MIKKO PELTOLA

Emotion–Attention Interactions in Infants’ Face Processing

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ABSTRACT

The exchange of emotional information through facial expressions is essential to early infant-caregiver interaction. The ability to process and comprehend information from facially communicated emotional signals develops significantly throughout the first year of life. One manifestation of this development during the second half of the first year is infants' increased attention to fearful rather than happy and emotionally neutral facial expressions. The four studies reported in this dissertation were intended to characterize the emotional modulation of attention in further detail by investigating the developmental emergence of and the critical factors underlying the attentional prioritization of fearful expressions in infancy.

Study I reported evidence of the emergence of enhanced attention to fearful faces between 5 and 7 months. While the data from 7-month-old infants replicated earlier findings of longer looking and larger attention-sensitive brain responses to fearful than happy faces, no differences were observed with either measure in 5-month-old infants. Studies II-IV utilized a novel paradigm to examine 7-month-old infants' disengagement of attention from facial expression stimuli toward non-emotional distractor stimuli and the critical factors that may underlie infants' attentional bias to fearful faces. These studies showed that fearful faces modulate infants' attention disengagement by increasing the latency and decreasing the frequency of eye movements from the centrally presented face toward the peripheral distractor stimulus. This effect was absent for faces that had been rated as novel as a fearful expression but lacking equal emotional signal value (Study II) and for neutral faces that had fearful eyes (Study III), the most prominent visual feature of a fearful expression. Finally, in Study IV, infants showed a larger deceleration of heart rate orienting response to fearful faces, resembling the autonomic response to threat-related stimuli typically observed in adults.

In light of these data, it is suggested that the turn of the second half of the first year is a period during which critical developmental changes take place in the way infants perceive, experience, and learn fear. At a developmental phase during which

infants typically begin to move independently, emotional significance of sensory stimuli becomes integrated with the functioning of attentional control mechanisms. The persistent bias to prefer fearful expressions over other stimuli presumably enables relatively efficient associative learning about the contexts in which fearful emotions are expressed by the caregivers (e.g., situations involving impending danger). In terms of brain function, the development of emotion-attention interactions may reflect the emergence of functional connections between structures sensitive to the emotional significance of sensory stimuli (amygdala) and cortical areas implicated in attentional control and emotion regulation (prefrontal, orbitofrontal, and anterior cingulate cortices).

LIST OF ORIGINAL PUBLICATIONS

This dissertation consists of the following four publications, which will be referred to in the text by their Roman numerals I – IV:

I Peltola, M.J., Leppänen, J.M., Mäki, S., & Hietanen, J.K. (2009). Emergence of enhanced attention to fearful faces between 5 and 7 months of age. *Social Cognitive and Affective Neuroscience, 4,* 134-142. Copyright © 2009 by Oxford University Press. Reproduced with permission.

II Peltola, M.J., Leppänen, J.M., Palokangas, T., & Hietanen, J.K. (2008). Fearful faces modulate looking duration and attention disengagement in 7-month-old infants. *Developmental Science, 11,* 60-68. Copyright © 2008 by John Wiley and Sons. Reproduced with permission.

III Peltola, M.J., Leppänen, J.M., Vogel-Farley, V.K., Hietanen, J.K., & Nelson, C.A. (2009). Fearful faces but not fearful eyes alone delay attention disengagement in 7-month-old infants. *Emotion, 9,* 560-565. Copyright © 2009 by the American Psychological Association. Reproduced with permission.

IV Leppänen, J., Peltola, M.J., Mäntymaa, M., Koivuluoma, M., Salminen, A., & Puura, K. (2010). Cardiac and behavioral evidence for emotional influences on attention in 7-month-old infants. *International Journal of Behavioral Development, 34,* 547-553. Copyright © 2010 by SAGE Publications. Adapted with permission.

1. INTRODUCTION

Throughout the course of evolution, survival and well-being have been contingent on one's ability to monitor the environment for potential signals of danger and reward (Williams, 2006; Öhman, 2009). In addition to detecting signals implying imminent threat or pleasure in the physical environment, humans are particularly adept at recognizing even subtle variation in emotional states expressed on others' faces in the social environment (Adolphs, 2002). These elementary social-cognitive processes and the specialized neural circuitry they are based upon lay the foundation for the sophisticated ability of humans to acquire knowledge about the physical and social world through observing others (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007; Olsson & Phelps, 2007). Adaptive behavior also requires sensitivity to the contextual determinants of facially communicated emotion because facial expressions may not always provide direct indications of the origin of the emotion conveyed but can act more as indirect referents to some external or internal source eliciting a change in emotional state (e.g., Aviezer et al., 2008). A fearful facial expression, for example, could be interpreted as conveying fear toward the observer but it may equally reflect the signaller's fearful response to a threatening stimulus or event in the vicinity.

Reading and transmitting facial communicative signals is especially important for a preverbal infant. Without the aid of words, infant-caregiver interaction relies on the communication of emotions, intentions, and needs via the nonverbal channels of the face, body, touch, and vocal prosodic cues (Feldman, 2007). Despite recent progress in studying the development of emotion-processing in infancy (Leppänen & Nelson, 2009), significant gaps in our knowledge of infants' emotion-processing abilities and the neural and cognitive mechanisms subserving these abilities are nevertheless evident. This dissertation attempts to characterize the developmental emergence of infants' enhanced attention to emotionally salient facial signals in the first year of life.

In this introductory chapter, I will first describe studies reporting prioritization of attention to and enhanced processing of emotionally significant signals in adults and discuss the mechanisms that may underlie such phenomena. I will then review research on early brain development and the emergence of infants' ability to perceive and recognize facial expressions of emotion. Finally, I will provide a framework for the present set of studies by describing the developmental foundations and available evidence for the interaction between emotional and attentional processes in infants.

1.1 Emotional modulation of attention in adults

A fundamental property of attention is its limited processing capacity. We are constantly faced with an abundance of stimuli but able to consciously attend to only a subset of available information at any given moment (Broadbent, 1958). Conscious, "top-down" controlled evaluation of the relevance of all incoming stimuli to our current goals would create an excessive burden for the brain's executive attention system. It is likely that such constraints have led certain types of information to gain "privileged" or even automatic access to awareness and to deploy attentional resources. Emotional stimuli represent one such type of sensory information.

There is now ample evidence showing how emotionally and motivationally signifcant stimuli – be they positive or negative in valence – substantially modulate attention and perception (for reviews, see Vuilleumier, 2005; Williams, 2006). Emotional significance can be defined as the relevance of a given stimulus in relation to our core motivation to minimize danger and maximize pleasure (Williams, 2006). Within this framework, stimuli that hold either a direct or a more ambiguous association with threat (e.g., predators, images of violence, angry or fearful emotional expressions) are particularly likely to be subject to rapid and persistent capture of attentional resources as well as enhanced perceptual processing (Vuilleumier, 2005; Öhman, 2009).

1.1.1 Introduction to methods

Before reviewing the experimental studies on the influence of emotional information on attentional and perceptual processing and their neural mechanisms, I will briefly introduce the methodology that is commonly used in exploring such issues. A variety of tasks have been used to study whether emotional information has a biasing effect on attentional and perceptual functions that is not similarly observed for neutral stimuli (see Bishop, 2008; Vuilleumier, 2005, for reviews). Performance is typically measured with manual responses that reflect the speed and accuracy of detecting the presence or categorizing the content of various target stimuli. The direction of the effects, e.g., whether ongoing processing is facilitated or interfered by emotion, is dependent on the task demands.

The impact of stimulus content on the orienting of attention in the spatial domain has often been studied with variations of the probe detection paradigm (MacLeod, Mathews, & Tata, 1986). In the task, two stimuli (e.g., an angry and a happy face) are first presented simultaneously on the screen for a brief period of time after which they disappear and a target stimulus (e.g., a small asterisk) appears at a location previously occupied by one of the two stimuli. Facilitation of attention is inferred if there is a tendency for the manual responses to be consistently faster at the location of one of the preceding stimuli. Another way to measure whether emotional stimuli are associated with an automatic capture of attention is to employ paradigms involving a "competition" between emotional and target stimuli. Competition for attentional resources can be provoked by presenting emotional stimuli as task-irrelevant distractors (e.g., performing a letter discrimination task with letters superimposed on a facial expression stimulus; Bishop, Jenkins, & Lawrence, 2007) or by using emotional stimuli to provide incorrect cues as to the spatial location at which the target will appear (e.g., presenting an emotional stimulus on the right side of the screen, followed by the target stimulus on the left; Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2004). The influence of emotion on early visual processing and the perceptual threshold of detecting the presence of different stimuli have typically been examined with rapid serial visual presentation (RSVP) paradigms. In an RSVP task, a stream of very rapidly changing stimuli is presented and the participant's task is to report whether a target stimulus (e.g., a fearful or a happy face) appeared among the stream of stimuli (Milders, Sahraie, Logan, & Donnellon, 2006).

Of the brain imaging methods for studying the neural correlates of emotion-processing, the two most commonly used are electroencephalography (EEG) and functional magnetic resonance imaging (fMRI). EEG is used to record electrical activity from the scalp surface caused by a large number of postsynaptic potentials in the underlying cortex (Davidson, Jackson, & Larson, 2000). The advantages of EEG in human brain research include its temporal accuracy in tracing brain activity in the millisecond range (Davidson et al., 2000) and its suitability for use in all age populations, even in newborns, because it is relatively easy to apply and does not require extensive restriction of motion (DeBoer, Scott, & Nelson, 2007). A major factor complicating the interpretation of EEG data is its questionable spatial resolution, i.e., the fact that the activity recorded from a single electrode does not reliably indicate that the activity originates from the cortical tissue right underneath the electrode because intervening structures, most notably the skull, cause smearing of the electrical signal (Michel et al., 2004). Novel techniques such as independent component analysis (Makeig, Debener, Onton, & Delorme, 2004) have been developed to provide spatially more accurate estimates of the underlying sources of scalp-recorded activity.

A traditional way of analyzing electrical brain activity with EEG is to measure event-related brain potentials (ERPs). ERPs are averaged amplitude fluctuations in the EEG signal that reflect synchronous activity of a large number of cortical neurons in response to a discrete stimulus or event (Fabiani, Gratton, & Coles, 2000; Handy, 2005). Averaging over multiple repetitions of the same stimulus category or event is considered to cancel out much of the “noise” (i.e., random brain activity and artefacts from various sources) to enable observation of the brain’s underlying neural activity related to the mental operation of interest (Fabiani et al., 2000). In adult studies, ERPs to faces, facial expressions, and other emotional stimuli have been measured with various stimulus presentation paradigms, including the attention paradigms outlined above. As a result, different ERP components (i.e., discrete positive or negative amplitude deflections) have been observed which are considered to reflect perceptual and attentional processes during the perception of different social and emotional stimuli. Adult face processing studies typically focus on the N170 component, which is a negative amplitude shift most prominent on posterior electrode sites at around 170 ms post-stimulus (see Rossion & Jacques, 2008, for a review). The N170 is considered to reflect the activation of cortical areas sensitive to the processing of the structural configuration of faces (i.e., perceiving a face as a face) as it has been consistently observed to show a more negative peak amplitude for faces than houses, cars, or other non-face objects (Rossion & Jacques, 2008). Another component related to the themes of the present thesis is “early posterior negativity” (EPN), which is an ongoing shift in the negative direction at around 200-350 ms post-stimulus in posterior areas. Differences in the magnitude of the EPN are considered to reflect selective attention to and elaborated perceptual processing of those stimuli that show relatively larger negativity in the EPN waveform (Codispoti, Ferrari, Junghöfer, & Schupp, 2006; Schupp et al., 2007).

Research on the neural mechanisms of emotion-processing has also benefited greatly from modern brain imaging techniques such as functional magnetic resonance imaging (fMRI), which provides estimates of regional brain activity by measuring hemodynamic responses (i.e., changes in blood oxygen levels) in the brain during different mental operations (Huettel, Song, & McCarthy, 2004; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). The advantage of fMRI over EEG/ERP methods is in superior spatial accuracy, which also enables accurate anatomical and functional localization for deeper (i.e., subcortical) structures beneath the cortex. It is also possible to analyze brain function on a network-level by measuring how activity patterns in different areas of the brain are correlated (Huettel et al., 2004). The disadvantages of fMRI include a poor temporal resolution that hinders observations of real-time neural operations and its sensitivity to movement artefacts, which prevents the use of fMRI with infants and small children while awake (Huettel et al., 2004).

Finally, there is also a long tradition in studying the responses of the autonomic nervous system during the perception of emotions (Bradley, 2009; Lang, Bradley, & Cuthbert, 1997). Autonomic responses, such as deceleration or acceleration of heart rate or changes in the activity of the sweat glands, are largely controlled by the deeper structures of the brain and therefore provide a view to automatically evoked psychophysiological responses during emotion perception (Bradley, 2009).

1.1.2 Behavioral evidence

Studies have converged in showing that in diverse tasks sensitive to various components of attentional and perceptual processing, as outlined above, emotionally significant information captures attention and is prioritized in the information processing stream. In visual probe detection tasks, attention tends to be automatically allocated towards threat-related stimuli (e.g., fearful faces) over simultaneously presented neutral stimuli, indicated by faster manual responses (Holmes, Green, & Vuilleumier, 2005; Pourtois, Grandjean, Sander, & Vuilleumier, 2004) and also eye movements (Bannerman, Milders, de Gelder, & Sahraie, 2009) to the direction cued by the threat-related stimulus. Automatic capture of processing resources is shown in slower responses to the target when emotionally negative stimuli provide incorrect spatial location cues (Koster et al., 2004) or are irrelevant and distracting for the task at hand (Fenske & Eastwood, 2003; Georgiou et al., 2005).

The benefits of emotion for early visual processing are highlighted by studies applying the RSVP paradigm, in which participants are more likely to detect (i.e., become aware of) fearful faces than happy or neutral faces in the RSVP stream (De Martino, Kalisch, Rees, & Dolan, 2009; Milders et al., 2006; Yang, Zald, & Blake, 2007). It is noteworthy that in the study of Yang et al. (2007), the mere presentation of the eyes of a fearful face was sufficient to produce these effects, suggesting that the eye region provides the information critical to perceiving the face as fearful. Phelps, Ling, and Carrasco (2006) even observed that the mere presentation of rapidly flashed fearful faces enhanced the participants' sensitivity to detect contrast differences in subsequently presented low-contrast stimuli, providing evidence that transient changes in emotional context exert an influence on early visual processing, i.e., making people actually see better in the presence of emotionally salient stimuli. Altogether, the data indicate that starting from the early stages of visual processing, emotionally significant stimuli (and particularly stimuli associated with threat) are given precedence over competing information in order to guide attention to the most relevant features in the environment (Vuilleumier, 2005).

1.1.3 Neural mechanisms

Findings from studies that have recorded ERPs during the perception of emotional stimuli parallel the behavioral findings described above by showing amplification of electrical activity for emotionally significant stimuli in brain areas associated with perceptual and attentional functioning (Adolphs, 2002; Vuilleumier, 2005). The N170 has been repeatedly shown to have a larger amplitude for fearful than happy or neutral faces (Batty & Taylor, 2003; Blau, Maurer, Tottenham, & McCandliss, 2007; Leppänen, Moulson, Vogel-Farley, & Nelson, 2007; Leppänen, Hietanen, & Koskinen, 2008; Stekelenburg & de Gelder, 2004; Williams, Palmer, Liddell, Song, & Gordon, 2006), possibly indicating increased neural activation in cortical areas sensitive to the processing of the structural configuration of faces (e.g., Williams et al., 2006). Similarly, enhanced EPN responses to highly arousing emotional scenes (Schupp et al., 2007) and fearful/angry faces (Leppänen, Kauppinen, Peltola, & Hietanen, 2007; Leppänen et al., 2008; Schupp et al., 2004) have been observed, providing electrophysiological correlates of selective attention and elaborated perceptual representations for emotionally salient material.

The amplitude modulation of the face-sensitive N170 component is typically considered to reflect enhanced activation in areas of the posterior temporal cortex such as the fusiform gyrus (Rossion & Jacques, 2008). Corroborating the ERP findings, fMRI studies have also shown increased neural responses to fearful than happy/neutral faces in the fusiform area and visual cortex (Vuilleumier, Armony, Driver, & Dolan, 2001; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). Thus, the response of the fusiform area that typically shows selectivity for faces over non-face stimuli (Kanwisher, McDermott, & Chun, 1997) is further augmented by the emotional content of the face. The activation of these posterior visual processing areas to fearful faces correlates (Morris et al., 1998) with activity in the amygdala, a collection of cell nuclei located in the medial temporal lobe (Whalen & Phelps, 2009). The amygdala typically shows a robust response to emotional faces and to fearful faces in particular (Hariri et al., 2002; Morris et al., 1996; Morris et al., 1998; Vuilleumier et al., 2001; Whalen et al., 2001). Moreover, the mere presentation of fearful eye whites (Whalen et al., 2004) or fearful eyes embedded in an otherwise neutral face (Morris, deBonis, & Dolan, 2002) appear to be sufficient to trigger increased amygdala activation, highlighting the critical role of the eye region in detecting fear in faces (cf. Yang et al., 2007). Finally, areas of the prefrontal cortex (PFC) such as the orbitofrontal (OFC) and anterior cingulate cortex (ACC) are also often activated by the perception of threat-related stimuli (Nili, Goldberg, Weizman, & Dudai, 2010; Ochsner & Gross, 2005; Pessoa, 2009; Pezawas et al., 2005; Vuilleumier et al., 2001) and show a correlation with activation of the amygdala (Bishop et al., 2007; Hare et al., 2008; Pezawas et al., 2005).

The pattern of brain activation during the processing of emotional faces under different task demands has begun to reveal the key components of the brain network that mediates the influence of emotional stimuli on attentional and perceptual processing, with the amygdala implicated as a central hub in this network (Vuilleumier, 2005). The amygdala has traditionally been associated with generating and learning fearful responses to threat-related stimuli (such as predators) in animals and humans (Phelps & LeDoux, 2005). These include "fear bradycardia", i.e., the rapid slowing of heart rate with accompanied behavioral "freezing" when an animal is confronted with a threatening stimulus (Bradley, 2009; Kapp, Supple, & Whalen, 1994). As has become evident with modern brain imaging techniques such as fMRI, the amygdala also shows increased activation to relatively milder threat-related stimuli such as fearful faces (or even to simple features such as fearful eyes; Morris et al., 2002; Whalen et al., 2004) which typically do not trigger any subjective feelings of fear in the participants (Whalen, 1998). This has led to a broader view of the amygdala as a "vigilance system" that serves to provide a rough evaluation for incoming sensory stimuli about their significance and to bias the attentional and perceptual systems to engage in deeper processing of stimuli deemed potentially relevant (Pessoa & Adolphs, 2010; Vuilleumier, 2005; Whalen et al., 2009).

Modulation of attention and perception is enabled by the vast connectivity of the amygdala with other brain regions, including projections to and from the visual cortex, fusiform gyrus, and regions of the prefrontal cortex, including the anterior cingulate and orbitofrontal cortices (for reviews, see Bauman & Amaral, 2008; Pessoa & Adolphs, 2010; Phelps & LeDoux, 2005). One mechanism through which the amygdala can participate in enhancing the visual processing of fearful expressions is a pathway through projections from the amygdala to the cholinergic neurons of the basal forebrain (Whalen, 1998). Thus, activation of the amygdala during the perception of fearful faces may increase the release of the neurotransmitter acetylcholine, which in turn produces transient increases in excitability (i.e., lowered firing thresholds) of face-sensitive neurons in the fusiform gyrus (Bentley, Vuilleumier, Thiel, Driver, & Dolan, 2003; Whalen, 1998). It is possible that in situations where different stimuli compete for attentional resources (as in probe detection tasks), such enhanced sensory representation may serve to bias attentional selection in favor of emotional stimuli and even suppress cortical responsivity to competing stimuli (Carlson, Reinke, LaMontagne, & Habib, in press; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2006; Vuilleumier, 2005).

Prefrontal brain structures such as the ACC are typically implicated in various cognitive functions (Bush, Luu, & Posner, 2000; Miller & Cohen, 2001) but for present purposes it is relevant to note that they have an important role in controlling the direction and maintaining the focus of attention (Bush et al., 2000; Casey et al., 1997; Posner & Rothbart, 2007). Another central PFC function is emotion regulation, which operates through inhibition of amygdala activation through neurons in the PFC (Pezawas et al., 2005). These operations are reflected in the concurrent activation of the ACC and the amygdala during the perception of emotionally salient stimuli (Nili et al., 2010; Ochsner & Gross, 2005; Pessoa, 2009; Pezawas et al., 2005) and particularly during tasks that entail suppressing unwanted shifts of attention toward distractors (Bishop et al., 2007; Hare et al., 2008; Vuilleumier et al., 2001). In summary, a widespread network of brain areas appears to be activated during the perception of emotional stimuli (Figure 1) and involves areas that process sensory information, evaluate the emotional significance of incoming stimuli, and areas that control attention and emotional reactions to the stimuli.

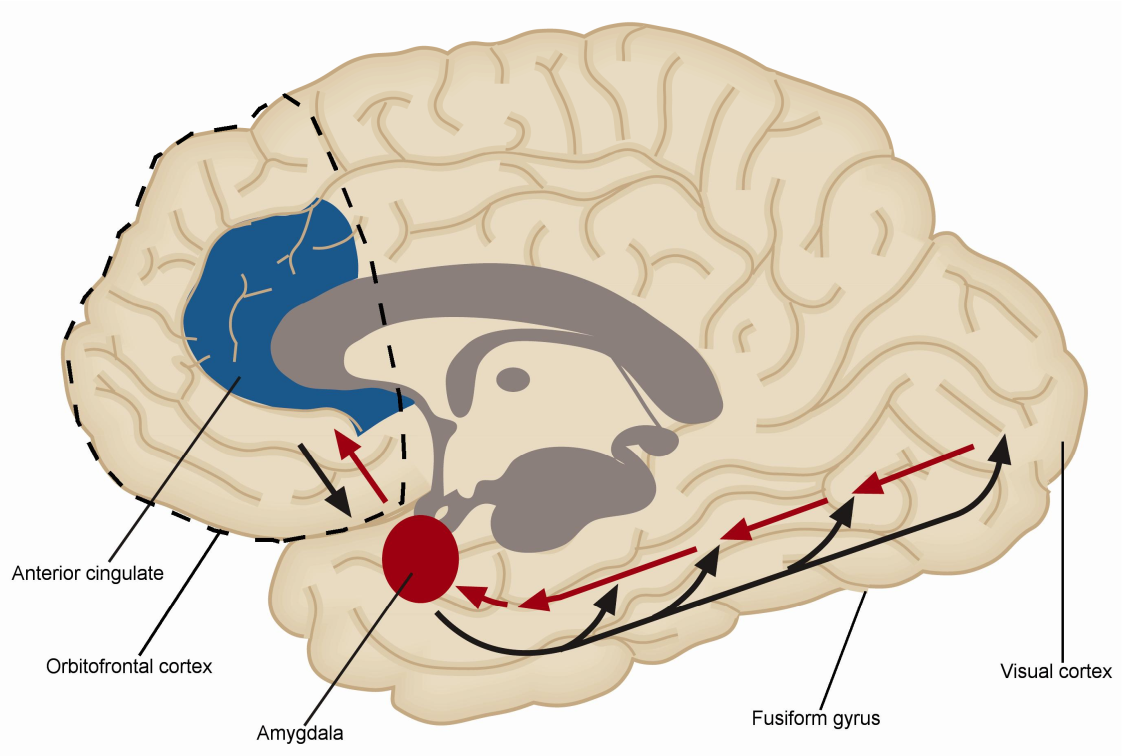

FIGURE 1. Some of the key brain areas and their reciprocal connections involved in the processing of emotional visual stimuli. The area within the dashed line approximates the area covered by the prefrontal cortex. Adapted with permission of Leppänen (2007).

1.2 Early development of face processing and attention

Before turning to the developmental emergence of emotional face processing skills, some background for the associations between brain development, face perception, and attention during infancy is presented. In general, rather little is currently known about the early development of the brain network that supports attentional allocation to and preferential processing of emotionally salient stimuli. The methods for measuring brain activity in infants currently only permit recording of cortical activity, thus the putative activation of the amygdala or other subcortical sources during the perception of facial expressions remains unobservable.

1.2.1 Face processing

At birth, infants' visual acuity is poor (Banks & Salapatek, 1983), making it unlikely that the infant would be able to discern subtle differences from facially communicated emotional signals. Infants do, however, show a very early interest in looking at faces (Goren, Sarty, & Wu, 1975) which is suggested to be driven by an innate preference for coarsely face-like stimuli (Johnson, 2005b). The extensive experience with observing others' faces that infants accumulate during the first months of life gradually leads to more finely tuned representations of faces and the different information that faces convey (e.g., identity, expression, and direction of others' attention; Johnson, 2005b; Nelson, 2001). Face processing abilities have typically been studied with different variations of the habituation paradigm (Fantz, 1964). For example, Quinn and Tanaka (2009) repeatedly showed 3- to 7-month-old infants an image of a female face in 15-second trials. After habituation (i.e., a decrement in looking time), the familiarized stimulus was replaced by a preference test stimulus pair which included the familiar face and a face of the same female to which minor featural or configural changes had been made (i.e., the size or relative distance of the eyes or mouth had been altered). Infants' ability to perceive the change in the test stimulus face was inferred from a preference in looking longer at the face that had been altered. The infants showed sensitivity in detecting configural changes especially in the eye region (i.e., when the distance between the eyes changed).

A number of other studies have also suggested that infants show an early-emerging sensitivity to process information from the eyes (see Gliga & Csibra, 2007; Senju & Johnson, 2009, for reviews). Even newborn infants look longer at faces with the eyes open vs. closed (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000) as well as at faces with direct vs. averted eye gaze (Farroni, Csibra, Simion, & Johnson, 2002). Studies utilizing eye tracking cameras that provide spatially detailed information about infants' eye movements toward different images also indicate that while scanning faces and facial expressions, infants between 4 and 7 months of age tend to fixate mostly on the eye region and less on the mouth area than do adults (Hunnius, de Wit, Vrins, & von Hofsten, in press). The adult-like triangular scanning pattern which involves switching visual focus between the eyes and mouth appears to emerge by 10 months of age (Libertus, Needham, & Pelphrey, 2007, March).

On a neural level, Johnson (2005a, b) has suggested that the early preference for face-like information is largely controlled by subcortical structures such as the superior colliculus, pulvinar, and amygdala. After the first months, face processing becomes increasingly subservient to cortical systems that gradually, possibly via synaptic pruning and reorganization, acquire much of the selectivity in processing facial information that is observed in adults (i.e., in the fusiform area; Johnson, 2005a; Johnson, Grossmann, & Cohen Kadosh, 2009). The development of cortical face processing systems has also been investigated by recording ERPs from young infants while they perceive faces and other stimuli. The N170 component that is measured in adults is not present with a similar timing and topography in infant ERPs. Two longer-latency components, N290 and P400 (the numbers corresponding to approximate latency of the peak in milliseconds), however, seem to share some of the same functional properties as the N170 (see de Haan, Johnson, & Halit, 2007, for a review). The negative-going shift in the N290 component is already more negative to faces than to Fourier-transformed control stimuli at 3 months of age (Halit, Csibra, Volein, & Johnson, 2004) and is modulated by the inversion of the face (i.e., when the face is presented upside-down) by 12 months of age in the same way as is the N170 in adults (Halit, de Haan, & Johnson, 2003). At 4 months of age, infants also show a larger N290 ERP amplitude for faces with direct than averted eye gaze (Farroni et al., 2002). Like the N170, the positive-going P400 component peaks faster with faces than with objects by 6 months of age (de Haan & Nelson, 1999) and, also similarly as in adults, is longer in latency for inverted than upright faces by 12 months of age (Halit et al., 2003). Together, the existing ERP data point to an increasing specialization in the cortical mechanisms responsive to faces (e.g., the fusiform area) during infancy (de Haan et al., 2007).

1.2.2 Attention

Studies have also provided insights on the early development of the frontal cortical structures that are part of the adult emotion-processing network. In general, frontal areas mature relatively late in development with changes in synapse formation and myelinization continuing even into adolescence (Giedd et al., 1999; Johnson, 2005a). Many of the functions performed by the frontal cortex are, nevertheless, already present in various tasks during infancy (e.g., Holmboe, Fearon, Csibra, Tucker, & Johnson, 2008) and the development of frontal cortical structures has a crucial role in the development of attentional abilities during the first year of life (Johnson, 2005a). The general developmental course of attention during the first year of life highlights an emerging ability to voluntarily regulate attentional focus between different stimuli competing for attention. During the first 2-3 months of life, it is characteristic for an infant to show “sticky fixation”, a marked inability to shift the eyes (i.e., attention) from one fixated location to another (Hood, 1995; Hunnius & Geuze, 2004). According to Johnson (2005a), the young infant’s difficulty in disengaging attention is due to visual orienting being driven largely by subcortical structures such as the superior colliculus in the early stages of ontogeny.

With the maturation of cortical structures (such as the ACC) after the first months of life, infants gain greater endogenous control over their visual orienting and eye movements (Colombo, 2001; Johnson, 2005a). The development of shifting attention away from an attended location to another has often been studied with a task in which peripheral stimuli are presented to attract attention to their location after attention has first been engaged on a central stimulus (i.e., the gap/overlap task; Aslin & Salapatek, 1975). For example, Hunnius and Geuze (2004) presented 6- to 26-week-old infants with the mother’s face or an abstract dynamic stimulus on the center of the screen for 1-2 seconds, followed by a peripheral stimulus for 5 seconds. On gap (or “non-competition”) trials, the central stimulus disappeared when the peripheral stimulus appeared whereas on overlap (“competition”) trials the central stimulus remained on the screen throughout the trial. Between 1 and 3 months of age, infants moved their eyes to the peripheral target on only a small proportion of the overlap trials (ca. 20% of trials), reflecting an immature ability to disengage attention from a stimulus under foveal vision. By 6 months of age, however, the frequency and latency of orienting to peripheral stimuli reaches an adult level of performance with attention shifts conducted on ca. 80% of the trials (Csibra, Tucker, & Johnson, 1998; Hunnius & Geuze, 2004). Prefrontal control is also highlighted in tasks that motivate the infant to inhibit reflexive saccades (i.e., eye movements) toward first-appearing sudden-onset distractor stimuli by increasing the saliency of subsequent target stimuli appearing at another spatial location (i.e., the anticipatory looking task; Johnson, 1995; see also Sheese, Rothbart, Posner, White, & Fraundorf, 2008). The ability to inhibit such reflexive saccades appears to be increasingly mastered by 4- to 6-month-old infants (Colombo, 2001; Johnson, 1995). These early attentional control skills have been suggested to form the basis for the more general skills of *executive attention* observed in older children as an emerging capacity for self-regulation and behavioral control, primarily governed by the ACC (Posner & Rothbart, 2007; Posner, Rothbart, Sheese, & Tang, 2007).

Infant ERP studies also suggest a role for the ACC and prefrontal regions in the allocation of attention to visual stimuli. One of the most studied infant ERP components is the Nc, a large negative deflection most prominent on central and frontal electrode sites at around 350-600 ms after stimulus onset (Csibra, Kushnerenko, & Grossmann, 2008; de Haan, 2007). In various stimulus presentation paradigms, the Nc has been shown to have a larger response to infrequent or novel stimuli (Courchesne, Ganz, & Norcia, 1981; Grossmann, Gliga, Johnson, & Mareschal, 2009; Nelson & Collins, 1991), reflecting an attentional capture by unexpected stimuli. In addition to responding to the novelty/frequency dimension of the stimuli, the Nc is also modulated by the personal meaning or importance of the stimulus being processed in that it is larger for the infant's mother's vs. stranger's face and for familiar vs. unfamiliar toys (de Haan & Nelson, 1997, 1999). Altogether, the Nc can be considered to represent a valid index of the strength of infants' attention allocation to a given stimulus (Csibra et al., 2008; de Haan, 2007). To explore the underlying cortical generators of the Nc, Reynolds and Richards (2005) applied independent component analysis with equivalent current dipole modeling for infants' EEG signal. These techniques suggested that the activity generating the Nc amplitude differences to different experimental conditions originated in prefrontal areas such as the inferior and medial frontal gyri and the ACC.

Richards and colleagues have also provided detailed insights into the autonomic responses associated with different phases of attentional orienting to visual stimuli, notably with the measurement of heart rate (HR) having become an invaluable tool in the study of infant attention (see Reynolds & Richards, 2007, for a review). The relatively automatic *orienting* of attention to new stimuli appearing in the visual field is accompanied by a rapid deceleration (i.e., slowing) of HR (Lewis, Kagan, Campbell, & Kalafat, 1966; Richards & Casey, 1992). The orienting response is most likely controlled by the subcortical reticular activating system in the midbrain and brain stem which innervates the parasympathetic fibers that decelerate the HR (Mesulam, 1983; Reynolds & Richards, 2007). In the second phase, if the infant engages in processing the stimulus, HR is maintained on a decelerated level, reflecting *sustained attention* and more voluntary cognitive processing of stimulus content. The magnitude and duration (which can last up to tens of seconds) of this phase corresponds to differences in looking time at stimuli varying in complexity and meaningfulness (e.g., static achromatic dots vs. dynamic film clips; Courage, Reynolds, & Richards, 2006). The infant's engagement in sustained attention is also indicated by lowered distractibility by sudden peripheral stimuli during the decelerated HR (Lansink & Richards, 1997). The ACC is associated with sustained HR deceleration in that the Nc ERP component is relatively larger during this HR-defined phase of attention and, as described above, the cortical generators of the Nc have been traced to the ACC (Reynolds & Richards, 2005; Richards, 2003). Finally, during the *attention termination* phase, HR accelerates to pre-stimulus level while attention is disengaged from the stimulus and the infant is no longer actively encoding the stimulus content even though his/her eyes may still remain on the stimulus (Colombo, Richman, Shaddy, Greenhoot, & Maikranz, 2001; Richards & Casey, 1992).

