Neuropsychologia 126 (2019) 62–68

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Emotion processing in the infant brain: The importance of local information

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ARTICLE INFO

Keywords:
Spatial frequency
Emotion
Development
Event related potential

ABSTRACT

Facial expressions provide crucial information for an infant's social and cognitive development. Expressions are discriminated based on specific basic-level information, such as global and local information represented in spatial frequencies. Research in adults suggests that different neural pathways are involved in emotion discrimination, each activated by specific spatial frequency ranges. However, in infants the involvement of spatial frequencies in emotion discrimination is unknown. In the current study we investigated the effect of manipulating spatial frequency information in the face on emotion discrimination. Infants aged 9–10 months (N = 61) viewed happy, fearful, and neutral faces. The faces contained either lower (related to global information) or higher spatial frequencies (related to local information). Brain activity in response to the faces was measured with electroencephalography. Interest was in the effect of emotion and spatial frequency on the amplitude of the N290, P400, and Nc components. Amplitudes of the N290 and P400 components differed between happy versus fearful or neutral faces, although only in the higher, and not the lower, spatial frequency condition. Amplitude of the Nc components differed between happy versus fearful or neutral faces regardless of spatial frequency condition. These results reveal the importance of higher spatial frequencies for emotion discrimination in infants (particularly at the N290 and P400 components). We related these findings to current models on the neural basis of facial-emotion processing.

1. Introduction

Facial expressions provide crucial information for infants' behavior and development. For instance, when infants start to crawl, their parent's expressions can warn them about possible dangerous situations in their environment that should be avoided (Sorce et al., 1985). During the first year of life, infants become able to discriminate between emotions in a face (for a review see: Grossmann, 2010; Leppänen and Nelson, 2009; Pascalis and Kelly, 2009). However, the neural basis of facial-emotion processing is not well understood. Previous research in adults revealed multiple brain areas that are involved in emotion discrimination and provided models on the brain pathways via which visual information reaches these areas (Johnson, 2005, 2015; Leppänen and Nelson, 2009). However, due to the spatial limitations of neural measures currently applied in infants, we are not yet able to directly test these models in infancy. In the present study we aimed to test aspects of these models to gain more insight in the neural basis of facial-emotion processing in infancy. Specifically, we investigated which visual information, that is lower and higher spatial frequencies, infants use to discriminate between emotions. Spatial frequencies were of particular interest because they are presumably processed via different pathways (Johnson, 2005, 2015).

Previous research in adults indicates that multiple areas are involved in emotion discrimination. The so-called emotion-processing network includes subcortical and cortical brain areas, such as the amygdala, orbitofrontal cortex (OFC), superior temporal sulcus (STS), and fusiform gyrus (FG; for a review see: Leppänen and Nelson, 2009). It has been suggested that this emotion-processing network emerges early in life (Leppänen and Nelson, 2009). Indeed, many studies reveal that infants' brain activity is modulated by emotion type (Table 1, but note the absence of an effect in Hoehl et al. (2008) and Vanderwert et al. (2015)). These studies showed that several components of the event related potential (ERP) differ between emotions. The N290 and P400 components are thought to relate to perceptual processing of emotional faces in infants, and are suggested to form the precursor of the adult N170 component (De Haan and Nelson, 1999; Halit et al., 2003). Furthermore, the Nc component is thought to relate to attentional processing of the face (Nelson and Monk, 2001; Richards, 2003). The modulation of these components by the emotional content of a face indicates that the infant brain processes emotions differently. However,

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http://dx.doi.org/10.1016/j.neuropsychologia.2017.09.006
Received 1 February 2017; Received in revised form 30 August 2017; Accepted 4 September 2017
Available online 07 September 2017
0028-3932/

Table 1
Overview of studies on emotion discrimination comparing at least two emotions.

