriceau, Roth, & Sullivan, 2010) and monkeys (Bauman & Amaral, 2008). This pattern is thought to serve important adaptive functions with respect to bonding with the caregiver during the earliest stages of postnatal development by increasing approach through the reduction of fear (Tottenham, 2012). This may therefore be seen as a highly preserved developmental mechanism in altricial species. Although infants' expression and perception of fear in comparison to happiness has been assigned such a critical role in early socioemotional development, to date it is not known whether and when the perception of body expressions in others evokes sensitive responses linked to motivational brain processes in infants.

In prior work it has been shown that the frontal cortex plays a mediating role in processing, experiencing, and regulating emotions (Davidson, 1992; Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Fox, 1991). Specifically, previous studies in adults and infants measuring asymmetrical frontal brain activity in the alpha frequency band suggest that the lateralization of cortical activity measured at frontal electrode sites is associated with different motivational tendencies and can be seen as an index of approach or withdrawal motivations (Davidson, 1984; Davidson & Fox, 1982; Harmon-Jones, 2003). In particular, it has been shown that the motivation to approach is associated with relatively greater left frontal cortical activity, whereas relatively greater right frontal cortical activity is associated with the motivation to withdraw (Buss et al., 2003; Coan, Allen, & Harmon-Jones, 2001; Davidson, 1984, 1992; Davidson & Fox, 1982; Harmon-Jones, 2003). More specifically, work with adults suggests that fear is considered to elicit withdrawal-related behavioral tendencies and that this is typically associated with greater right frontal activation (Coan & Allen, 2003; Coan et al., 2001; Tomarken, Davidson, & Henriques, 1990).

Frontal EEG alpha asymmetry has also been examined in early development. For example, in a study by Davidson and Fox (1982) frontal EEG alpha asymmetry was examined in 10-month-old infants who were presented with happy and sad facial expressions. In line with the notion that the perception of emotional expressions results in different motivational tendencies in the perceiver, in this study, happy facial expressions elicited greater relative left frontal activation than sad facial expressions that elicited greater relative right frontal activation (Davidson & Fox, 1982). Moreover, in infants it has been shown that the experience of particular emo-

tional states is associated with systematic differences in frontal EEG alpha asymmetry. Specifically, expressing withdrawal-related behaviors in 6-month-old infants was associated with greater relative right frontal EEG asymmetry (Buss et al., 2003), while exhibiting approach-related behaviors (smiling) resulted in greater relative left frontal EEG asymmetry in 10-month-old infants (Fox & Davidson, 1988). This indicates that the perception of emotions in others and the experience of emotional states are reflected in systematic changes in frontal EEG alpha asymmetry in infants.

The aim of the current study was to extend previous ERP findings (Missana, Atkinson, and Grossmann, 2014) regarding infants' emerging sensitivity to emotional body expressions by investigating the effects of perceiving dynamic fearful and happy body expressions on frontal EEG alpha asymmetry patterns in 4- and 8-month-old infants. Based on the prior work reviewed above, we had three main predictions. First, we predicted that 8-month-old infants, but not 4-month-old infants, show differential responding to emotional body expressions (developmental hypothesis). Second, we predicted that 8-month-old infants' frontal EEG alpha asymmetry patterns only differ when the emotional body expressions are presented in an upright orientation (orientation specificity hypothesis). Third, in terms of the asymmetry patterns, we predicted that 8-month-olds show (a) greater right frontal EEG asymmetry to fearful expressions, indexing a tendency to withdraw, and (b) greater left frontal EEG asymmetry to happy expressions, indexing a tendency to approach (emotion sensitivity hypothesis).

Materials and Methods

Participants

The experiment was based on EEG data collected from a previous study with 4- and 8-month-old infants (Missana, Atkinson, & Grossmann, 2014). The sample consisted of twenty 4-month-old infants aged between 123 and 137 days (10 females, median age = 129 days, range = 14 days) and twenty 8-month-old infants between 230 and 259 days (nine females, median age = 251, range = 29 days). An additional fifteen 4-month old infants aged between 122 and 138 days (eight females, median age = 133 days, range = 16 days) and twenty 8-month-old infants aged between 230 and 259 days (10 females, median age = 251 days, range = 29 days) were tested but were excluded from the final sample due to fussiness ($n = 5$) or too many artifacts ($n = 30$). Infants excluded from the final analysis did not systematically differ in gender, age, or maternal education from the included infants. Note that an attrition rate at this level is within the normal range for an infant ERP study (DeBoer, Scott, & Nelson, 2005). The infants were born full-term (between 37 and 41 weeks) and had a normal birth weight (>2500g). All infants came from a middle-class background in a medium-sized German city. Maternal education was assessed by obtaining information regarding the mother's final school degree. Maternal education was scored by using a ranking from 1 (lowest possible school degree in Germany) to 3 (highest possible school degree in Germany). For our sample the mean for maternal education was 2.67 ($SD = .56$).