1.3 Development of facial expression processing in infancy

There are fairly different perspectives on the developmental time-course of the ability to process emotional information from faces. Other views emphasize the role of experience-based gradual tuning to a range of emotional expressions during a protracted developmental course during infancy and childhood (Gao & Maurer, 2010; Nelson, 2001) while others postulate very early – even innate – abilities to process and react accordingly to caregivers' various expressive signals (Trevarthen & Aitken, 2001).

The basic prerequisites for reading signals of emotion from facial expressions have been suggested by some to be functional even in the neonatal period as newborn babies have been shown to be able to perform visual *discrimination* (i.e., the registration of changes in appearance) between different facial expressions posed by a live model (e.g., Field, Woodson, Greenberg, & Cohen, 1982). Such early findings have been questioned, however, with later studies finding no clear evidence of facial expression discrimination (i.e., longer looking when a change in a facial expression is presented) in newborns (Farroni, Menon, Rigato, & Johnson, 2007; Kaitz, Meschulach-Sarfaty, Auerbach, & Eidelman, 1988). Furthermore, even if newborns are able to perceive the visual differences between facial expressions, the most parsimonious explanation for the data that also acknowledges the limits of newborn visual acuity (Banks & Salapatek, 1983) would be that the neonates are merely detecting salient physical changes apparent in the different expressions (e.g., open vs. closed mouth) and, thus, no specific innate abilities related to the processing of facial expressions *per se* are necessarily implied (Leppänen & Nelson, 2006). In older infants (i.e., 3- to 7-month-olds), more stable evidence for the discrimination of most facial expressions has been found (de Haan & Nelson, 1998; Kuchuk, Vibbert, & Bornstein, 1986; Nelson, Morse, & Leavitt, 1979; Schwartz, Izard, & Ansul, 1985; Young-Browne, Rosenfeld, & Horowitz, 1977).

More sophisticated abilities relating to the *recognition* and *categorization* of different facial expressions have been investigated with a more complex variant of the traditional habituation paradigm, i.e., the multiple-exemplar habituation-recovery task which is a tool for measuring infants' ability to compute invariant patterns from variable exemplars of a stimulus category (Aslin, 2007). Typically, infants are first shown successive examples of different individuals portraying the same emotion (e.g., happiness). After the infant's looking time to the pictures has decreased below a prespecified habituation criterion, a test trial is presented in which two novel individuals are shown side by side, one showing the habituated expression (i.e., happiness) and the other a novel expression (e.g., fear). Facial expression recognition is inferred from a "recovery" (i.e., increase) of looking time towards the face portraying the novel emotional category. Studies using the habituation-recovery paradigm converge in showing that by the age of 3 to 5 months, infants are already adept at recognizing happiness from faces over variation in poser identity and intensity of the smile (Bornstein & Arterberry, 2003; Caron, Caron, & Myers, 1982). Studies with slightly older infants have also provided evidence for infants' recognition of surprised faces by 5 to 7 months of age (Caron et al., 1982; Ludemann & Nelson, 1988).

Evidence for the ability to recognize other expressions of emotion, such as fear and anger, is less consistent and the habituation order of the expression categories appears as a critical factor for the recognition effects to occur. Some studies have shown recovery of looking at happy faces after being habituated to fearful or angry faces (Serrano, Iglesias, & Loeches, 1992, 1995) while many others have not (Caron, Caron, & Myers, 1985; Kotsoni, de Haan, & Johnson, 2001; Ludemann & Nelson, 1988; Nelson et al., 1979; Nelson & Dolgin, 1985; Phillips, Wagner, Fells, & Lynch, 1990). For example, Nelson, Morse, and Leavitt (1979) first habituated 7-month-old infants to happy or fearful expressions presented by different models, and then tested recognition by presenting the habituated expression paired with a novel expression, both presented by a novel model. The infants recognized happy faces from fearful faces (i.e., recovery of looking was observed for the novel fearful expression). However, when first habituated to fearful faces, the infants did not reliably indicate that they recognized the previously encountered fearful expressions from happy faces (i.e., the infants did not look longer at the novel happy expression). Thus, in light of the habituation-recovery data, infants presumably acquire fairly stable perceptual representations early in development for the facial expressions they observe most frequently during the first months of life (i.e., smiling faces; Malatesta & Haviland, 1982) while less frequently encountered negative emotions are associated with more incomplete perceptual representations, impeding stable categorization of expressions over multiple examples.

Recent studies have also begun to examine whether the brain responses that putatively precede the adult N170 are sensitive to the emotional expression of faces similarly as has been observed in adults. Leppänen, Moulson et al. (2007) showed repeated presentations of fearful, happy, and neutral faces to a group of 7-month-old infants while ERPs were recorded. The analyses focused on the N290 and P400 components. A significant difference was observed in the P400 component, which had a higher peak amplitude for fearful than happy or neutral faces whereas the N290 did not differ between emotional expressions. The authors (Leppänen, Moulson et al., 2007) concluded that this finding indicates a role for affective content in modulating very early perceptual responses to faces already by 7 months of age. Two other studies have also reported evidence for discrimination between fearful and angry faces at the level of N290 and P400 components, although finding opposite results concerning the direction of the ERP differences between the two expressions (Hoehl & Striano, 2008; Kobiella, Grossmann, Reid, & Striano, 2008).

Altogether, the conclusions about the developmental time-course of infants' ability to recognize different emotional expressions remain tentative. The data concerning the recognition of fearful and angry faces is particularly controversial, with the habituation-recovery studies often finding no evidence of recognition but the more recent ERP assessments providing evidence of discrimination at the level of early visual brain responses. However, as the ERP studies have not had multiple identities presenting various examples of the different expression categories, it is difficult to evaluate whether the differences in ERP amplitudes actually arise from emotional category recognition or from more simple visual discrimination between the expressions.

1.4 Emotional modulation of attention in infants

In attempting to account for the lack of recognition effects for fearful faces in the habituation-recovery paradigm, it has been proposed that infants may have a tendency to spontaneously orient their attention toward fearful faces (Kotsoni et al., 2001; Leppänen & Nelson, 2006). Such enhanced attention to fearful faces could override the looking time effects that would evince for the perceptual recognition of the fearful expression category even when the infant shows habituation to individual examples of fearful habituation stimuli. The influence of emotional stimuli on infants' attention has been studied by measuring the duration of looking at different types of emotional stimuli as well as brain responses known to be associated with the strength of attention allocation. Number of studies utilizing such measures concur in showing that at least from 7 months of age, infants display an attentional bias toward fearful faces (Leppänen & Nelson, 2009).

For example, when two different facial expressions are shown side by side on a computer screen for a period of 10-20 seconds, 7-month-old infants spontaneously look longer at fearful than at happy faces (Kotsoni et al., 2001; Leppänen, Moulson et al., 2007; Nelson & Dolgin, 1985). The advantage of such a *visual paired comparison* (VPC) paradigm is that it involves two competing inputs for attentional resource allocation, creating a situation in which the infant has to choose which stimulus requires more visual processing. As no preceding habituation procedure is used, the looking time differences in the VPC task appear to reflect spontaneous attentional biases that the infant brings to the laboratory. To date, no studies have used the VPC paradigm to examine whether a similar looking time bias occurs in younger infants, with the exception of Farroni et al. (2007) who in fact observed that 2- to 4-day-old newborn infants had a tendency to look longer at the side of a happy than a fearful face. Bornstein and Arterberry (2003) presented images of fearful and happy facial expressions sequentially (i.e., one by one) and did not observe any differences in the duration of looking at these faces in 5-month-old infants.

Studies recording ERPs during repeated presentation of faces have observed larger Nc amplitudes for fearful than happy faces in 7-month-olds (de Haan, Belsky, Reid, Volein, & Johnson, 2004; Grossmann et al., 2011; Leppänen, Moulson et al., 2007; Nelson & de Haan, 1996). Again, the data from younger infants are limited. By measuring Nc responses to neutral and fearful faces with the eyes looking toward or away from a laterally presented object, Hoehl and Striano (2010) found no differences in the Nc between the two expressions in 3-month-old infants. Note that the cortical generators of the Nc have been traced to the ACC (Reynolds & Richards, 2005; Richards, 2003), which is known to have an important role in controlling the direction and maintaining the focus of attention (Bush et al., 2000; Casey et al., 1997; Posner & Rothbart, 2007). Thus, it is plausible to interpret the ERP modulation in 7-month-old infants as reflecting increased recruitment of cortical attention systems during the perception of fearful faces (Leppänen & Nelson, 2009).

Taken together, some interesting parallels between adults' emotion-attention interactions and infants' attentional and emotional face processing development can be drawn. In adults, prefrontal structures such as the ACC are connected to areas that respond to the emotional relevance of stimuli (i.e., the amygdala) for integrating the emotional value of sensory stimuli in the control of attentional focus and for regulation of negative affect (Hare et al., 2008; Pessoa, 2009; Pezawas et al., 2005). In infants, prefrontal structures and in particular the ACC are proposed to have a central role in the development of early executive mechanisms enabling control of attention disengagement and eye movements (Colombo, 2001; Johnson, 2005a; Posner et al., 2007). Such basic attentional control skills appear to be well-developed by the age of 6 months (Johnson, 2005a), by the time infants also begin to show evidence for a more sophisticated ability to recognize different facial expressions (Leppänen & Nelson, 2006) as well as to exhibit increased attention to emotionally salient fearful faces (Leppänen & Nelson, 2009). Thus, it is a conceivable hypothesis that from 6 months onwards, the emotional value of sensory stimuli could become integrated with and hence modulate the operation of frontal attentional control systems.

The present studies approached this hypothesis by first examining in detail the age at which infants begin to show increased attention to fearful faces. Second, facial expression stimuli were used together with an established infant attention paradigm (i.e., the gap/overlap task; Aslin & Salapatek, 1975). As the task involves a competition for attentional resources between centrally presented faces and peripheral distractor stimuli, it will likely measure operations that are sensitive to PFC functioning, such as disengagement of attention and controlled inhibition of reflexive saccades (cf. Colombo, 2001; Holmboe et al., 2008; Johnson, 2005a; Posner et al., 2007). This approach was postulated to more closely reflect infants' *actively controlled* attentional reactions toward facial expressions than, for example, the traditional VPC paradigm.

2. AIMS OF THE STUDY

Building on our current understanding of the development of infants' ability to process emotional information from faces, the studies reported in this dissertation were designed to further characterize the interaction between emotional and attentional processes in infancy and to specifically explore whether attentional control processes are influenced by emotional facial expression stimuli. The first specific aim was to determine the age at which infants begin to show an attentional bias toward fearful faces (Study I). A common aim for Studies II-IV was to investigate whether facial expressions of emotion modulate the disengagement component of attention, possibly reflecting an ability of emotional information to modulate the functioning of frontally mediated attentional control systems already at an early age. Studies II and III were also intended to determine whether the mere novelty and unfamiliarity of fearful faces are sufficient to account for infants' attentional bias toward fearful faces (Study II) and whether infants display an adult-like increased attention to the salient information present in the eye region of fearful faces (Study III). Finally, Study IV sought to determine the heart rate responses associated with enhanced attention to fearful faces in infants. In a broader framework, the studies were hypothesized to corroborate the assertion that the prefrontally mediated ability to control attention and eye movements interacts with the emerging ability to "read" emotional signal value from facial expressions to guide attention to the most salient and impending signals of emotion (i.e., fearful faces).

The focus of the studies was particularly on infants' processing of fearful faces, instead of other expressions of negative valence, such as anger or sadness, for the following reasons. First, as the effects of emotion on attention are putatively conveyed by a neural circuitry of which the amygdala is a key element, it is important to note that in adults most robust amygdala activation is commonly observed for fearful faces (Davis & Whalen, 2001; Whalen et al., 2001). Although both angry and fearful faces are associated with threat, the source of the threat is inherently more ambiguous in fear, while ambiguity and uncertainty *per se* are often regarded as critical factors in activating the amygdala (Davis & Whalen, 2001; Herry et al., 2007; Kim et al., 2004; Pessoa, 2010). Second, the majority of those infant studies that provide the most significant background for the present studies compared responses between fearful and happy/neutral faces (Bornstein & Arterberry, 2003; Hoehl & Striano, 2010; Kotsoni et al., 2001; Leppänen, Moulson et al., 2007). Thus, the data collected by investigating the developmental emergence of and the factors associated with infants' enhanced attention to fearful (instead of angry) faces will be more readily interpreted in light of earlier studies using comparable stimulus material.

2.1 Development of enhanced attention to fearful faces

To draw reliable conclusions about the developmental emergence of enhanced attention to fearful faces, different age groups should be presented with comparable measures of attention. Currently, there is a lack of research investigating the putative developmental transitions in infants' attention to emotional faces. As reviewed in the introduction, the majority of the studies measuring looking times with the VPC task as well as those measuring attention-sensitive Nc ERP responses to facial expressions have been conducted on 7-month-old infants. While a few published investigations have applied similar methodology to older infants (Grossmann, Striano, & Friederici, 2007; Hoehl & Striano, 2010; LoBue & DeLoache, 2010), the available data are more scarce for infants younger than 7 months. Studies with 3- to 5-month-old infants showing no evidence of attentional biases to fearful faces in terms of looking time (Bornstein & Arterberry, 2003) or ERPs (Hoehl & Striano, 2010) may be taken to suggest that the attentional bias toward fearful faces emerges between 5 and 7 months of age. Study I sought to test this hypothesis by measuring looking times and attention-sensitive brain responses to fearful and happy faces in 5- and 7-month-old infants.

2.2 Novelty preference and attention to facial expressions

The exact stimulus parameters that modulate the Nc component are not adequately known because in different studies, a larger Nc has been found to be related to the novelty/unexpectedness (Courchesne et al., 1981; Grossmann et al., 2009; Nelson & Collins, 1991) or the personal/emotional significance of the stimuli (de Haan & Nelson, 1997, 1999). Consequently, it has been questioned whether the Nc modulation by fearful faces observed in 7-month-old infants is merely due to a lack of experience with fearful faces by 7 months of age, i.e., a novelty response (Nelson & de Haan, 1996; Vaish, Grossmann, & Woodward, 2008). Indeed, Malatesta and Haviland (1982) observed 60 mother-infant dyads during the early months of the infant's life and concluded that in a typical rearing environment, the infant's visual experience with facial expressions other than smiling and neutral expressions remains somewhat limited at least until 6 months of age. In addition to the modulation of the Nc by stimulus novelty, it is typical for infants to look longer at novel than familiar stimuli (Fantz, 1964). More specifically, when confronted with a stimulus, a process of matching the perceived stimulus with a corresponding representation stored in memory is initiated. If the match found is incomplete or if no match can be found, the novel stimulus is subjected to increased processing in order to construct a neuronal representation of it (Cohen & Gelber, 1975; Sokolov, 1963).

Therefore, it is essential to explore the most parsimonious interpretation for 7-month-old infants' consistently observed attentional bias toward fearful faces. It has not been explicitly tested to what extent the variation in infants' attention to different emotional faces is governed by the degree of unfamiliarity of the expressions. Fearful faces, obviously, have qualities related to both novelty and emotional significance, making it complicated to ascertain which dimension dominates in driving the attentional effects in infants. Study II approached this issue by comparing infants' attention to fearful faces and to novel control expressions which were reasoned to be equally unfamiliar as fearful faces but lacking a similar emotional signal value. It was hypothesized that if an attentional preference for novelty is a constitutive factor in infants' attentional bias toward fear, the novel, non-emotional faces should result in similar effects on attention in the gap/overlap task (i.e., increased looking time and inhibition of attention disengagement).

2.3 Modulation of attention by fearful eyes

When adult participants view face stimuli, featural changes in the eye region that are prominently expressed in fearful faces (i.e., raised eyebrows and enlarged eyes with an increased exposure of the white sclera) appear to be sufficient to trigger similar modulation of attention (Yang et al., 2007) and emotion-related brain responses (Morris et al., 2002; Whalen et al., 2004) as prototypical fearful expressions. Also, when viewing faces, a large amount of visual scanning is typically directed around the eyes (Henderson, Williams, & Falk, 2005). Studies investigating emotion recognition from faces in which different facial areas are only sparsely exposed in each individual trial (Smith, Cottrell, Gosselin, & Schyns, 2005) or studies with an amygdala-lesioned participant with a scanning deficit regarding the eye region of faces (Adolphs et al., 2005) have provided further evidence for the critical role of the eye region in providing “diagnostic” information particularly when the task is to recognize fear from faces.

Recall from the introduction that infants also show an early-emerging tendency to process information from the eyes (Gliga & Csibra, 2007; Hunnius et al., in press; Senju & Johnson, 2009). Johnson (2005b) suggested that a fearful face might be the optimal stimulus to activate the amygdala-centered emotion-processing system in early ontogeny because a) infants are responsive to high-contrast, low spatial frequency (LSF) information from early on (Banks & Salapatek, 1983), b) the amygdala activates robustly to coarse LSF visual information in adults (Vuilleumier, Armony, Driver, & Dolan, 2003), and c) the high-contrast eye region in fearful faces provides salient LSF input.

Study III examined the possibility that, as with adults, also in infancy the perception of wide-open fearful eyes alone is sufficient to produce enhanced attentional effects. This study utilized corneal-reflection eye tracking to gather detailed information about how 7-month-old infants visually scan different facial expressions. The role of the eye region was investigated by comparing responses to fearful faces with those to a neutral face in which the eyes had been replaced by fearful eyes. It was hypothesized that if the increased allocation of attention to fearful faces in infants is driven by the information provided by enlarged eyes, the infants should (a) direct their visual scanning pattern to a larger extent toward the eyes for both fearful faces and neutral faces with fearful eyes than toward happy and neutral faces, and (b) exhibit inhibition of attention disengagement from both fearful faces and neutral faces with fearful eyes in the overlap task.

2.4 Cardiac correlates of enhanced attention

The orienting response to new stimuli appearing in the visual field is accompanied by a rapid deceleration of heart rate (HR) that is most likely controlled by subcortical mechanisms (Reynolds & Richards, 2007). Importantly, studies with animals indicate that activity in the amygdala modulates the magnitude of the HR deceleration response (Kapp et al., 1994). The amygdala-mediated “fear bradycardia” is evident in most mammals and it is accompanied by a rapid slowing of HR and behavioral “freezing” when the animal is confronted with a threatening stimulus such as a predator (Bradley, 2009). An equivalent of the animal response to threats in human adults is a rapid and sustained HR deceleration during the perception of emotionally negative stimuli, such as aversive scenes or angry faces (Bradley, Lang, & Cuthbert, 1993; Codispoti, Bradley, & Lang, 2001; Kolassa & Miltner, 2006; Libby, Lacey, & Lacey, 1973). Bradley (2009; Lang & Bradley, 2010) has argued that such cardiac orienting response to threat-related cues may reflect the activation of an evolutionarily old defensive motivational system that serves to guide attention to salient features in the environment in order to facilitate perceptual processing and extraction of information about potentially significant stimuli.

Whether similar, potentially amygdala-mediated, emotional enhancement of the cardiac component of the autonomic response could already be observed in infancy has not so far been investigated. However, as there is a reliably documented correspondence between changes in HR and automatic (i.e., orienting) as well as more controlled (i.e., sustained engagement) stages of attentional processing in infants (Reynolds & Richards, 2007), incorporating HR measures into infants’ emotional stimulus processing has the potential to provide important insights into the relative roles of automatic and controlled attentional reactions in infants’ emotion-attention interactions. To this end, Study IV included HR measurement in the overlap task to assess infants’ cardiac reactivity to emotional face stimuli. On the basis of earlier ERP studies showing rapid modulation of attention-sensitive brain responses to fearful and neutral/happy expressions (Leppänen, Moulson et al., 2007; Nelson & de Haan, 1996), it was predicted that infants exhibit a relatively enhanced cardiac orienting reflex to fearful facial expressions. It was further hypothesized that the greater attentional engagement with fearful facial expressions is also evident at a later stage of processing, resulting in prolonged maintenance of the heart rate deceleration and inhibition of attention disengagement in the context of fearful facial expressions.

3. METHODS AND RESULTS

3.1 Study I

Methods of Study I

A group of 5-month-old (*n* = 29) and a group of 7-month-old (*n* = 29) infants participated in Study I. ERP data on 18 five-month-olds and 20 seven-month-olds providing ≥10 artefact-free trials for both happy and fearful stimulus conditions were analyzed. Artefact-free looking time data in the visual paired comparison (VPC) task were obtained from 23 five-month-olds and 26 seven-month-olds. Eight of the infants in the ERP sample and 14 of the infants in the VPC sample were tested twice (i.e., at both ages).

Visual and electrophysiological indices of infants' allocation of attention to fearful and happy faces were measured with ERPs (in a repeated presentation procedure) and looking times (in a VPC paradigm), both shown to be sensitive to the level of attention directed to fearful and happy faces in earlier studies with 7-month-old infants (de Haan et al., 2004; Leppänen, Moulson et al., 2007; Nelson & de Haan, 1996). In the ERP task, fearful and happy faces were presented repeatedly in random order, 1000 ms each, while continuous EEG was recorded from 30 scalp locations. The facial expression stimuli were obtained from the NimStim set of facial expressions (Tottenham et al., 2009) as well as from our own laboratory stimulus database. Prior to data collection, adult observers (*n* = 18) were asked to rate the images to ensure that the images from our own database matched the standardized NimStim stimuli in terms of fearfulness and happiness. The statistical analyses of the ERP task were focused on amplitudes of the Nc component. To analyze the Nc, standard procedures (e.g., Hoehl & Striano, 2010; Leppänen, Moulson et al., 2007) were followed by calculating amplitude averages for fearful and happy faces within a time window of 350–600 ms for electrodes C3 and C4, located lateral to the central vertex.

After the ERP task, the electrode cap was removed and two 10-second VPC trials with a happy and a fearful face were presented. The faces were 12° apart and their left-right positioning on the screen alternated between the trials and was counterbalanced between participants. Looking times (which were averaged across the two trials) at fearful and happy faces were recorded with a video camera mounted on top of the monitor.

Results of Study I

The grand average ERPs measured from electrodes C3 and C4 for 5- and 7-month-old infants are shown in Figure 2. As can be observed, both age groups showed a prominent Nc response during 350-600 ms post-stimulus. Only in the 7-month-olds' group, however, was this attentional response modulated by the emotion displayed on the stimulus face. Thus, while the responses to fearful and happy faces were of equal magnitude in the 5-month-olds' group, 7-month-old infants had significantly larger Nc amplitudes for fearful than for happy faces.

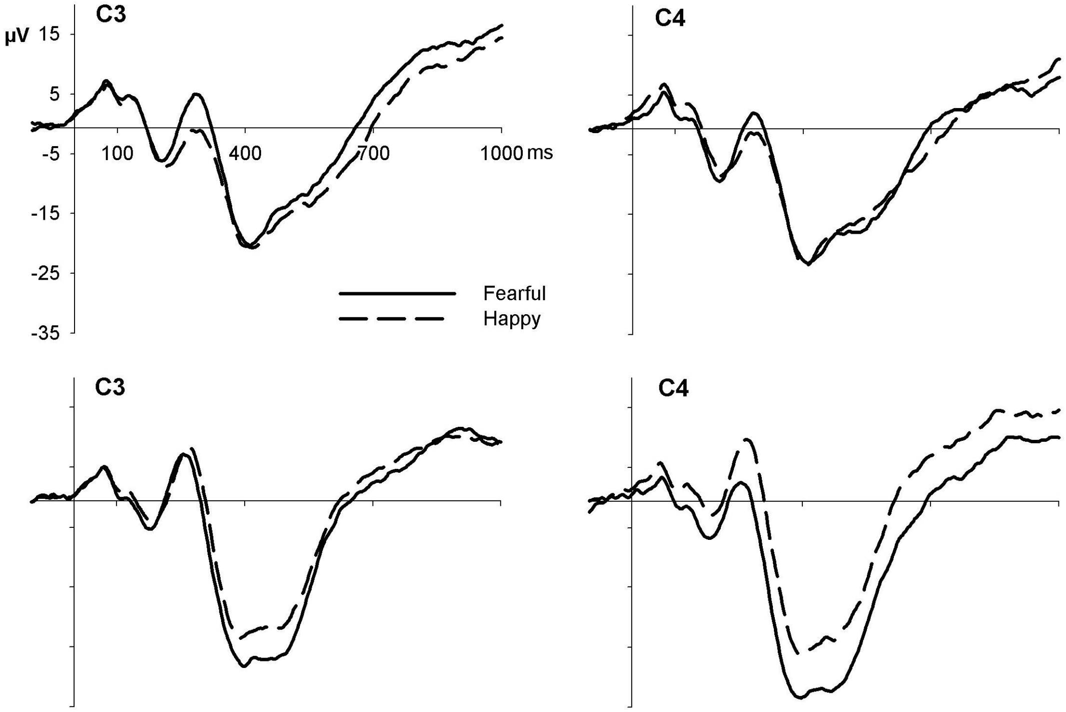

FIGURE 2. Grand average ERP waveforms for fearful and happy faces over the left (C3) and right (C4) hemisphere. The data from 5-month-old infants are displayed in the top graphs and the 7-month-olds' data in the bottom graphs.

An identical pattern of results emerged for the VPC data (Figure 3). There was no indication of a bias to look at one of the facial expressions more than the other in the 5-month-olds' group. The 7-month-olds, however, looked significantly longer at fearful than at happy faces.

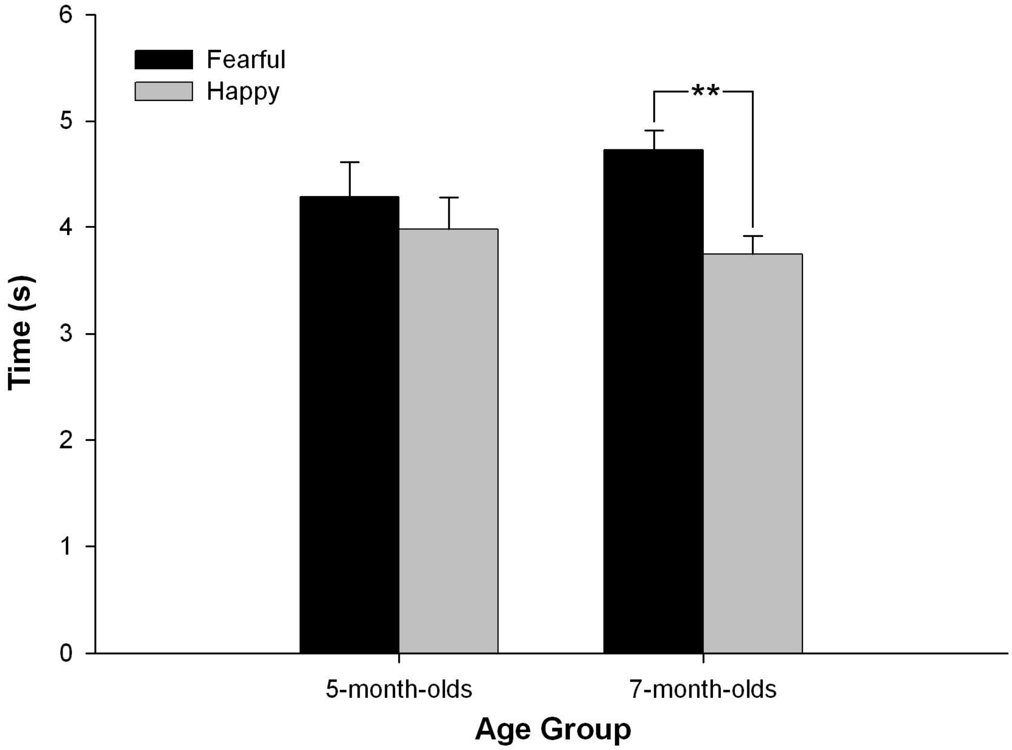

FIGURE 3. Average looking times in the VPC task for fearful and happy faces in 5- and 7-month-old infants. (Note: ** denotes statistical significance at the level of *p* < .01.)

As some infants participated in the experiment at both ages, additional analyses were run to control for the possible influence of the number of times an infant participated in the experiment. A marginal interaction between facial expression, hemisphere, and the number of visits in the laboratory (once or twice) was observed in the 7-month-olds' ERP data. This was due to the infants participating only once showing larger Nc amplitudes for fearful faces in the right (C4) but not in the left (C3) hemisphere, while the infants who participated at both ages showed bilaterally a larger Nc for fearful than happy faces at 7 months of age. There was no influence of the number of visits on the VPC data.

3.2 Study II

Methods of Study II

In Study II, the participants were a group of 7-month-old infants (*n* = 28). After excluding some participants due to fussiness or excessive movement artefacts, 27 infants remained in the analyses of the looking time task and 17 infants in the gap/overlap task data analyses.

First, all participants completed a short looking time task in which fearful, happy, novel, and control faces (taken from our own laboratory stimulus database) were each presented once individually on the screen for 20 seconds (see Figure 4 for examples of the stimuli). In the novel, non-emotional expression, the lips were closed, the cheeks were blown full of air, and the eyes were wide open. Prior to data collection, a rating study with a group of adults (*n* = 12) confirmed that the novel expressions were perceived as novel as the fearful faces but they were rated low on fearfulness and happiness. The control face was a face-shaped visual noise image that was included as a control stimulus to examine the potential effects of the presence of faces *per se* on attention-related measures. This stimulus was created by randomizing the phase spectra of a face and holding the color spectra constant (as was done by Halit et al., 2004). The order of stimulus presentation was randomized across participants. A hidden video camera mounted on top of the monitor was used to record the infants' looking times (i.e., longest individual fixations and total looking time) toward the faces during the 20-second trials.

FIGURE 4. Examples of the stimuli used in Study II.

After the looking time assessment, an overlap task with the same facial stimuli was presented. In this task (see Figure 5 for an illustration), the infant's attention was first attracted to the center of the screen with an attention-getter (a red circle expanding from 0.4° to 4.3° in a continuous fashion). Once the infant fixated on the attention-getter for at least a second, a face was presented on the center of the screen. After 1000 ms, the face was flanked by a peripheral stimulus (i.e., a checkerboard pattern) equiprobably 13.6° on the left or right for 3000 ms. The dependent variable was disengagement frequency (i.e., the percentage of trials on which the infant made a saccade from the face toward the peripheral stimulus). In addition to the overlap trials, half of the trials were "gap" trials on which the central stimulus face disappeared from the screen 200 ms prior to the presentation of the peripheral stimulus, creating a transitional blank screen between the presentation of the face and the peripheral stimulus. As Study II was our first to examine attention disengagement from facial expressions in infants, gap trials were included for two reasons. First, it enabled us to test the overall validity of the modified task, i.e., whether the overlap trials with facial expression stimuli do indeed result in a standard "gap effect" (i.e., less frequent and slower saccades toward the peripheral stimuli on overlap trials; Csibra et al., 1998; Frick, Colombo, & Saxon, 1999; Hunnius & Geuze, 2004). Second, because the offset of the central stimulus obviates the need to disengage attention (Colombo, 2001), the inclusion of the gap condition enabled us to determine whether the possible effects of emotional expressions on attention are specifically due to the disengagement component of attention (i.e., evident only in the overlap condition) and not to more general influences on attentional shifting (i.e., evident also in the gap condition).

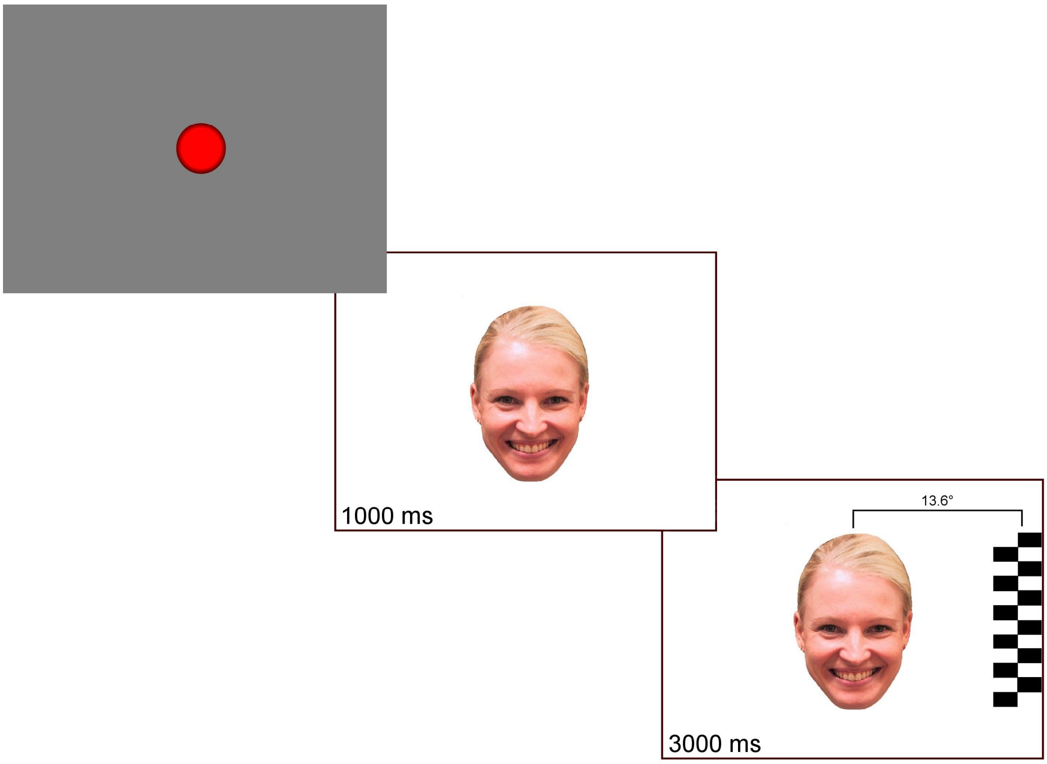

FIGURE 5. The sequence of events during a single overlap trial. On gap trials, the face was removed 200 ms before the appearance of the peripheral stimulus.