Study	Age (months)	Included number of participants	Presented emotion					Result: peak amplitude		
			Happy	Neutral	Sad	Fearful	Angry	N290	P400	Nc
Grossmann et al. (2007)	7	20	1				1	–	–	H > A
	12	20	1				1	–	H > A	n.s.
de Haan et al. (2004)	7	36	1	1		1		–	–	F > H
Hoehl et al. (2008)	7	14		1		1		–	–	n.s.
Hoehl and Striano (2008)	7	13				1	1	A > F	A > F	n.s.
Hoehl and Striano (2010a)	3	21	1	1				–	–	H > N
Hoehl and Striano (2010b)	3–4	15		1		1		n.s.	–	n.s.
	6–7	18		1		1		n.s.	–	n.s.
	9–10	17		1		1		n.s.	–	F > N
Kobiella et al. (2008)	7	17				1	1	A > F	F > A	A > F
Leppanen et al. (2007)	7	15	1	1		1		n.s.	F > NF > H	F > H
Nelson and de Haan (1996)	7	19	1			1		n.s.	n.s.	F > H
	7	19				1	1	n.s.	n.s.	n.s.
Parker et al. (2005)	8–32	33	1		1	1	1	A > S > F	F > S	n.s.
Peltola et al. (2009)	5	18	1			1		–	–	n.s.
	7	20	1			1		–	–	F > H
Rigato et al. (2010)	4	28	1			1		n.s.	n.s.	H > F
Stahl et al. (2010)	6	46		1			1	–	–	N > A
Taylor-Colls and Pasco Fearon (2015)	7	40	1	1		1		–	–	F > NF > H
Vanderwert et al. (2015)	7	34	1			1	1	n.s.	n.s.	–
Yrttiaho et al. (2014)	5	75	1	1		1		(N + H) > F	F > (N + H)	–
	7	100	1	1		1		(N + H) > F	F > (N + H)	–
van den Boomen et al. (current study)	9–10	60	1	1		1		H > (N + F)	H > (N + F)	H > (N + F)

Note. In the result columns, a horizontal line indicates that the peaks are not investigated, n.s. indicates no significant effect, and > indicates a higher amplitude.
H = Happy; N = Neutral; S = Sad; F = Fearful; A = Angry.

the applied methods limit conclusions regarding the pathways involved in emotion processing.

According to the dual route model of face processing, faces are processed through two interconnected brain pathways: a subcortical route and a cortical route (Johnson, 2005, 2015). The cortical route connects the visual cortex with the STS and the FG, whereas the subcortical route provides visual information via the thalamus to the amygdala and OFC. These brain pathways might operate on different basic-level visual information (Johnson, 2005, 2015). Presumably, the subcortical route operates on lower spatial frequency information. The cortical route carries mainly higher spatial frequency information. Lower spatial frequencies are suggested to support, more than higher spatial frequencies, the processing of the global configuration of the face (i.e. global visual information). In contrast, higher spatial frequencies are suggested to support, more than lower spatial frequencies, the encoding of detailed visual information such as sharp edges present in a face (i.e. local visual information; Goffaux and Rossion, 2006; Morrison and Schyns, 2001). Taken together, current models state that brain areas in the emotion-processing network receive information from a subcortical and cortical route that operate on different spatial frequency information. Consequently, the spatial frequency information used to discriminate between emotions might indicate which pathways are involved.

Support for a differential involvement of lower and higher spatial frequency information in processing emotions in the brain comes from research in school-age children and adults (e.g. Deruelle et al., 2008; Pourtois, Dan, Grandjean, Sander, and Vuilleumier, 2005; Vlamings et al., 2010a; Vlamings et al., 2010b). Interestingly, the involvement of lower and higher spatial frequency information in emotion discrimination appears to change across development. That is, in children brain activity differs between emotions when faces contain lower (Vlamings et al., 2010a) or higher (Vlamings et al., 2010b) spatial frequencies. In adults this difference is found for faces containing lower spatial frequencies (e.g. Pourtois et al., 2005; Vlamings et al., 2009; but see for varying effects on behavior: Goren and Wilson, 2006; Kumar and Srinivasan, 2011). Yet, it is still unknown whether infants can discriminate emotions based on lower or higher spatial frequency information. Behavioral studies suggest that in newborns the subcortical route and lower spatial frequencies are involved in face processing, while the cortical route and higher spatial frequencies come into play later in infancy (Johnson, 2005, 2015). For example, Simion and colleagues (Simion et al., 1998) demonstrated that newborns show a face-related preference when face-like stimuli were presented to the temporal visual field, which feeds preferentially into the subcortical visual pathway. This preference was not found when newborns observed stimuli in the nasal visual field, which feeds mainly into the cortical pathway. Whether older infants discriminate emotions based on both spatial frequency ranges is not investigated. Research in infants is important, because it might provide a baseline for future studies on early markers of atypical development such as in children with Autism Spectrum Disorder who extensively rely on higher spatial frequencies in processing of emotions (Vlamings et al., 2010b).