All parents gave written informed consent prior to the study and were paid for their children's participation. The children were given a toy after the session.

Stimuli

The stimulus material consisted of 2-s clips of point-light body movements displaying eight different fearful and eight different happy expressions (from Atkinson et al., 2012), which were presented upright and inverted (see Figure 1). Stimulus motion was equated across the two emotion categories by selecting eight expressions from the original set of 10 for each emotion, such that the differences in the means of three similar measures of stimulus motion were as small as possible.

Procedure

The infants were seated on their parent's lap in a dimly lit, sound-attenuated, and electrically shielded room during testing. To rule out the possibility that the parents influence the infants' responses to the stimuli, we asked the parents not to talk to or interact with their infant during the course of the experiment. Furthermore, we instructed the parents to look at the infant but not at the screen and the sessions were video-recorded so that trials during which the parent interacted with the infant could be excluded from the analysis. The stimuli were presented in the center of the screen on a black background, using a 70-Hz, 17-in computer screen at a distance of 70 cm. To attract the infants' attention to the screen, each point-light body expression clip was preceded by an alerting sound and a fixation cross (1000 ms), followed by a black screen (400 ms), followed by the stimuli (2000 ms). During the intertrial interval, infants were presented with an abstract screensaver for the purpose of keeping infants' attention. The stimuli were presented in a randomized order with the exception that no two stimuli with the same emotion and orientation combination were presented consecutively. The sessions were videorecorded to control for infants' attention to the screen. The EEG session ended when the infant became fussy or inattentive.

EEG Measurement

The EEG was recorded from 27 Ag/AgCl electrodes attached to an elastic cap (EasyCap GmbH, Herrsching, Germany) using the 10–20 system of electrode placement. The data were online referenced to the CZ electrode and offline rereferenced to the algebraic mean of the left and right mastoid electrode. The horizontal electrooculogram (EOG) was recorded from two electrodes (F9,

F10), which are part of the cap located at the outer canthi of both eyes. The vertical EOG was recorded from an electrode on the supraorbital ridge (Fp2), which is part of the cap and an additional single electrode on the infraorbital ridge of the right eye. The EEG was amplified using a Porti-32/M-REFA amplifier (Twente Medical Systems International, EJ Oldenzaal, Netherlands) and digitized at a rate of 500 Hz. Electrode impedances were kept between 5 and 20 k Ω .

EEG Measures of Asymmetrical Activation

Frequency analysis of the EEG data was performed using the *FieldTrip* software (<http://fieldtrip.fcdonders.nl/>; Oostenveld, Fries, Maris, & Schoffelen, 2011) in combination with custom-made MATLAB scripts. The raw EEG data were high-pass filtered with a cut-off frequency of 3 Hz to reduce slow drifts and removing DC components. The recordings were segmented into epochs of 4000 ms duration, lasting from 1000 ms prior stimulus onset until 1000 ms postvideo offset. Epochs were visually inspected and excluded from further analyses if they were contaminated by large nonstereotyped artifacts (e.g., gross muscle activity or movement artifacts). Remaining stereotyped artifacts (originating, e.g., from eyeblinks or eye movements, tonic muscle activity, or pulse artifacts) were corrected using a signal processing procedure (Jung et al., 2000) based on independent component analysis. The segmented EEG data were decomposed into 24 independent components by application of the symmetric FastICA algorithm. Independent components representing physiological or electrode artifacts were identified by visual inspection of the components' scalp topographies, frequency spectra, and single-trial time courses. They were removed from the data before back projection to the electrode space. For the analysis of event-related oscillations, time-frequency representations of artifact-cleaned single trials were computed using Morlet wavelets with a width of five cycles. The mean alpha power during the processing of point-light body expressions was estimated by averaging the squared magnitude of the complex wavelet transform coefficients across trials (separately for happy upright, happy inverted, fearful upright, and fearful inverted body expressions), over time points and frequency bins. Power values were obtained in the alpha frequency band from 4 to 8 Hz where the majority of power was localized. It has been shown that the alpha frequency range changes with development and is generally lower in infants and children than in adults (Marshall, Bar-Haim, & Fox, 2002; Stroganova, Orekhova, & Posikera, 1999). Prior work shows that peaks of alpha power were observed in the frequency range of 6–9 Hz in infants, suggesting that this range is most suitable for studying alpha power in infancy (Bell & Fox, 1994; Marshall et al., 2002). Because even lower frequency ranges were used in other work with infants (Fox & Davidson, 1987, 1988; Henderson, Fox, & Rubin, 2001), we decided to visually inspect our data to determine the appropriate frequency range. This visual inspection of the data revealed that in our infant groups the maximum power was found in the range of 4 to 8 Hz and we therefore focused our analysis on this range. Mean alpha power values were log-transformed using the natural logarithm function (\ln) to normalize their distribution. EEG alpha power asymmetry scores were calculated for midfrontal (F3, F4) electrodes during a time window of 700 to 1100 ms post stimulus onset. The selection of electrodes for our analysis was based on