Results of Study II

In the looking time task, the infants looked significantly longer at fearful than visual noise faces as measured by average looking times and longest individual fixation lengths (Figure 6). None of the other differences in looking times were significant.

In the gap/overlap task, saccades toward the peripheral stimuli were generally less frequent (59% vs. 98%) and of longer latency (594 vs. 434 ms) during overlap than gap trials respectively, clearly showing that the overlap trials exerted an influence on attention disengagement. On gap trials there were no differences between the stimulus faces in the frequency of saccades toward the peripheral stimuli. On overlap trials, however, saccades toward the peripheral stimuli were significantly less frequent from fearful than from happy and visual noise faces (Figure 6). The novel expression did not differ from any of the other faces in saccade frequency.

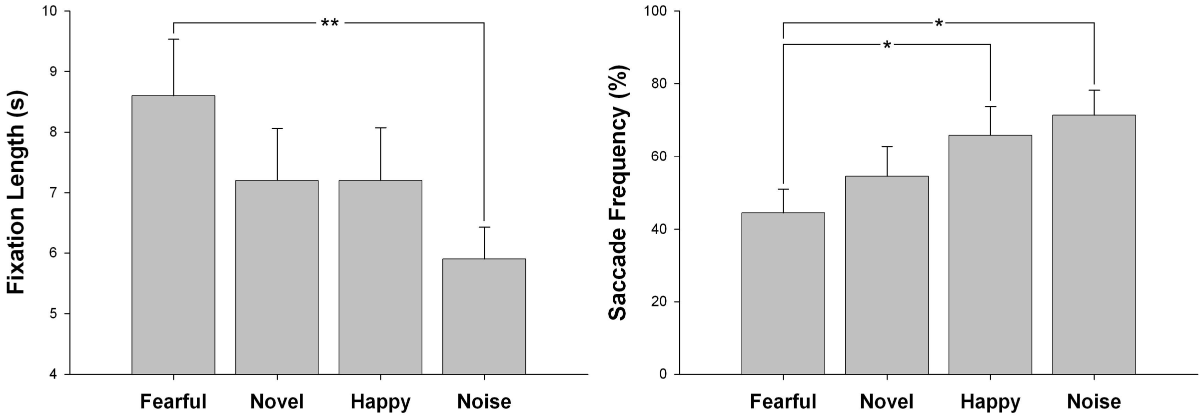

FIGURE 6. Left: longest individual fixations for the different faces in the looking time task. Right: the average frequency of saccades toward the peripheral stimuli on overlap trials. * $p < .05$; ** $p < .01$.

3.3 Study III

Methods of Study III

Eye tracking data were analyzed from a sample of 15 seven-month-old infants. An additional 13 infants were tested but excluded from the data analyses because of prematurity, poor eye tracker calibration, fussiness, or excessive movement artefacts resulting in less than five good trials in one or more stimulus conditions in the overlap task.

This study utilized the corneal-reflection eye tracking technique (see Gredebäck, Johnson, & von Hofsten, 2010, for a review) to acquire spatially detailed information about infants' visual processing of different facial expressions. The eye-tracker monitor had embedded cameras that recorded the reflection of an infrared light source on the cornea relative to the pupil from both eyes of the infant at a frequency of 50 Hz (i.e., every 20 ms). The average spatial accuracy of the eye-tracking system (Tobii 1750; http://www.tobii.com) was in the range of 0.5 to 1°, which approximates to a 0.5 to 1 cm area on the screen with a viewing distance of 60 cm. The experiment started with the calibration of the eye tracker cameras by presenting an animated stimulus sequentially at 5 different locations of the screen until the infant had fixated on all of them.

After calibration, the data collection began with a short visual scanning task in which fearful, happy, and neutral facial expressions (obtained from the NimStim set; Tottenham et al., 2009), and a neutral face with fearful eyes were each presented twice for 10 seconds in the center of the screen (see Figure 7 for examples of the stimuli). The neutral face with fearful eyes was produced with image-editing software by cutting the eyes from a fearful face and superimposing them on the same model's neutral eyes. All four expressions were first presented in random order, and then repeated in a different random order. For the analyses of visual scanning of different areas of the face, multiple areas of interest (AOIs) were manually defined around the eyes, nose, mouth, forehead, and the contour of the head. The analyses of the scanning patterns were conducted on the percentage of looking time at each AOI in relation to the total time spent looking at the expression across both trials.

Shortly after the scanning task, an overlap task with the same facial expressions posed by another model was presented. The dependent variable was saccade latency (i.e., the time from the onset of the peripheral stimulus to the initiation of an eye movement towards it). To this end, the task was slightly modified from Study II. First, no gap trials were included in order to increase the number of overlap trials. Second, to enhance the attention-grabbing properties of the peripheral stimuli and to increase the number of saccades directed at them, the peripheral stimulus flickered by alternating its contrast polarity at a 10-Hz frequency for the first 1000 ms of its appearance.

Results of Study III

Infants' typical visual scanning patterns for the four different facial expressions are presented in Figure 7. The scanning patterns for the expressions were very similar and no significant differences between the expressions were found. Thus, for all expressions, the infants spent the most time scanning the eye region (*M* = 53% of the total time spent looking at the face), followed by the forehead, nose, mouth, and the face contour.

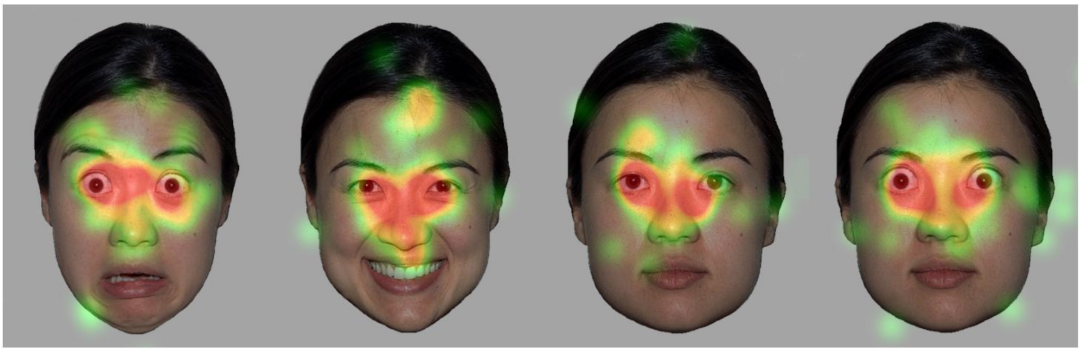

FIGURE 7. Heatmaps illustrating the typical scanning patterns for the four facial expressions, i.e., areas in which the majority of fixations were directed.

In the overlap task, the manipulation of the salience of the peripheral stimuli by adding flicker was successful in increasing the average proportion of saccades away from the face stimuli (84% vs. 59% in Studies III and II respectively). The facial expression of the central stimulus had a significant effect on saccade latencies toward the peripheral stimuli (Figure 8). It took significantly longer for the infants to shift their attention away from fearful than from happy faces, neutral faces, and neutral faces with fearful eyes.

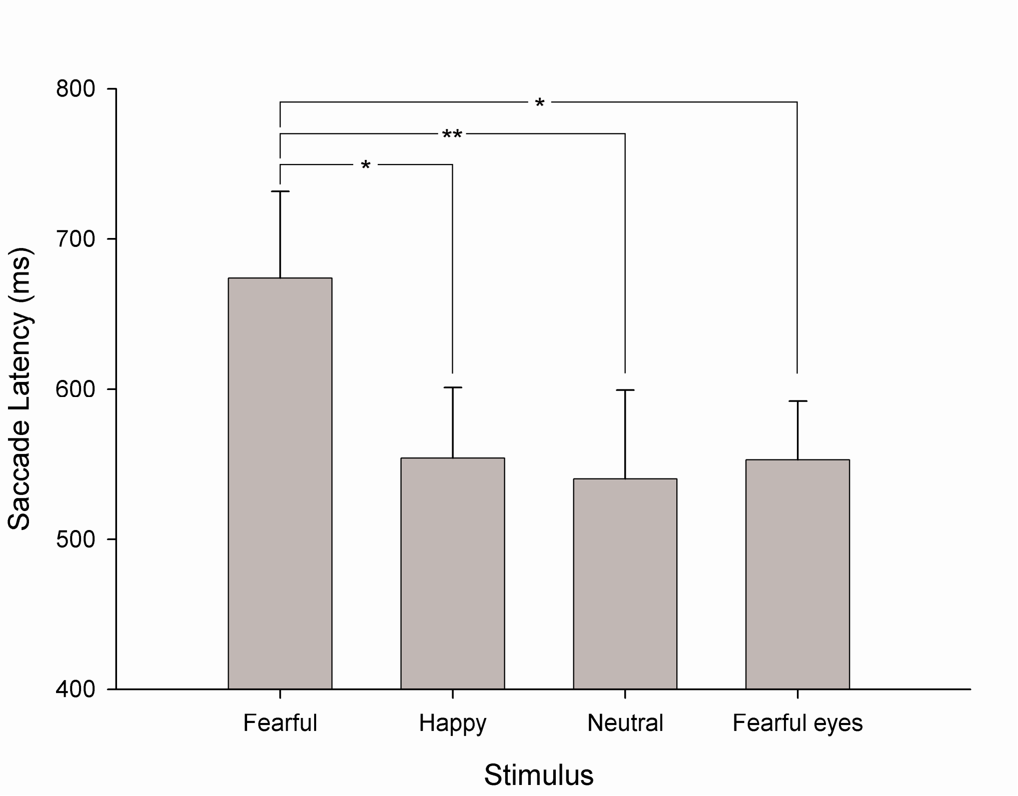

FIGURE 8. Average saccade onset latencies from the central stimulus toward the peripheral stimulus. * $p < .05$; ** $p < .01$.

3.4 Study IV

Methods of Study IV

The final sample consisted of 42 seven-month-old infants. Data from an additional 8 infants were analyzed but excluded from the final sample due to technical difficulties in heart rate recording, movement artefacts resulting in fewer than 2 acceptable trials in some experimental conditions, or low quality of the heart rate recording and extreme heart rate change scores (>3 standard deviations from the group mean).

To measure infants' heart rate and attention disengagement from facial expressions, the overlap task without gap trials was used with fearful, happy, neutral, and visual noise faces (obtained from the laboratory stimulus database). The electrocardiogram (ECG) was recorded with two electrodes placed on the participant's chest. Offline, QRS complexes (corresponding to the depolarization of the ventricles; Andreassi, 2000) were identified from the ECG signal and interbeat intervals (IBIs; the time intervals between two successive R-waves) were calculated. Finally, the IBIs in 500-ms intervals ranging from 1000 ms prior to trial onset to 4000 ms post-stimulus were converted into beats per minute (BPM) and averaged across different trials within each stimulus condition. The analyses were performed on the HR change scores calculated by subtracting the BPM in each 500-ms interval from the BPM during the 1000-ms prestimulus interval (cf. Richards & Turner, 2001). Accordingly, negative change score values indicate HR deceleration while positive values indicate HR acceleration during stimulus viewing.

Results of Study IV

The results of the behavioral data paralleled those of Studies II and III. Thus, when compared to visual noise, neutral, and happy faces, saccades away from fearful faces were significantly slower and less frequent.

As can be observed from Figure 9, all stimulus conditions resulted in a HR deceleration response that occurred primarily during the first 1000 ms of stimulus presentation and subsequently returned to prestimulus levels. The analysis of the HR change scores for the whole trial duration (4000 ms) did not result in differences between stimulus conditions. However, when the analysis was confined to the first 1000 ms of stimulus presentation (i.e., the phase of the initial HR orienting response and prior to the onset of the peripheral stimulus), fearful faces resulted in a significantly steeper HR deceleration than happy and neutral facial expressions. Finally, the magnitude of the initial HR deceleration for fearful faces was *negatively* correlated with the magnitude of the fear-effect on the frequency of saccades toward the peripheral stimuli. This correlation indicated that the cardiac deceleration response to fearful expressions was attenuated in those infants who exhibited relatively greater amount of saccade suppression.

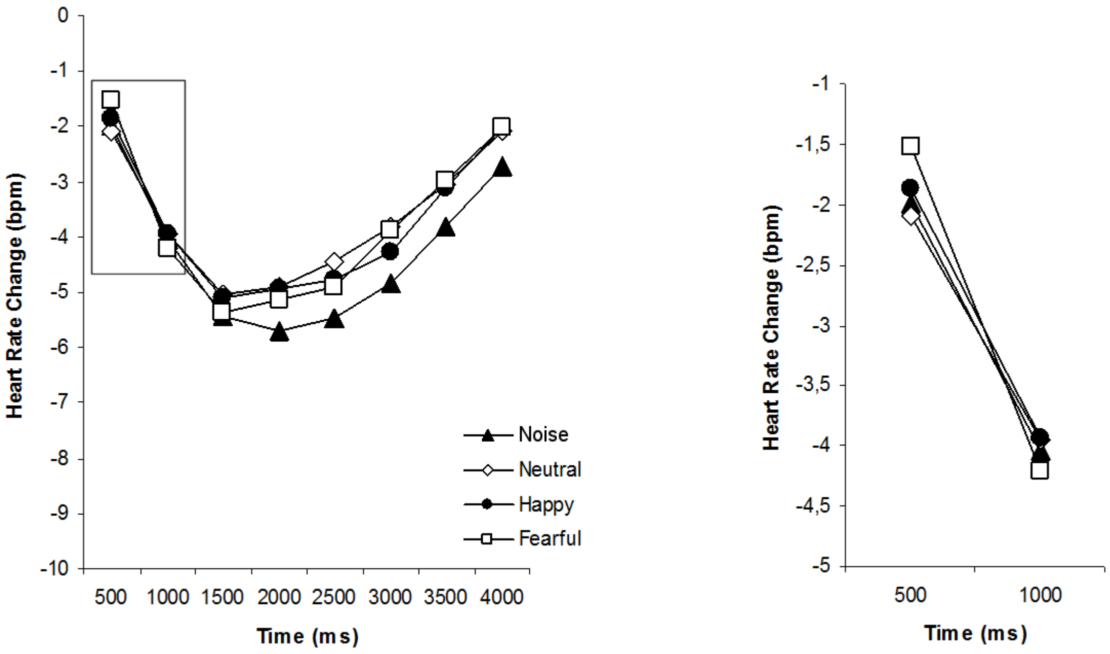

FIGURE 9. Heart rate change scores, reflecting the difference (in BPM) between the mean HR during a 1000-ms prestimulus baseline and HR during the 4000-ms stimulus-viewing period (graph on the left). The framed time segment in the graph is enlarged on the right to show the HR change scores during the first second of stimulus viewing (i.e., the phase of the initial HR orienting response and the time period preceding the onset of the peripheral stimulus).

4. DISCUSSION

The ability to process and comprehend information from facially communicated emotional signals makes substantial progress throughout the first year of life. One manifestation of this development in the second half of the first year is infants' attentional bias and heightened interest in fearful facial expressions. The present series of studies aimed to characterize this bias in greater detail by investigating the developmental emergence of and the critical factors underlying the attentional prioritization of emotionally salient fearful expressions in infancy. Study I provided evidence that enhanced attention to fearful faces emerges between 5 and 7 months of age. While 7-month-old infants' data replicated earlier findings of longer looking times and more pronounced attention-sensitive brain responses to fearful than to happy faces, no differences were observed with either measure in 5-month-olds. In the following studies, 7-month-olds' attention to facial expression stimuli that were paired with non-emotional distractor stimuli was examined with the overlap paradigm. Studies II-IV converged in showing that fearful faces exerted a consistent influence on infants' attention disengagement, increasing the latency and decreasing the frequency of saccades toward the peripheral stimulus. A similar effect was absent for faces that had been rated as novel as a fearful expression but lacking equal emotional significance (Study II) and for neutral faces with fearful eyes, the most prominent individual feature of a fearful expression (Study III). Finally, in Study IV, it was shown that infants also exhibit an adult-like deceleration of heart rate in response to fearful faces.

In the following, I will first evaluate the results observed in light of the hypotheses stated in the chapter outlining the aims of the present studies. After that, I will discuss the results in relation to a broader hypothesis that the turn of the second half of the first year is a period during which critical developmental changes take place in the way infants perceive, experience, and learn fear. Finally, I will discuss the implications of the present results on the development of the brain networks responsible for emotion, attention, and their interaction.

4.1 Evaluation of the results

4.1.1 The novelty hypothesis

I first consider the results of Studies I-III in relation to the assumption that infants' increased attention to fearful faces is driven primarily by the unfamiliarity and novelty of these expressions in a typical infant's rearing environment (e.g., Nelson & de Haan, 1996; Vaish et al., 2008). Although the novelty hypothesis has not been explicitly tested, the assumption favoring novelty in infants' processing of fearful faces gained moderate support from a study by de Haan et al. (2004). The study showed that 7-month-old infants who scored high on temperamental positive affectivity and who also had relatively more emotionally positive mothers (i.e., who putatively expressed fearful and other negative expressions less often than emotionally less positive mothers, although this was not explicitly controlled for) looked longer at and had larger Nc amplitudes for fearful than happy faces. This effect was interpreted to reflect relatively less experience with negative emotional displays in these infants and, therefore, a more marked attentional response to a novel stimulus category.

The data reported in the present studies, however, did not provide unambiguous support for the novelty hypothesis. In Study II, an expression which was rated as equally novel and which also contained overlapping visual features with a fearful face (i.e., wide-open eyes) was not associated with a similar prolonged looking time and lower frequency of saccades toward the peripheral stimulus as was the case with fearful faces. Although no ratings were obtained in Study III, the neutral face with fearful eyes could also be considered a novel and atypical stimulus for the infants but, again, it did not have the same effect as fearful faces on saccades toward the peripheral stimulus. Also, the lack of differences in looking times and ERP amplitudes between fearful and happy faces in 5-month-old infants in Study I appears to contradict a novelty-based account. After all, fearful faces most certainly are as infrequently encountered stimuli for 5-month-olds as they are for 7-month-olds (cf. Malatesta & Haviland, 1982). Of course, the possibility remains that the novelty response to fearful faces was obscured in the 5-month-olds due to an incompletely represented perceptual category for happy expressions (i.e., rendering the happy faces also somewhat novel). Although this issue was not directly assessed in Study I, the possibility of such an effect seems rather unlikely in light of earlier research which has shown proficient encoding of happy expressions over variation in poser identity and smile intensity with 5-month-old infants (e.g., Bornstein & Arterberry, 2003). Naturally, these findings warrant replication and as the direct contrast between novel and fearful faces was not statistically significant in Study II, caution should be exercised before making strong inferences regarding the novelty assumption on the basis of the present data.

It is, however, important to reiterate some of the findings described in the introduction which suggest that in addition to novelty, the personal or emotional significance of the stimulus being processed modulates infants' attention. First, infants also show a *familiarity* preference that manifests, for example, in larger attention-sensitive Nc amplitudes to mother's vs. stranger's face and for familiar vs. unfamiliar toys (de Haan & Nelson, 1997, 1999). These findings imply that the emotional saliency or significance of the perceived stimuli may override the memory-based preference for material that is incompletely (or not at all) represented in memory. Second, Grossmann et al. (2007) presented 7-month-olds with angry and happy faces and – in contrast to studies comparing attention allocation to fearful and happy faces – observed a longer looking time and a larger Nc amplitude for happy than for angry faces. This result poses a challenge to a novelty-based account because angry expressions are undoubtedly similarly unfamiliar to 7-month-olds as are fearful expressions (cf. Malatesta & Haviland, 1982). Taken together, it may be concluded in light of the data presented here and in earlier studies that the mere novelty of fearful faces *per se* is not sufficient to account for the attentional effects observed in 7-month-old infants in the present as well as in numerous other studies.

4.1.2 Fearful eyes

The data from Study III indicate that 7-month-old infants' attentional bias to fearful expressions cannot be intepreted straightforwardly as a response to enlarged fearful eyes. Instead, infants appear to preferentially pay attention to the eye region for a variety of facial expressions and not in any particular way for fearful faces. Similar indifference in the relative amount of scanning the eyes over neutral, sad, happy, angry, and fearful expressions in 4- and 7-month-old infants was recently reported by Hunnius et al. (in press). Furthermore, fearful eyes alone were not associated with a delayed disengagement of attention following the onset of the peripheral stimuli. These results appear to be partially at odds with some studies in adults (Morris et al., 2002; Whalen et al., 2004; Yang et al., 2007) which have shown that the mere perception of fearful eyes is sufficient to trigger similar modulation of attention and emotion-related brain activation as prototypical fearful expressions.

However, there are also other findings suggesting that the eyes may not be exclusively responsible for modulating attention and associated brain responses to fearful faces. Asghar et al. (2008), for example, found comparable activation in the amygdala for whole fearful faces, fearful eyes alone, and fearful faces with the eye region masked. Likewise, Leppänen et al. (2008) measured similar differentiation in posterior visual ERP responses (the EPN component) between fearful and neutral expressions both when the eyes of a fearful face were covered with sunglasses or presented in isolation (i.e., in a letterbox view). It was also found, however, that the reaction times to categorize the stimulus as fearful vs. neutral were shorter when the whole face instead of the eye region alone was visible, indicating that, compared to salient eye region cues, whole face fearful expressions provide additional "diagnostic" cues (e.g., featural changes in the mouth region) that permit faster and more accurate discrimination performance in adults. Infants, on the other hand, may not have similar flexibility in utilizing information from multiple facial sources and seem to require a full prototypical expression to detect the face as fearful. A potential caveat in this interpretation could be, however, that for the neutral face with fearful eyes, only the eyes – and thus not the raised eyebrows – were transferred from the fearful expression in Study III. The potential significance of such a seemingly minor difference was highlighted in the results of Leppänen et al. (2008), who found that in adults the ERP modulation by fearful relative to neutral faces disappeared when the eyes *and* eyebrows (but not the eyes alone) were covered. Similarly, to determine the importance of different facial "action units" (i.e., characteristic facial muscle movements) in the recognition of different facial expressions, Kohler et al. (2004) concluded that for fearful expressions, correct recognition is most strongly associated with the presence of enlarged eyes and raised inner eyebrows. The relative contributions of different information sources in the eye region (i.e., the amount of white sclera relative to the pupil, raised eyebrows etc.) in accounting for the effects of fearful expressions on attention and perception in infants await further resolution.

4.1.3 Attentional mechanisms

In evaluating the evidence of an attentional bias for fearful faces in the overlap task, a question of paramount importance concerns the mechanisms possibly underlying the modulation of attention disengagement. Specifically, is the suppression of attention disengagement from fearful faces most likely due to a) a *difficulty* in disengaging attention, b) *diminished perceptual sensitivity* to peripheral stimuli while attention is held by the face presented at foveal vision, or c) a *bias to not respond* to non-emotional peripheral stimuli, i.e., endogenously controlled attentional selection? In the article reporting the data of Study II (Peltola, Leppänen, Palokangas, & Hietanen, 2008), an argument was taken in favor of a difficulty in disengaging attention from threat-related stimuli, a position I am inclined to reconsider at this point. The reasons for favoring a difficulty-based account were based on findings in adults showing impaired attention disengagement from threat-related stimuli (e.g., Georgiou et al., 2005; Koster et al., 2004) as well as on infant studies that have observed an approximately 80% probability of disengagement during overlap trials even from salient stimuli such as the mother's face or a dynamic abstract stimulus (Hunnius & Geuze, 2004).

However, it may not be reasonable to make direct comparisons between adult and infant studies because infants (as opposed to adults), of course, are not given any verbal instructions to shift their eyes from the face toward the target, and as a result, may not necessarily be motivated to do so. The abilities to disengage attention as well as to hold visual focus on a preferred stimulus are well developed by the age of 7 months (Colombo, 2001; Johnson, 2005a). Thus, even though peripheral stimuli induce covert shifts of attention to their location (Johnson, Posner, & Rothbart, 1994; Richards, 2000), infants are able to inhibit overt eye movements away from the central stimulus if motivated to do so. Accordingly, the finding of an increase in saccade probability after the saliency of the peripheral stimulus was enhanced by flickering its contrast polarity (Study III) is consistent with earlier studies (e.g., Finlay & Ivinskis, 1984) and in line with the suggestion by Hunnius and Geuze (2004) that infants process the content of peripheral stimulation covertly but regulate their eye movements as a function of the content of both the central and peripheral stimuli. To directly evaluate whether difficulty in attention disengagement plays a role in infants' attention to fearful faces in the overlap task, one could present infants with a task in which their motivation to shift attention away from the face is increased, for example, by presenting an incentive, e.g., an interesting dynamic stimulus, when the infants correctly shift their eyes toward the peripheral stimulus.

Apart from a difficulty in disengagement or diminished perceptual sensitivity to peripherally presented stimuli, it is interesting to consider the effect of fear on attention disengagement in the overlap task as endogenously controlled attention (i.e., a response bias) to the signal conveyed by fearful faces. Some support for an endogenous mechanism is provided by studies that have combined signal detection analyses with heart rate-defined assessment of attention (Hicks & Richards, 1998; Richards, 1997). Hicks and Richards (1998) presented 8- to 26-week-old infants with static and dynamic peripheral stimuli alongside dynamic central stimuli during phases of attention and inattention (as defined by HR deceleration and its return to baseline level). Utilizing signal detection analyses, estimates for infants' sensitivity to detect the peripheral stimulus (d' index) and the bias against shifting attention away from the central stimulus (response bias β) were calculated. These estimates were considered to reflect the influence of the central stimulus on infants' peripheral perceptual sensitivity (d') and on more controlled response decision processes (β) operating at a later stage of the processing sequence (e.g., Massaro & Cowan, 1993). It was found that the infants were more likely to withhold shifting attention away from the center when attention was engaged in the focal stimulus and that this effect was best explained by differences in β but not in d'. In other words, the authors (Hicks & Richards, 1998) concluded that increased attention to the central stimulus was associated with controlled inhibition of the eye movement response but not with decreased sensitivity to detect the presence of a stimulus in the peripheral vision. One could further test whether centrally presented fearful faces have any effects on perceptual sensitivity to peripherally presented stimuli by recording ERPs during the overlap task. Shifts of attention to peripheral stimuli are typically preceded by an increase of early ERP responses (e.g., P1, a sharp positive peak at around 100 ms post-stimulus) in visual cortex contralateral to the stimulus (e.g., in the right occipital cortex following a left visual field stimulus; Hillyard & Anllo-Vento, 1998; Richards, 2005). It could be hypothesized that if centrally presented fearful faces suppress perceptual sensitivity to competing stimuli, the P1 triggered by the peripheral stimuli should be relatively smaller during fearful than happy central stimuli.

4.1.4 Cardiac correlates

Incorporating HR measurement into the overlap paradigm was considered to provide additional insights into the relative roles of automatic and controlled attentional mechanisms in contributing to the emotional modulation of attention in the overlap task. In Study IV, fearful faces were associated with larger HR deceleration but this effect was confined to the first 1000 ms post-stimulus (i.e., the time period preceding the onset of the peripheral stimulus). Fearful faces did not result in a prolonged maintenance of the HR deceleration, which could have indicated an effect on sustained attention and possibly more voluntary attentional engagement with fear. The emotional modulation of the rapid initial HR orienting is more akin to an obligatory attentional response to threat-related stimuli that is commonly observed in adults as well as in animals (Bradley, 2009). In animals, such “fear bradycardia” is controlled by signals emanating from the amygdala (Kapp et al., 1994) and serves to facilitate extraction of information about the source of the potential threat (Bradley, 2009). It would be tempting to interpret the infants’ enhanced HR orienting response to fear as an obligatory reflex to threat-related stimuli that serves to facilitate perceptual processing and that is controlled by an amygdala-centered subcortical circuitry. The precise function of the enhanced orienting is obscured, however, by the correlational analyses in Study IV which did not readily indicate that the cardiac orienting response corresponds to a relatively stronger inhibition of saccades away from fearful faces. The negative correlation between the magnitude of the orienting response during the first 1000 ms and the subsequent tendency to not respond to the peripheral stimulus suggests that different mechanisms may mediate enhanced initial orienting to and subsequent attentional prioritization of fearful faces, the latter possibly reflecting more controlled response processes.

The HR data from Study IV left open whether fearful faces would also result in a more pronounced and sustained HR deceleration which could provide indications regarding the hypothesis that the influence of fearful faces on attention is due to controlled regulation of attention (i.e., a response bias, cf. Hicks & Richards, 1998).

It is probable that the overlap paradigm is not optimal for revealing sustained HR effects due to the short stimulus presentation times and rapid rate of stimulus changes. It is important to note, however, that our more recent data (Peltola, Leppänen, & Hietanen, 2010) provides some support for a suggestion that there is a correspondence between the magnitude of HR deceleration over the whole trial and the behavioral response to peripheral stimuli. In that study, analyses of HR modulation as a function of attentional response type (i.e., whether the infant did or did not make a saccade toward the distractor) were made possible by presenting only fearful and happy faces and shortening the trial duration, thereby obtaining a larger number of trials for data analyses. Briefly, it was found that in addition to a larger HR deceleration to fearful faces in general, an interaction was found in that the HR deceleration was significantly larger during fearful face trials on which the infant did not make a saccade toward the peripheral stimulus than during happy face trials with no saccades. For trials on which a saccade was made, no difference in the magnitude of HR deceleration between fearful and happy faces was observed. Thus, the bias to attend preferentially to fearful faces is accompanied by a concomitant increase in the cardiac orienting response which is sustained until the end of the trial.

4.2 Developmental change in fear processing

Studies showing no attentional bias for fearful faces in infants aged 5 months or younger (Bornstein & Arterberry, 2003; Hoehl & Striano, 2010) as well as the differential results for the two age groups in Study I demonstrate that the attentional bias to favor fearful faces emerges between 5 and 7 months of age. Considering other developmental phenomena observed at this age, it is intriguing to note that stranger anxiety, i.e., increased vigilance regarding less familiar conspecifics, typically begins to appear at around the same age of 6 to 9 months (Cassidy & Shaver, 2008). With a laboratory setting that involved a stranger gradually approaching the infant, Braungart-Rieker, Hill-Soderlund, and Karrass (2010) examined the developmental course of fearful reactivity from 4 to 16 months of age. The greatest increase in fear reactivity was observed between 4 and 8 months, with the 4-month-olds, on average, showing very little fear of the stranger. There appears therefore to be a developmental correspondence between infants' enhanced attentiveness to fearful facial signals and putatively amygdala-mediated emotional fear responses such as stranger anxiety. The data from human infants are paralleled by research in macaque monkeys showing that infant monkeys – although already initiating exploratory social behavior during the first weeks of life – take between 2 and 4 months (roughly equaling 8-month-old human infants) before they start to respond to threat-related stimuli, such as others' facial expressions and unfamiliar conspecifics, with increasing sensitivity and species-typical fear reactions (Bauman & Amaral, 2008; Suomi, 1999). Together, these findings point to an absence of a heightened responsivity to threat-related stimuli during the early phases of development. Vaish et al. (2008) even argued for the existence of a "positivity bias" during the first half-year as there are some findings of longer looking times at happy than fearful expressions in newborns (Farroni et al., 2007) and at happy than angry expressions in 4- to 6-month-old infants (LaBarbera, Izard, Vietze, & Parisi, 1976; Wilcox & Clayton, 1968).

Regarding the possible experience-mediated mechanisms that could contribute to the observed changes in infants' sensitivity to fearful faces, it is relevant to note the advent of self-produced locomotion, i.e., the onset of crawling, which takes place typically at around the turn of the second half of the first year (Adolph, Vereijken, & Denny, 1998). Research by Campos and colleagues has shown that significant changes in infants' socioemotional environment take place when the infant starts to move independently (see Campos et al., 2000, for a review). For instance, caregivers typically start to show increased variability in their expressive behaviors toward the infant, including a heightened propensity to display emotionally negative facial signals in situations involving potential harm or misconduct in attempting to regulate the infant's actions (Campos, Kermoian, & Zumbahlen, 1992). As a result, facial expressions begin to gain more direct referential significance, which may enable infants to form associations between emotional signals and different contextual events. Whether such developmental mechanisms could account for the age differences in Study I is not known. Some doubt is cast on this by unpublished data analyses from Study I showing no differences in the magnitude of the attentional bias to fear in 7-month-old infants who already had or did not have experience of crawling by the time of testing. Thus, while there is little doubt that by the age of 12 months infants have learned to utilize adults' facial expressions as providing referential information to guide their attention and behavior (e.g., Carver & Vaccaro, 2007; Mumme & Fernald, 2003), probably due to extensive experience with adults using facial expressions as means to regulate the infant's behavior, it is doubtful whether such experience could explain the emergence of enhanced attention to fearful facial displays at 7 months of age.