The current study investigated the effects of the presence of lower versus higher spatial frequency information on emotion discrimination in 9- to 10-month old infants. At this age, infants are expected to show robust emotion processing and have sufficient attention span to include multiple conditions in the experiment. We studied the effects of spatial frequency on discrimination of neutral, fearful, and happy emotions. Emotion discrimination was evaluated at three components in the ERP, being the N290, P400, and Nc. We expect an effect of emotion on the amplitude of all three components. Previous studies (De Haan and Nelson, 1999; Halit et al., 2003; Nelson and Monk, 2001; Richards, 2003) indicated that effects on the N290 and P400 would indicate that perceptual discrimination between emotions is present in infants. Effects on the Nc would suggest differences in allocation of attention towards the different emotional faces. Interaction effects were expected for all components as well, in which case we would be interested in whether the emotion effect on amplitude would be larger for lower or higher spatial frequencies. More specifically, based on the previously described models we expected that emotion effects on the N290 and P400 amplitude would be largest for faces containing higher spatial frequencies. These components supposedly relate to perceptual processing in the FFA and STS, which might receive higher spatial frequency information via the visual cortex (Johnson, 2005, 2015). On the contrary, we expected emotion effects on the Nc component to be largest for faces containing lower spatial frequencies. This component might relate to attention processes and activity in the OFC, which is suggested to receive lower spatial frequency information via the amygdala (Johnson, 2005, 2015).

2. Methods

2.1. Participants

The final sample consisted of 61 9–10 month-old infants (31 males) with an average age of 303 days (9.9 months; range: 279–330 days; stdev: 11.0). An additional 16 infants were tested but excluded from analyses due to refusal to wear the EEG cap (N = 1), excessive motion in combination with lack of attention (N = 14), or medical reason (N = 1). All infants were born full-term (38–42 weeks), had normal birth weight, and no developmental delays or abnormalities in visual or auditory processing, as reported by the health-care system.

The medical ethical committee of the University Medical Center Utrecht approved the study, in accordance with the Declaration of Helsinki. All parents or guardians gave written informed consent prior to participation, after explanation of the procedure. Children received a toy after participation.

2.2. Stimuli and procedure

2.2.1. Stimuli

Face stimuli consisted of photographs of 10 facial identities each depicted under 3 emotional conditions taken from the MacBrain Face Stimulus Set.[1] Using Photoshop, all stimuli were cropped, turned into grey scale and matched for size (19.4 × 14.0 degrees of visual angle at a viewing distance of 57 cm). Faces had a neutral or fearful expression, and were filtered with a low- (LSF; < 2 cycles per degree) or high-pass (HSF; > 6 cycles per degree) spatial frequency filter. The LSF and HSF stimuli differed in terms of Root Mean Square (RMS) contrast (LSF: 25 cd/m2; HSF: 8 cd/m2). This created a 3 (emotion: neutral, fearful, happy) × 2 (SF: LSF, HSF) condition design (Fig. 1).

2.2.2. Procedure

During testing the infant was seated in a highchair or on the mothers lap. The stimuli were presented on a 23-in. screen with a resolution of 1920 × 1080 pixels, and a refresh rate of 60 Hz, in two blocks of 20 stimuli per condition, in random order for 800 ms, with a jittered interstimulus interval between 700 and 1000 ms. Completion of all trials took 7.5 min (excluding breaks and attention reorientation). A video camera was placed on top of the screen for online observation. When the infant was not looking at the screen, the experiment was paused and attention was reoriented by a sound played by the computer or a moving stimulus on the screen. Stimuli were presented until the infant became too fussy or bored to attend. Video recordings were additionally used for off-line coding of attention. Unattended trials were discarded from analyses. The average number of attended trials was 165 (stdev: 29; range: 73–215) for included participants.

2.3. ERP recording, preprocessing, and peak analysis

2.3.1. ERP recording

EEG activity was recorded from 32 electrodes using a Biosemi Active Two EEG system (Biosemi, Amsterdam, The Netherlands). Electrodes were positioned at standard EEG recording locations according to the international 10/20 system. During recording, EEG was sampled at a rate of 2048 Hz. Two electrodes in the cap, the CMS (Common Mode Sense) and DRL (Driven Right Leg) provided an active ground.