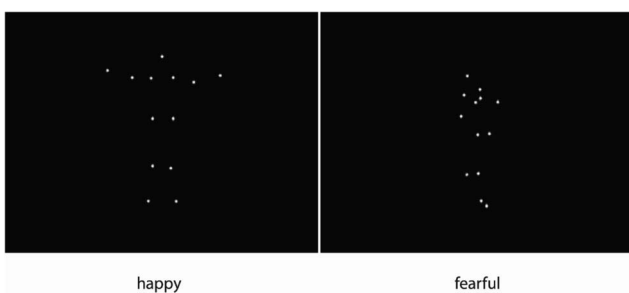


Figure 1. This figure provides an example of the point-light display stimuli. The figure shows two still frames taken at the maximum of the emotional expression. Image from “Tuning the Developing Brain to Emotional Body Expressions” by Missana, Atkinson, and Grossmann, 2014, *Developmental Science*. Reprinted with permission.

prior infant and children studies that examined frontal EEG asymmetry responses (Davidson & Fox, 1982; Fox & Davidson, 1988; Missana, Grigutsch, & Grossmann, 2014; Pickens, Field, & Nawrocki, 2001). We chose the time window for our analysis based on prior work using ERPs (Missana, Atkinson, & Grossmann, 2014). For this purpose, it is important to keep in mind that we used dynamic stimuli that changed from a neutral display (the actor standing in a neutral position) to the expression of the respective emotion. In this dynamic context, the emotional expression unfolds over time and the detection of differences between emotions does not occur before 700 ms, as demonstrated in previous work using ERPs (Missana, Atkinson, and Grossmann, 2014). Our time window for the frontal EEG alpha asymmetry analysis therefore only started at 700 ms after movement onset. The time window chosen is shorter than in prior studies but still long enough to fully capture oscillations within the frequency range of interest for our analysis (4–8 Hz). Specifically, at 6 Hz, a time window of 400 ms, as used in the current analysis, is more than twice as long as a cycle of the alpha oscillation which is at $T = 167$ ms (calculation based on the formula $T = 1/f$). The scores were obtained by subtracting left log-transformed alpha power values from the corresponding right log-transformed values ($\ln(\text{right}) - \ln(\text{left})$). It has been shown that increases in alpha power are associated with decreased cerebral activation and vice versa (Goldman, Stern, Engel, & Cohen, 2002; Laufs et al., 2003). The asymmetry score reflects the power in one hemisphere relative to the power in the opposite hemisphere. Higher scores on this metric suggest relatively greater left activity (Davidson, 1988).

For the group of 4-month-old infants, the mean number of trials seen per condition was 17.81. The mean number of trials included in the EEG alpha asymmetry analysis was 12.65 for the fearful upright condition, 12.60 for happy upright, 12.60 for fearful inverted, and 12.35 for the happy inverted condition. For the group of 8-month-olds the mean number of trials seen per condition was 19.98. The mean number of trials included in the EEG alpha asymmetry analysis was 14.50 for the fearful upright condition, 15.00 for the happy upright condition, 14.60 for fearful inverted, and 14.75 for the happy inverted condition. The number of trials used for final analyses did not differ by condition or age, all $F_s < .263$.

For statistical analysis, differences between mean EEG alpha asymmetry scores across experimental conditions were assessed by an omnibus repeated-measures analysis of variance (ANOVA) with emotion (happy vs. fearful) and orientation (upright vs. inverted) as within-subjects factors and age (4 months vs. 8 months) as between-subjects factor. As in prior work (Davidson & Fox, 1982), to ascertain that effects are specific to frontal electrodes, asymmetry scores were also computed for central electrodes (C3, C4) and parietal electrodes (P3, P4) for comparison reasons.

