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Abbreviations

Ag/AgCl = silver-silver chloride

cm = centimeter

EEG = electroencephalography

e.g. = example given

EOG = electrooculography

ERP = event-related brain potential

fMRI = functional magnetic resonance imaging

fNIRS = functional near-infrared spectroscopy

Hz = Hertz

IBQ-R = Infant Behavior Questionnaire – Revised

i.e. = in example

IRI = Interpersonal Reactivity Index

LPP = late positive potential

ms = milliseconds

mPFC = medial prefrontal cortex

Nc = negative component

μV = micro Volt

OFC = orbito-frontal cortex

Pc = positive component

PLD = point-light displays

ROI = regions of interest

s = second

Part 1

Introduction

“For me, context is the key - from that comes the understanding of everything.”-

Kenneth Noland

1 General Introduction

1.1 Perception of emotions

Humans are fundamentally social beings. In our daily lives, we interact with each other by decoding social and emotional cues from one another. In doing so, we not only rely on verbal communication but also on non-verbal modes of communication. Moreover, we communicate in these various forms in order to interpret others’ intentions and feelings. This in turn allows us to reciprocate to others’ needs and helps us to build long-term social relationships (Frith, 2009; Izard et al., 2001).

One critical aspect of social interactions is detecting and interpreting emotions. Facial and body expressions are important signals that help us interpret emotional cues from others (Belin, Campanella, & Ethofer, 2012). Much research investigating emotion perception has focused on facial expressions as they are considered as one of the most immediate means of conveying emotional information (Belin et al., 2012).Emotions expressed by the face are vital cues that guide our behavior during social interactions(Frith, 2009b). Recently, there has been a growing interest in understanding the role of emotions expressed by bodies. Body expressions are effective when one is communicating emotional information over large distances since it is difficult to decipher emotional information from facial expressions over large distances (de Gelder, 2009). There is evidence from the literature which suggests that adults can readily detect and discriminate between emotions expressed by human bodies (Coulson, 2004; Shaarani & Romano, 2007).

The ability to interact with one another by responding to emotional cues begins early in infancy well before the onset of spoken language. From birth, infants establish a bond with their primary caregiver by communicating via emotional cues. During the first year of life, infants are not only capable of expressing emotions by themselves but they also develop the ability to identify and differentiate between emotions that are expressed by others (de Haan & Matheson, 2009).Both behavioral as well as neuroscientific accounts suggest that the ability to detect and discriminate between negative and positive facial expressions develops around the age of 7 months, during the first year of life(Grossmann, Striano, & Friederici, 2007; Schwartz, Izard, & Ansul, 1985).More recently, researchers have shown that the ability to detect and discriminate between body emotions emerges around 8 months of age (Missana, Atkinson, & Grossmann, 2015; Missana, Rajhans, Atkinson, & Grossmann, 2014; Zieber, Kangas, Hock, & Bhatt, 2014). This is concurrent with previous developmental accounts that have demonstrated the ability to sensitively respond to emotional facial and vocal cues emerges at a similar age (Grossmann, 2013; Peltola, Leppänen, Mäki, & Hietanen, 2009b).

Emotional valence of the stimuli largely influences the way one perceives emotions. Studies have found that adults as well as infants consider negative expressions of emotions to be more salient than positive emotions (Ducette & Soucar, 1974; Vaish, Grossmann, & Woodward, 2008). Interestingly, this bias towards negative emotions (fear) begins in infancy between 5 to 7 months of age (Grossmann, Oberecker, Koch, & Friederici, 2010; Grossmann, Striano, & Friederici, 2005; Missana et al., 2015; Missana et al., 2014; Peltola et al., 2009b). The early emergence of this fear bias has important evolutionary implications since it prepares individuals at an early age to avoid potential threats from the environment (Vaish et al., 2008).

Apart from helping individuals to avoid threatening situations, studies have shown that fearful expressions (displaying distress) can also elucidate altruistic behavior. For example, kidney donors show heightened and psychopaths show decreased perceptual sensitivity to fear in others (Marsh & Blair, 2008; Marsh et al., 2014). Furthermore, these effects have been specifically found for fearful expressions and not angry expressions thus indicating a specific link between fear processing and altruistic behavior. Surprisingly, this link between emotional responsiveness to fear and altruism has only been examined in adults (Marsh, Kozak, & Ambady, 2007). To our knowledge, there have been no studies that have looked at the developmental emergence of this association between fear processing and altruism and potential similarities and differences across cultures.

1.2 Why context matters in emotion perception?

Emotion perception is a complex process and it does not involve simply reading the expression from the stimulus. Contradictory to the approach adopted by Ekman & Friesen. (1971), there is more to emotion research than just identifying six basic expressions of emotions and categorizing them as universal. Typically, research involving emotion perception has mostly focused on displaying isolated images of faces or body expressions (Adolphs, 2002; Atkinson, 2013; Atkinson, Dittrich, Gemmell, & Young, 2004). However, emotional expressions are rarely viewed as isolated entities and the social context in which emotions are expressed needs to be taken into account. Some of the contextual elements that aid in the comprehension of emotions include: the individual perceiving the emotional expression, the stimulus displaying the emotional expression, and the social situation in which the emotion is both expressed as well as perceived (Hess & Hareli, 2015).