2.3.2. Preprocessing

Using Brain Vision Analyser software (version 2.0; Brainproducts GmbH) and Matlab (version 2014b; The Mathworks, Natick, MA; Fieldtrip version 20160105[2]) we pre-processed the data. Data were resampled offline to 512 Hz, and filtered with a high-pass filter of .1 Hz (24 dB/oct), a low-pass filter of 30 Hz (24 dB/oct) and a notch filter of 50 Hz. In order to compute ERPs, epochs of 100 ms pre-stimulus (baseline) until 1000 ms post-stimulus were extracted from the continuous data. The data was demeaned, with baseline defined as 100 ms pre-stimulus until stimulus onset. Trials were removed in *single electrodes* when there were artefacts. Artefacts were defined as amplitudes below −200 or above 200 µV; a difference of more than 200 µV within 100 ms; a difference of less than 3 µV within 200 ms; or a voltage change of more than 50 µV per sampling point. An electrode was rejected if there were less than 5 artefact-free trials. Trials were removed *in all electrodes* (i.e. the full trial was removed) if the child blinked or looked away between 0 and 500 ms after stimulus onset (manually coded in the video; no EEG-based eye blink detection performed), or if more than 16% of electrodes contained artefacts as described above (based on previous research on face processing in infants, e.g. Halit et al., 2003). Finally, activity was referenced to the average of all included electrodes. For each stimulus condition an average of the ERP was created per electrode. Based on previous research in infants (Kobiella et al., 2008; Leppänen et al., 2007, 2009); participants were included in the data analyses if for each of the electrodes of interest (i.e. P3, PO3, O1, Oz, O2, PO4, P4, Cz, Fz, C3, C4, FC1, FC2) there were at least 10 segments per condition included in the average. The average number of included segments was 25 per condition (N290 and P400: Fear HSF: $M = 24.2$; $SE = 0.7$; Fear LSF: $M = 24.6$; $SE = 0.7$; Neutral HSF: $M = 26.9$; $SE = 0.8$; Neutral LSF: $M = 24.7$; $SE = 0.7$; Happy HSF: $M = 24.0$; $SE = 0.8$; Happy LSF: $M = 23.6$; $SE = 0.8$; Nc: Fear HSF: $M = 24.7$; $SE = 0.7$; Fear LSF: $M = 25.1$; $SE = 0.7$; Neutral HSF: $M = 27.5$; $SE = 0.8$; Neutral LSF: $M = 25.3$; $SE = 0.7$; Happy HSF: $M = 24.5$; $SE = 0.8$; Happy LSF: $M = 24.1$; $SE = 0.8$). There was a significant interaction between emotion and SF on the number of included trials for the N290 and P400 components ($F(2,120) = 12.7$; $p < 0.001$; $\eta^2 = 0.174$), and for the Nc component ($F(2,120) = 12.9$; $p < 0.001$; $\eta^2 = 0.177$). However, the number of included trials unlikely mediated the effects of emotion and SF on amplitude, because there were no significant correlations (all $p > 0.05$). Please refer to Appendix A for an extensive description of the analyses and results on the number of included trials and correlations with amplitude.

2.3.3. Component analyses

The components of interest were the N290, P400, and Nc. Mean amplitude within a time window of 200–325 ms (N290), 325–600 ms (P400) and 300–600 ms (Nc) was exported for further analyses on these components. Based on visual inspection of the P400 component, analyses were also performed on the early and late part of the P400. These analyses led to the similar conclusions regarding the effects of SF and emotion, and are described in Appendix B. Electrodes of interest were based on previous research (i.e. studies in Table 1 that included sufficient information to relate the described electrode of interest to the electrode of our 10–20 system), resulting in the P3, PO3, O1, Oz, O2, PO4 and P4 for the N290 and P400. For the Nc, electrodes of interest

[1] Development of the MacBrain Face Stimulus Set was overseen by Nim Tottenham and supported by the John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development. Please contact Nim Tottenham at tott0006@tc.umn.edu for information concerning the stimulus set.

[2] Fieldtrip is an open source Matlab toolbox for EEG and MEG analysis; (Oostenveld et al., 2011).