Results

Our analysis revealed a significant three-way interaction between the factors emotion, orientation, and age, $F(1, 38) = 7.125$, $p = .011$, partial $\eta^2 = 0.158$. Given that the factor age interacts with the experimental manipulation, further analyses were conducted for the two age groups separately to resolve this three-way interaction. Specifically, in agreement with our predictions (devel-

opmental hypothesis), we found that for the group of 8-month-old infants there was a significant interaction between the factors emotion and orientation, $F(1, 19) = 5.735$, $p = .027$, partial $\eta^2 = 0.232$, whereas no such interaction was observed in the group of 4-month-old infants. An additional analysis for a longer time window of 700 to 2000 ms revealed no significant interaction between the factors emotion, orientation, and age, $F(1, 38) = 1.031$, $p = .316$, suggesting that the effect is limited to the time window examined above (see Figure 2 for time-frequency plots of the EEG data from the 8- and 4-month-old infants, respectively). In addition, we controlled for effects of maternal education by conducting a repeated-measures ANOVA with the same factors (emotion, orientation, and age) as specified above and including maternal education as a covariate. This analysis revealed no main effects of maternal education or interactions with maternal education. Moreover, the Emotion \times Orientation \times Age interaction remained significant when controlling for maternal education, $F(1, 30) = 4.804$, $p = .036$.

Further analysis using paired-sample t -tests revealed a significant difference between the frontal EEG alpha asymmetry scores in 8-month-old infants in response to fearful expressions compared to happy expression in the upright orientation, $t(19) = 3.249$, $p = .004$. Critically, in line with our predictions (orientation specificity hypothesis), this effect was specific to the upright orientation as no significant differences in the EEG alpha asymmetry scores were found between the response to inverted fearful expressions and happy body expressions in the inverted orientation, $t(19) = -0.348$, $p = .732$.

As shown in Figure 3, fearful body expressions presented in an upright orientation were found to result in negative frontal EEG alpha asymmetry scores ($M = -0.087$, $SD = 0.19$), reflecting greater relative right frontal activation indicative of a motivational tendency to withdraw from fearful body expressions. In addition, as shown in Figure 3, happy expressions presented in an upright orientation were found to result in greater (positive) EEG alpha asymmetry scores ($M = 0.008$, $SD = 0.20$), reflecting greater relative left frontal activation indicative of a motivational tendency to approach happy body expressions. The pattern of results concerning the asymmetry responses evoked by fearful and happy expressions confirms our emotion sensitivity hypothesis. Note, however, that although the EEG alpha asymmetry score in response to upright happy expressions is positive, the value is very close to zero, implying that the asymmetry across hemispheres is rather small, speaking for a virtually symmetrical activation during this condition (see Table 1).

In additional analyses, t -tests were performed to test whether asymmetry scores differed from zero within the conditions. For both age groups no significant differences were found, all p values $> .019$ (p value threshold adjusted for multiple comparisons using Bonferroni correction; see Appendix).

We conducted an additional analysis in which we compared the frontal EEG asymmetry scores across the two age groups separately for happy and fearful expressions (upright orientation). This was done to find out whether the developmental difference across ages reported above is due to a change in the way in which 8-month-old infants respond to a specific emotion. Critically, this analysis revealed that EEG alpha asymmetry scores only differed across ages for the happy expression, $t(19) = -2.367$, $p = .029$ but not for the fearful expression, $t(19) = 0.189$, $p = .852$.