A novel approach in attempting to account for the mechanisms that might give rise to the rapid changes in infants' preferences for facial signals of emotion at the turn of the second half of the first year was provided by Leppänen and Nelson (2009) who considered such changes as a case of *experience-expectant* processes in brain development. Experience-expectant refers to a certain level of evolutionarily shaped "preparedness" in the developing neural circuits to "expect" the occurrence of sensory stimuli that are common to all members of a species such as basic elements of visual patterns (Greenough, Black, & Wallace, 1987). Thus, as a consequence of a lengthy evolution in species-typical environments, some neural circuits may be innately biased to adapt their firing patterns for certain classes of stimuli with relatively little exposure to ensure the development of stable and finely tuned neural representations for stimuli that the environment typically provides for all members of the species. Nelson (2001) adapted such a view as a framework for understanding the rapid rate of development in processing and recognizing human faces in early infancy. Newborn infants appear to have the capability to process some of the typical characteristics of faces, which manifests in neonates' visual preferences for coarsely face-like stimuli such as schematic patterns containing high-contrast features corresponding to the approximate location of the eyes and mouth (e.g., Simion, Valenza, Umilta, & Dalla Barba, 1998) and even for simple up-down asymmetrical patterns that contain more high-contrast elements in the upper half of the stimulus (Turati, Simion, Milani, & Umilta, 2002). The early-emerging preference for face-like information may have evolved to ensure that infants gain extensive experience with individual faces during early development and gradually develop the skills for making fine-grained discriminations between a large number of individual faces (Johnson, 2005b). Leppänen and Nelson (2009) argued for a similar developmental progression in the early emergence of the neural systems underlying the processing of emotional facial expressions. Thus, infants' attentional bias toward fearful faces may indicate a pre-wired readiness to attend preferentially to – and subsequently learn from – signals of high emotional salience, a readiness which is activated at the developmental phase during which infants typically begin self-produced locomotion and facial expressions begin to serve more regulative and referential functions. According to this view (Leppänen & Nelson, 2009), the preferential processing appears obligatory and does not necessitate the assumption that the infants are able to derive meaning from the fearful faces they pay attention to. The heightened interest in such signals, however, may promote the emerging ability to extract the meaning denoted by a fearful expression.

The question arises, however, why the prioritization of fearful faces does *not* emerge earlier than at six months? From an evolutionary point of view, enhanced attentiveness to facial signals of threat is a highly adaptive response that serves to foster rapid learning and, ultimately, survival in situations involving a potential threat (Öhman, 2009). From this perspective, it can be argued that it would be adaptive for the functional response to threat-related information to be evident very early in ontogeny (cf. Vaish et al., 2008). However, research in various altricial species has yielded evidence for an absence of fear-learning during early development which purportedly functions to optimize and protect the infant's attachment and proximity-seeking to the caregiver and, conversely, to prevent learning aversion toward the caregiver (Moriceau & Sullivan, 2005). For example, infant rat pups not only fail to learn aversion to a novel odor that is paired with a shock but actually increase their preference for the odor (Moriceau & Sullivan, 2006; Sullivan, Landers, Yeaman, & Wilson, 2000). After the young rat learns to walk and begins to progress toward independent life outside the nest after 10 days af age, fear of shock-paired odors is learned quickly (Languille, Richer, & Hars, 2009; Sullivan et al., 2000), reflecting an adaptation for learning imminent threats to survival while exploring outside the nest (Barr et al., 2009). Such a developmental shift in responding to threat-related stimuli is essentially dependent on the functional emergence of dopamine and glucocorticoid signaling in the amygdala (Barr et al., 2009; Moriceau, Wilson, Levine, & Sullivan, 2006), which begins to show enhanced responses during odor-shock conditioning only after the early sensitive period for attachment learning has passed (Sullivan et al., 2000).

Thus, early infancy in rats is marked by an inability to form threat-related associations and by a concurrent hyperactivation of systems guiding the young rat to seek proximity to a close attachment figure, even if subjected to abusive handling (Moriceau & Sullivan, 2005). Naturally, similar developmental changes in human infants have not been documented in such detail as in rodents. However, the superficial similarity in the developmental progression of rodents' fear-learning and infants' and macaques' putatively amygdala-mediated phenomena (i.e., wariness of strangers and increased attention to fearful faces) may provide the basis for a tentative hypothesis that in the human infant's life, too, the early phase of ontogeny during which the infant is most critically dependent upon parental care is associated with enhanced functioning of mechanisms supporting the creation of an attachment to the caregiver, coupled with an apparent inability to learn fear of the caregiver (cf. Moriceau, Roth, & Sullivan, 2010). Such a hypothesis remains to be tested experimentally. An extensive line of research in a "natural experiment" with children developing in deprived conditions in Romanian institutions, however, has provided indirect support for the hypothesis and further highlighted the importance of the timing of experiences mediating emotional development (Reeb, Fox, Nelson, & Zeanah, 2009). Children transferred to high-quality foster care before 6 months of age fare consistently better emotionally than those transferred after 6 months with a higher probability of having secure attachment and fewer behavioral problems (MacLean, 2003; Marcovitch et al., 1997; O'Connor et al., 2003). Such observations provide some support for the contention that amygdala-mediated emotional behaviors show a developmental progression that has evolved to ensure an early sensitive period for development of the infant-caregiver attachment bond (Reeb et al., 2009).

4.3 Emotion-attention interaction in the developing brain

The present findings that show 7-month-old infants paying increased attention to signals of potential threat (i.e., fearful faces) – also when attention is diverted elsewhere by distracting stimuli – suggest that during a developmental phase that marks a step toward becoming less dependent on caregivers, the emotional significance of social stimuli becomes integrated with the functioning of executive attention systems in order to guide attention towards biologically relevant information in the environment. Such biased attention would obviously benefit a locomotive infant by enabling rapid learning of potential risks through observing others' facial expressions (cf. Campos et al., 2000). In terms of brain function, interaction between perceptual processing and the systems controlling behavioral output requires functional interaction between cortical areas processing sensory information, structures that are responsive to the emotional significance of stimuli (e.g., orbitofrontal cortex and the amygdala), and the areas that are associated with attention control (e.g., ACC; Pessoa, 2009).

At present, we have no means to directly access the developmental state of such functional networks in the infant brain as the current methods for brain imaging in infants (such as EEG) only allow recording of activity from the scalp surface but not from deeper sources such as the amygdala. However, the present and earlier data provide some clues, albeit indirect, suggesting an interplay between systems controlling attention and emotion perception at an early age. First, the larger ERP responses to fearful faces in Study I and also in other studies (de Haan et al., 2004; Leppänen, Moulson et al., 2007; Nelson & de Haan, 1996) have their putative cortical generators in the ACC (Reynolds & Richards, 2005). This suggests that perhaps similarly as in adults (Pessoa, 2009; Pezawas et al., 2005; Vuilleumier et al., 2001), executive mechanisms that serve to provide control over the focus of attention as well as inhibitory feedback to the amygdala operate during the perception of emotionally evocative stimuli in 7-month-old infants. Second, the apparent sensitivity of infants in inhibiting their attention selectively to prototypical fearful faces over other potentially relevant and attention-grabbing stimulus features (novelty, distinctive eye region features) suggests a considerable level of specificity in the input utilized by the mechanisms inhibiting unwanted attention shifts to distracting stimuli in order to retain attention on the more salient source of information. Third, recent studies by Hoehl and colleagues showed larger Nc amplitudes when 6-month-old infants perceived a fearful face gazing at a novel object than when the fearful face was looking at the infant (Hoehl, Palumbo, Heinisch, & Striano, 2008; Hoehl & Striano, 2010). The Nc was also larger for separately presented novel objects after they had been associated with a fearful eye gaze than after being associated with a neutral eye gaze (Hoehl & Striano, 2010). In terms of emotion-attention interaction, these findings further indicate that infants' attentional resource allocation to emotionally neutral objects is sensitive to the emotional context in which the objects are presented (i.e., an object-directed fearful gaze implying that the object possesses an attribute that the infant should be wary of and pay attention to). Finally, Sheese et al. (2008) presented 6- and 7-month-old infants with an anticipatory looking task which is an early marker of executive attention control (i.e., control of visual orienting is indexed by looking at the location of an upcoming target prior to its appearance). The frequency of correct anticipatory looks was found to be positively correlated with a relatively more cautious approach to subsequently presented novel toys (i.e., a longer delay before interacting with and rather looking at than touching the toys), indicating an early-emerging correspondence between executive attention control and the regulation of emotional responding to novelty.

To conclude, the emerging executive attention skills may provide infants with more efficient regulation of responses to emotional stimuli and an ability to utilize emotional cues in the control of attentional focus. Posner and Rothbart (2007; Posner et al., 2007) provide a framework for the importance of the executive attention system for later socioemotional development. As a primary platform for executive functions, the ACC is hypothesized to form the basis for emotion regulation and empathy by "reading" and acting upon the signals emanating from the amygdala (Posner & Rothbart, 2007). Accordingly, a positive relation between executive abilities and empathic responding to others' distress have been observed in older children (e.g., Valiente et al., 2004). Whether infants' selective attention to others' facial expressions has any predictive value for the later development of empathic responding or whether there is a direct correspondence between rudimentary executive capacity and sensitivity to emotional cues in infancy provide fruitful avenues for future research. Nevertheless, the existing data can be taken to support a tentative hypothesis that the neural systems operating upon perception, emotional responding, and its regulation are already functionally linked in infancy.

4.4 Concluding remarks

To summarize, the present set of studies showed that the increased attention to fearful facial expressions a) emerges between 5 and 7 months of age, b) is reflected in infants' regulation of attention between faces and distractor stimuli, c) shows selectivity to prototypical fearful expressions in that no similar attentional modulation was observed for other potentially relevant stimulus features (i.e., novelty and enlarged fearful eyes), and d) bears a resemblance to adults' autonomic response to threat-related stimuli.

Some limitations regarding the interpretation of the results are noteworthy. First, although a developmental change in attention to emotional stimuli between 5 and 7 months of age was shown, no firm conclusions can be made regarding emotion-attention interactions during the later stages of infancy. It could happen, for example, that the relatively robust behavioral attentional biases for fearful faces may attenuate with age while the neural responses might still indicate differential responses to emotional faces. Second, while infants' responses to prototypical fearful faces showed a level of specificity over other potentially relevant stimulus features (novelty, enlarged eyes), it still remains to be reliably demonstrated that infants do actually respond to the emotional signal value inherent in fearful expressions (i.e., realize that the person is afraid). Third, individual differences in responding to emotional stimuli due to temperament, genetic predisposition (e.g., variation in amygdala-prefrontal functional connectivity induced by serotonin-linked genes; Pezawas et al., 2005) or other factors were not investigated. Potential early-emerging individual differences in attention to facial expressions could have important downstream effects on subsequent emotional and social development, particularly as emotional face processing and temperament-related variation in fearful reactivity have both been linked to amygdala functioning (cf. Fox, Henderson, Marshall, Nichols, & Ghera, 2005).

Emotion-attention interactions probed by our tests of facial emotion processing in infancy illustrate the emergence of a prioritization of emotional significance in processing social signals. Such an ability may provide a crucial scaffold for an infant with a newly found level of independence to navigate in an increasingly complex social and physical environment. An important goal for future studies is to elucidate the ways in which the early-emerging ability to regulate attention and behavior in response to emotional cues contributes to later behavioral and social development.

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REFERENCES

Adolph, K. E., Vereijken, B., & Denny, M. A. (1998). Learning to crawl. *Child Development, 69*, 1299-1312.

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

Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature, 433*, 68-72.

Andreassi, J. L. (2000). *Psychophysiology: Human behavior and physiological response* (4th ed.). Mahwah, NJ: Lawrence Erlbaum Associates, Inc.

Asghar, A. U. R., Chiu, Y., Hallam, G., Liu, S., Mole, H., Wright, H., et al. (2008). An amygdala response to fearful faces with covered eyes. *Neuropsychologia, 46*, 2364-2370.

Aslin, R. N. (2007). What's in a look? *Developmental Science, 10*, 48-53.

Aslin, R. N., & Salapatek, P. (1975). Saccadic localization of visual targets by the very young human infant. *Perception and Psychophysics, 17*, 293-302.

Aviezer, H., Hassin, R. R., Ryan, J., Grady, C., Susskind, J., Anderson, A., et al. (2008). Angry, disgusted, or afraid? Studies on the malleability of emotion perception. *Psychological Science, 19*, 724-732.

Banks, M. S., & Salapatek, P. (1983). Infant visual perception. In M. M. Haith, & J. J. Campos (Eds.), *Handbook of child psychology: Vol. 2. Infancy and developmental psychobiology* (4th ed., pp. 435-571). New York, NY: Wiley.

Bannerman, R. L., Milders, M., de Gelder, B., & Sahraie, A. (2009). Orienting to threat: Faster localization of fearful facial expressions and body postures revealed by saccadic eye movements. *Proceedings of the Royal Society B: Biological Sciences, 276*, 1635-1641.

Barr, G. A., Moriceau, S., Shionoya, K., Muzny, K., Gao, P., Wang, S., et al. (2009). Transitions in infant learning are modulated by dopamine in the amygdala. *Nature Neuroscience, 12*, 1367-1369.

Batki, A., Baron-Cohen, S., Wheelwright, S., Connellan, J., & Ahluwalia, J. (2000). Is there an innate gaze module? Evidence from human neonates. *Infant Behavior and Development, 23*, 223-229.

Batty, M., & Taylor, M. J. (2003). Early processing of the six basic facial emotional expressions. *Cognitive Brain Research, 17*, 613-620.

Bauman, M. D., & Amaral, D. G. (2008). Neurodevelopment of social cognition. In C. A. Nelson, & M. Luciana (Eds.), *Handbook of developmental cognitive neuroscience* (2nd ed., pp. 161-185). Cambridge, MA: MIT Press.

Bentley, P., Vuilleumier, P., Thiel, C. M., Driver, J., & Dolan, R. J. (2003). Cholinergic enhancement modulates neural correlates of selective attention and emotional processing. *Neuroimage, 20*, 58-70.

Bishop, S. J. (2008). Neural mechanisms underlying selective attention to threat. *Annals of the New York Academy of Sciences, 1129*, 141-152.

Bishop, S. J., Jenkins, R., & Lawrence, A. D. (2007). Neural processing of fearful faces: Effects of anxiety are gated by perceptual capacity limitations. *Cerebral Cortex, 17*, 1595-1603.

Blau, V., Maurer, U., Tottenham, N., & McCandliss, B. (2007). The face-specific N170 component is modulated by emotional facial expression. *Behavioral and Brain Functions, 3*, 7.

Bornstein, M. H., & Arterberry, M. E. (2003). Recognition, discrimination and categorization of smiling by 5-month-old infants. *Developmental Science, 6*, 585-599.

Bradley, M. M. (2009). Natural selective attention: Orienting and emotion. *Psychophysiology, 46*, 1-11.

Bradley, M. M., Lang, P. J., & Cuthbert, B. N. (1993). Emotion, novelty, and the startle reflex: Habituation in humans. *Behavioral Neuroscience, 107*, 970-980.

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

Broadbent, D. E. (1958). *Perception and communication*. London, UK: Pergamon Press.

Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences, 4*, 215-222.

Campos, J. J., Anderson, D. I., Barbu-Roth, M. A., Hubbard, E. M., Hertenstein, M. J., & Witherington, D. (2000). Travel broadens the mind. *Infancy, 1*, 149-219.

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

Carlson, J. M., Reinke, K. S., LaMontagne, P. J., & Habib, R. (in press). Backward masked fearful faces enhance contralateral occipital cortical activity for visual targets within the spotlight of attention. *Social Cognitive and Affective Neuroscience.*

Caron, R. F., Caron, A. J., & Myers, R. S. (1982). Abstraction of invariant face expressions in infancy. *Child Development, 53*, 1008-1015.

Caron, R. F., Caron, A. J., & Myers, R. S. (1985). Do infants see emotional expressions in static faces? *Child Development, 56*, 1552-1560.

Carver, L. J., & Vaccaro, B. G. (2007). 12-month-old infants allocate increased neural resources to stimuli associated with negative adult emotion. *Developmental Psychology, 43*, 54-69.

Casey, B. J., Trainor, R., Giedd, J., Vauss, Y., Vaituzis, C. K., Hamburger, S., et al. (1997). The role of the anterior cingulate in automatic and controlled processes: A developmental neuroanatomical study. *Developmental Psychobiology, 30*, 61-69.

Cassidy, J., & Shaver, P. R. (Eds.). (2008). *Handbook of attachment: Theory, research, and clinical applications* (2nd ed.). New York, NY: The Guilford Press.

Codispoti, M., Bradley, M. M., & Lang, P. J. (2001). Affective reactions to briefly presented pictures. *Psychophysiology, 38*, 474-478.

Codispoti, M., Ferrari, V., Junghofer, M., & Schupp, H. T. (2006). The categorization of natural scenes: Brain attention networks revealed by dense sensor ERPs. *Neuroimage, 32*, 583-591.

Cohen, L. B., & Gelber, E. R. (1975). Infant visual memory. In L. B. Cohen, & P. Salapatek (Eds.), *Infant perception: From sensation to cognition: Vol. 1. Basic visual processes* (pp. 347-403). New York, NY: Academic Press.

Colombo, J. (2001). The development of visual attention in infancy. *Annual Review of Psychology, 52*, 337-367.

Colombo, J., Richman, W. A., Shaddy, D. J., Greenhoot, A. F., & Maikranz, J. M. (2001). Heart rate-defined phases of attention, look duration, and infant performance in the paired-comparison paradigm. *Child Development, 72*, 1605-1616.

Courage, M. L., Reynolds, G. D., & Richards, J. E. (2006). Infants' attention to patterned stimuli: Developmental change from 3 to 12 months of age. *Child Development, 77*, 680-695.

Courchesne, E., Ganz, L., & Norcia, A. M. (1981). Event-related brain potentials to human faces in infants. *Child Development, 52*, 804-811.

Csibra, G., Kushnerenko, E., & Grossmann, T. (2008). Electrophysiological methods in studying infant cognitive development. In C. A. Nelson, & M. Luciana (Eds.), *Handbook of developmental cognitive neuroscience* (2nd ed., pp. 247-262). Cambridge, MA: MIT Press.

Csibra, G., Tucker, L. A., & Johnson, M. H. (1998). Neural correlates of saccade planning in infants: A high-density ERP study. *International Journal of Psychophysiology, 29*, 201-215.

Davidson, R. J., Jackson, D. C., & Larson, C. L. (2000). Human electroencephalography. In J. T. Cacioppo, L. G. Tassinary & G. G. Berntson (Eds.), *Handbook of psychophysiology* (2nd ed., pp. 27-52). Cambridge, UK: Cambridge University Press.

Davis, M., & Whalen, P. J. (2001). The amygdala: Vigilance and emotion. *Molecular Psychiatry, 6*, 13-34.

de Haan, M. (2007). Visual attention and recognition memory in infancy. In M. de Haan (Ed.), *Infant EEG and event-related potentials.* (pp. 101-143). New York, NY: Psychology Press.

de Haan, M., Belsky, J., Reid, V., Volein, A., & Johnson, M. H. (2004). Maternal personality and infants' neural and visual responsivity to facial expressions of emotion. *Journal of Child Psychology and Psychiatry, 45*, 1209-1218.

de Haan, M., Johnson, M. H., & Halit, H. (2007). Development of face-sensitive event-related potentials during infancy. In M. de Haan (Ed.), *Infant EEG and event-related potentials.* (pp. 78-99). New York, NY: Psychology Press.

de Haan, M., & Nelson, C. A. (1997). Recognition of the mother's face by six-month-old infants: A neurobehavioral study. *Child Development, 68*, 187-210.

de Haan, M., & Nelson, C. A. (1998). Discrimination and categorisation of facial expressions of emotion during infancy. In A. Slater (Ed.), *Perceptual development* (pp. 287-309). Hove, UK: Psychology Press.

de Haan, M., & Nelson, C. A. (1999). Brain activity differentiates face and object processing in 6-month-old infants. *Developmental Psychology, 35*, 1113-1121.

De Martino, B., Kalisch, R., Rees, G., & Dolan, R. J. (2009). Enhanced processing of threat stimuli under limited attentional resources. *Cerebral Cortex, 19*, 127-133.

DeBoer, T., Scott, L. S., & Nelson, C. A. (2007). Methods for acquiring and analyzing infant event-related potentials. In M. de Haan (Ed.), *Infant EEG and event-related potentials* (pp. 5-38). New York, NY: Psychology Press.

Fabiani, M., Gratton, G., & Coles, M. G. H. (2000). Event-related brain potentials. In J. T. Cacioppo, L. G. Tassinary & G. G. Berntson (Eds.), *Handbook of psychophysiology* (2nd ed., pp. 53-84). Cambridge, UK: Cambridge University Press.

Fantz, R. L. (1964). Visual experience in infants: Decreased attention to familiar patterns relative to novel ones. *Science, 146*, 668-670.

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

Farroni, T., Menon, E., Rigato, S., & Johnson, M. H. (2007). The perception of facial expressions in newborns. *European Journal of Developmental Psychology, 4*, 2-13.

Feldman, R. (2007). Parent-infant synchrony: Biological foundations and developmental outcomes. *Current Directions in Psychological Science, 16*, 340-345.

Fenske, M. J., & Eastwood, J. D. (2003). Modulation of focused attention by faces expressing emotion: Evidence from flanker tasks. *Emotion (Washington, D.C.), 3*, 327-343.

Field, T. M., Woodson, R., Greenberg, R., & Cohen, D. (1982). Discrimination and imitation of facial expression by neonates. *Science, 218*, 179-181.

Finlay, D., & Ivinskis, A. (1984). Cardiac and visual responses to moving stimuli presented either successively or simultaneously to the central and peripheral visual fields in 4-month-old infants. *Developmental Psychology, 20*, 29-36.

Fox, N. A., Henderson, H. A., Marshall, P. J., Nichols, K. E., & Ghera, M. M. (2005). Behavioral inhibition: Linking biology and behavior within a developmental framework. *Annual Review of Psychology, 56*, 235-262.

Frick, J. E., Colombo, J., & Saxon, T. F. (1999). Individual and developmental differences in disengagement of fixation in early infancy. *Child Development, 70*, 537-548.

Gao, X., & Maurer, D. (2010). A happy story: Developmental changes in children's sensitivity to facial expressions of varying intensities. *Journal of Experimental Child Psychology, 107*, 67-86.

Georgiou, G. A., Bleakley, C., Hayward, J., Russo, R., Dutton, K., Eltiti, S., et al. (2005). Focusing on fear: Attentional disengagement from emotional faces. *Visual Cognition, 12*, 145-158.

Giedd, J. N., Blumenthal, J., Jeffries, N. O., Castellanos, F. X., Liu, H., Zijdenbos, A., et al. (1999). Brain development during childhood and adolescence: A longitudinal MRI study. *Nature Neuroscience, 2*, 861-863.

Gliga, T., & Csibra, G. (2007). Seeing the face through the eyes: A developmental perspective on face expertise. *Progress in Brain Research, 164*, 323-339.

Goren, C. C., Sarty, M., & Wu, P. Y. K. (1975). Visual following and pattern discrimination of face-like stimuli by newborn infants. *Pediatrics, 56*, 544-549.

Gredebäck, G., Johnson, S., & von Hofsten, C. (2010). Eye tracking in infancy research. *Developmental Neuropsychology, 35*, 1-19.

Greenough, W. T., Black, J. E., & Wallace, C. S. (1987). Experience and brain development. *Child Development, 58*, 539-559.

Grossmann, T., Gliga, T., Johnson, M. H., & Mareschal, D. (2009). The neural basis of perceptual category learning in human infants. *Journal of Cognitive Neuroscience, 21*, 2276-2286.

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

Grossmann, T., Striano, T., & Friederici, A. D. (2007). Developmental changes in infants' processing of happy and angry facial expressions: A neurobehavioral study. *Brain and Cognition, 64*, 30-41.

Halit, H., Csibra, G., Volein, A., & Johnson, M. H. (2004). Face-sensitive cortical processing in early infancy. *Journal of Child Psychology and Psychiatry, 45*, 1228-1334.

Halit, H., de Haan, M., & Johnson, M. H. (2003). Cortical specialisation for face processing: Face-sensitive event-related potential components in 3- and 12-month-old infants. *Neuroimage, 19*, 1180-1193.

Handy, T. C. (2005). *Event-related potentials: A methods handbook*. Cambridge, MA: MIT Press.

Hare, T. A., Tottenham, N., Galvan, A., Voss, H. U., Glover, G. H., & Casey, B. J. (2008). Biological substrates of emotional reactivity and regulation in adolescence during an emotional go-nogo task. *Biological Psychiatry, 63*, 927-934.

Hariri, A. R., V, M., Tessitore, A., Kolachana, B., Fera, F., Goldman, D., et al. (2002). Serotonin transporter genetic variation and the response of the human amygdala. *Science, 297*, 400-403.

Henderson, J. M., Williams, C. C., & Falk, R. J. (2005). Eye movements are functional during face learning. *Memory & Cognition, 33*, 98-106.

Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science, 317*, 1360-1366.

Herry, C., Bach, D. R., Esposito, F., Di Salle, F., Perrig, W. J., Scheffler, K., et al. (2007). Processing of temporal unpredictability in human and animal amygdala. *Journal of Neuroscience, 27*, 5958-5966.

Hicks, J. M., & Richards, J. E. (1998). The effects of stimulus movement and attention on peripheral stimulus localization by 8- to 26-week-old infants. *Infant Behavior and Development, 21*, 571-589.

Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences of the United States of America, 95*, 781-787.

Hoehl, S., Palumbo, L., Heinisch, C., & Striano, T. (2008). Infants' attention is biased by emotional expressions and eye gaze direction. *Neuroreport, 19*, 579-582.

Hoehl, S., & Striano, T. (2008). Neural processing of eye gaze and threat-related emotional facial expressions in infancy. *Child Development, 79*, 1752-1760.

Hoehl, S., & Striano, T. (2010). The development of emotional face and eye gaze processing. *Developmental Science, 13,* 813-825.

Holmboe, K., Fearon, R. M. P., Csibra, G., Tucker, L. A., & Johnson, M. H. (2008). Freeze-frame: A new infant inhibition task and its relation to frontal cortex tasks during infancy and early childhood. *Journal of Experimental Child Psychology, 100*, 89-114.

Holmes, A., Green, S., & Vuilleumier, P. (2005). The involvement of distinct visual channels in rapid attention towards fearful facial expressions. *Cognition & Emotion, 19*, 899-922.

Hood, B. M. (1995). Visual selective attention in infants: A neuroscientific approach. In L. Lipsitt, & C. Rovee-Collier (Eds.), *Advances in infancy research, vol. 9* (pp. 163-216). Norwood, NJ: Ablex.

Huettel, S. A., Song, A. W., & McCarthy, G. (2004). *Functional magnetic resonance imaging*. Sunderland, MA: Sinauer Associates.

Hunnius, S., de Wit, T. C. J., Vrins, S., & von Hofsten, C. (in press). Facing threat: Infants' and adults' visual scanning of faces with neutral, happy, sad, angry, and fearful emotional expressions. *Cognition & Emotion.*

Hunnius, S., & Geuze, R. H. (2004). Gaze shifting in infancy: A longitudinal study using dynamic faces and abstract stimuli. *Infant Behavior and Development, 27*, 397-416.

Johnson, M. H. (1995). The inhibition of automatic saccades in early infancy. *Developmental Psychobiology, 28*, 281-291.

Johnson, M. H. (2005a). *Developmental cognitive neuroscience: An introduction* (2nd ed.). Oxford, UK: Blackwell.

Johnson, M. H. (2005b). Subcortical face processing. *Nature Reviews Neuroscience, 6*, 766-774.

Johnson, M. H., Grossmann, T., & Cohen Kadosh, K. (2009). Mapping functional brain development: Building a social brain through interactive specialization. *Developmental Psychology, 45*, 151-159.

Johnson, M. H., Posner, M. I., & Rothbart, M. K. (1994). Facilitation of saccades toward a covertly attended location in early infancy. *Psychological Science, 5*, 90-93.

Kaitz, M., Meschulach-Sarfaty, O., Auerbach, J., & Eidelman, A. (1988). A reexamination of newborns' ability to imitate facial expressions. *Developmental Psychology, 24*, 3-7.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17*, 4302-4311.

Kapp, B. S., Supple, W. F.,Jr, & Whalen, P. J. (1994). Effects of electrical stimulation of the amygdaloid central nucleus on neocortical arousal in the rabbit. *Behavioral Neuroscience, 108*, 81-93.

Kim, H., Somerville, L. H., Johnstone, T., Polis, S., Alexander, A. L., Shin, L. M., et al. (2004). Contextual modulation of amygdala responsivity to surprised faces. *Journal of Cognitive Neuroscience, 16*, 1730-1745.

Kobiella, A., Grossmann, T., Reid, V. M., & Striano, T. (2008). The discrimination of angry and fearful facial expressions in 7-month-old infants: An event-related potential study. *Cognition & Emotion, 22*, 134-146.

Kohler, C. G., Turner, T., Stolar, N. M., Bilker, W. B., Brensinger, C. M., Gur, R. E., et al. (2004). Differences in facial expressions of four universal emotions. *Psychiatry Research, 128*, 235-244.

Kolassa, I. T., & Miltner, W. H. (2006). Psychophysiological correlates of face processing in social phobia. *Brain Research, 1118*, 130-141.

Koster, E. H., Crombez, G., Van Damme, S., Verschuere, B., & De Houwer, J. (2004). Does imminent threat capture and hold attention? *Emotion, 4*, 312-317.

Kotsoni, E., de Haan, M., & Johnson, M. H. (2001). Categorical perception of facial expressions by 7-month-old infants. *Perception, 30*, 1115-1125.

Kuchuk, A., Vibbert, M., & Bornstein, M. H. (1986). The perception of smiling and its experiential correlates in three-month-old infants. *Child Development, 57*, 1054-1061.

LaBarbera, J. D., Izard, C. E., Vietze, P., & Parisi, S. A. (1976). Four- and six-month-old infants' visual responses to joy, anger, and neutral expressions. *Child Development, 47*, 535-538.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). Motivated attention: Affect, activation and action. In P. J. Lang, R. F. Simons & M. T. Balaban (Eds.), *Attention and orienting: Sensory and motivational processes* (pp. 97-135). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Lang, P. J., & Bradley, M. M. (2010). Emotion and the motivational brain. *Biological Psychology, 84*, 437-450.

Languille, S., Richer, P., & Hars, B. (2009). Approach memory turns to avoidance memory with age. *Behavioural Brain Research, 202*, 278-284.

Lansink, J. M., & Richards, J. E. (1997). Heart rate and behavioral measures of attention in six-, nine-, and twelve-month-old infants during object exploration. *Child Development, 68*, 610-620.

Leppänen, J. M. (2007). Depressioon liittyvät emotionaaliset muutokset ja niiden hermostollinen perusta. *Duodecim, 123*, 297-303.

Leppänen, J. M., Hietanen, J. K., & Koskinen, K. (2008). Differential early ERPs to fearful versus neutral facial expressions: A response to the salience of the eyes? *Biological Psychology, 78*, 150-158.

Leppänen, J. M., Kauppinen, P., Peltola, M. J., & Hietanen, J. K. (2007). Differential electrocortical responses to increasing intensities of fearful and happy emotional expressions. *Brain Research, 1166*, 103-109.

Leppänen, J. M., Moulson, M. C., Vogel-Farley, V. K., & Nelson, C. A. (2007). An ERP study of emotional face processing in the adult and infant brain. *Child Development, 78*, 232-245.

Leppänen, J. M., & Nelson, C. A. (2006). The development and neural bases of facial emotion recognition. In R. V. Kail (Ed.), *Advances in child development and behavior, vol. 34* (pp. 207-246). San Diego, CA: Academic Press.

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

Lewis, M., Kagan, J., Campbell, H., & Kalafat, J. (1966). The cardiac response as a correlate of attention in infants. *Child Development, 37*, 63-71.

Libby, W. L.,Jr., Lacey, B. C., & Lacey, J. I. (1973). Pupillary and cardiac activity during visual attention. *Psychophysiology, 10*, 270-294.

Libertus, K., Needham, A., & Pelphrey, K. A. (2007, March). *An eye-tracking study of face perception: From infancy to adulthood*. Poster presented at the Biennial Meeting of the Society for Research in Child Development, Boston, MA.

LoBue, V., & DeLoache, J. S. (2010). Superior detection of threat-relevant stimuli in infancy. *Developmental Science, 13*, 221-228.

Logothetis, N. K., Pauls, J., Augath, M., Trinath, T., & Oeltermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature, 412*, 150-157.

Ludemann, P. M., & Nelson, C. A. (1988). Categorical representation of facial expressions by 7-month-old infants. *Developmental Psychology, 24*, 492-501.

MacLean, K. (2003). The impact of institutionalization on child development. *Development and Psychopathology, 15*, 853-884.

MacLeod, C., Mathews, A., & Tata, P. (1986). Attentional bias in emotional disorders. *Journal of Abnormal Psychology, 95*, 15-20.

Makeig, S., Debener, S., Onton, J., & Delorme, A. (2004). Mining event-related brain dynamics. *Trends in Cognitive Sciences, 8*, 204-210.

Malatesta, C. Z., & Haviland, J. M. (1982). Learning display rules: The socialization of emotion expression in infancy. *Child Development, 53*, 991-1003.

Marcovitch, S., Goldberg, S., Gold, A., Washington, J., Wasson, C., Krekewich, K., et al. (1997). Determinants of behavioural problems in Romanian children adopted in Ontario. *International Journal of Behavioral Development, 20*, 17-31.

Massaro, D. W., & Cowan, N. (1993). Information processing models: Microscopes of the mind. *Annual Review of Psychology, 44*, 383-425.

Mesulam, M. M. (1983). The functional anatomy and hemispheric specialization for directed attention: The role of the parietal lobe and its connectivity. *Trends in Neurosciences, 6*, 384-387.

Michel, C. M., Murray, M. M., Lantz, G., Gonzalez, S., Spinelli, L., & Grave de Peralta, R. (2004). EEG source imaging. *Clinical Neurophysiology, 115*, 2195-2222.