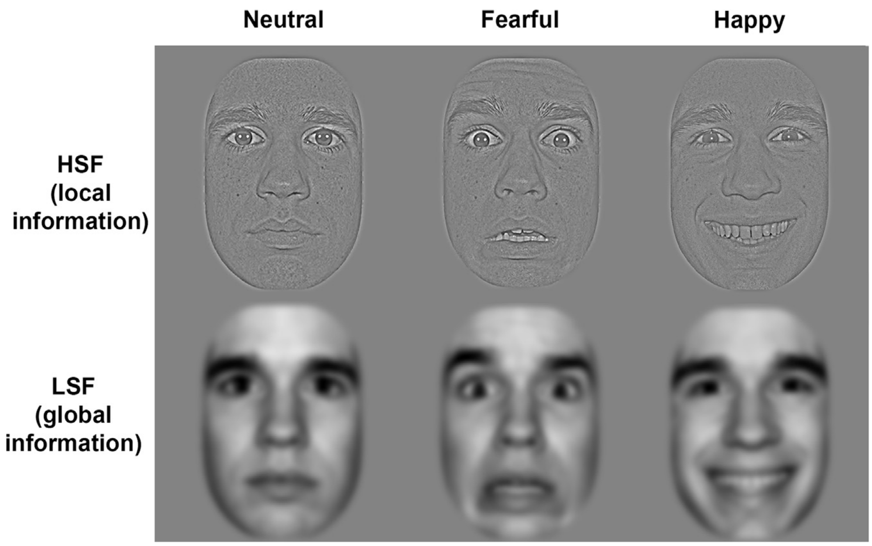

Fig. 1. Example of fearful, neutral, and happy low SF (LSF; global) and high SF (HSF; local) filtered face stimuli.

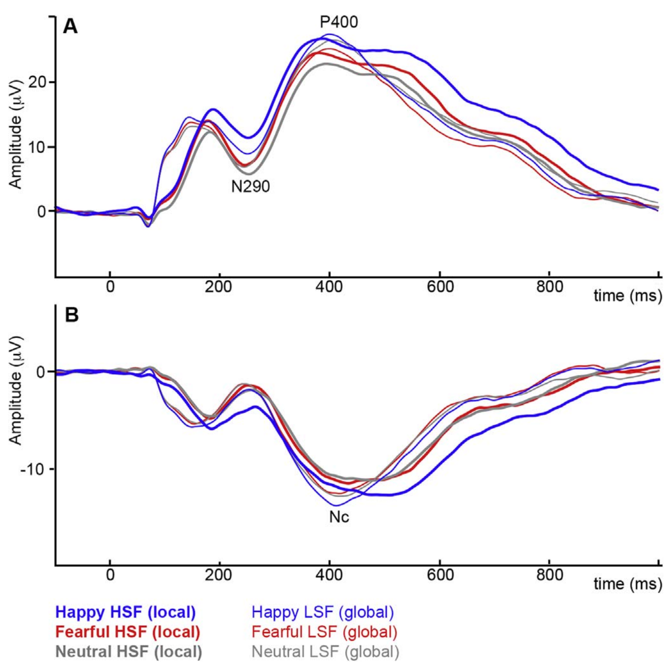

Fig. 2. Grand averages at the pooled electrodes for N290 and P400 (A) and Nc (B) evoked by local (thick lines) or global (thin lines) faces with happy (blue), fearful (red), or neutral (grey) expression. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

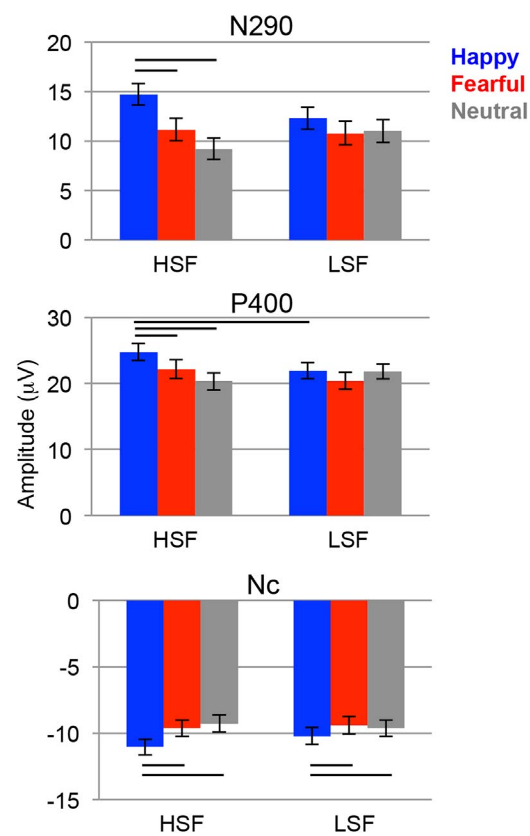

Fig. 3. Means and Standard Errors of N290, P400 and Nc amplitudes, evoked by facial expressions with HSF (local) or LSF (global) content. Black connecting lines represent significant differences between the emotions ($p < 0.05$). Note that the significant effect at the Nc amplitude represents a main effect of emotion.