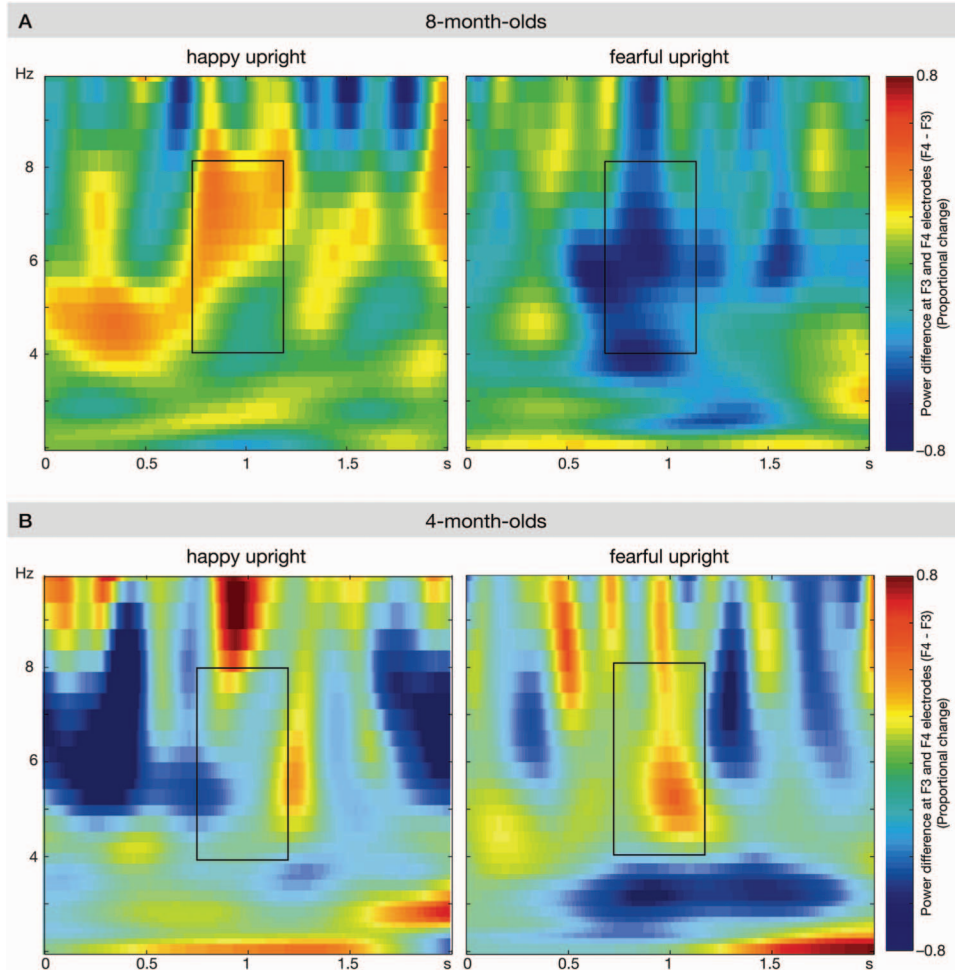


Figure 2. This figure shows the power changes relative to baseline for 2 s after stimulus onset and in the frequency range of 2 to 10 Hz in A) 8-month-old infants and B) 4-month-old infants. Each plot depicts the difference power at F4 and F3 electrode sites for happy and fearful upright body expressions. The rectangles represent the analyzed time window and frequency range.

Specifically, for the happy expressions, in the group of the 4-month-olds, we observed a negative EEG alpha asymmetry score ($M = -0.1148, SD = 0.20$), indexing right frontal activation, whereas, in the group of the 8-month-olds, we observed a positive

EEG alpha asymmetry score ($M = 0.008, SD = 0.20$) indexing left (or symmetrical) frontal activation.

Importantly, no effects were found at central electrodes, $F(1, 38) = 0.396, p = .533$ and at parietal electrodes, $F(1, 38) = 1.218,$

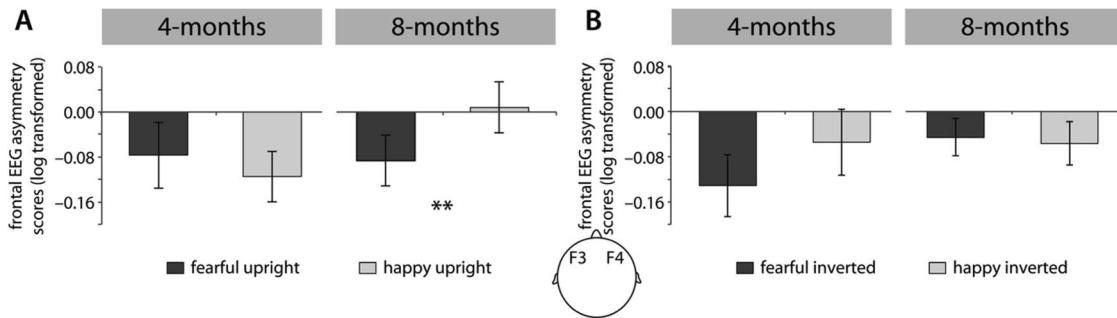


Figure 3. This figure shows 4- and 8-month-old infants' frontal EEG alpha asymmetry scores (log transformed) in response to fearful and happy upright (A) and inverted (B) presented body expressions. $** p \leq .01$.

Table 1
Frontal EEG Alpha Asymmetry Scores for 4- and 8-Month-Old Infants in Response to Happy Upright, Happy Inverted, Fearful Upright, and Fearful Inverted Presented Body Expressions

	N	Electrodes	Asymmetry scores (M ± SD)			
			Happy upright	Fearful upright	Happy inverted	Fearful inverted
4-month-olds	20	F3/F4	-0.115 ± 0.20	-0.077 ± 0.23	-0.055 ± 0.26	-0.131 ± 0.25
8-month-olds	20	F3/F4	0.008 ± 0.20	-0.087 ± 0.19	-0.057 ± 0.17	-0.046 ± 0.15

$p = .277$. This is indicative of the specific involvement of the frontal region compared to central and parietal regions (Davidson & Fox, 1982).