Milders, M., Sahraie, A., Logan, S., & Donnellon, N. (2006). Awareness of faces is modulated by their emotional meaning. *Emotion, 6*, 10-17.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience, 24*, 167-202.

Moriceau, S., Roth, T. L., & Sullivan, R. M. (2010). Rodent model of infant attachment learning and stress. *Developmental Psychobiology, 52,* 651-660.

Moriceau, S., & Sullivan, R. M. (2005). Neurobiology of infant attachment. *Developmental Psychobiology, 47*, 230-242.

Moriceau, S., & Sullivan, R. M. (2006). Maternal presence serves as a switch between learning fear and attraction in infancy. *Nature Neuroscience, 9*, 1004-1006.

Moriceau, S., Wilson, D. A., Levine, S., & Sullivan, R. M. (2006). Dual circuitry for odor-shock conditioning during infancy: Corticosterone switches between fear and attraction via amygdala. *Journal of Neuroscience, 26*, 6737-6748.

Morris, J. S., deBonis, M., & Dolan, R. J. (2002). Human amygdala responses to fearful eyes. *Neuroimage, 17*, 214-222.

Morris, J. S., Friston, K. J., Buchel, C., Frith, C. D., Young, A. W., Calder, A. J., et al. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain, 121*, 47-57.

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

Mumme, D. L., & Fernald, A. (2003). The infant as onlooker: Learning from emotional reactions observed in a television scenario. *Child Development, 74*, 221-237.

Nelson, C. A. (2001). The development and neural bases of face recognition. *Infant and Child Development, 10*, 3-18.

Nelson, C. A., & Collins, P. F. (1991). Event-related potential and looking-time analysis of infants' responses to familiar and novel events: Implications for visual recognition memory. *Developmental Psychology, 27*, 50-58.

Nelson, C. A., & de Haan, M. (1996). Neural correlates of infants' visual responsiveness to facial expressions of emotion. *Developmental Psychobiology, 29*, 577-595.

Nelson, C. A., & Dolgin, K. G. (1985). The generalized discrimination of facial expressions by seven-month-old infants. *Child Development, 56*, 58-61.

Nelson, C. A., Morse, P. A., & Leavitt, L. A. (1979). Recognition of facial expressions by seven-month-old infants. *Child Development, 50*, 1239-1242.

Nili, U., Goldberg, H., Weizman, A., & Dudai, Y. (2010). Fear thou not: Activity of frontal and temporal circuits in moments of real-life courage. *Neuron, 66*, 949-962.

Ochsner, K. N., & Gross, J. J. (2005). The cognitive control of emotion. *Trends in Cognitive Sciences, 9*, 242-249.

O'Connor, T. G., Marvin, R. S., Rutter, M., Olrick, J. T., Britner, P. A., & The English and Romanian Adoptees Study Team. (2003). Child–parent attachment following early institutional deprivation. *Development and Psychopathology, 15*, 19-38.

Öhman, A. (2009). Of snakes and faces: An evolutionary perspective on the psychology of fear. *Scandinavian Journal of Psychology, 50*, 543-552.

Olsson, A., & Phelps, E. A. (2007). Social learning of fear. *Nature Neuroscience, 10*, 1095-1102.

Peltola, M. J., Leppänen, J. M., & Hietanen, J. K. (2010). *Enhanced cardiac and attentional responding to fearful faces in 7-month-old infants.* Manuscript submitted for publication.

Peltola, M. J., Leppänen, J. M., Palokangas, T., & Hietanen, J. K. (2008). Fearful faces modulate looking duration and attention disengagement in 7-month-old infants. *Developmental Science, 11*, 60-68.

Pessoa, L. (2009). How do emotion and motivation direct executive control? *Trends in Cognitive Sciences, 13*, 160-166.

Pessoa, L. (2010). Emotion and cognition and the amygdala: From "what is it?" to "what's to be done?". *Neuropsychologia, 48*, 3416-3429.

Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: From a 'low road' to 'many roads' of evaluating biological significance. *Nature Reviews Neuroscience, 11*, 773-783.

Pezawas, L., Meyer-Lindenberg, A., Drabant, E. M., Verchinski, B. A., Munoz, K. E., Kolachana, B. S., et al. (2005). 5-HTTLPR polymorphism impacts human cingulate-amygdala interactions: A genetic susceptibility mechanism for depression. *Nature Neuroscience, 8*, 828-34.

Phelps, E. A., & LeDoux, J. E. (2005). Contributions of the amygdala to emotion processing: From animal models to human behavior. *Neuron, 48*, 175-187.

Phelps, E. A., Ling, S., & Carrasco, M. (2006). Emotion facilitates perception and potentiates the perceptual benefits of attention. *Psychological Science, 17*, 292-299.

Phillips, R. D., Wagner, S. H., Fells, C. A., & Lynch, M. (1990). Do infants recognize emotion in facial expressions? Categorical and "Metaphorical" evidence. *Infant Behavior and Development, 13*, 71-84.

Posner, M. I., & Rothbart, M. K. (2007). Research on attention networks as a model for the integration of psychological science. *Annual Review of Psychology, 58*, 1-23.

Posner, M. I., Rothbart, M. K., Sheese, B. E., & Tang, Y. (2007). The anterior cingulate gyrus and the mechanism of self-regulation. *Cognitive, Affective & Behavioral Neuroscience, 7*, 391-395.

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

Pourtois, G., Schwartz, S., Seghier, M. L., Lazeyras, F., & Vuilleumier, P. (2006). Neural systems for orienting attention to the location of threat signals: An event-related fMRI study. *Neuroimage, 31*, 920-933.

Quinn, P. C., & Tanaka, J. W. (2009). Infants' processing of featural and configural information in the upper and lower halves of the face. *Infancy, 14*, 474-487.

Reeb, B. C., Fox, N. A., Nelson, C. A., & Zeanah, C. H. (2009). The effects of early institutionalization on social behavior and underlying neural correlates. In M. de Haan, & M. R. Gunnar (Eds.), *Handbook of developmental social neuroscience* (pp. 477-496). New York, NY: The Guilford Press.

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

Reynolds, G. D., & Richards, J. E. (2007). Infant heart rate: A developmental psychophysiological perspective. In L. A. Schmidt, & S. J. Segalowitz (Eds.), *Developmental psychophysiology: Theory, systems, and methods* (pp. 173-212). Cambridge, UK: Cambridge University Press.

Richards, J. E. (1997). Peripheral stimulus localization by infants: Attention, age, and individual differences in heart rate variability. *Journal of Experimental Psychology: Human Perception and Performance, 23*, 667-680.

Richards, J. E. (2000). Localizing the development of covert attention in infants with scalp event-related potentials. *Developmental Psychology, 36*, 91-108.

Richards, J. E. (2003). Attention affects the recognition of briefly presented visual stimuli in infants: An ERP study. *Developmental Science, 6*, 312-328.

Richards, J. E. (2005). Localizing cortical sources of event-related potentials in infants' covert orienting. *Developmental Science, 8*, 255-278.

Richards, J. E., & Casey, B. J. (1992). Development of sustained visual attention in the human infant. In B. A. Campbell, H. Hayne & R. Richardson (Eds.), *Attention and information processing in infants and adults: Perspectives from* *human and animal research* (pp. 30-60). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Richards, J. E., & Turner, E. D. (2001). Extended visual fixation and distractibility in children from six to twenty-four months of age. *Child Development, 72*, 963-972.

Rossion, B., & Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *Neuroimage, 39*, 1959-1979.

Schupp, H. T., Öhman, A., Junghöfer, M., Weike, A. I., Stockburger, J., & Hamm, A. O. (2004). The facilitated processing of threatening faces: An ERP analysis. *Emotion, 4*, 189-200.

Schupp, H. T., Stockburger, J., Codispoti, M., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2007). Selective visual attention to emotion. *Journal of Neuroscience, 27*, 1082-1089.

Schwartz, G. M., Izard, C. E., & Ansul, S. E. (1985). The 5-month-old's ability to discriminate facial expressions of emotion. *Infant Behavior and Development, 8*, 65-77.

Senju, A., & Johnson, M. H. (2009). The eye contact effect: Mechanisms and development. *Trends in Cognitive Sciences, 13*, 127-134.

Serrano, J. M., Iglesias, J., & Loeches, A. (1992). Visual discrimination and recognition of facial expressions of anger, fear, and surprise in 4- to 6-month-old infants. *Developmental Psychobiology, 25*, 411-425.

Serrano, J. M., Iglesias, J., & Loeches, A. (1995). Infants' responses to adult static facial expressions. *Infant Behavior and Development, 18*, 477-482.

Sheese, B. E., Rothbart, M. K., Posner, M. I., White, L. K., & Fraundorf, S. H. (2008). Executive attention and self-regulation in infancy. *Infant Behavior and Development, 31*, 501-510.

Simion, F., Valenza, E., Umilta, C., & Dalla Barba, B. (1998). Preferential orienting to faces in newborns: A temporal-nasal asymmetry. *Journal of Experimental Psychology: Human Perception and Performance, 24*, 1399-1405.

Smith, M. L., Cottrell, G. W., Gosselin, F., & Schyns, P. G. (2005). Transmitting and decoding facial expressions. *Psychological Science, 16*, 184-189.

Sokolov, E. N. (1963). *Perception and the conditioned reflex*. New York, NY: Macmillan.

Stekelenburg, J. J., & de Gelder, B. (2004). The neural correlates of perceiving human bodies: An ERP study on the body-inversion effect. *Neuroreport, 15*, 777-780.

Sullivan, R. M., Landers, M., Yeaman, B., & Wilson, D. A. (2000). Good memories of bad events in infancy. *Nature, 407*, 38-39.

Suomi, S. J. (1999). Attachment in rhesus monkeys. In J. Cassidy, & P. R. Shaver (Eds.), *Handbook of attachment: Theory, research, and clinical applications.* (pp. 181-197). New York, NY: Guilford Press.

Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., et al. (2009). The NimStim set of facial expressions: Judgments from untrained research participants. *Psychiatry Research, 168*, 242-249.

Trevarthen, C., & Aitken, K. J. (2001). Infant intersubjectivity: Research, theory, and clinical applications. *Journal of Child Psychology and Psychiatry, 42*, 3-48.

Turati, C., Simion, F., Milani, I., & Umilta, C. (2002). Newborns' preference for faces: What is crucial? *Developmental Psychology, 38*, 875-882.

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

Valiente, C., Eisenberg, N., Fabes, R. A., Shepard, S. A., Cumberland, A., & Losoya, S. H. (2004). Prediction of children's empathy-related responding from their effortful control and parents' expressivity. *Developmental Psychology, 40*, 911-926.

Vuilleumier, P. (2005). How brains beware: Neural mechanisms of emotional attention. *Trends in Cognitive Sciences, 9*, 585-594.

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2001). Effects of attention and emotion on face processing in the human brain: An event-related fMRI study. *Neuron, 30*, 829-841.

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience, 6*, 624-631.

Vuilleumier, P., Richardson, M. P., Armony, J. L., Driver, J., & Dolan, R. J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature Neuroscience, 7*, 1271-1278.

Whalen, P. J. (1998). Fear, vigilance, and ambiguity: Initial neuroimaging studies of the human amygdala. *Current Directions in Psychological Science, 7*, 177-188.

Whalen, P. J., Davis, F. C., Oler, J. A., Kim, H., Kim, M. J., & Neta, M. (2009). Human amygdala responses to facial expressions of emotion. In P. J. Whalen, & E. A. Phelps (Eds.), *The human amygdala* (pp. 265-288). New York, NY: The Guilford Press.

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

Whalen, P. J., & Phelps, E. A. (2009). *The human amygdala*. New York, NY: The Guilford Press.

Whalen, P. J., Shin, L. M., McInerney, S. C., Fischer, H., Wright, C. I., & Rauch, S. L. (2001). A functional MRI study of human amygdala responses to facial expressions of fear versus anger. *Emotion, 1*, 70-83.

Wilcox, B. M., & Clayton, F. L. (1968). Infant visual fixation on motion pictures of the human face. *Journal of Experimental Child Psychology, 6*, 22-32.

Williams, L. M. (2006). An integrative neuroscience model of "significance" processing. *Journal of Integrative Neuroscience, 5*, 1-47.

Williams, L. M., Palmer, D., Liddell, B. J., Song, L., & Gordon, E. (2006). The 'when' and 'where' of perceiving signals of threat versus non-threat. *Neuroimage, 31*, 458-467.

Yang, E., Zald, D. H., & Blake, R. (2007). Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion, 7*, 882-886.

Young-Browne, G., Rosenfeld, H. M., & Horowitz, F. D. (1977). Infant discrimination of facial expressions. *Child Development, 48*, 555-562.

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Emergence of enhanced attention to fearful faces between 5 and 7 months of age

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The adult brain is endowed with mechanisms subserving enhanced processing of salient emotional and social cues. Stimuli associated with threat represent one such class of cues. Previous research suggests that preferential allocation of attention to social signals of threat (i.e. a preference for fearful over happy facial expressions) emerges during the second half of the first year. The present study was designed to determine the age of onset for infants' attentional bias for fearful faces. Allocation of attention was studied by measuring event-related potentials (ERPs) and looking times (in a visual paired comparison task) to fearful and happy faces in 5- and 7-month-old infants. In 7-month-olds, the preferential allocation of attention to fearful faces was evident in both ERPs and looking times, i.e. the negative central mid-latency ERP amplitudes were more negative, and the looking times were longer for fearful than happy faces. No such differences were observed in the 5-month-olds. It is suggested that an enhanced sensitivity to facial signals of threat emerges between 5 and 7 months of age, and it may reflect functional development of the neural mechanisms involved in processing of emotionally significant stimuli.

Keywords: facial expression; attention; event-related potentials; looking time; infants

INTRODUCTION

The ability to recognize salient emotional and social cues and prioritize them over other competing stimuli is critical for adaptive behaviour. Indeed, behavioural and neuroimaging studies in adults have provided evidence for enhanced processing of threat-related signals, such as fearful facial expressions (Vuilleumier, 2005; Williams, 2006). The impact of emotional salience on attention and perception is reflected, for example, in preferential allocation of attention to fearful over simultaneously presented neutral faces (Pourtois *et al.*, 2004; Holmes *et al.*, 2005), lower detection threshold for fearful than happy/neutral faces in rapid serial presentation conditions (Milders *et al.*, 2006), and improved visual contrast sensitivity following fearful face cues (Phelps *et al.*, 2006). Neuroimaging and event-related potential (ERP) studies have also provided evidence for enhanced neural responses to fearful faces in the visual cortex (Morris *et al.*, 1998; Batty and Taylor, 2003; Vuilleumier *et al.*, 2004; Williams *et al.*, 2006; Leppänen *et al.*, 2007a).

The developmental origins for the enhanced processing of social signals of threat are not known in detail and emotional face processing in general is considered to follow a protracted developmental course throughout childhood and adolescence (Leppänen and Nelson, 2006). Previous research, however, suggests that a rudimentary capacity to prefer salient emotional cues emerges by the second half of the first year. There is converging evidence that at 7 months of age, infants allocate attention preferentially to fearful over happy expressions. When looking times have been measured to paired presentations of fearful and happy faces (i.e. a visual paired comparison procedure; VPC), 7-month-olds have been shown to spontaneously look longer at fearful than happy expressions (Nelson and Dolgin, 1985; Kotsoni *et al.*, 2001; Leppänen *et al.*, 2007b). In studies investigating attention allocation to emotional faces by recording ERPs, 7-month-olds typically display a larger negativity at frontocentral recording sites 400 ms after stimulus onset for fearful as compared to happy faces (Nelson and de Haan, 1996; de Haan *et al.*, 2004; Leppänen *et al.*, 2007b). This ‘Negative central’ (Nc) component is thought to reflect an obligatory attentional response to salient, meaningful and, in visual memory paradigms, to infrequent stimuli [see de Haan (2007) for review]. The cortical sources of the infant Nc have been localized in the anterior cingulate region (Reynolds and Richards, 2005), corroborating its role in attention regulation (cf. Bush *et al.*, 2000). Finally, our previous study (Peltola *et al.*, 2008) showed that 7-month-old infants disengaged their attention significantly less frequently from centrally presented fearful faces than happy faces or control stimuli in order to shift attention to peripheral targets. These results paralleled those found in adults (e.g. Georgiou *et al.*, 2005).

Although there is growing evidence for 7-month-old infants’ attentional bias for fearful faces, the age of onset for such a bias is not known. The majority of infant ERP studies on emotional face processing has centred on

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7-month-old infants (Nelson and de Haan, 1996; de Haan *et al.*, 2004; Grossmann *et al.*, 2007; Leppänen *et al.*, 2007b), and, to our knowledge, there are no published studies investigating younger infants' ERP responses to fearful emotional expressions [but see Hoehl *et al.* (2008) for related research]. Studies with human newborns (Farroni *et al.*, 2007) and macaque monkeys (Bauman and Amaral, 2008) indicate that at the early stages of development, infants are not particularly sensitive to fearful faces and other facial signals of threat. There is even some evidence for an early 'positivity bias' (Vaish *et al.*, 2008) as earlier studies found longer looking times to happy than angry/frowning and neutral sequentially presented expressions in 5-month-old infants (LaBarbera *et al.*, 1976; Wilcox and Clayton, 1968). Behavioural studies employing a habituation-recovery paradigm to examine infants' ability to categorize multiple exemplars of an expression to a single class have provided evidence that at the age of 5 months, infants are able to recognize happy expressions (Caron *et al.*, 1982), even when they have been habituated to different intensities of smiles posed by different models (Bornstein and Arterberry, 2003). Interestingly, in an additional looking time assessment with happy and fearful faces, 5-month-olds did not show an attentional preference for either happy or fearful faces (i.e. there were no differences in looking times between these expressions; Bornstein and Arterberry, 2003).

In the present study, we examined with electrophysiological and behavioural methods whether enhanced visual attention to fearful faces is already present at 5 months of age. A standard visual ERP paradigm with happy and fearful faces was first presented to 5- and 7-month-old infants, after which they saw a VPC presentation with two 10-second trials of happy/fearful face pairs. For 7-month-olds, we hypothesized to replicate the previous findings of a larger Nc and longer looking time for fearful than happy faces (Nelson and de Haan, 1996; de Haan *et al.*, 2004; Leppänen *et al.*, 2007b). On the basis of the previous literature (e.g. Bornstein and Arterberry, 2003), we did not expect to see a similar attentional bias in 5-month-old infants.

METHODS

Participants

For the ERPs, the final sample consisted of 18 5-month-old and 20 7-month-old infants. EEG was also recorded from an additional 11 5-month-old and 9 7-month-old infants, who were excluded from the ERP analyses due to fussiness or excessive movement artefacts resulting in <10 good trials. VPC data were analysed from 23 5-month-olds and 26 7-month-olds. VPC data from six infants were discarded due to a side bias (i.e. looking at one stimulus for <5% out of the total looking time for each trial), from two infants due to experimenter error, and from one infant due to fussiness. The parents of the participants were contacted through birth records and local Child Welfare Clinics, and all testing sessions were scheduled within 1 week of the infants' 5th- or 7th-month birthday. All infants were full term (37–42 weeks), with a birth weight of >2400 g, and free from postnatal visual or neurological abnormalities. Approval for the study was obtained from the research permission committee of the Department of Social Services and Health Care of the city of Tampere.

Eight of the infants in the ERP sample and 14 of the infants in the VPC sample were tested twice (i.e. at both ages). The potential influence of repeated testing was taken into account in data analyses, as described below.

Stimuli and task procedure

The stimuli were colour images of fearful and happy facial expressions posed by four female models. All stimuli were presented on a white background and cropped to exclude all non-face features. Two of the four stimulus models were taken from our own laboratory stimulus database and the other two were from the MacBrain Face Stimulus Set (Tottenham *et al.*, in press). Prior to data collection, a group of adults ($n = 18$), rated the stimuli for fearfulness and happiness on a scale from 1 to 7. The ratings confirmed that the fearful ($M = 5.9$; range = 5.2–6.6) and happy ($M = 6.1$; range = 5.6–6.5) expressions were considered good and equally intense examples of the respective emotions. Consistent with the methodology used in prior infant studies, each infant was presented with expressions of only one model. Different models were, however, used in the ERP and VPC tasks. The infants who participated in the experiment twice saw the faces of the two remaining models on their second visit. With a looking distance of 60 cm, the stimuli measured 15.4° and 10.8° of vertical and horizontal visual angle, respectively.

Upon arrival to the laboratory, the experimental procedure was described and signed consent was obtained from the parent. EEG was recorded while the infants were sitting on their parents lap in front of a 19-inch LCD monitor surrounded by black panels. Fearful and happy faces were shown repeatedly for 1000 ms in random order.[1] Between the stimuli, a black-and-white $4^\circ \times 4^\circ$ checkerboard stimulus was presented on the centre of the screen to attract the infants' attention. The checkerboard flickered for the first 1000 ms at 4 Hz and then remained stationary. The experimenter monitored the infants' looking behaviour through a hidden video camera mounted above the monitor and initiated each trial only when the infants were attending at the stationary checkerboard stimulus. The trials on which the infant blinked or turned his/her eyes away from the face during stimulus presentation were marked online as bad by the experimenter. Trials were presented until the infant became too fussy or inattentive to continue, but with a maximum of 150 trials. On average, 72.3 (SD = 25.4;

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[1] In the ERP task, the infants were also shown, along fearful and happy faces, face-shaped matched visual noise images in which the phase spectra of the model's face were randomized, but the amplitude and the colour spectra were held constant (cf. Halit *et al.*, 2004). The data for these stimuli are not reported here.

range = 28–149) trials were presented during the EEG recording. Stimulus presentation was controlled by Neuroscan Stim software running on a 3.4 GHz desktop computer.

After the EEG recording, the electrode cap was removed and two 10-s VPC trials with a happy and a fearful face were presented. On one trial, a happy face was on the left, on the other trial, a fearful face was on the left. The faces were presented 12° apart (ear to ear). The left-right positioning of the two expressions was counterbalanced between participants. The infants' looking behaviour was recorded with the video camera for offline analyses. The VPC trials were presented with E-Prime software (Psychology Software Tools Inc., www.pstnet.com/eprime).

Acquisition and analysis of the electrophysiological data

Continuous EEG was recorded with 30 Ag–AgCl electrodes mounted in an elastic cap (Quik-Cap) and placed according to the 10–20 system. Neuroscan QuikCell liquid electrolyte electrode application technique was used to obtain electrode impedances <10 kΩ. Linked mastoids served as the reference. EOG electrodes were left out as pilot testing indicated the majority of the infants being markedly intolerant for those electrodes. However, great care was taken to ensure that the final data were free of ocular artefacts by (i) the experimenter monitoring the infants' eyes continuously during stimulus presentation (and marking trials with eye movements as bad) and (ii) by visually inspecting the EEG for all trials, as described below. The data were sampled at 500 Hz, band-pass filtered from 0.1 to 100 Hz and stored on a computer disk for offline analyses by Scan 4.3 software. Offline, the data were lowpass-filtered at 30 Hz, segmented to 1100 ms epochs starting 100 ms before the presentation of each stimulus and baseline-corrected against the mean voltage during the 100-ms pre-stimulus period. Trials marked as bad online by the experimenter were removed, and the epochs were also visually inspected for artefacts. Trials with motion artefacts resulting from head or body movements, high-frequency EMG artefacts or the activity exceeding A-D values were discarded. Furthermore, for the electrodes above the eyes (Fp1, Fp2), trials with the amplitude exceeding 100 μV were discarded. Infants with <10 good trials in either of the experimental conditions (fearful and happy faces) were excluded from the analyses. For the infants included in the analyses, there were no significant differences in the number of good fearful and happy trials between age groups (5-month-olds: fearful $M = 16.5$, happy $M = 16.4$; 7-month-olds: fearful $M = 17.4$, happy $M = 18.8$), $F(1, 36) = 1.7$, $P > 0.2$.

Attention-sensitive brain responses to the stimuli were examined by analysing the Nc component. There are also other infant ERP components that have been recently associated with the processing of facial expressions, most importantly the posterior N290 and P400 (Leppänen *et al.*, 2007b, in press; Kobiella *et al.*, 2008). However, as the primary focus of our study was on processes related to visual attention, and because the electrode cap used in the present study has a rather sparse coverage of posterior regions where the N290 and P400 components are most prominent, we will only report data on the Nc component. The relation of the Nc and attention is well established and the frontocentral regions where the Nc is most prominent were well covered in the present measurement. To analyse the Nc component, amplitude averages were calculated within a time window of 350–600 ms for electrodes C3 and C4. This time window and these recording sites were chosen on the basis of previous literature (de Haan *et al.*, 2004; Leppänen *et al.*, 2007b) and our own data (i.e. inspection of individual infants' average ERP plots) showing the most prominent Nc amplitudes on central electrodes within this time window. For both age groups, Nc amplitudes were subjected to a 2 × 2 analysis of variance (ANOVA) with Expression (fearful, happy) and Hemisphere (left, right) as within-subject factors.

Analysis of the behavioural data

The video recordings of the infants' looking behaviour during VPC trials were coded by an observer blind to the left–right positioning of the fearful and happy faces. Queen's Video Coder (Baron *et al.*, 2001) was used to analyse the total time the infants spent looking at the stimulus on the left and right side for each trial. To ensure the reliability of the coding, another observer coded ~25% of the recordings (13 infants). Pearson correlations between the two observers' coding of the participants' total looking times during individual VPC trials ranged from 0.95 to 1. The analyses were performed on the total looking time for fearful and happy faces, averaged across the two trials.

RESULTS

Electrophysiological data

The grand average ERPs measured from frontocentral electrode sites for 5- and 7-month-old infants are shown in Figures 1 and 2, respectively. For the 5-month-olds, an ANOVA showed no main effects or interactions involving Expression or Hemisphere, $F\text{s} < 2.2$. Thus, the average Nc amplitudes were no greater for fearful ($M = -16.3\,\mu V$; SD = 11.1) than happy ($M = -16.8\,\mu V$; SD = 12.7) faces at 5 months of age. For the 7-month-olds' ERP data, however, an ANOVA resulted in main effects of Hemisphere, $F(1, 19) = 5.3$, $P < 0.05$, and Expression, $F(1, 19) = 8.6$, $P < 0.01$, but no interaction between them, $F \leq 1$. Thus, the mean amplitudes within 350–600 ms after stimulus onset were generally more negative over the right than the left hemisphere. More importantly, the Nc amplitudes were significantly greater for fearful ($M = -24.9\,\mu V$; SD = 8.0) as compared to happy ($M = -18.9\,\mu V$; SD = 9.7) faces in 7-month-old infants.

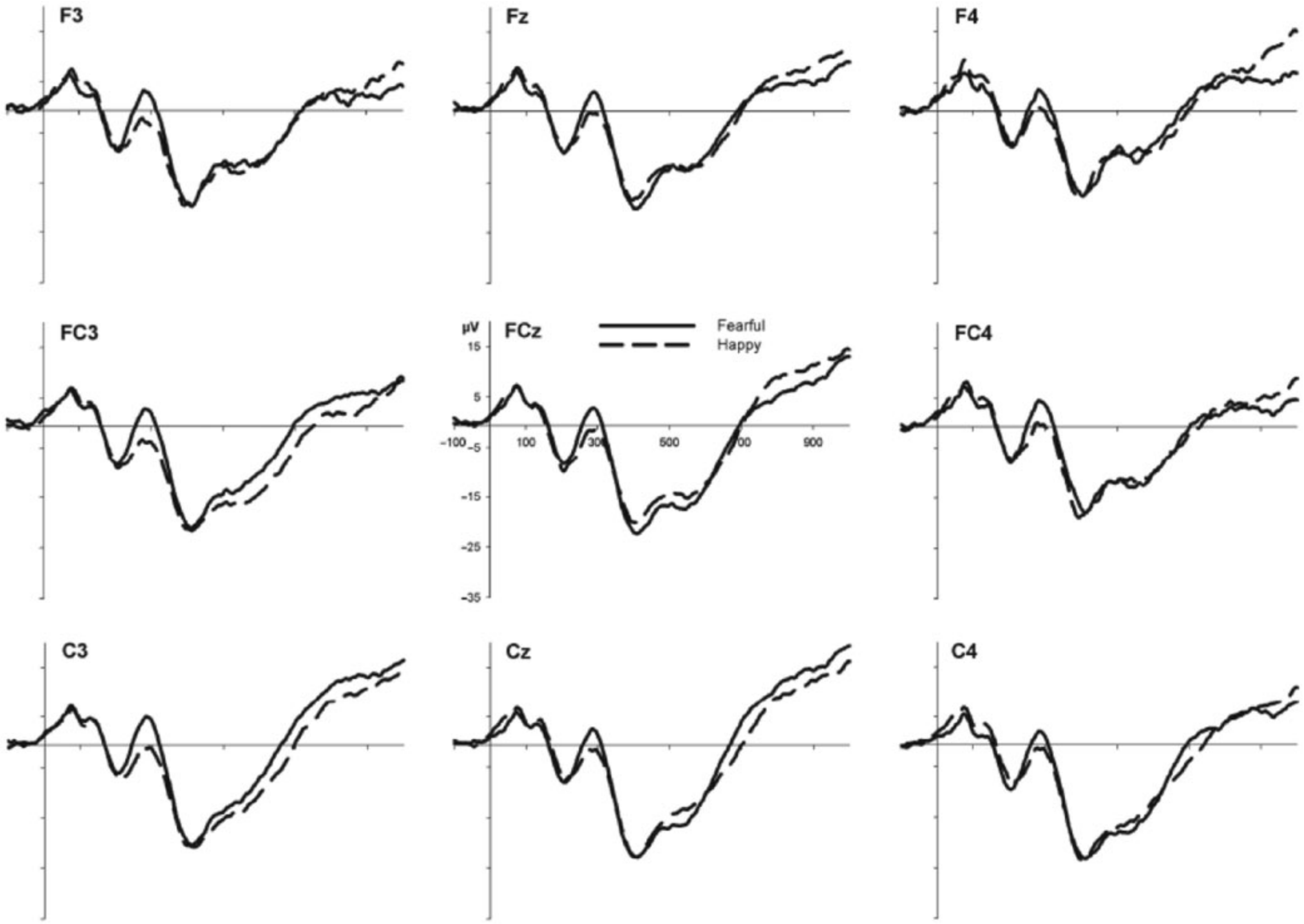

Fig. 1 Grand average ERP waveforms for fearful and happy faces over the left (F3, FC3, C3), central (Fz, FCz, Cz) and right (F4, FC4, C4) frontocentral region for the 5-month-old infants.

Behavioural data

The average looking times for fearful and happy faces in the VPC are presented in Figure 3. As can be inspected, 5-month-olds showed no significant difference in looking times for fearful ($M = 4.3$ s; SD $= 1.6$) and happy ($M = 4.0$ s; SD $= 1.5$) faces, $F(1, 22) = 0.47$, $P > 0.4$. However, 7-month-olds looked significantly longer at fearful ($M = 4.7$ s; SD $= 0.9$) when compared with happy ($M = 3.8$ s; SD $= 0.8$) faces, $F(1, 25) = 13.1$, $P < 0.01$.

Control analyses

As there were infants who contributed to the data at both 5 and 7 months of age, additional analyses were warranted to examine any possible differences between infants who participated once and twice. And indeed, for the 7-month-olds' ERP data, there was a marginal three-way interaction including Expression (2), Hemisphere (2) and Visit (2: once, twice), $F(1, 18) = 4.8$, $P < 0.06$. For the 7-month-old infants who participated only once, a two-way ANOVA indicated a marginal Expression × Hemisphere interaction, $F(1, 11) = 4.0$, $P < 0.08$. Pairwise comparisons showed a larger Nc for fearful than happy faces in the right hemisphere, $P \leq 0.05$, but not in the left hemisphere, $P > 0.6$. Instead, in infants participating at both 5 and 7 months of age, a two-way ANOVA showed a significant main effect for Expression due to larger Nc for fearful than happy faces, $P < 0.01$, but no Expression × Hemisphere interaction, $F(1, 7) = 1.1$, $P > 0.3$.

A 2 (Expression) × 2 (Visit) ANOVA with the 7-month-olds' VPC data did not yield a significant two-way interaction, $F(1, 24) = 0.49$, $P > 0.4$, indicating that the looking times were longer for fearful than happy faces irrespective of whether the infants were on their first or second visit at 7 months of age, both Ps $\leq .05$.