were C3, Cz, C4, FC1, FC2 and Fz. Although based on previous research some additional electrodes of interest could be identified, those electrodes were excluded based on low data quality in most of the participants (i.e. P7, P8, T7, T8, F3 and F4) or unclear components of interest (i.e. Pz). To limit the number of statistical comparisons, analyses were performed for the average amplitude over all electrodes of interest Figs. 2 and 3. Please refer to Appendix C for analyses on single electrodes. These analyses led to the same conclusions regarding effects of SF and emotion. Furthermore, they revealed that the reported effects were most evident at medial electrodes. (Table 2)

Main interest was in the interaction between SF (LSF; HSF) and emotion (neutral; fearful; happy). Repeated measures ANOVAs were performed with SF and emotion as independent variables, with mean activity as dependent variable. If this interaction would be significant, paired *t*-tests would be performed between emotions for each SF to study whether discrimination between emotions depends on SF. Furthermore, we would perform a paired *t*-test between HSF and LSF for the fearful, neutral and happy faces to study whether processing of the emotion itself depends on the SF content of the face. For all reported analyses, the alpha value was set at 0.05 and all post-hoc analyses are corrected for multiple testing using Bonferroni correction.

Table 2
Means and standard errors (in μV) of N290, P400 and Nc amplitudes, evoked by facial expressions with HSF (local) or LSF (global) content.

	N290		P400		Nc	
	LSF	HSF	LSF	HSF	LSF	HSF
Happy	12.3 (1.1)	14.7 (1.1)	21.9 (1.2)	24.7 (1.3)	−10.2 (.6)	−11.0 (.6)
Fear	10.7 (1.2)	11.1 (1.2)	20.4 (1.3)	22.2 (1.4)	−9.4 (.6)	−9.6 (.6)
Neutral	11.0 (1.2)	9.2 (1.1)	21.8 (1.1)	20.3 (1.3)	−9.6 (.6)	−9.3 (.7)

3. Results

3.1. N290 component

Repeated measures ANOVA on N290 mean amplitude revealed a significant interaction between SF and emotion ($F(2;120) = 5.9$; $p = 0.004$; $\eta^2 = 0.090$). Furthermore, there was a main effect of emotion ($F(2;120) = 18.11$; $p < 0.001$; $\eta^2 = 0.232$) with more positive amplitudes for happy than fearful ($p < 0.001$) or neutral faces ($p < 0.001$). There was no main effect of SF ($F(1;60) = 0.26$; $p = 0.612$; $\eta^2 = 0.004$). Based on the interaction, we performed paired *t*-tests to investigate whether emotion effects were present for each SF, and whether the SF content affected processing of each of the emotions. Paired *t*-tests (against alpha = 0006 due to 9 comparisons) revealed that in the HSF condition, happy faces evoked more positive amplitudes than fearful ($t(60) = -4.3$; $p < 0.001$) and neutral faces ($t(60) = 6.3$; $p < 0.001$). No significant differences were found for other comparisons (all $p > 0.018$).

3.2. P400 component

Repeated measures ANOVA on P400 mean amplitude revealed an interaction between emotion and SF ($F(2; 120) = 7.7$; $p = 0.001$; $\eta^2 = 0.114$). Furthermore, there was a main effect of emotion ($F(2;120) = 9.8$; $p < 0.001$; $\eta^2 = 0.141$) with more positive amplitudes for happy than fearful ($p = 0.002$) or neutral faces ($p < 0.001$). There was no main effect of SF ($F(1;60) = 2.7$; $p = 0.106$; $\eta^2 = 0.043$). Similar to the results reported for the N290 component, paired *t*-tests (against alpha = 0006 due to 9 comparisons) for the P400 revealed in the HSF condition significantly more positive amplitudes evoked by happy than fearful ($t(60) = -2.9$; $p = 0.005$) and neutral faces ($t(60) = 5.6$; $p < 0.001$). Furthermore, happy HSF faces evoked significantly more positive amplitudes compared to happy LSF faces ($t(60) = 3.1$; $p = 0.003$). No significant differences were found for other comparisons (all $p > 0.040$).