Nonparametric tests (chi-square and binomial sign tests) were conducted to further examine potential differences in the number of infants showing particular frontal EEG asymmetry responses during the experimental conditions. Specifically, this analysis revealed a significant difference in the lateralization patterns (left vs. right) when comparing between ages (4 vs. 8 months) for upright happy expressions, $\chi^2(1, N = 40) = 4.912, p = .027$, but not for upright fearful expressions, $\chi^2(1, N = 40) = .921, p = .337$ (see Table 2). This corroborates the results obtained from our parametric analysis presented above by showing that only for the happy condition significantly more 8-month-old infants exhibited a lateralization to the left hemisphere in their frontal EEG asymmetry response.

In addition, only for the group of the 8-month-old infants we found a marginally significant difference in the lateralization patterns (left vs. right) when comparing between emotions (happy vs. fearful), $\chi^2(1, N = 20) = 3.6, p = .058$ (see Table 3). No such difference in the lateralization patterns across emotions was observed in the group of 4-month-old infants, $\chi^2(1, N = 20) = 1.667, p = .197$ (see Table 3). This corroborates the results obtained from our parametric analysis presented above by showing that differences in lateralization patterns across emotions were found only for the 8-month-old infants.

Moreover, our data show that 17 out of twenty 8-month-old infants (85%) exhibited higher asymmetry scores to happy upright bodies indicative of a relative shift of frontal asymmetry patterns from right to left in response to happy body expressions, and a binomial sign test revealed that this is a significant difference in terms of the lateralization patterns, $p = .003$. Similar to the prior analysis, for the group of 4-month-old infants no such difference was obtained, $p = .503$, because only 8 out of twenty 4-month-old infants (40%) showed higher asymmetry scores to happy upright bodies.

Discussion

The current study investigated the early development of the neural sensitivity to emotional body expressions by measuring frontal EEG alpha asymmetry patterns in response to dynamic fearful and happy body expressions in 4- and 8-month-old infants. Our results revealed that 8-month-old infants, but not 4-month-old infants, showed differences in their frontal EEG alpha asymmetry patterns distinguishing between fearful and happy body expressions. This finding is in line with prior ERP work showing that over the course of the first year of life the human brain becomes tuned to emotional body expressions (Missana, Atkinson, & Grossmann, 2014). More generally, the ontogenetic emergence of the neural sensitivity to emotional body expressions, evident in our results, occurs at a time in development when facial and vocal emotion processing capacities undergo similar change (Grossmann, Oberecker, Koch, & Friederici, 2010; Peltola et al., 2009). The current findings therefore provide further evidence for accounts that regard emotion perception as a unified ability that develops in concert across various processing channels (face, voice, and body) (Heberlein & Atkinson, 2009).

In the current study we used PLD stimuli that provided little static form information but contain the essential motion cues that allow adult observers to recognize emotions from body motion (Atkinson, Dittrich, Gemmell, & Young, 2004; Atkinson, Tunstall, & Dittrich, 2007) and showed that 8-month-old infants can distinguish between emotions on the basis of these motion cues by using frontal EEG alpha asymmetry measures. This finding critically extends prior work that has investigated infants' perception of biological motion from PLDs (Bertenthal, 1993; Hirai & Hiraki, 2005; Reid, Hoehl, & Striano, 2006) by demonstrating that infants are not only sensitive to biological motion but can also extract specific information concerning the emotional state of the biological agent.

Furthermore, in line with our prediction that 8-month-old infants' frontal EEG alpha asymmetry patterns only differ when the

Table 2
Differences in Frontal EEG Alpha Asymmetry Patterns (Left Versus Right) When Comparing Between Ages (4 vs. 8 Months) for Upright Presented Bodies (χ^2 Values and p Values)

	N	Frontal asymmetry							
		Happy upright		χ^2	p	Fearful upright		χ^2	p
		Left	Right			Left	Right		
4-month-olds	20	6	14	4.912	.027	10	10	.921	.337
8-month-olds	20	13	7			7	13		

Table 3
Differences in Frontal EEG Alpha Asymmetry Patterns (Left vs. Right) When Comparing Between Emotions (Happy vs. Fearful) for Upright Presented Bodies (χ^2 Values and p Values)