DISCUSSION

We examined with ERP and looking time measures whether enhanced visual attention to fearful faces emerges between 5 and 7 months of age or whether it is already present at 5 months of age. For the 7-month-olds, the results replicated earlier findings of a larger Nc component and longer looking times for fearful than happy faces. The 5-month-olds,

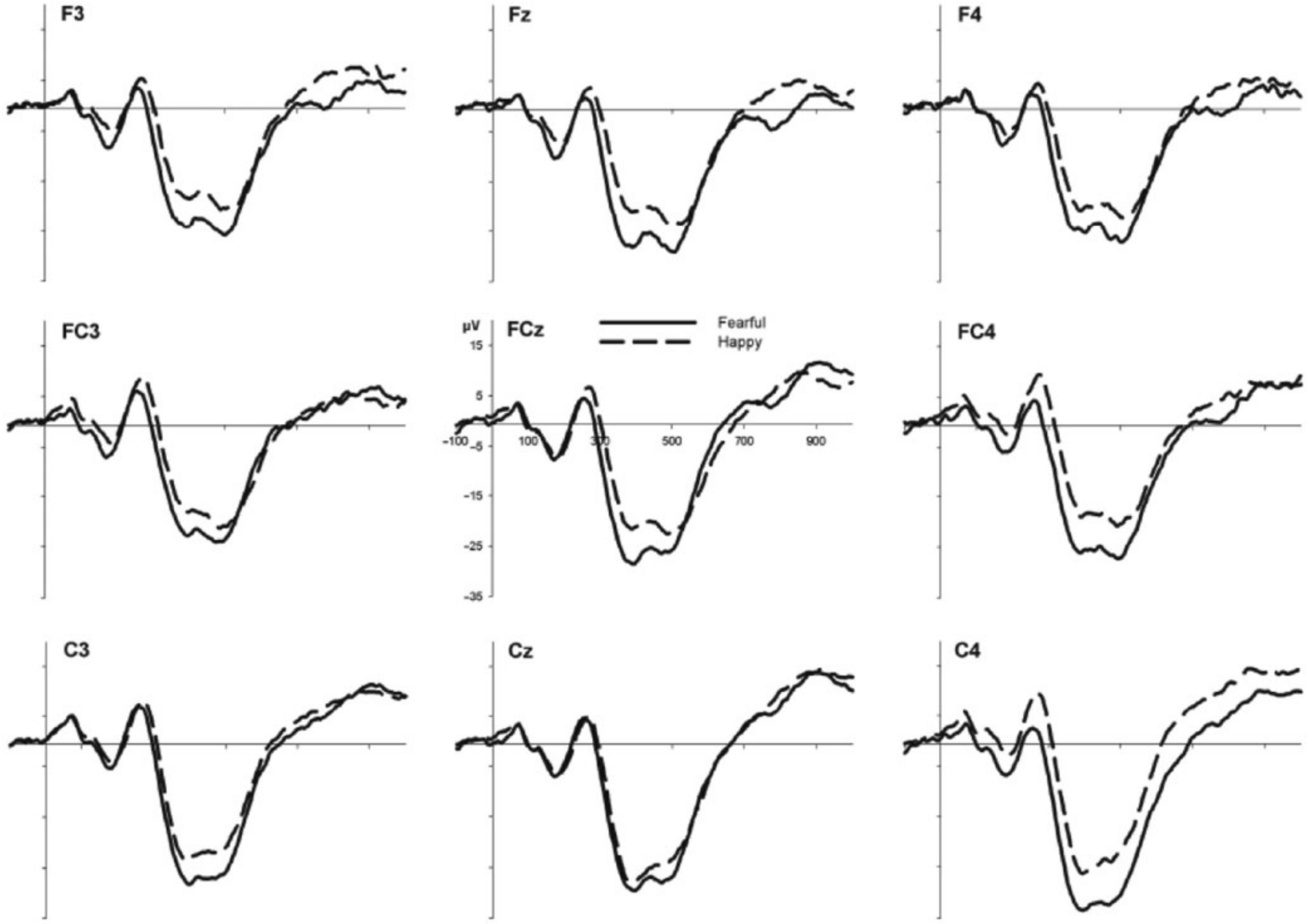

Fig. 2 Grand average ERP waveforms for fearful and happy faces over the left (F3, FC3, C3), central (Fz, FCz, Cz) and right (F4, FC4, C4) frontocentral region for the 7-month-old infants.

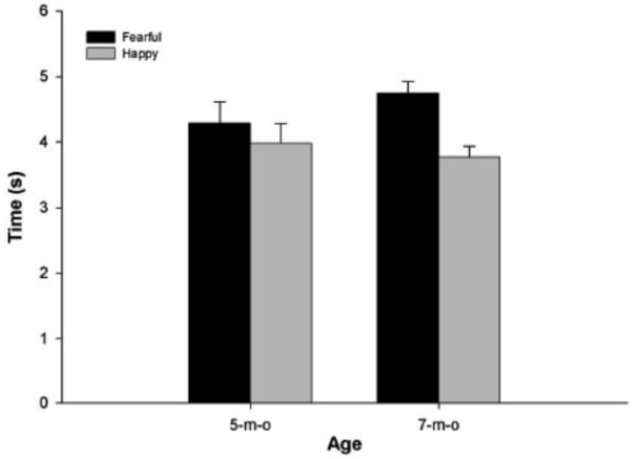

Fig. 3 Average looking times for fearful and happy faces in 5- and 7-month-old infants in the VPC task.

however, showed an Nc of a similar magnitude for fearful and happy faces, and they also looked equally long at both expressions. It is important to note that the absence of the effects in 5-month-olds was not due to lower-quality data: the younger infants showed a prominent Nc response, provided an equal number of trials for the ERP analyses with the older infants, and looked, on average, at the faces in the VPC task as long as the 7-month-olds.

Thus, the differential pattern of results in 5- and 7-month-old infants implies that the attentional bias for fearful faces emerges at around 7 months of age. An interesting issue is, of course, whether the stronger allocation of attention to fearful faces in 7-month-olds reflects emotional processing, i.e. whether it is the *emotional signal value* of a fearful face, which is detected and reacted to with increased attention. Fearful faces are considered as potent stimuli for activating the neural mechanisms responsible for detecting and reacting to threat-related signals and potential dangers in the environment (Whalen, 1998). The amygdala is seen as an integral neural structure in associating emotional significance to environmental stimuli and producing a cascade of responses serving rapid alerting and optimal perceptual functioning when encountering signals of threat (Vuilleumier, 2005; Williams, 2006). Indeed, in adults, fearful facial expression cues have been shown to result in enhanced attentional and perceptual processing

(Holmes *et al.*, 2005; Milders *et al.*, 2006; Phelps *et al.*, 2006) as well as increased skin conductance responses (Williams *et al.*, 2005). Furthermore, there is a wealth of neuroimaging and ERP evidence for an enhanced neural activation for fearful as compared to happy and neutral faces in the visual occipitotemporal cortex, a process also considered to result from the modulatory influence of the amygdala (Morris *et al.*, 1998; Vuilleumier *et al.*, 2004; Williams *et al.*, 2006; Vuilleumier and Pourtois, 2007; Leppänen *et al.*, 2007a).

It is currently unclear whether a similar subcortical modulatory mechanism could be functional already in early human development. Current neuroimaging techniques (e.g. fMRI) are not feasible for studying the involvement of the amygdala circuitry in infants' face processing. Moreover, as ERPs reflect mostly cortical postsynaptic activity, the putative amygdala-mediated modulation of ERP activity has to be considered tentatively. Nevertheless, there is some intriguing indirect evidence suggesting that the second half of the first year may be an important turning point in the development of brain systems that underlie sensitivity to signals of threat conveyed by others' faces (Leppänen and Nelson, 2009). In macaque monkeys, the connections between various cortical areas and the amygdala are relatively mature shortly after birth (Nelson *et al.*, 2002). Interestingly, infant monkeys at around 2 months of age (roughly equalling 8-month-old human infants) become increasingly sensitive to threat-related stimuli, including others' facial expressions (Bauman and Amaral, 2008). At the same age, monkeys also start to exhibit fear of unfamiliar conspecifics (Suomi, 1999), in close resemblance to the stranger anxiety displayed by human infants from 6 to 7 months of age (Kagan and Herschkowitz, 2005).

As mentioned in the introduction, the neural generators of the Nc component in infant ERPs have been suggested to be located in prefrontal regions, mainly in the anterior cingulate cortex (ACC; Reynolds and Richards, 2005). ACC has been implicated with various functions [see Bush *et al.* (2000) for review]. For the present purposes, it is interesting to note that in adults, coactivation of ACC and the amygdala has been observed during the processing of fearful faces (Morris *et al.*, 1998; Vuilleumier *et al.*, 2001). ACC activation in such tasks has been associated with the regulation of attentional, behavioural and emotional responses to threat-related stimuli (Morris *et al.*, 1998; Bush *et al.*, 2000; Elliott *et al.*, 2000). In this light, it is tempting to hypothesize that the larger Nc response to fearful faces in 7-month-old infants would reflect stronger ACC activity resulting, in turn, from an increased response in the amygdala. Naturally, we make this inference about infants' ERP data with great caution, because the time-course of the development of the amygdala and its functional connectivity with ACC and related cortical attention networks is not known.

In addition to the development of the neural circuitry for processing affective significance, it is important to consider the experience-mediated mechanisms that could also be responsible for the observed changes in infants' sensitivity to fearful faces. It has been noted that changes in infants' locomotive abilities (e.g. the onset of crawling at around 7 months) are associated with increased variability in caregivers' expressive behaviours as well as changes in infants' monitoring of such cues [see Campos *et al.* (2000) for review]. These changes may form the basis for referential emotional communication as emotional signals start to gain a more direct function in regulating the infant's behaviour. In parallel, developmental changes in infants' general information processing abilities may also bring about changes in the efficiency of associating emotional meaning to a broader range of stimuli (Vaish *et al.*, 2008). However, despite such important developmental progression occurring at around the same age period as the effects observed in the present study, it is not known to what extent the attentional bias for fearful faces could be accounted for by experience-mediated mechanisms. Exact data on the number of occasions a typical 7-month-old has observed fearful faces is lacking. However, our own experience as well as anecdotal evidence from parents suggests that such direct experience with fearful faces remains very limited at this age period (cf. Malatesta and Haviland, 1982).

The absence of facial expression effects in 5-month-olds in the present study suggests that the perceptual systems of younger infants do not detect the informational value conveyed by fearful faces. At this age, smiling faces are an emotionally salient stimulus to the infants as a result of repeated and affectively rewarding interactions with a smiling caregiver. Indeed, there is some earlier evidence for a looking time bias to happy expressions in younger infants (Wilcox and Clayton, 1968; LaBarbera *et al.*, 1976, but see Bornstein and Arterberry, 2003). In this vein, we could have even expected attention to be allocated more strongly towards happy faces. However, although happy faces are undoubtedly emotionally salient cues, their impact on the allocation of attentional resources in 5-month-olds might not be expected to be comparable to the impact of fearful faces later in development. Theories of affective significance processing propose that once an individual begins to associate different cues with threat- and reward-related qualities, threat-related emotional cues are given precedence on a short time scale, resulting in rapid alerting and possibly interruption of ongoing activity, while positive cues do not require such immediate action but might instead act as reinforcers for an organism to continue with the ongoing activity (Cacioppo *et al.*, 1999; Williams, 2006; Vaish *et al.*, 2008).

On the other hand, it is interesting to note that a recent study (Hoehl *et al.*, 2008) suggests that even infants as young as 3 months old are sensitive to the emotional signal value of fearful faces. In their study, 3-month-olds' Nc was larger for objects that had been preceded by an image of a fearful face gazing towards the same object when compared with objects that had been paired with a neutral gaze. A direct comparison between that study and the present results is problematic as Hoehl *et al.* did not report ERPs time-locked to the faces. Nevertheless, it seems possible that, similarly to adults (Adams and Kleck, 2003), averted gaze enhances the processing of fearful faces already at 3 months of age. However, an alternative perceptual/low-level interpretation of the results of Hoehl *et al.* (2008) is that the enlarged fearful eyes produced a more robust attentional orienting response towards the object than neutral eyes did. This may have resulted in enhanced visual processing of (and a larger Nc for) the object. In this case, no processing of the emotional signal of the preceding face would be necessarily involved.

Seven-month-old infants' visual preference for fearful faces has also been interpreted as a response to stimuli that are merely unfamiliar to the infants (i.e. novel; Nelson and de Haan, 1996; Vaish *et al.*, 2008). Indeed, it has been shown that during the first half of their first year, infants encounter negative facial expressions rarely in their environment (Malatesta and Haviland, 1982). However, the present findings cannot be easily interpreted as novelty responses. We did not observe an attentional bias in 5-month-olds, to whom fearful faces are, if anything, at least as unfamiliar as they are for 7-month-olds. Furthermore, our previous study (Peltola *et al.*, 2008) showed that novel grimaces lacking emotional signal value but rated as equally novel as the fearful faces did not have an attention holding effect on 7-month-olds' visual attention as fearful faces did. One could also argue that the 5-month-olds had a weaker stored representation of a happy face than the older infants. If this was the case, it could obviously attenuate the novelty response toward fearful faces in the younger age group, as novelty would have an impact on the processing of both fearful and happy expressions. Although we had no means to assess this issue directly in the present study, the possibility for such an age effect seems rather unlikely in light of previous research. Namely, it has been shown that at the age of 5 months, infants are already able to generalize from multiple exemplars (identities) of happy faces a category of a happy face, even when smiles with varying intensities are used during habituation (e.g. Bornstein and Arterberry, 2003).

There are also previous studies comparing infants' responses to novel and familiar stimuli, which indicate that infant attention is sensitive to the meaningfulness and emotional content of stimuli. First, de Haan and Nelson (1997, 1999) studied 6-month-old infants and found a larger Nc for familiar than unfamiliar stimuli (mother's face vs stranger's face and familiar vs unfamiliar toys), whereas no effects of stimulus familiarity on looking times were found. Second, a study investigating 7-month-old infants' processing of angry expressions, which are obviously also relatively unfamiliar to infants at this age, actually found a larger Nc and longer looking times to happy as compared to angry faces (Grossmann *et al.*, 2007). This finding also suggests that simply the negative emotional valence of fearful faces is not responsible for the attentional modulation. Anger and fear share the same valence and yet they seem to produce opposing effects on 7-month-olds' attention. However, a replication of this result and further testing with different negative emotions (e.g. sadness) is needed to critically test whether infants' attentional responses are modulated by a specific (negatively valenced) expression rather than by negatively valenced emotions in general. Indeed, it could also be the case that the 7-month-olds in Grossmann *et al.* (2007) did not yet recognize the emotional signal value of angry faces, which led to stronger allocation of attention to emotionally more meaningful expressions (i.e. happy faces). Another interesting result of that study was that at 12 months of age, infants showed an adult-like stronger negativity in their ERP responses to angry faces. Thus, in relation to our own data, it could be tentatively suggested that the processing of fearful and angry faces might develop along different developmental trajectories during infancy, with infants becoming reactive to fearful faces at an earlier point in development.

An unexpected finding of the present study was that the number of times an infant participated in the experiment had an influence on the observed effects. Importantly, the main finding of larger Nc and longer looking times for fearful than happy faces was observed in both groups of 7-month-old infants (i.e. in those who participated once and those who participated twice). There was, however, a difference in the laterality of the Nc effect, so that the infants participating only once at 7 months of age showed a larger Nc for fearful than happy faces in the right but not in the left hemisphere recording site, while the infants who participated twice at both 5 and 7 months of age showed the differential responses in both hemispheres. The reasons for this unexpected difference are not entirely clear and given that the interaction was marginal, cautiousness must be exercised in interpreting it. We note, however, that the right-lateralized effect in infants who participated only once can be seen to parallel previous observations of a right hemisphere bias in adults' and infants' face processing (de Schonen and Mathivet, 1990; de Haan and Nelson, 1997, 1999; Nelson, 2001). The bilateral effect in those infants who participated twice may reflect a training effect, i.e. observing repeated presentations of fearful and happy faces twice within a 2-month period resulted in a more robust and bilateral attentional response for fearful faces. It is an interesting possibility, however, that such small amount of practice could produce observable group differences in processing fearful faces.

The present study is limited in that as we used only static faces presented on the screen, we are not able to make straightforward conclusions about when in development infants begin to process fearful faces differentially in real-life settings where infants are most often faced with dynamic and multimodally communicated emotional expressions. Indeed, it has been observed that infants become sensitive to multimodally communicated expressions earlier in development than to visually presented facial expressions alone (Flom and Bahrick, 2007). Studies in adults suggest that the recognition of dynamically presented facial expressions might recruit a different neural circuitry than static faces (e.g. Kilts *et al.*, 2003); however, studies on infants' brain responses to dynamic expressions are lacking [but see Grossmann *et al.* (2008)]. Another limitation concerns the possible differences between age groups in their visual scanning patterns for fearful and happy faces as we did not obtain eye tracking data. Previous data indicate that amygdala activation (Adolphs *et al.*, 2005) and ERP modulation (Schyns *et al.*, 2007) by fearful faces are associated with fixations targeted at the eye region of fearful faces. Thus, interpreting the present results, it remains possible that the 5-month-olds directed their fixations relatively less on the eye region while scanning fearful faces, which could result in an attenuated amygdala response. However, although research on infants' visual scanning patterns of emotional faces is scarce, existing evidence (Hunnius *et al.*, 2007) as well as our own unpublished data suggest that already from 4 months of age infants direct their fixations pronouncedly on the eye region while looking at different emotional faces. Finally, a replication of the present findings with larger independent samples and a statistically significant interaction between age groups would yield stronger evidence for a developmental change between 5 and 7 months.

In summary, the present study extended previous research on the development of emotional face processing in infancy by showing that the bias to allocate attention more strongly to fearful than happy emotional expressions appears to emerge between 5 and 7 months of age. As the 5-month-olds did not show enhanced attention to fearful faces, which they very rarely encounter in their rearing environment, it seems rather unlikely that the observed effects in 7-month-olds would be accountable merely by the novelty of fearful faces. It is possible that the attentional effects reflect functional developmental changes in brain mechanisms (e.g. the amygdala), which participate in evaluating the emotional significance of stimuli and generating enhanced responses toward stimuli signalling potential threat. Also, as reviewed earlier, the effects are observed at around the same age period when infants begin to show other putatively amygdala-mediated emotional responses, such as stranger anxiety. Together, these findings suggest that 7-month-old infants may already have some understanding of the emotional signal value of fearful expressions although further research is required to determine the level of sophistication of these early abilities.

REFERENCES

Adams, R.B., Jr, Kleck, R.E. (2003). Perceived gaze direction and the processing of facial displays of emotion. *Psychological Science*, *14*, 644–7.

Adolphs, R., Gosselin, F., Buchanan, T.W., Tranel, D., Schyns, P., Damasio, A.R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature*, *433*, 68–72.

Baron, M.J., Wheatley, J., Symons, L., Hains, C.R., Lee, K., Muir, D. (2001). *The Queen's Video Coder* (http://psyc.queensu.ca/vidcoder/). Department of Psychology, Queen's University, Canada.

Batty, M., Taylor, M.J. (2003). Early processing of the six basic facial emotional expressions. *Cognitive Brain Research*, *17*, 613–20.

Bauman, M.D., Amaral, D.G. (2008). Neurodevelopment of social cognition. In: Nelson, C.A., Luciana, M., editors. *Handbook of Developmental Cognitive Neuroscience,* 2nd edn. Cambridge, MA: MIT Press, pp. 161–85.

Bornstein, M.H., Arterberry, M.E. (2003). Recognition, discrimination and categorization of smiling by 5-month-old infants. *Developmental Science*, *6*, 585–99.

Bush, G., Luu, P., Posner, M.I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, *4*, 215–22.

Cacioppo, J.T., Gardner, W.L., Berntson, G.G. (1999). The affect system has parallel and integrative processing components: form follows function. *Journal of Personality and Social Psychology*, *76*, 839–55.

Campos, J.J., Anderson, D.I., Barbu-Roth, M.A., Hubbard, E.M., Hertenstein, M.J., Witherington, D. (2000). Travel broadens the mind. *Infancy*, *1*, 149–219.

Caron, R.F., Caron, A.J., Myers, R.S. (1982). Abstraction of invariant face expressions in infancy. *Child Development*, *53*, 1008–15.

de Haan, M. (2007). Visual attention and recognition memory in infancy. In: de Haan, M., editor. *Infant EEG and event-related potentials.* New York: Psychology Press, pp. 101–43.

de Haan, M., Belsky, J., Reid, V., Volein, A., Johnson, M.H. (2004). Maternal personality and infants' neural and visual responsivity to facial expressions of emotion. *Journal of Child Psychology and Psychiatry*, *45*, 1209–18.

de Haan, M., Nelson, C.A. (1997). Recognition of the mother's face by six-month-old infants: a neurobehavioral study. *Child Development*, *68*, 187–210.

de Haan, M., Nelson, C. A. (1999). Brain activity differentiates face and object processing in 6-month-old infants. *Developmental Psychology*, *35*, 1113–21.

de Schonen, S., Mathivet, E. (1990). Hemispheric asymmetry in a face discrimination task in infants. *Child Development*, *61*, 1192–205.

Elliott, R., Rubinsztein, J.S., Sahakian, B.J., Dolan, R.J. (2000). Selective attention to emotional stimuli in a verbal go/no-go task: an fMRI study. *Neuroreport*, *11*, 1739–44.

Farroni, T., Menon, E., Rigato, S., Johnson, M.H. (2007). The perception of facial expressions in newborns. *European Journal of Developmental Psychology*, *4*, 2–13.

Flom, R., Bahrick, L.E. (2007). The development of infant discrimination of affect in multimodal and unimodal stimulation: the role of intersensory redundancy. *Developmental Psychology*, *43*, 238–52.

Georgiou, G.A., Bleakley, C., Hayward, J., et al. (2005). Focusing on fear: attentional disengagement from emotional faces. *Visual Cognition*, *12*, 145–58.

Grossmann, T., Johnson, M.H., Lloyd-Fox, S., et al. (2008). Early cortical specialization for face-to-face communication in human infants. *Proceedings of the Royal Society B*, *275*, 2803–11.

Grossmann, T., Striano, T., Friederici, A.D. (2007). Developmental changes in infants' processing of happy and angry facial expressions: a neurobehavioral study. *Brain and Cognition*, *64*, 30–41.

Halit, H., Csibra, G., Volein, A., Johnson, M.H. (2004). Face-sensitive cortical processing in early infancy. *Journal of Child Psychology and Psychiatry*, *45*, 1228–334.

Hoehl, S., Wiese, L., Striano, T. (2008). Young infants' neural processing of objects is affected by eye gaze direction and emotional expression. *PLoS ONE*, *3*, e2389.

Holmes, A., Green, S., Vuilleumier, P. (2005). The involvement of distinct visual channels in rapid attention towards fearful facial expressions. *Cognition and Emotion*, *19*, 899–922.

Hunnius, S., de Wit, T.C.J., von Hofsten, C. (2007). *Infants' visual scanning of faces with happy, angry, fearful, and neutral expression*. Poster presented at the biennial meeting of the Society for Research in Child Development, Boston, MA.

Kagan, J., Herschkowitz, N. (2005). *A young mind in a growing brain*. Mahwah, NJ: Lawrence Erlbaum Associates.

Kilts, C.D., Egan, G., Gideon, D.A., Ely, T.D., Hoffman, J.M. (2003). Dissociable neural pathways are involved in the recognition of emotion in static and dynamic facial expressions. *Neuroimage*, *18*, 156–68.

Kobiella, A., Grossmann, T., Striano, T., Reid, V.M. (2008). The discrimination of angry and fearful facial expressions in 7-month-old infants: an event-related potential study. *Cognition and Emotion*, *22*, 134–46.

Kotsoni, E., de Haan, M., Johnson, M.H. (2001). Categorical perception of facial expressions by 7-month-old infants. *Perception*, *30*, 1115–25.

LaBarbera, J.D., Izard, C.E., Vietze, P., Parisi, S.A. (1976). Four- and six-month-old infants' visual responses to joy, anger, and neutral expressions. *Child Development*, *47*, 535–8.

Leppänen, J.M., Kauppinen, P., Peltola, M.J., Hietanen, J.K. (2007a). Differential electrocortical responses to increasing intensities of fearful and happy emotional expressions. *Brain Research*, *1166*, 103–9.

Leppänen, J.M., Moulson, M.C., Vogel-Farley, V.K., Nelson, C.A. (2007b). An ERP study of emotional face processing in the adult and infant brain. *Child Development*, *78*, 232–45.

Leppänen, J.M., Nelson, C.A. (2006). The development and neural bases of facial emotion recognition. In: Keil, R.V., editor. *Advances in child development and behavior*, Vol. 34. San Diego: Academic Press, pp. 207–46.

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

Leppänen, J.M., Richmond, J., Moulson, M.C., Vogel-Farley, V.K., Nelson, C.A. (in press). Categorical representation of facial expressions in the infant brain. *Infancy*.

Malatesta, C.Z., Haviland, J.M. (1982). Learning display rules: the socialization of emotion expression in infancy. *Child Development*, *53*, 991–1003.

Milders, M., Sahraie, A., Logan, S., Donnellon, N. (2006). Awareness of faces is modulated by their emotional meaning. *Emotion*, *6*, 10–17.

Morris, J.S., Friston, K.J., Buchel, C., Frith, C.D., Young, A.W., Calder, A.J., et al. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, *121*, 47–57.

Nelson, C.A. (2001). The development and neural bases of face recognition. *Infant and Child Development*, *10*, 3–18.

Nelson, C.A., Bloom, F.E., Cameron, J.L., Amaral, D., Dahl, R.E., Pine, D. (2002). An integrative, multidisciplinary approach to the study of brain-behavior relations in the context of typical and atypical development. *Development and Psychopathology*, *14*, 499–520.

Nelson, C.A., de Haan, M. (1996). Neural correlates of infants' visual responsiveness to facial expressions of emotion. *Developmental Psychobiology*, *29*, 577–95.

Nelson, C.A., Dolgin, K.G. (1985). The generalized discrimination of facial expressions by seven-month-old infants. *Child Development*, *56*, 58–61.

Peltola, M.J., Leppänen, J.M., Palokangas, T., Hietanen, J.K. (2008). Fearful faces modulate looking duration and attention disengagement in 7-month-old infants. *Developmental Science*, *11*, 60–8.

Phelps, E.A., Ling, S., Carrasco, M. (2006). Emotion facilitates perception and potentiates the perceptual benefits of attention. *Psychological Science*, *17*, 292–9.

Pourtois, G., Grandjean, D., Sander, D., Vuilleumier, P. (2004). Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex*, *14*, 619–33.

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

Schyns, P.G., Petro, L.S., Smith, M.L. (2007). Dynamics of visual information integration in the brain for categorizing facial expressions. *Current Biology*, *17*, 1580–5.

Suomi, S.J. (1999). Attachment in rhesus monkeys. In: Cassidy, J., Shaver, P.R., editors. *Handbook of attachment: theory, research, and clinical applications*. New York: Guilford Press, pp. 181–97.

Tottenham, N., Tanaka, J.W., Leon, A.C., McCarry, T., Nurse, M., Hare, T.A., et al. (in press). The NimStim set of facial expressions: judgments from untrained research participants. *Psychiatry Research*.

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

Vuilleumier, P. (2005). How brains beware: neural mechanisms of emotional attention. *Trends in Cognitive Sciences*, *9*, 585–94.

Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J. (2001). Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron*, *30*, 829–41.

Vuilleumier, P., Pourtois, G. (2007). Distributed and interactive brain mechanisms during emotion face perception: evidence from functional neuroimaging. *Neuropsychologia*, *45*, 174–94.

Vuilleumier, P., Richardson, M.P., Armony, J.L., Driver, J., Dolan, R.J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature Neuroscience*, *7*, 1271–8.

Whalen, P.J. (1998). Fear, vigilance, and ambiguity: initial neuroimaging studies of the human amygdala. *Current Directions in Psychological Science*, *7*, 177–88.

Wilcox, B.M., Clayton, F.L. (1968). Infant visual fixation on motion pictures of the human face. *Journal of Experimental Child Psychology*, *6*, 22–32.

Williams, L.M. (2006). An integrative neuroscience model of "significance" processing. *Journal of Integrative Neuroscience*, *5*, 1–47.

Williams, L.M., Das, P., Liddell, B., Olivieri, G., Peduto, A., Brammer, M.J., et al. (2005). BOLD, sweat and fears: fMRI and skin conductance distinguish facial fear signals. *Neuroreport*, *16*, 49–52.

Williams, L.M., Palmer, D., Liddell, B.J., Song, L., Gordon, E. (2006). The 'when' and 'where' of perceiving signals of threat versus non-threat. *Neuroimage*, *31*, 458–67.

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REPORT

Fearful faces modulate looking duration and attention disengagement in 7-month-old infants

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Abstract

The present study investigated whether facial expressions modulate visual attention in 7-month-old infants. First, infants' looking duration to individually presented fearful, happy, and novel facial expressions was compared to looking duration to a control stimulus (scrambled face). The face with a novel expression was included to examine the hypothesis that the earlier findings of greater allocation of attention to fearful as compared to happy faces could be due to the novelty of fearful faces in infants' rearing environment. The infants looked longer at the fearful face than at the control stimulus, whereas no such difference was found between the other expressions and the control stimulus. Second, a gap/overlap paradigm was used to determine whether facial expressions affect the infants' ability to disengage their fixation from a centrally presented face and shift attention to a peripheral target. It was found that infants disengaged their fixation significantly less frequently from fearful faces than from control stimuli and happy faces. Novel facial expressions did not have a similar effect on attention disengagement. Thus, it seems that adult-like modulation of the disengagement of attention by threat-related stimuli can be observed early in life, and that the influence of emotionally salient (fearful) faces on visual attention is not simply attributable to the novelty of these expressions in infants' rearing environment.

Introduction

One of the functions of the emotional brain systems is to scan the environment for the presence of biologically relevant stimuli and to guide attention and processing resources towards these stimuli (Vuilleumier, 2005; Williams, 2006). In environments where multiple stimuli compete for attention, stimuli which are relevant to our core motivation to minimize danger and maximize pleasure are given precedence, and they are subjected to the most rapid processing (Williams, 2006). Indeed, behavioural studies with adults using facial expressions as emotional stimuli indicate that attention is preferentially allocated to threat-related stimuli (e.g. fearful faces) over simultaneously presented neutral stimuli (Holmes, Green & Vuilleumier, 2005). Viewing fearful and angry faces may also cause a delay in disengaging attention from them, particularly in individuals with elevated levels of anxiety (Georgiou, Bleakley, Hayward, Russo, Dutton, Eltiti & Fox, 2005). Subcortical brain structures, especially the amygdala, have been suggested to play an important role in the recognition of fearful faces and in the interaction of emotional and attentional processes (Vuilleumier, 2005). With its dense connections with cortical and other subcortical areas, the amygdala subserves rapid alerting (Liddell, Brown, Kemp, Barton, Das, Peduto, Gordon & Williams, 2005) and allocation of attention to emotionally significant stimuli (Adolphs, Gosselin, Buchanan, Tranel, Schyns & Damasio, 2005).

Although progress has been made in understanding emotion–attention interactions in adults, little is known, however, about how these interactions develop. The development of visual attention *per se* has been extensively studied and several paradigms to study attention in infants and young children have been developed (Colombo, 2001). Therefore, examining how emotionally significant stimuli affect infants' performance in these attention-sensitive tasks may provide important insights into the early development of emotion–attention interactions.

A component of spatial attention that emerges in the early stages of postnatal development and that may be susceptible to emotional influences is the disengagement of attention. Disengagement is considered as the stage of spatial orienting when the processing of a stimulus in a current location has to be terminated before shifting attention to a new location (Posner & Petersen, 1990). Between 1 and 3 months of age, infants show apparent difficulties in disengaging fixation from foveated stimuli

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in order to shift attention to peripherally presented stimuli ('sticky fixation'; Hood, 1995). In the following months, this tendency wanes gradually (Hunnius & Geuze, 2004). Such development has been associated with the maturation of frontal and parietal structures enabling greater cortical control over the disengagement and shifting of spatial attention (Johnson, 2005a). The development of attentional disengagement has been studied with the gap/overlap task (Aslin & Salapatek, 1975; Hood, Willen & Driver, 1998). In a typical version of this task, the infant is first presented with a central fixation stimulus. After a short delay (e.g. 1000 ms), a peripheral target appears. On gap trials, the central stimulus is removed prior to the appearance of the target, whereas on overlap trials, the central stimulus remains present throughout the trial. The critical difference between these conditions is that on overlap trials, attention has to be disengaged from the central fixation, whereas on gap trials, disengagement from fixation is not needed (Colombo, 2001). Between 1 and 3 months of age, infants move their eyes to the peripheral target on only a small proportion of the overlap trials (ca. 20% of trials; Hunnius & Geuze, 2004). By 6 months of age, however, the frequency and latency of orienting to targets on overlap trials reaches an adult level of performance (Csibra, Tucker & Johnson, 1998; Hunnius & Geuze, 2004). However, it is currently not known whether the emotional significance of the central stimulus has an influence on the frequency or latency of attention disengagement in infancy.

Facial expressions may be particularly well suited stimuli to start examining whether emotional significance influences attention in infancy. Even newborns are able to perceive the difference between happy, surprised, and sad facial expressions (Field, Woodson, Greenberg & Cohen, 1982), although it is possible that these discriminations are based on some salient low-level stimulus features (e.g. open vs. closed mouth). By the age of 5 to 7 months, infants are able not only to discriminate between facial expressions but also to categorize expressions posed by different models into a common class, although this ability may be limited to happy and surprised expressions (see Leppänen & Nelson, 2006, for a review). By the age of 5 to 7 months, infants also start to show some sensitivity to the emotional signal value of facial expressions. For example, in 5-month-old infants, the magnitude of an eye blink startle to loud noise is modulated by facial expressions, so that viewing angry faces augments and viewing happy faces reduces the magnitude of the blink (Balaban, 1995). Furthermore, 7-month-old infants show a visual preference for fearful faces over happy faces, i.e. the infants look longer at a fearful face when it is presented simultaneously with a happy face in a visual paired comparison task (VPC; Kotsoni, de Haan & Johnson, 2001; Nelson & Dolgin, 1985). Greater allocation of attention to fearful faces has also been demonstrated in electrophysiological studies which have shown that the 'Negative central' (Nc) component of the event-related potential (ERP) is larger for fearful than happy faces in 7-month-old infants (de Haan, Belsky, Reid, Volein & Johnson, 2004; Leppänen, Moulson, Vogel-Farley & Nelson, 2007; Nelson & de Haan, 1996). The Nc component is thought to reflect the orienting of processing resources to attention-grabbing stimuli (Nelson & Monk, 2001; Richards, 2003).