3.3. Nc component

Repeated measures of ANOVA on the Nc mean activity revealed a main effect of emotion ($F(2,120) = 7.4$; $p = 0.001$; $\eta^2 = 0.110$). There was no interaction ($F(2,120) = 1.2$; $p = 0.316$; $\eta^2 = 0.019$) or main effect of SF ($F(1,60) = 0.57$; $p = 0.452$; $\eta^2 = 0.009$). Pairwise comparisons revealed that happy faces evoked more negative amplitudes compared to fearful (Bonferroni corrected $p = 0.008$) or neutral ones (Bonferroni corrected $p = 0.002$). No significant difference in amplitude was found between the fearful and neutral faces ($p > 0.99$).

Overall, analyses reveal that differential processing of emotions was mainly seen in the HSF condition between happy and the other emotions. For the Nc component happy faces were discriminated from fearful and neutral ones independently of the presence of higher or lower spatial frequency information.

4. Discussion

This study investigated the effect of local and global information (as manipulated by spatial frequencies) on emotion discrimination in infants. Infants viewed emotional faces, that either contained lower spatial frequencies (related to global information) or higher spatial frequencies (related to local information). To study emotion discrimination, we investigated whether the amplitude of the evoked N290, P400, and Nc components differed between emotions. It is suggested that the N290 and P400 relate to perceptual processing and that the Nc relates to attentional processing of emotions (De Haan and Nelson, 1999; Halit et al., 2003; Nelson and Monk, 2001; Richards, 2003). The results revealed that the presence of lower versus higher spatial frequency information affected whether infants could discriminate between emotions. At the N290 and P400, happy faces could be discriminated from neutral and fearful faces when only higher, but not only lower, spatial frequency information was available. At the Nc, happy faces were discriminated from neutral and fearful ones independent of the presence of lower or higher spatial frequency information. At all components there was no discrimination of fearful from neutral faces when either lower or higher spatial frequency information was available.

The present results in infants indicate a differential involvement of lower and higher spatial frequency information in emotion processing, although only for perceptual (i.e. N290 and P400) and not attentional (i.e. Nc) processing. This is in line with previous research in adults and children (Deruelle et al., 2008; Pourtois et al., 2005; Vlamings et al., 2009, 2010a, 2010b). These results can be placed within current models concerning the neural basis of facial-emotion processing. According to the emotion-processing network, perceptual processing of emotions occurs in the fusiform gyrus (FG) and the superior temporal sulcus (STS) (see Leppänen and Nelson (2009) for an extensive overview of this emotion-processing network). These areas are suggested to receive higher spatial frequency information via the visual cortex. Top-down attentional modulation of perceptual processes is thought to occur via the orbitofrontal cortex (OFC). The OFC, in addition to the amygdala, is suggested to receive lower spatial frequency information through a subcortical pathway. Presumably there are connections between the OFC and the perceptual areas (i.e. FG and STS) that forward lower and higher spatial frequency information (Leppänen and Nelson, 2009). Assuming this model is correct, we could speculate that at 10 months the connections from the OFC to the perceptual areas are too weak to forward the lower spatial frequency information that is necessary for emotion discrimination. Connections from perceptual areas to the OFC might be strong enough to forward the necessary higher spatial frequency information. This might at least partly explain why in the present study perceptual processes (i.e. N290 and P400) differ between happy and other emotions only when higher spatial frequency information is present, while the presence of lower or higher spatial frequency information does not affect attentional processes (i.e. Nc).

This explanation does not take into account that at least some lower spatial frequency information is likely to reach the FG and STS via the visual cortex. That is, lower and higher spatial frequency information reach the visual cortex, respectively via the magnocellular and parvocellular pathway (Mishkin and Ungerleider, 1982; Nassi and Callaway, 2009). The parvocellular pathway is thought to continue into the ventral stream and magnocellular pathway into the dorsal stream. While the FG and STS are part of the ventral stream and thus mainly receive higher spatial frequency information, the ventral and dorsal streams interact (Mishkin and Ungerleider, 1982; Nassi and Callaway, 2009). Consequently, at least some lower spatial frequency information is likely to reach the FG and STS via the visual cortex as well. It is yet unexplained why lower spatial frequency information that reaches these areas via the visual cortex is insufficient for emotion discrimination. Future studies should reveal the specific underlying mechanisms for the absence of perceptual emotion discrimination based on lower spatial frequency information at 9–10 months of age.