	N	Frontal asymmetry							
		8-month-olds		χ^2	p	4-month-olds		χ^2	p
		Left	Right			Left	Right		
Happy upright	20	13	7	3.6	.058	6	14	1.667	.197
Fearful upright	20	7	13			10	10		

emotional body expressions are presented in an upright orientation (orientation specificity hypothesis), we found that inversion of the body motion disrupts the discrimination between emotions, suggesting that 8-month-old infants require upright body motion to successfully extract emotional information. This is similar to what is already known from adults (Atkinson et al., 2007; Atkinson et al., 2012) and it is also in agreement with work showing inversion effects for the perception of faces in the first year of life (de Haan, Pascalis, & Johnson, 2002). The disruption of emotion discrimination by body inversion can be seen as evidence for the developmental emergence of configural processing of body motion. Namely, rather than relying on individual features of the body that are also present in the inverted stimulus, 8-month-olds need to see the configuration of body features in order for the discrimination process to take place.

The frontal EEG alpha asymmetry differences between fearful and happy stimulus conditions are unlikely to be the result of differences in low-level motion properties between the two stimulus sets. This is because, first, we controlled for the amount of dot motion across the happy and fearful expressions and, second, the frontal EEG alpha asymmetry differences between emotions were not observed for the inverted stimuli, in which the available dynamic information is identical to that available in the upright stimuli. Thus, 8-month-olds are likely to be using higher-level motion cues to discriminate between the emotions (see Atkinson et al., 2007).

The frontal EEG alpha asymmetry patterns in response to the individual emotions observed in the current study confirmed our prediction regarding infants' emerging emotion sensitivity. Specifically, we found that 8-month-olds show greater relative right frontal EEG asymmetry to fearful expressions, indexing a tendency to withdraw, and greater relative left frontal EEG asymmetry to happy expressions, indexing a tendency to approach. These results are in line with previous findings indicating that (a) the perception and experience of happy expressions elicited greater relative left frontal activation associated with approach tendencies (Davidson & Fox, 1982; Fox & Davidson, 1988) and (b) the perception and experience of fear is related to withdrawal-related motivational tendencies and is associated with greater right frontal activation (Buss et al., 2003; Coan & Allen, 2003; Coan et al., 2001; Tomarken et al., 1990). Our findings support the general notion that the frontal cortex plays a role in processing emotional information and that this can already be traced in infancy (Fox, 1991; Grossmann, 2013b). More specifically, extending prior work with 10-month-old infants based on using facial expressions of emotion (Davidson & Fox, 1982), this finding provides evidence for specific changes in the motivational tendencies that are asso-

ciated with perceiving emotional body cues. This suggests that perceiving others' emotional expressions engenders basic motivational processes in 8-month-old infants. Having such brain processes in place early in development might serve as a vital basis for guiding social behavior in terms of informing decisions as to whom (or what) to approach or avoid (Hamlin, Wynn, & Bloom, 2007). Clearly, future work with infants is needed to examine a possible link between the neural responses, similar to those measured in the current study, and overt social behavior.

With respect to infants' emerging neural sensitivity to emotional body expressions, it is also important to discuss that our results revealed that frontal EEG alpha asymmetry scores only differed across ages in response to the happy expressions but not in response to the fearful expressions. This suggests that the developmental change that takes place between 4 and 8 months mainly affects the processing of happy body expressions. The finding that developmental changes occur for processing happy body expressions stands in contrast to prior ERP work on infant facial expression processing, showing developmental changes with respect to processing fearful expressions (e.g., Peltola et al., 2009). This might point to potential differences in infants' perception of emotion from bodies and faces but is more likely to be explained by differences in using dynamic when compared to static expressions. This is because recent work with 8-month-old infants shows that using static body postures results in similar ERP responses (enhanced Nc) to fearful bodies as seen for fearful faces (Missana, Rajhans, Atkinson, & Grossmann, 2014). This discrepancy between dynamic and static displays of body expressions might have something to do with the fact that the dynamic stimuli used in the current study to portray happiness are perceived as infant-directed action or as "motionese" by the infants. Specifically, parents have been shown to modify their bodily movements in a variety of ways when interacting with infants (Brand, Baldwin, & Ashburn, 2002) and infants display strong preferences for motionese when compared to adult-directed movements (Brand & Shallcross, 2008). Critically, for the current study motionese is characterized by exaggerated positive affect in body movement similar to the happy body movement portrayed in our point-light displays. Therefore, it is possible that infants' responses to happy body expressions are related to their preference for motionese. Regardless of this issue, our finding is in line with previous work on emotional body expression processing using ERPs (Missana, Atkinson, & Grossmann, 2014). Specifically, prior work reported that infant ERP responses (in particular the Pc) changed in its amplitude between 4 and 8 months of age in response to happy expressions (more positive in older infants), indexing the recognition of positive expressions. Note that these EEG measures have been shown to tap