Although the preference for fearful faces implies that emotional significance modulates infants' visual attention, there are open questions that require further clarification. First, in typical rearing environments, infants are exposed mainly to positive facial expressions and rarely to fearful faces (Malatesta & Haviland, 1982). This raises the possibility that it is the novelty of fearful faces rather than their emotional signal value that attracts infants' attention (Nelson & Dolgin, 1985). Second, although infants look longer at fearful faces, it is not known which specific component of attention is affected by fearful expressions. Research with adults (Georgiou *et al.*, 2005) has shown delayed attentional disengagement from fearful faces, and infant studies (Colombo, 1995; Frick, Colombo & Saxon, 1999) have shown that looking duration to non-emotional stimuli is positively correlated with attention disengagement latency. These findings may be taken to suggest that the commonly observed longer looking times to fearful faces in infants reflect an influence of fearful expressions on attentional disengagement.

In the present study, two behavioural tasks were used to examine the influences of emotional significance and novelty of facial expressions on looking duration and attention disengagement in 7-month-old infants. First, looking durations to individually presented fearful and happy facial expressions and to novel expressions were measured and compared to those for a control stimulus (scrambled face). Second, a gap/overlap paradigm was employed to examine the effects of facial expressions on the disengagement of attention. Based on previous data in infants (e.g. Ludemann & Nelson, 1988), we hypothesized that infants would look longer at fearful faces compared to happy faces and control stimuli. We also hypothesized that fearful faces would exert an influence on attention by inhibiting attention disengagement, i.e. infants would find it more difficult to disengage attention from fearful faces than from happy faces and control stimuli. Finally, to determine whether the effects of fearful faces on visual attention can be separated from the effects of novelty and unfamiliarity, we examined whether novel facial expressions and fearful expressions have similar effects on looking times and attention disengagement.

Methods

Participants

The final sample consisted of 28 7-month-old infants (14 boys; mean age 210 days; *SD* = 2.8; birth weight at least

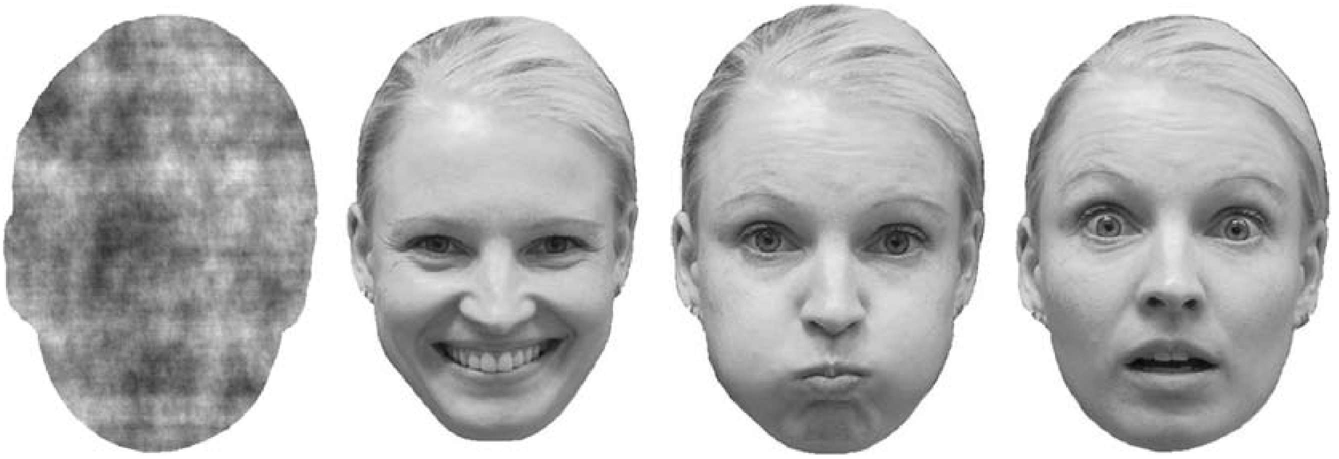

Figure 1 *Examples of the stimuli used in the present study.*

Table 1 *Happiness, novelty, and fearfulness ratings for the stimuli used in the present study (scale 1–7). Ratings for the stimuli from the NimStim face stimulus set are shown in parentheses*

	Face				
Rating	Happy	Novel	Fearful	F(2, 22)	Post-hoc tests
Happiness	5.6 (5.2)	2.2	2.2 (1.8)	44.8**	Happy > Novel & Fear
Novelty	1.6 (1.8)	4.9	5.0 (5.0)	32.2**	Happy < Novel & Fear
Fearfulness	1.3 (1.2)	2.3	5.7 (5.8)	231.9**	Fear > Novel > Happy

Note: ** $p < .01$.

2400 g). At the time of testing, the infants were healthy and free of visual or neurological abnormalities. An additional three infants were tested but excluded from all analyses due to prematurity (gestational age 37 weeks or less). The participants were recruited through Child Welfare Clinics. Parents who expressed their interest in participating in research were contacted by telephone.

Stimuli and apparatus

The face stimuli (Figure 1) were colour images of two female models portraying a happy, fearful, or a novel facial expression. In the novel expression, lips were closed, cheeks were blown full of air, and eyes were clearly open. The control stimuli were face-shaped images that were created by randomizing the phase spectra of the faces of the two models while maintaining the amplitude and colour spectra constant (following the procedure described by Halit, Csibra, Volein & Johnson, 2004). The faces measured 15.4° and 10.8° of vertical and horizontal visual angle, respectively.

The validity of the facial expressions was tested by asking 12 adults to rate the expressions on a scale from 1 to 7 depending on how happy, novel, and fearful the faces seemed to them. Besides the expressions used in the present study, happy and fearful facial expressions from an existing stimulus set (the NimStim Face Stimulus Set; Tottenham, Borscheid, Ellertsen, Markus & Nelson, 2002) were included as reference stimuli. Importantly, as can be inspected from Table 1, happy and fearful faces were evaluated as good examples of the respective emotions, and the ratings obtained for the faces in the present study were highly similar to the ratings for stimuli taken from an existing stimulus set. The novel expressions were perceived as novel as the fearful faces but they were rated low on fearfulness and happiness.

The experimental session took place in a darkened room. Infants sat on their parent's lap in a 1 m × 2 m booth in front of a 17-inch computer monitor, with a distance of 60 cm between the infant's eyes and the monitor. The monitor was surrounded by black panels leaving only the screen visible for the infant. A hidden digital video camera was mounted above the monitor, and infants' eye movements were recorded throughout the experiment with the camera and a DVD recorder for off-line analyses. E-Prime software (Schneider, Eschman & Zuccolotto, 2002) was used to control the stimulus presentation.

Procedure

Upon arrival at the laboratory, the experimental procedure was described, and all parents gave written consent. The actual experiment consisted of a looking duration task and a gap/overlap task, presented in this order for all participants. Half of the participants saw images of face model A and the other half saw images of model B.

Looking duration task

Each of the three facial expressions and the control stimulus was presented once for a 20-second period on the centre of the screen. The order of the stimulus presentation was randomized across participants. Before each trial, the infant's attention was drawn to the centre of the screen by a red circle which expanded to 4.3° in a continuous fashion. The experimenter monitored the infant's behaviour between the trials, and initiated the next stimulus with a key-press when the child was attending to the red circle.

Gap/overlap task

This task was administered immediately after the looking duration task. Again, the experimenter initiated each trial when the child was attending to the red circle. The trial started with the presentation of the central stimulus (i.e. one of the three different faces or the control stimulus), and 1000 ms after the onset of the central stimulus, a peripheral target was presented 13.6° equiprobably either to the left or right of the central stimulus. The target stimulus was a black-and-white checkerboard pattern, subtending a visual angle of 15.4° and 4.3° vertically and horizontally, respectively. The target was visible for 3000 ms. On gap trials, the central stimulus was removed 200 ms prior to the presentation of the target. On overlap trials, the central stimulus remained present on the screen throughout the trial (see Figure 2). The central stimuli (i.e. a happy, fearful, or a novel face, or the control stimulus) and the gap/overlap trials were presented in a random order with the constraint that none of the facial expressions was presented more than two consecutive times. The experiment was continued until the infant became inattentive or too fussy to continue (approximately 15 minutes).

Data analyses

Video coding

The video records from both the looking duration task and the gap/overlap task were coded off-line by an independent observer who was blind to the stimulus condition. The analyses were carried out with the Queen's Video Coder (Baron, Wheatley, Symons, Hains, Lee & Muir, 2001) which allowed frame-by-frame playback of the video recording.

For the looking duration task, (a) total looking time to each image (i.e. the accumulated looking time from separate fixations toward the stimulus during the 20-second period), and (b) the length of the longest individual fixation (i.e. peak look) to each image were calculated. The data from one infant were excluded from the looking time analyses due to excessive movements, thus leaving 27 participants (14 boys) for the analyses.

In the gap/overlap task, the infants completed an average of 40 trials. On average, 7.5 (*SD* = 5.6) trials were excluded due to excessive movements or anticipatory eye movements (i.e. eye movement latencies < 200 ms after target onset; Canfield & Haith, 1991). Infants with less than two scorable responses within any of the experimental conditions were excluded from the analyses, which resulted in the exclusion of nine infants. A further two infants were excluded due to technical errors, thus leaving 17 infants (eight boys) for the analyses. The included infants had on average 4.93 (*SD* = 1.24) scorable trials per condition.[1] Of the scorable trials, the percentages of correct responses (i.e. the child moved his/her eyes toward the target), fixations (i.e. the child did not move his/her eyes from the central face during the trial), and false responses (i.e. the child looked to the opposite side of the target) were calculated. The percentages of

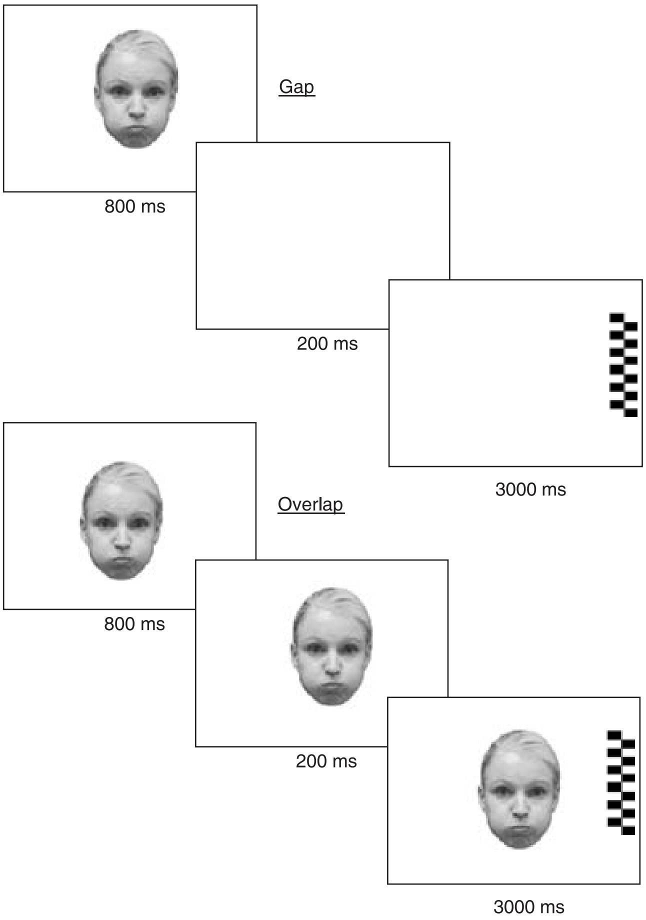

Figure 2 *Examples of gap and overlap trials with a novel face.*

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[1] The mean number of scorable responses (with standard deviations in parentheses) for control, happy, novel, and fearful stimuli were 5.1 (1.5), 5.4 (1.5), 4.5 (1.3), and 5.0 (1.7) in the gap condition, and 4.9 (1.7), 4.5 (1.4), 5.0 (1.5), and 5.2 (1.3) in the overlap condition. The differences in the number of scorable responses were not significant between the gap and overlap conditions nor within these conditions, all *ps* > .4, except that on gap trials, novel faces had less scorable responses than happy faces, $t = 4.67$, $p < .01$. We note, however, that this difference did not affect the conclusions of the study, as the main analyses were based on the infants' performance on overlap trials.

correct and fixation responses were the primary dependent variable as false responses were nearly absent in both gap and overlap conditions. Additionally, the latency of the first saccade toward the target (i.e. the time interval from target onset to eye movement onset) was calculated. However, as many infants had too few correct responses on overlap trials (due to increased number of fixation responses), the analysis of the latency differences between different faces was considered uninformative (cf. Hood *et al.*, 1998).

Statistical analyses

As the values of some of the test variables were not normally distributed, common transformation techniques (e.g. natural logarithm and square root) were employed in an attempt to normalize the data. As normal distribution was not obtained with the transformations for any of the other variables except the peak look data, nonparametric methods were used to analyse the data. Two-way factorial analyses were conducted using repeated-measures analyses of variance (ANOVAs) on rank transformed data (as described by Conover, 1999), one-way analyses by using Friedman's rank test and paired comparisons by using Wilcoxon's signed-ranks test. With the normally distributed peak look data, a repeated-measures ANOVA and *t*-tests (with Bonferroni correction) were used. For clarity, the figures show the untransformed values.

The reliability of the coding was ensured by having another independent observer (who was blind to the stimulus condition) code 30% of the recordings. For the looking duration task, the Pearson correlations of the two observers' measurements of each infant's looking times to different stimuli were on average .96 and .97 for the total looking time and peak looks, respectively. For the gap/overlap task, the interobserver agreement (Cohen's kappa) for the infants' response on individual trials was on average .84.

Results

Looking duration task

The total looking times and the durations of peak looks are shown in Figure 3. The total looking times were marginally different for control (M = 12.9 s), happy (M = 13.4 s), novel (M = 14.0 s), and fearful (M = 14.7 s) stimuli, F_R = 7.37, *df* = 3, *p* = .06 (Friedman's test). Paired comparisons indicated that the difference between fearful faces and control stimuli was significant, *z* = –2.81, *p* < .05 (Wilcoxon's test), whereas the expected difference between fearful and happy faces or any of the other differences was not significant, all *p*s > .4.

The analysis of logarithmically transformed peak look times revealed significant differences between control (M = 5.9 s), happy (M = 7.2 s), novel (M = 7.2 s), and fearful (M = 8.6 s) stimuli, *F*(3, 78) = 3.60, *p* < .02. The peak looks were significantly longer to fearful faces than to control stimuli, *t*(26) = 3.61, *p* < .01. None of the other differences were significant, all *p*s > .6.

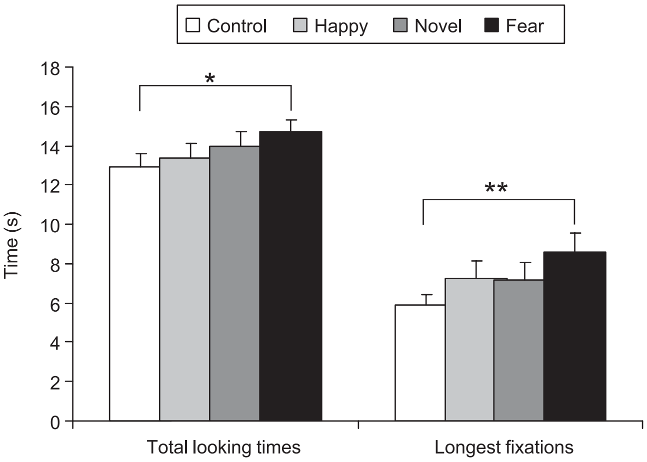

Figure 3 *Total looking times and longest fixations to each stimulus in the looking duration task.*
Note: * $p < .05$; ** $p < .01$.

Gap/overlap task

The eye movement latencies were generally shorter on gap trials than on overlap trials (434 ms vs. 594 ms), *z* = –2.53, *p* < .01. Figure 4 shows that this 'gap effect' was also reflected in the higher percentage of correct responses in the gap as compared to overlap condition. A 2 (Condition: gap, overlap) × 4 (Stimulus: control, happy, novel, fear) ANOVA conducted on rank scores yielded a significant interaction, *F*(3, 48) = 4.15, *p* < .02. The percentage of correct responses on gap trials was generally high and there were no significant differences in the proportion of correct responses between different faces, all *p*s > .3. However, in the overlap condition, the proportion of correct responses differed significantly between stimuli, F_R = 11.52, *df* = 3, *p* < .01. There were significantly fewer correct responses in the overlap condition to fearful (44.5%) than to happy faces (65.8%), *z* = –2.67, *p* < .05 and to control stimuli (70.1%), *z* = –2.95, *p* < .05. A reverse pattern emerged for fixation responses, F_R = 11.52, *df* = 3, *p* < .01. Thus, on overlap trials, the infants fixated significantly more frequently to fearful (54.4%) as compared to happy faces (34.2%), *z* = –2.61, *p* = .05, and to control stimuli (28.9%), *z* = –2.76, *p* < .05. The novel face did not differ from the other stimuli in the percentage of correct (54.5%) and fixation (44.4%) responses, all *p*s > .2.

Correlational analyses

To examine the possible associations between the performance in the two tasks (cf. Frick *et al.*, 1999), looking time was correlated with the performance in the gap/overlap task. The correlations between both looking

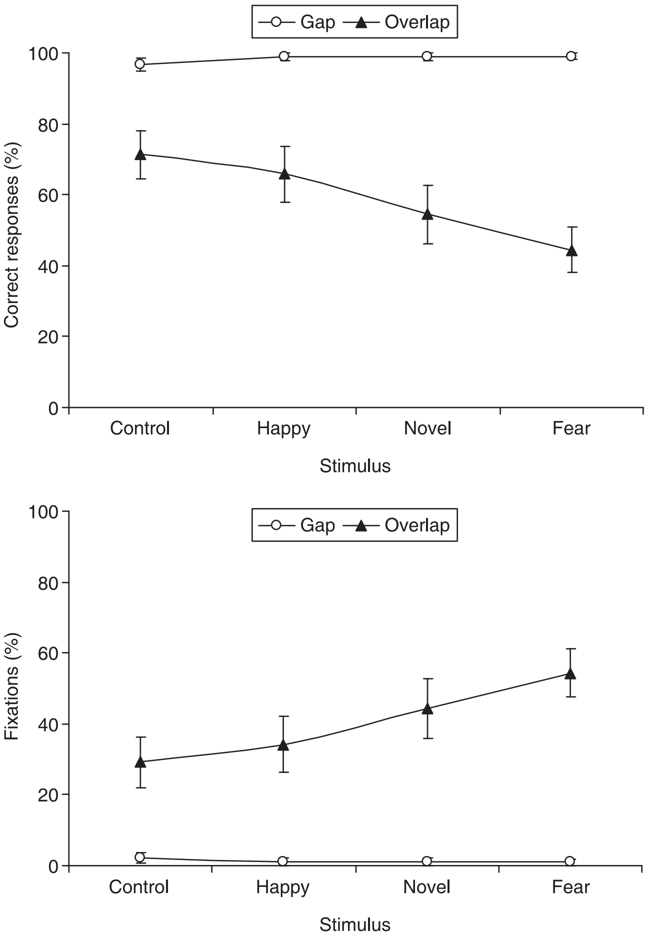

Figure 4 *The percentages of correct and fixation responses (i.e. no movement) in the gap and overlap conditions.*

duration measures and the percentages of correct and fixation responses were generally in the expected direction, i.e. looking duration was negatively correlated with the mean percentage of correct responses and positively correlated with the mean percentage of fixation responses. However, none of these correlations was statistically significant, all *p*s > .05.

Discussion

The present results are generally consistent with the hypothesis that facial expressions exert an influence on infants' visual attention. Results from the looking duration task showed that looking times to fearful faces differed significantly from looking times to the control stimulus, whereas happy and novel faces were not looked at longer compared to the control stimulus. In contrast to the hypotheses, the difference between fearful and happy faces was not significant. Although there is no ready interpretation for this unexpected result, two methodological points should be mentioned. First, in the present study, looking times were measured to four different stimuli, whereas previous studies have typically contrasted only happy and fearful faces. Second, we presented the stimuli sequentially, but it is possible that a paired stimulus presentation design would have been more sensitive in eliciting differential looking behaviour to happy and fearful faces (e.g. Kotsoni *et al.*, 2001; Nelson & Dolgin, 1985). Nelson and Dolgin (1985) speculated that when the faces are seen individually, infants might not be able to differentiate the informational value between happy and fearful faces, as opposed to when the faces are presented simultaneously. Another possibility is, of course, that the visual differentiation of the facial expressions is more efficient when the faces are presented simultaneously as opposed to sequential presentation. One might also speculate that the visual preference for fearful over happy faces is most likely observed when there is competition for attentional resources between stimuli. However, as both behavioural (de Haan & Nelson, 1998; Ludemann & Nelson, 1988) and ERP (de Haan *et al.*, 2004; Leppänen *et al.*, 2007; Nelson & de Haan, 1996) studies have reported fear preference with sequentially presented stimuli, the suggestion of the greater sensitivity of the paired presentation in eliciting differential allocation of attention should be considered as tentative.

The hypothesis concerning the effect of fearful faces on attentional disengagement was also supported. This was evidenced by an increased number of fixation responses (i.e. no movement) during overlap trials, when the foveated stimulus was a fearful face. Thus, it seems that adult-like modulation of the disengagement component of attention by threat-related stimuli can be observed in infants as young as 7 months old. One might argue that the less frequent saccades toward the target during overlap trials with fearful faces could be due to a voluntary inhibition of saccades (i.e. the infants *wanting* to fixate on the fearful face), and not due to *difficulties* in disengaging fixation. However, this possibility seems rather unlikely, as in previous studies with 6-month-old infants, orienting toward the peripheral target has been consistently observed on approximately 80% of the overlap trials (e.g. Csibra *et al.*, 1998; Hunnius & Geuze, 2004), even when the foveated stimulus has been meaningful and obviously interesting, such as the mother's face talking and smiling or an abstract stimulus with motion (Hunnius & Geuze, 2004). Whether disengagement latencies from fearful faces are also longer in infants remains an open issue. A limitation of the present study was that there were too few correct responses on overlap trials to calculate the eye movement latencies for different stimuli (cf. Hood *et al.*, 1998). It is also noteworthy that we cannot make strong assumptions about the association between looking duration and attention disengagement on the basis of the present data. The correlations between looking duration and performance on overlap trials were in the right direction, albeit not significant. One possible explanation for this lack of significant correlation is that the association between looking duration and disengagement might dissipate by the age of 7 months, when infants already exhibit a rather well-developed ability to disengage attention (Blaga & Colombo, 2006).

What is it in a fearful face that captures infants' attention? Besides conveying information about the presence of a potential threat, fearful faces are also novel stimuli to infants at this age (Malatesta & Haviland, 1982). Nevertheless, it appears that novelty *alone* is not sufficient to account for the previously observed behavioural and electrophysiological responses to fearful faces, as the novel face did not differ from the control image and the happy face in looking time and in the frequency of attention disengagement in the present study. However, the novelty hypothesis of infants' preference for fearful faces cannot be completely ruled out, as a direct comparison did not reveal significant differences between fearful and novel faces in either task in the current study.

An alternative possibility remains that salient low-level features, such as wide open eyes, capture attention in infants (Nelson & Dolgin, 1985). It has been suggested that low-frequency information of the eye region (i.e. the size of the white sclera around the iris) is especially relevant in the detection and recognition of fear from faces (Adolphs *et al.*, 2005; Johnson, 2005b; Whalen, Kagan, Cook, Davis, Kim, Polis, McLaren, Somerville, McLean, Maxwell & Johnstone, 2004). Furthermore, infants show sensitivity to the information present in the eye region very early in development (Farroni, Csibra, Simion & Johnson, 2002). Thus, fearful faces may be particularly suitable stimuli for drawing infants' attention to faces (Johnson, 2005b). In the present stimuli, the size of the eye white was largest in the fearful face, followed by the novel and happy faces. By inspecting the mean looking times and fixation percentages, it is interesting to note that the results follow a similar linear pattern (i.e. looking times and fixation percentages increase with respect to how much eye white is visible). However, as not all of the differences were significant, caution should be exercised when making inferences concerning the size of the eye whites on the basis of our findings.

It is also important to consider whether the findings of infants' enhanced attention are specific with respect to fearful expressions *per se*, or whether they extend to other negatively valenced expressions, such as anger. Interestingly, 7-month-old (Grossmann, Striano & Friederici, 2007) and younger infants (LaBarbera, Izard, Vietze & Parisi, 1976) have been found to look less at angry as compared to happy faces. Furthermore, the finding of larger Nc amplitude to happy as compared to angry faces in 7-month-old infants (Grossmann *et al.*, 2007) also suggests that at this age, infants do not exhibit an attentional bias toward angry faces. Together, these findings can be taken to suggest that angry faces would not cause less frequent disengagement of attention in the gap/overlap task as was shown for fearful faces in the present study. However, it remains for future studies to empirically test this hypothesis.

The specific neural mechanisms which delay/inhibit disengagement from threatening stimuli are not known (Phelps, 2006). However, the amygdala is involved in contributing to an enhanced neural activation in the visual cortex when viewing fearful faces (e.g. Morris, Friston, Büchel, Frith, Young, Calder & Dolan, 1998). When there is competition for attentional resources (e.g. between a central face and a peripheral stimulus), such enhanced sensory representations may act to bias attentional selection in favour of emotional or threatening stimuli (Vuilleumier, 2005). There is also evidence (Pourtois, Schwartz, Seghier, Lazeyras & Vuilleumier, 2006) suggesting that the activation of parietal areas involved in the shifting of attention is suppressed by threat-related stimuli, and such response may produce transient unresponsiveness to competing stimuli. Although it remains unanswered whether the amygdala modulates sensory processing in human infants, it is interesting to note that studies with macaque monkeys have shown that the reciprocal connections between the amygdala and different cortical regions are established soon after birth (Nelson, Bloom, Cameron, Amaral, Dahl & Pine, 2002). However, one should be cautious in making strong inferences, as, for example, amygdala responses have been shown to be stronger for neutral compared to fearful faces in 11-year-old children (Thomas, Drevets, Whalen, Eccard, Dahl, Ryan & Casey, 2001).

In conclusion, the present study showed that perceiving a fearful facial expression has an influence on attention disengagement in 7-month-old infants. This influence was not simply attributable to the novelty of these faces. These findings provide the first pieces of evidence that adult-like emotion–attention interactions can be demonstrated in young infants. The findings also encourage further use of facial expression stimuli together with established attention-sensitive paradigms in studying the development of emotion–attention interactions. It also remains for future studies to determine whether the low-frequency information of the eye region is critical in attracting infants' attention to fearful faces.

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References

Adolphs, R., Gosselin, F., Buchanan, T.W., Tranel, D., Schyns, P., & Damasio, A.R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature*, **433**, 68–72.

Aslin, R.N., & Salapatek, P. (1975). Saccadic localization of visual targets by the very young human infant. *Perception and Psychophysics*, **17**, 293–302.

Balaban, M.T. (1995). Affective influences on startle in five-month-old infants: reactions to facial expressions of emotions. *Child Development*, **66**, 28–36.

Baron, M.J., Wheatley, J., Symons, L., Hains, C.R., Lee, K., & Muir, D. (2001). *The Queen's video coder* (http://psyc.queensu.ca/~vidcoder). Department of Psychology, Queen's University, Canada; http://psyc.queensu.ca/vidcoder/

Blaga, O.M., & Colombo, J. (2006). Visual processing and infant ocular latencies in the overlap paradigm. *Developmental Psychology*, **42**, 1069–1076.

Canfield, R.L., & Haith, M.M. (1991). Young infants' visual expectations for symmetric and asymmetric stimulus sequences. *Developmental Psychology*, **27**, 198–208.

Colombo, J. (1995). On the neural mechanisms underlying developmental and individual differences in visual fixation in infancy: two hypotheses. *Developmental Review*, **15**, 97–135.

Colombo, J. (2001). The development of visual attention in infancy. *Annual Review of Psychology*, **52**, 337–367.

Conover, W.J. (1999). *Practical nonparametric statistics* (3rd edn.). New York: Wiley.

Csibra, G., Tucker, L.A., & Johnson, M.H. (1998). Neural correlates of saccade planning in infants: a high-density ERP study. *International Journal of Psychophysiology*, **29**, 201–215.

de Haan, M., Belsky, J., Reid, V., Volein, A., & Johnson, M.H. (2004). Maternal personality and infants' neural and visual responsivity to facial expressions of emotion. *Journal of Child Psychology and Psychiatry*, **45**, 1209–1218.

de Haan, M., & Nelson, C.A. (1998). Discrimination and categorization of facial expressions of emotion during infancy. In A.M. Slater (Ed.), *Perceptual development: Visual, auditory, and language perception in infancy* (pp. 287–309). London: UCL Press.

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

Field, T.M., Woodson, R., Greenberg, R., & Cohen, D. (1982). Discrimination and imitation of facial expression by neonates. *Science*, **218**, 179–181.

Frick, J.E., Colombo, J., & Saxon, T.F. (1999). Individual and developmental differences in disengagement of fixation in early infancy. *Child Development*, **70**, 537–548.

Georgiou, G.A., Bleakley, C., Hayward, J., Russo, R., Dutton, K., Eltiti, S., & Fox, E. (2005). Focusing on fear: attentional disengagement from emotional faces. *Visual Cognition*, **12**, 145–158.

Grossmann, T., Striano, T., & Friederici, A.D. (2007). Developmental changes in infants' processing of happy and angry facial expressions: a neurobehavioral study. *Brain and Cognition*, **64**, 30–41.

Halit, H., Csibra, G., Volein, A., & Johnson, M.H. (2004). Face-sensitive cortical processing in early infancy. *Journal of Child Psychology and Psychiatry*, **45**, 1228–1234.

Holmes, A., Green, S., & Vuilleumier, P. (2005). The involvement of distinct visual channels in rapid attention towards fearful facial expressions. *Cognition and Emotion*, **19**, 899–922.

Hood, B.M. (1995). Shifts of visual attention in the human infant: a neuroscientific approach. In C. Rovee-Collier & L. Lipsett (Eds.), *Advances in infancy research* (Vol. 9; pp. 163–216). Norwood, NJ: Ablex.

Hood, B.M., Willen, D., & Driver, J. (1998). Adult's eyes trigger shifts of visual attention in human infants. *Psychological Science*, **9**, 131–134.

Hunnius, S., & Geuze, R.H. (2004). Gaze shifting in infancy: a longitudinal study using dynamic faces and abstract stimuli. *Infant Behavior and Development*, **27**, 397–416.

Johnson, M.H. (2005a). *Developmental cognitive neuroscience* (2nd edn.). Oxford: Blackwell.

Johnson, M.H. (2005b). Subcortical face processing. *Nature Reviews Neuroscience*, **6**, 766–774.

Kotsoni, E., de Haan, M., & Johnson, M.H. (2001). Categorical perception of facial expressions by 7-month-old infants. *Perception*, **30**, 1115–1125.

LaBarbera, J.D., Izard, C.E., Vietze, P., & Parisi, S.A. (1976). Four- and six-month-old infants' visual responses to joy, anger, and neutral expressions. *Child Development*, **47**, 535–538.

Leppänen, J.M., Moulson, M.C., Vogel-Farley, V.K., & Nelson, C.A. (2007). An ERP study of emotional face processing in the adult and infant brain. *Child Development*, **78**, 232–245.

Leppänen, J.M., & Nelson, C.A. (2006). The development and neural bases of facial emotion recognition. In R.V. Kail (Ed.), *Advances in child development and behaviour* (Vol. 34; pp. 207–246). San Diego, CA: Academic Press.

Liddell, B.J., Brown, K.J., Kemp, A.H., Barton, M.J., Das, P., Peduto, A., Gordon, E., & Williams, L.M. (2005). A direct brainstem-amygdala-cortical 'alarm' system for subliminal signals of fear. *Neuroimage*, **24**, 235–243.

Ludemann, P., & Nelson, C.A. (1988). Categorical representation of facial expressions by 7-month-old infants. *Developmental Psychology*, **24**, 492–501.

Malatesta, C.Z., & Haviland, J.M. (1982). Learning display rules: the socialization of emotion expression in infancy. *Child Development*, **53**, 991–1003.

Morris, J.S., Friston, K.J., Büchel, C., Frith, C.D., Young, A.W., Calder, A.J., & Dolan, R.J. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, **121**, 47–57.

Nelson, C.A., Bloom, F.E., Cameron, J., Amaral, D., Dahl, R., & Pine, D. (2002). An integrative, multidisciplinary approach to the study of brain–behaviour relations in the context of typical and atypical development. *Development and Psychopathology*, **14**, 499–520.

Nelson, C.A., & de Haan, M. (1996). Neural correlates of infants' visual responsiveness to facial expressions of emotion. *Developmental Psychobiology*, **29**, 577–595.

Nelson, C.A., & Dolgin, K. (1985). The generalized discrimination of facial expressions by 7-month-old infants. *Child Development*, **56**, 58–61.

Nelson, C.A., & Monk, C. (2001). The use of event-related potentials in the study of cognitive development. In C.A. Nelson & M. Luciana (Eds.), *Handbook of developmental cognitive neuroscience* (pp. 125–136). Cambridge, MA: MIT Press.

Phelps, E.A. (2006). Emotion and cognition: insights from studies of the human amygdala. *Annual Review of Psychology*, **57**, 27–53.

Posner, M.I., & Petersen, S.E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, **13**, 25–42.

Pourtois, G., Schwartz, S., Seghier, M.L., Lazeyras, F., & Vuilleumier, P. (2006). Neural systems for orienting attention to the location of threat signals: an event-related fMRI study. *Neuroimage*, **31**, 920–933.

Richards, J.E. (2003). Attention affects the recognition of briefly presented visual stimuli in infants: an ERP study. *Developmental Science*, **6**, 312–328.

Schneider, W., Eschman, A., & Zuccolotto, A. (2002). *E-Prime user's guide*. Pittsburgh, PA: Psychology Software Tools Inc.