The presence of discriminating happy faces from neutral and fearful faces at 9–10 months replicates previous studies in younger infants (de Haan et al., 2004; Hoehl and Striano, 2010a; Leppänen et al., 2007; Peltola et al., 2009; Taylor-Colls and Pasco Fearon, 2015; Yrttiaho et al., 2014). The effect was present at all three investigated ERP components, and shows that perceptual- and attention-related components are sensitive to the difference between positive versus other emotions (happy versus fearful or neutral expressions). However, previous neurocognitive findings indicated that infants can also discriminate negative from other negative or neutral emotions (as reflected in comparisons between fearful and neutral, angry, or sad faces; Hoehl and Striano, 2008, 2010b; Kobiella et al., 2008; Leppänen et al., 2007; Parker et al., 2005; Taylor-Colls and Pasco Fearon, 2015; Yrttiaho et al., 2014). The lack of discriminating fearful from neutral faces in the present study contradicts these previous findings and is not yet taken into account in the proposed relation to the models (Johnson, 2005, 2015; Leppänen and Nelson, 2009). An explanation for the discrepancy between present and previous findings could reside in the effects of filtering that removed information from the faces. This had two consequences: firstly, the faces looked different from real-life faces, which could make emotion discrimination more difficult. Under such circumstances, it could be speculated that infants are better in discrimination of positive than negative emotions. Infants could be more skilled in processing positive emotions, since this skill arises earlier in life than processing negative ones (Porto et al., 2016). A second consequence of filtering is that neither of the faces contained mid-band spatial frequencies (i.e. the visual information in between lower and higher spatial frequency information). Possibly, infants require this information to discriminate fearful expressions. Mid-band frequencies are suggested to be important for emotion recognition in older children and adults as well (Gao and Maurer, 2011). To gain further insight in the neural basis of facial-emotion processing, a next step will be to compare neural processing of different types of emotional faces filtered to contain only lower, higher or mid-band spatial frequencies with unfiltered emotional faces. This would increase knowledge on the roles of spatial frequency content, valence, and experience or familiarity on infants' emotion discrimination.

While interpreting the current results, the scope and consequently the limitations of the study should be taken into account. The current stimuli were filtered to contain specific spatial frequency information. Consequently, only limited conclusions can be drawn regarding face processing of unfiltered, real-life, faces. Furthermore, while manipulating spatial frequencies, the luminance contrast of the stimulus changes as well. In adults, this contrast change does not account for effects of spatial frequencies on processing of emotions (Vlamings et al., 2009). However, since both contrast sensitivity and spatial frequency processing develop throughout childhood, possible effects of contrast differences between spatial frequency conditions cannot be excluded. In addition, a test-retest study conducted in a subset of the current sample showed low test-retest reliability for the effects of spatial frequency and emotional content on the face-sensitive ERPs (Munsters et al., 2017). Consequently, no conclusions can be drawn regarding emotion processing in individual participants. Nonetheless, the test-retest study showed that the results from the current design are replicable at a group level (Munsters et al., 2017). In contrast to the current findings the test-retest study however revealed differential processing of fearful and neutral faces at the N290 and P400 components in the high spatial frequency condition. This differential processing is also reported in some previous studies, but not in others (see Table 1 for an overview). Further research is needed to unravel those contracting findings.

Overall, the current study revealed that perceptual processes (as reflected in the N290 and P400 components) differ between happy and other emotions when only higher spatial frequency information (related to local information) is available, but not when only lower spatial frequency (related to global information) is present. Furthermore, processes related to attention allocation (reflected in the Nc component) differ between happy and other emotions regardless of the available spatial frequency information. These findings enhance the knowledge on how infants process emotional faces.

Funding sources

The Consortium on Individual Development (CID) financed this study. CID is funded through the Gravitation program of the Dutch Ministry of Education, Culture, and Science and the NWO (Grant No. 024.001.003). The funding source had no involvement in the study design, data collection, analyses and interpretation of data, writing the report, and in the decision to submit the article for publication.

Acknowledgements

The authors thank parents and children for participating in the study. We also are grateful to Esther Eijlers, Aliegriet Pol, Malu Parson, Paula Rompes, and the employees at the KinderKennisCentrum of Utrecht University for their help in set-up of the study and data collection. The Consortium on Individual Development (CID) financed this study. CID is funded through the Gravitation program of the Dutch Ministry of Education, Culture, and Science and the NWO (Grant No. 024.001.003). The funding source had no involvement in the study design, data collection, analyses and interpretation of data, writing the report, and in the decision to submit the article for publication.

Conflict of interest

The authors declare no conflict of interest.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2017.09.006.

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