into distinct processes that differ in their functional relevance (Missana, Grigutsch, & Grossmann, 2014): as the ERP measure (Pc) is a neural correlate of recognition memory (Grossmann et al., 2006; Nelson et al., 1998), whereas the frontal EEG alpha asymmetry measure is a neural correlate of motivational tendencies (Davidson, 1984; Davidson & Fox, 1982; Harmon-Jones, 2003). We therefore propose that the current findings in conjunction with the prior ERP work (Missana, Atkinson, & Grossmann, 2014) are best interpreted as supporting the notion of a developmental transition in infants' emotion perception from body motion cues characterized by changes in recognition memory and motivational brain processes. These changes are likely to represent highly interdependent processes, as recognition of an emotion is required for motivational responses to occur.

Indeed, our analysis also revealed that the observed effects were limited to a time window of 700 to 1100 ms after movement onset. This is the same time window during which 8-month-old infants' ERP responses differed between fearful and happy dynamic body expressions (Missana, Atkinson, & Grossmann, 2014). In this context, it is important to mention that although the frontal EEG alpha asymmetry effects were observed at frontal electrodes, the ERP differences in prior work were seen at temporal and parietal electrodes. The differential topography of effects suggests that the discrimination (as indexed by ERPs) and motivational evaluation of body expressions (as indexed by frontal asymmetry) occur at similar points in time, but rely on spatially distinct brain processes. The fact that frontal EEG alpha asymmetry patterns and ERP responses tap into distinct brain processes is in line with recent work using dynamic emotional facial expressions in 8-month-old infants (see Missana, Grigutsch, & Grossmann, 2014). Nonetheless, in future studies, to better understand the nature of the brain processes elicited by viewing emotional expressions, it will be important to further investigate how ERP and frontal EEG alpha asymmetry effects interrelate and contribute to the perception of emotion. This points to a general need in understanding infants' perception of emotion as a complex emerging ability reflected in various psychologically relevant brain processes.

Finally, it is important to discuss the limitations of the current study by suggesting ways of how to address remaining issues in future studies. First, the current paradigm should be extended to other ages (beyond infancy) to further investigate the developmental trajectory of the perception of emotional body expressions. In particular, prior work has shown that there are considerable differences between 8-month-old infants and adults in their frontal EEG alpha asymmetry patterns observed in response to emotional facial expressions (Missana, Grigutsch, & Grossmann, 2014). This indicates that older infants' responses are not yet adult-like but development occurs beyond infancy with respect to the motivational processes evoked by viewing facial expression and this may generalize to viewing body expressions. Second, future work with infants is needed to assess whether there is a link between the neural responses, similar to those measured in the current study, and approach and withdrawal behaviors in response to emotional body expressions. Specifically, one possibility is to combine EEG measurements with behavioral preference tests as used in prior work with infants (Hamlin et al., 2007) to test whether, during the viewing of the expression, frontal EEG asymmetry patterns of a person are associated with approach of or withdrawal from that person during a preference test. Third, to better understand the

developmental process that underpins emotion perception from body cues, future work is needed to systematically examine what factors contribute to individual differences in emotional body expression processing in infancy. In the current study we controlled for effects of maternal education. However, prior work with 8-month-old infants shows that other maternal variables such as maternal empathic concern and duration of exclusive breastfeeding, as well as infant temperament, are associated with marked differences in infants' ERP responses to static emotional body postures (Krol, Rajhans, Missana, & Grossmann, 2014; Rajhans, Missana, Krol, & Grossmann, 2014). It is thus important to examine whether these factors are also linked to individual differences in frontal EEG alpha asymmetry.

In summary, the current findings have shed new light on the developmental, perceptual, and neural processes that underpin the sensitivity to emotional body expressions thereby critically extending and informing accounts of emotion processing. In particular, our results demonstrate that during the first year of life the human brain becomes sensitive to the motivational significance conveyed by emotional body expressions.

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Appendix

t-Values and *p*-Values for *t*-Tests Against Zero for 4- and 8-Month-Old Infants' Frontal EEG Alpha Asymmetry Scores in Response to Happy Upright, Happy Inverted, Fearful Upright, and Fearful Inverted Presented Body Expressions

	4-month-olds		8-month-olds	
	<i>t</i>	<i>p</i> *	<i>t</i>	<i>p</i> *
Happy upright	−2.553	.019	.177	.862
Happy inverted	−.928	.365	−1.473	.157
Fearful upright	−1.520	.145	−1.937	.068
Fearful inverted	−2.388	.027	−1.401	.177

* Uncorrected *p* value.

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