Thomas, K.M., Drevets, W.C., Whalen, P.J., Eccard, C.H., Dahl, R.E., Ryan, N.D., & Casey, B.J. (2001). Amygdala response to facial expressions in children and adults. *Biological Psychiatry*, **49**, 309–316.

Tottenham, N., Borscheid, A., Ellertsen, K., Marcus, D.J., & Nelson, C.A. (2002, April). Categorization of facial expressions in children and adults: establishing a larger stimulus set. Poster presented at the Annual Meeting of the Cognitive Neuroscience Society, San Francisco.

Vuilleumier, P. (2005). How brains beware: neural mechanisms of emotional attention. *Trends in Cognitive Sciences*, **9**, 585–594.

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

Williams, L.M. (2006). An integrative neuroscience model of 'significance' processing. *Journal of Integrative Neuroscience*, **5**, 1–47.

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Cardiac and behavioral evidence for emotional influences on attention in 7-month-old infants

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To examine the ontogeny of emotion-attention interactions, we investigated whether infants exhibit adult-like biases in automatic and voluntary attentional processes towards fearful facial expressions. Heart rate and saccadic eye movements were measured from 7-month-old infants (*n* = 42) while viewing non-face control stimuli and neutral, happy, and fearful facial expressions flanked after 1000 ms by a peripheral distractor. Relative to neutral and happy expressions, fearful expressions resulted in a greater cardiac deceleration response during the first 1000 ms of face-viewing and in a relatively long-lasting suppression of face-to-distractor saccades. The results suggest that the neural architecture for the integration of emotional significance with automatic attentional orienting as well as more voluntary attentional prioritization processes is present early in life.

Humans constantly monitor others' faces for signs of different emotional states and are skilled at utilizing these cues to acquire knowledge about the physical and social world (Herrmann et al., 2007; Olsson & Phelps, 2007). Developmental work in human infants suggests that the foundations of these social-cognitive abilities emerge in early infancy. By the second half of the first year, infants' visual system is sufficiently developed to discriminate most facial expression contrasts and infants begin to exhibit enhanced attention to affectively salient facial expressions (e.g., expressions that signal potential danger, de Haan & Nelson, 1998; Leppänen & Nelson, 2006, 2009). Seven-month-old infants look longer at a fearful than happy facial expression in a paired comparison task (Kotsoni *et al.*, 2001; Nelson & Dolgin, 1985) and are less likely to move their gaze from a centrally presented fearful face to a peripheral target than from a non-face control stimulus (Peltola et al., 2008). Recordings of event-related brain potentials (ERPs) to facial expressions in 7-month-old infants have further shown that visual and attention-sensitive ERPs are enhanced when infants are viewing fearful facial expressions (Hoehl et al., 2008; Leppänen et al., 2007; Nelson & de Haan, 1996; Peltola et al., 2009a).

In the present study, we aimed at further examining the mechanisms that underlie infants' enhanced attention to fearful facial expressions. In particular, the goal of this study was to measure changes in heart rate to examine whether infants' initial orienting reflex to the stimulus is modulated by affective significance. Evidence for such an effect would suggest that information about facial expressions is rapidly coded and begins to bias attentional engagement in the very early stages of stimulus processing.

Previous studies in animal and human adults have shown that attention to external stimuli is accompanied by a rapid deceleration of the heart rate (Bradley, 2009). This deceleration response is observed in human infants from the first months of postnatal life (Lewis et al., 1966) and it may index an automatic and largely subcortically mediated orienting reflex towards the stimulus (Reynolds & Richards, 2007). A recent study with 3- to 12-month-old infants (Courage et al., 2006) showed that the magnitude of the cardiac deceleration response was invariable across different stimuli (i.e., geometric patterns, faces, and dynamic films), although differences between stimulus categories were observed in later stages of stimulus processing when the decelerated heart rate level was maintained and the infant was engaged in more voluntary cognitive processing of the stimulus (i.e., dynamic film clips began to attract more attention). It is possible, however, that even the earliest stages of attentional processing might be modulated by affective significance. For example, studies in adults have shown that the heart rate deceleration response is augmented when the subject is viewing unpleasant scenes or angry facial expressions (Bradley et al., 1993; Kolassa & Miltner, 2006). Also, the neural systems that are involved in processing facial expressions of emotions (i.e., the amygdala) are closely linked with those subcortical systems that control heart rate deceleration (Kapp et al., 1994).

To examine the orienting reflex to different facial expressions, we measured changes in heart rate from 7-month-old infants while they were viewing neutral, happy, and fearful facial expressions flanked after 1000 ms of picture viewing with a peripheral distractor. We focused on 7-month-old infants because previous studies have shown that reliable visual discrimination of facial expressions emerges between 5 and 7 months of age (Flom & Bahrick, 2007) and that the attentional preference for fearful facial expressions is not present in newborns or in 5-month-old infants but is consistently found in 7- and 13-month-old infants (Chen & Johnson, 2008; Farroni et al., 2007; Peltola et al., 2009a). Based on previous ERP findings of relatively rapid differentiation of neutral/happy and fearful expressions in infants (i.e., at ~ 400 ms post-stimulus, see e.g., Nelson & de Haan, 1996) and the hypothesis that some of the emotion-related brain systems mature early in development, we predicted that infants exhibit relatively enhanced cardiac orienting reflex to fearful facial expressions. We further predicted that the greater attentional engagement with fearful facial expressions is also evident at a later stage of processing, resulting in prolonged maintenance of the heart rate deceleration and reduced frequency of face-to-distractor saccades in the context of fearful facial expressions.

Methods

Participants. The participants in the present study were a subgroup of infants in an ongoing longitudinal project designed to examine the continuity of emotional development from infancy to childhood (infants for whom HR data were available were included in the present study). The final sample consisted of 42 7-month-old infants (20 females, mean age = 215.6 days; *SD* = 3.2). All infants were born full term (≥37 weeks), had a birth weight of >2400 g and no history of visual or neurological abnormalities. Data from an additional 8 infants were analyzed but excluded from the final sample due to technical difficulties in heart rate recording (*n* = 1), movement artifact resulting in fewer than 2 good trials in some experimental conditions (*n* = 4), or low quality of the heart rate recording and extreme heart rate change scores (>3 *SD* from group mean, *n* = 3). Approval for the project was obtained from the ethical committee of the local university hospital and an informed, written consent was obtained from the parent.

Stimuli and Procedure. The stimuli were color images of neutral, happy, and fearful facial expressions of two female models as well as a face-shaped matched visual noise image created from each model's face by randomizing the phase spectra of the model's face and holding the color spectra constant. The non-face control stimuli were added to examine potential effects of the presence of a face *per se* on attention-related measures. With a 60-cm viewing distance, each of the four faces measured 15.4° and 10.8° of vertical and horizontal visual angle, respectively. Prior to data collection, a group of adults (*n* = 18) rated the facial expressions for happiness and fearfulness on a scale from 1 to 7. The ratings confirmed that the happy (*M* = 5.9) and fearful (*M* = 6.2) facial expressions used were considered good examples of the respective emotions.

Infants were seated on the parent's lap while stimuli were presented with a 19-inch computer monitor that was surrounded by black panels. A hidden video camera recorded the infant's looking behavior and enabled the experimenter to control stimulus presentation. To measure infants' heart rate and behavioral responses to facial expressions, the "overlap" task was used. [1] In this task (Figure 1), each trial was started with the presentation of a red circle that expanded from 0.4° to 4.3° in a continuous fashion on the center of the screen. As soon as the infant fixated this stimulus, the experimenter pressed a key to present one of the four different face stimuli on the center of the screen on a white background. After 1000 ms, the face stimulus was flanked by a peripheral distractor stimulus 13.6° equiprobably on the left or right for 3000 ms. The distractors were black-and-white vertically arranged circles or a checkerboard pattern, measuring 15.4° and 4.3° vertically and horizontally, respectively. During the overlap task, every infant saw only one model's face (approximately half of the participants saw model A and the other half model B). Stimuli were presented in random order with the

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[1] The first 14 infants in the present sample started the experiment with a short looking time task in which the infant accumulated 20-s of looking time for each of the 4 experimental stimuli. This task was omitted from the procedure for the remaining participants because our interim analyses indicated that the task was insensitive to stimulus category differences. No differences were found in the results reported in this paper between those infants who underwent and those who did not undergo the looking time task. Because there were no other differences in the experimental procedure, the data were collapsed across the two groups.

constraint that the same face was presented no more than twice in a row and the target on the same side of the screen no more than three times in a row. The trials were presented until the infant had accumulated at least five trials per stimulus category. Some of the infants accumulated more trials but only the first five trials in each stimulus category were included in the analysis. Five trials per condition was considered sufficient given that previous studies using heart rate and saccade measures have generally included relatively few trials per condition (i.e., 2-5 trials, see Courage et al., 2006; Peltola et al., 2008).

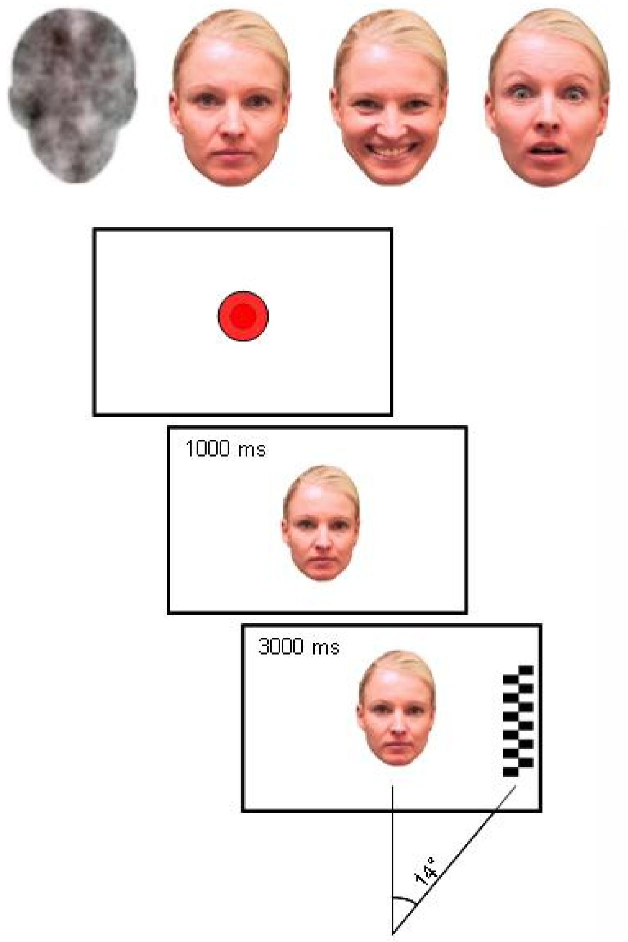

Figure 1. Examples of the facial expression stimuli used in the experiment and an illustration of the sequence of events in the overlap task.

Acquisition and analysis of the HR data. Electrocardiogram (ECG) was recorded throughout the picture viewing session with two pre-gelled and self-adhesive electrodes placed on the participant’s chest. The ECG was band-pass filtered from 0.05 to 30 Hz, amplified with a gain of 1000 (Range, +/-2750 μV; Accuracy .084 μV/LSB), and stored on a computer disk at the sample rate of 1000 Hz (Neuroscan/Synamps). Offline, heart rate data were analyzed by using an in-house (Matlab-based) algorithm to identify QRS complexes in the ECG signal, and to measure the time intervals between two successive R-waves (interbeat intervals or IBI). After computer-based detection of peaks, the data were manually corrected for falsely detected and missing peaks. Also, trials contaminated by artifact, movement, anticipatory saccades (i.e., eye movements commenced within 160 ms after distractor onset), or incorrect saccades (eye movements away from the face that were not directed towards the distractor) were removed from the analyses. The mean number of trials retained in the HR analysis was 4.6 (*SD* = 0.7), with no difference between stimulus conditions (*p* > .10). For the scorable trials, the IBIs in a time interval starting 1000 ms prior to stimulus presentation and extending to 4000 ms post-stimulus were quantified and assigned to 500-ms intervals by weighting each IBI by the proportion of the 500-ms interval occupied by that IBI (see Richards & Turner, 2001). Finally, IBIs were converted to beats per minute and averaged across different trials within each facial expression condition.

Analysis of the behavioral data. An observer who was blind to the stimulus condition coded the video records of infant behavior by using video editing software with frame-by-frame playback (VirtualDubMod 1.5.10.2). Trials with excessive movement, anticipatory eye movements, and “incorrect” responses were excluded from the analysis. The mean number of retained and scorable trials was 4.75 (*SD* = 0.6). There were no differences in the number of scorable trials between stimulus conditions (*p* > .10). Scorable trials were analyzed for the proportion of trials with a distractor-directed saccade (i.e., the child moved his/her eyes toward the distactor during a time window from 160 to 3000 ms after the onset of the peripheral distractor) out of the total number of scorable trials (i.e., a sum of trials with distractor-directed saccade and trials on which the child did not move his/her eyes from the central face within the specified time window). Saccade latencies were also coded but are reported as complementary analyses because latency data are missing for some participants due to lack of distractor-directed saccades in some conditions. To establish the reliability of the data coding procedures, another independent observer who was blind to the stimulus condition coded 6 of the recordings (14%). Although the proportion of double-coded participants was smaller than the conventional 30%, we considered it sufficient to demonstrate that the simple coding procedures employed in the present study were highly reliable. The interobserver agreement (Cohen’s Kappa) for the classification of responses to different response categories (i.e., target-directed saccade present, saccade absent, non-scorable trial) was 1.0. Pearson correlations of the two observers judgements of the latency of the saccades were on average .99 (range .96-1).

Results

Heart rate. The mean heart rate during the 1-s baseline period did not differ between control (*M* = 132.8, *SD* = 11.0), neutral (*M* = 133.6, *SD* = 10.8), happy (*M* = 133.6, *SD* = 10.7), and fearful (*M* = 133.7, *SD* = 11.4) facial expressions, *p* > .05. Figure 2 shows the average change in heart rate from the baseline period to the stimulus viewing period (in 0.5-s intervals). An 8 (Time) × 4 (Facial expression) repeated measures analysis of variance (ANOVA) on the HR change scores revealed a significant main effect of time, *F*(7, 287) = 22.6, *p* < .001. As shown in Figure 2, the heart rate decelerated during the first 1.5-s of stimulus viewing and subsequently returned towards the baseline level. The largest deceleration was observed from 0-500 to 500-1000 ms, and a smaller but still significant deceleration from 500-1000 to 1000-1500 ms, *p*s < .001.

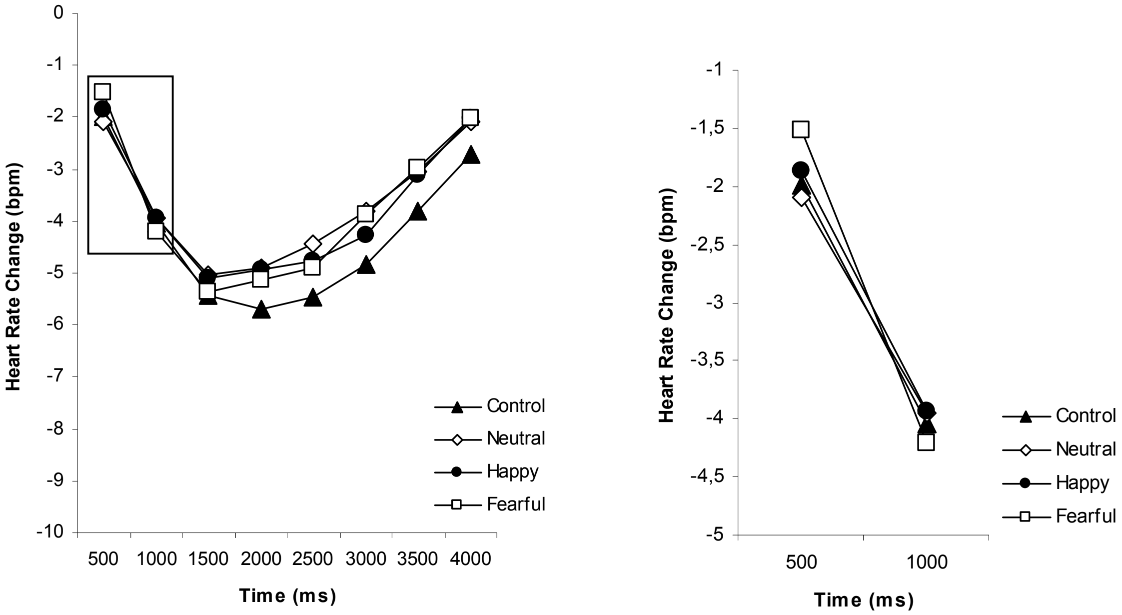

Figure 2. Heart rate change scores, reflecting the difference between the mean heart rate during a 1000-ms prestimulus baseline and heart rate during the 4000-ms stimulus-viewing period (graph on the left). The framed time segment in the graph is enlarged on the right to show the heart rate change scores during the first second of stimulus viewing (i.e., the time period preceding the onset of the distractor stimulus).

The overall ANOVA yielded no significant main effect of Emotion or Emotion × Time interaction, *p*s > .05. Given the a priori hypothesis of differences in the orienting phase of attention, we next conducted an additional analysis to examine differences between emotional expressions in the magnitude of the initial heart rate deceleration response. This analysis was confined to the first 1000 ms of stimulus viewing because the deceleration response was most robust in this time period and the response was not disrupted by the distractor stimulus. It is of note that in many previous studies with infants (e.g., Courage et al., 2006), the orienting phase has been identified for each individual infant separately as the first five successive heart rate peaks with longer interbeat intervals than the median of five pre-stimulus peaks. This procedure could not be followed in the present study due to the relatively short baseline period and the rapid rate of heart rate changes (apparently arising from faster stimulus presentation rate in the present as compared to previous studies). A 4 (Emotion) × 2 (Time: 0-500, 500-1000) ANOVA on the heart-rate difference scores from 0 to 1000 ms post-stimulus revealed no significant main effect of Emotion, but there was a significant Emotion × Time interaction, *F*(3, 123) = 3.0, $p < .05$. Planned contrasts showed no difference between non-face control stimulus and neutral expressions or between neutral and happy expressions in the size of the heart rate deceleration from 0 to 1000 ms, *p*s > .10. However, there was a significant difference in the deceleration response between neutral and fearful expressions, *F*(1, 123) = 7.9, $p < .01$, and between happy and fearful expressions, *F*(1, 123) = 3.7, $p < .05$, reflecting a relatively steeper deceleration of the heart rate for fearful facial expressions (see Figure 2, right).

Behavioral measures. The mean probabilities of distractor-directed saccades in each facial expression condition are shown in Figure 3. Because the saccade probability data were not normally distributed, they were analyzed by using non-parametric Friedman's rank test and Wilcoxon's signed-ranks test (paired comparisons). There was a significant effect of stimulus category on saccade probability, $F_R = 40.8$, *df* = 3, $p < .001$. Pairwise comparisons showed no difference in saccade frequency between the non-face control stimuli (*M* = .95, *SD* = .12) and neutral facial expressions (*M* = .92, *SD* = .16), $p > .05$, or between neutral and happy expressions (*M* = .90, *SD* = .15), $p > .05$. However, compared to neutral and happy expressions, fearful expressions resulted in significantly fewer saccades, (*M* = .75, *SD* = .24, zs > 3.7, *p*s < .001).

The mean latency of all distractor-directed saccades was 517.7 ms (*SD* = 182.6). To analyze the effect of facial expression on saccadic reaction times, the mean latency of saccades that occurred in a time window from 160 to 1000 ms following distractor onset were calculated for each facial expression condition. Saccades longer than 1000 ms (~2.5 *SD* above the group mean) were excluded to eliminate the effect of extremely long saccadic reaction times on the mean scores. The percentage of excluded trials did not differ significantly between control (*M* = 2.6 %, *SD* =11.9), neutral (*M* = 4.8 %, *SD* =11.5), happy (*M* = 4.4 %, *SD* =10.3), and fearful (*M* = 8.0 %, *SD* =19.8) stimulus conditions, $p > .10$. A one-way repeated measures ANOVA yielded a significant effect of emotional expressions on saccade latency, *F*(3, 114) = 12.9, $p < .001$. Paired t-tests showed no significant difference in saccade latency between control (*M* = 386 ms, *SD* = 98 ms) and neutral (*M* = 413 ms, *SD* = 89 ms) expressions or neutral and happy (*M* = 431 ms, *SD* = 88 ms) expressions, but a significant difference between neutral and fearful (*M* = 493, *SD* = 112) as well as happy and fearful expression, *p*s ≤ .001.

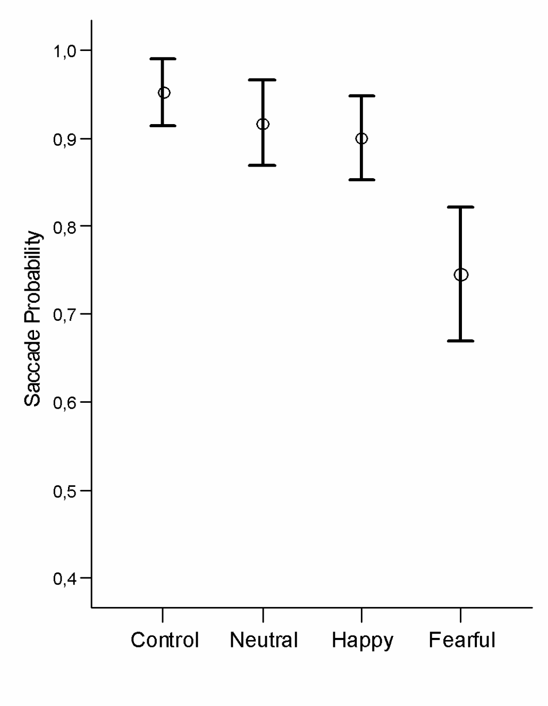

Figure 3. Mean probability of distractor-directed saccades as a function of facial expression. (Error bars represent a 95% confidence interval for the mean).

***Relations between heart rate and behavioral measures*.** The results reported above showed that fearful facial expressions modulate the cardiac deceleration response as well as the probability of saccades to peripheral distractors. We next examined the potential relation of these two phenomena, in particular, whether the magnitude of the fear-effect on heart rate deceleration from 0 to 1000 ms post-stimulus was correlated with and predicted the magnitude of the fear-effect on saccade probability. For the purpose of this analysis, we calculated the size of the cardiac deceleration response to neutral expressions (Neutral_{1000}-Neutral_{0}) and the size of the cardiac deceleration response to fearful expressions (Fearful_{1000}-Fearful_{0}), and used the difference between these two indices (i.e., (Neutral_{1000}-Neutral_{0}) - (Fearful_{1000}-Fearful_{0}) as a measure of the fear-effect on cardiac orienting. Positive values of this difference score indicate a relatively larger cardiac deceleration response to fearful expressions. We also calculated the difference in the saccade probability between neutral and fearful expressions ($\text{Neutral}_{\text{prob}}$-$\text{Fearful}_{\text{prob}}$) and used this difference score as a measure of the fear-effect on saccades to the distractor stimuli. Again, positive values indicate a relatively greater inhibition of saccades in the context of fearful expressions. There was a significant *negative* correlation between the fear-effect on the cardiac orientation and the fear-effect on saccades to the distractors, $r = -.40, p < .01$. A similar negative correlation was observed when happy instead of neutral expressions were used as a baseline condition against which the effects of fearful expressions were calculated, $r = -.30$, $p = .05$. These negative correlations indicated that relatively greater cardiac deceleration in response to fearful expressions did not predict greater suppression of saccades to the distractor stimulus later in the stimulus sequence. Instead, it appears that the cardiac deceleration response to fearful expressions was attenuated in those infants who exhibited relatively greater amount of saccade suppression.

Discussion

The present results provided some evidence for enhanced cardiac deceleration response to fearful expressions in 7-month-old infants. The results also showed that fearful expressions cause infants to inhibit saccades from a centrally presented face to a peripheral distractor. These findings extend previous research by suggesting that emotional expressions may influence different stages of infants' attentional engagement with the stimulus.

Consistent with prior research, a clear cardiac deceleration response was evident for all facial expressions during the first 1000-1500 ms of stimulus viewing. This deceleration was of relatively larger size for fearful expressions. The enhanced cardiac orienting response to signals of negative emotion in infants is consistent with the findings of larger cardiac orienting to facial expressions of anger (Kolassa & Miltner, 2006) and emotional scenes (Bradley et al., 1993) in adults. In studies with adults, the deceleration phase of the heart rate change scores has typically not been analyzed separately for emotion effects but inspection of the figures published in the context of these studies shows that the larger heart rate response to emotionally negative stimuli arises during the first 500 or 1000 ms of stimulus viewing (Bradley et al., 1993; Kolassa & Miltner, 2006). The surface similarity of the initial part of the infants' and adults' deceleration response suggests that a common (possibly amygdala-centered) neural network may mediate this effect (Kapp et al., 1994). Bradley (2009) drew a parallel between the enhanced cardiac orienting response in humans and the slowing of the heart rate in the context of threatening cues in animals (i.e., bradycardia), and noted that the cardiac deceleration may be part of a defense-related orienting reflex that acts to facilitate perceptual processing and extraction of information about potentially significant stimuli.

After the initial deceleration response, infants' heart rate is typically maintained at the decelerated level if the visual stimulation is prolonged (Reynolds & Richards, 2007). In this sustained attention stage, the heart rate deceleration is typically of larger magnitude and longer duration to salient stimuli such as film clips, reflecting infants' greater voluntary attentional engagement with these stimuli (e.g., Courage et al., 2006). Although expected, such sustained HR deceleration to fearful expressions was not observed in the present study. It is likely, however, that the present paradigm was not optimal for revealing such sustained effects due to the short duration of the stimuli, the presentation of the distractors, and the relatively rapid rate of stimulus changes.

Consistent with prior research (Peltola et al., 2008; Peltola et al., 2009b), the present results also showed that fearful expressions inhibit saccades toward peripheral distractors. Interestingly, the magnitude of the fear-effect on heart rate deceleration was *negatively* correlated with the magnitude of the fear-effect on saccade probability. This suggests that different mechanisms may mediate enhanced initial orienting towards fearful expressions and subsequent prioritization of attention to these expressions. A similar dissociation of the orienting mechanisms and more voluntary attentional mechanisms is suggested by previous findings showing that the orienting phase of attention is attenuated (i.e., shortened in duration) and the more voluntary sustained attention phase enhanced (i.e., prolonged in duration) when infants are presented with interesting dynamic stimuli (Courage et al., 2006). Although brain activity was not measured in the present study, it is interesting to speculate on the basis of previous work that the enhanced initial orienting response to fearful expressions may reflect a relatively automatic response that is mediated by subcortical systems involved in heart rate control (Kapp et al., 1994) whereas the effects of fearful facial expressions on saccadic eye movements may involve more voluntary attention regulation processes, possibly mediated by connections between the amygdala and eye movement control circuits in the prefrontal cortex (Johnson, 2005; Munoz & Everling, 2004; Pessoa, 2009).

Besides the underlying mechanisms, it is important to consider the specific stimulus attributes that are important for eliciting the observed changes in heart rate and overt attention. In interpreting the differential attention to fearful facial expressions, a reference is often made to the affective salience of these cues; that is, they may be perceived as signals of the presence of a potential danger in the environment or as ambiguous signals that require further processing to be understood (Whalen, 1998). An alternative possible interpretation is that infants respond to some other attributes of fearful expressions such as their novelty in infants' social environment or distinctively large eyes (a feature that may also affect infants' attention). These alternative possible explanations were not controlled in the present study. Previous studies have, however, shown that novel non-emotional grimaces (i.e., blown-up cheeks and enlargened eyes), that are equal in their estimated frequency of occurrence as fearful facial expressions, and neutral faces with enlargened eyes fail to produce similar effects on attention as fearful expressions do (Peltola et al., 2008, 2009b). These results provide some support for interpreting the attentional bias towards fearful expressions in terms of affective processes and argue against the possibility that the bias is simply attributable to novelty or some distinctive visual features. It is clear, however, that further research is needed to attain more conclusive evidence on this important question.

In sum, the present study leaves open whether more sustained attention phases, as defined by a prolonged heart rate deceleration, are affected by emotional significance. Such effects are perhaps most likely to occur when infants are presented with longer-lasting and possibly dynamic facial expressions. This question notwithstanding, the present study provides an important additional piece of evidence to support the hypothesis that emotion-attention interactions begins to emerge during the second half of the first year. In particular, the present data raise the possibility that emotional significance is integrated with the functioning of different attention-related mechanisms, including mechanisms that regulate initial orientation to the stimulus as well as mechanisms that underlie more voluntary processing and prioritization of behaviorally relevant stimuli. Such emotion-attention interactions appear to be in place at a developmental time point when social signals of emotions become behaviorally relevant and are most likely to occur in the infant's environment. That is, when infants start to locomote and actively explore the environment, they may also start to use others' facial expressions to acquire knowledge about objects that are safe and can be approached and objects that are potentially harmful and should be avoided (Sorce et al., 1985).

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References

Bradley, M. M. (2009). Natural selective attention: Orienting and emotion. *Psychophysiology, 46*, 1-11.

Bradley, M. M., Lang, P. J., & Cuthbert, B. N. (1993). Emotion, novelty, and the startle reflex: Habituation in humans. *Behavioral Neuroscience, 107*, 970-980.

Chen, F. S., & Johnson, S. C. (2008). *Infants' attention to emotional expressions: Evidence for attachment-based individual differences.* Paper presented at the International Conference on Infant Studies, Vancouver, Canada.

Courage, M. L., Reynolds, G. D., & Richards, J. E. (2006). Infants' visual attention to patterned stimuli: Developmental change from 3- to 12-months of age. *Child Development, 77*, 680-695.

de Haan, M., & Nelson, C. A. (1998). Discrimination and categorization of facial expressions of emotion during infancy. In A. M. Slater (Ed.), *Perceptual development: Visual, auditory, and language perception in infancy* (pp. 287-309). London: University College London Press.

Farroni, T., Menon, E., Rigato, S., & Johnson, M. H. (2007). The perception of facial expressios in newborns. *European Journal of Developmental Psychology, 4*, 2-13.

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

Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science, 317*(5843), 1360-1366.

Hoehl, S., Palumbo, L., Heinisch, C., & Striano, T. (2008). Infants' attention is biased by emotional expressions and eye gaze direction. *Neuroreport, 19*(5), 579-582.

Johnson, M. H. (2005). *Developmental cognitive neuroscience* (2nd ed.). Oxford: Blackwell Publishing Ltd.

Kapp, B. S., Supple, W. F., & Whalen, P. J. (1994). Effects of electrical stimulation of the amygdaloid central nucleus on neocortical arousal in the rabbit. *Behavioral Neuroscience, 108*, 81-93.

Kolassa, I.-T., & Miltner, W. H. R. (2006). Psychophysiological correlates of face processing in social phobia. *Brain Research, 1118*(1), 130-141.

Kotsoni, E., de Haan, M., & Johnson, M. H. (2001). Categorical perception of facial expressions by 7-month-old infants. *Perception, 30*, 1115-1125.

Leppänen, J. M., Moulson, M. C., Vogel-Farley, V. K., & Nelson, C. A. (2007). An erp study of emotional face processing in the adult and infant brain. *Child Development, 78*(1), 232-245.

Leppänen, J. M., & Nelson, C. A. (2006). The development and neural bases of facial emotion recognition. In R. V. Keil (Ed.), *Advances in child development and behavior* (Vol. 34, pp. 207-245). San Diego: Academic Press.

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

Lewis, M., Kagan, J., Campbell, H., & Kalafat, J. (1966). The cardiac response as a correlate of attention in infants. *Child Development, 37*, 63-71.

Munoz, D. P., & Everling, S. (2004). Look away: The anti-saccade task and the voluntary control of eye movement. *Nature Reviews Neuroscience, 5*(3), 218-228.

Nelson, C. A., & de Haan, M. (1996). Neural correlates of infants' visual responsiveness to facial expressions of emotions. *Developmental Psychobiology, 29*, 577-595.

Nelson, C. A., & Dolgin, K. (1985). The generalized discrimination of facial expressions by 7-month-old infants. *Child Development, 56*, 58-61.

Olsson, A., & Phelps, E. A. (2007). Social learning of fear. *Nature Neuroscience, 10*(9), 1095-1102.

Peltola, M. J., Leppänen, J. M., Mäki, S., & Hietanen, J. K. (2009a). The emergence of enhanced attention to fearful faces between 5 and 7 months of age. *Social Cognitive and Affective Neuroscience*(4), 134-142.

Peltola, M. J., Leppänen, J. M., Palokangas, T., & Hietanen, J. K. (2008). Fearful faces modulate looking duration and attention disengagement in 7-month-old infants. *Developmental Science, 11*, 60-68.

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

Pessoa, L. (2009). How do emotion and motivation direct executive control? *Trends in Cognitive Sciences, 13*(4), 160.

Reynolds, G. D., & Richards, J. E. (2007). Infant heart rate: A developmental psychophysiological perspective. In L. A. Schmidt & S. J. Segalowitz (Eds.), *Developmental psychophysiology* (pp. 106-117). Cambridge: Cambridge Press.

Richards, J. E., & Turner, E. D. (2001). Extended visual fixation and distractability in children from six to twenty-four months of age. *Child Development, 72*, 963-972.

Sorce, F. F., Emde, R. N., Campos, J. J., & Klinnert, M. D. (1985). Maternal emotional signaling: Its effect on the visual cliff behavior of 1-year-olds. *Developmental Psychology, 21*, 195-200.

Whalen, P. J. (1998). Fear, vigilance, and ambiguity: Initial neuroimaging studies of the human amygdala. *Current Directions in Psychological Science, 7*, 177 – 188.