In the recent years, evidence has accumulated to suggest that context plays an important role in the way adults perceive emotions. For example, (Righart & de Gelder, 2006) investigated the influence of social scene (context) on emotion perception by using event-related potentials (ERPs). Their results suggest that when an emotional face is presented to participants with a context conveying similar emotional information, their N170 was enhanced, thus indicating the significance of context (scene) during emotion perception. Furthermore, differences in culture also have an effect on how an individual attends to contextual factors when processing emotional information. More specifically, (Masuda et al., 2008) demonstrated that adults in East Asian cultures rely more on the surrounding context when processing emotions than adults in Western cultures. Apart from culture, emotions expressed by bodies also serve as powerful contexts when interpreting emotions from faces as well as voices (Aviezer, Trope, & Todorov, 2012; De Gelder, 2006; Meeren, van Heijnsbergen, & De Gelder, 2005; Righart & De Gelder, 2006). Thus, the context in which the emotion is embedded is critical for adults' processing of emotions.

Based on a review of mounting evidence concerning contextual effects on emotion processing in adults, Barrett, Mesquita, & Gendron., (2011) have outlined a model that stipulates three types of contexts. According to this there are three essential types of context-based effects in adults: (1) Perceiver-based context effects, (2) Stimulus-based context effects, and (3) Culture- based context effects. The following sections (1.2.1, 1.2.2, 1.2.3) aim to describe these context-based effects in more detail.

1.2.1 Perceiver-based context effects: The role of perceiver in emotion perception

The perceiver plays a central and ubiquitous role in the perception of emotions. The extent to which a perceiver attends to emotional stimuli might depend on a number of factors such as the perceivers' motives, past experiences, and their affective states (Showers & Cantor, 1985). Furthermore, the emotional state of individuals influences recognition of emotions (Niedenthal, Brauer, Halberstadt, & Innes-Ker, 2001). In this study, participants' emotional states were manipulated by inducing an emotional state with a combination of film and music. Participants were then presented with movie clips in which facial emotions dynamically changed into a different emotion. Niedenthal et al., (2001) found that the emotional state of the participants enabled them to detect changes in emotional expressions during the movie clip. Apart from the individuals' personal motives, past experiences, and their affective states, differences in their personality, temperament, and genotype also influence the way they perceive emotions (Hamann & Canli, 2004). In particular, Hall. (2006) showed a correlation between self-reported aggression and perception of angry expressions in others, suggesting that a greater tendency to experience aggression is related to a greater sensitivity to anger in others. Besides behavioral evidence, neuroimaging studies have also suggested associations between individual differences in personality and emotion perception (Amin, Constable, & Canli, 2004; Canli et al., 2001). For example, Canli et al., (2001) used fMRI to examine whether personality traits are localized to specific brain regions. Thus, it is essential to consider these variations and their contribution towards our understanding of individuals' emotional responses and emotional experiences.

Surprisingly, very little is known about the developmental emergence of individual differences and their association with emotion perception. Only recently, researchers have found links between genetic variation in neurotransmitter systems and differences in infants' brain responses to facial expressions of emotion (Grossmann et al., 2011). Furthermore, variation in infants' temperament has also been associated with emotion regulation and expression (De Haan, Belsky, Reid, Volein, & Johnson, 2004; Grossmann, 2013; Grossmann et al., 2011; Martinos, Matheson, & de Haan, 2012). In particular, Martinos et al., (2012) found that the infants' tendency to express and regulate their negative emotions was associated with differences in their allocation of attention to negative (fearful) facial expressions. However, it remains unclear whether these associations between infant temperament and individual differences in neural emotion processing are specific to facial expressions or can also be observed in response to emotional information from other relevant sources such as body expressions. Clearly, more research in this area is required to address the developmental origins of individual differences that influence and provide a context for the perception of emotions.

1.2.2 Stimulus-based context effects: The role of various stimuli in emotion perception

Human beings perceive emotions from their environment via multiple sources such as faces, voices, and bodies. Over the past decades, studies investigating emotion perception have been based on presenting facial expressions of emotions in isolation (Adolphs, 2002). However, emotion perception is a multi-sensory process and emotional information is rarely conveyed through one sensory channel but is rather communicated simultaneously via multiple channels, such as faces, voices, and bodies. Several studies have addressed the question of how emotional information conveyed via different modalities is integrated. For example, de Gelder & Vroomen. (2000) showed that adults are capable of integrating emotional information from vocal and facial cues. This has been corroborated by evidence from electrophysiological and functional neuroimaging studies (Pourtois, de Gelder, Bol, & Crommelinck, 2005; Pourtois, de Gelder, Vroomen, Rossion, & Crommelinck, 2000). Moreover, the ability to integrate emotional information from facial and vocal cues begins early in development (Grossmann, Striano, & Friederici, 2006). For example, Grossmann and colleagues (2006) used ERP measures to demonstrate that infants at the age of 7 months detected incongruence between facial and vocal expressions by showing an enhanced negative component towards incongruent facial and vocal expressions.

Apart from faces and voices, body expressions also play a significant role in conveying emotional information. In fact, body expressions are considered to be the most evolutionarily conserved and immediate means of communicating emotional information(De Gelder, 2006). Moreover, there is evidence from the adult literature, which shows that adults can readily detect and discriminate between emotions displayed by body expressions (Atkinson, 2013; de Gelder, 2009). Recent work has provided developmental insights into the perception of emotional body expressions. Based on this work, it has become clear that the ability to perceive and respond to emotional body expressions begins in the first year of life. In particular, Zieber et al., (2014) performed a series of behavioral experiments and showed that 6.5-month-old infants sensitively respond to emotional body expressions and are able to match emotional information from body expressions to corresponding vocal cues. Furthermore, Missana et al. (2015) examined the neural underpinnings of emotional body processing with the help of ERPs in 4 and 8- month-old infants. The results from this study indicated that 8-month-old infants, but not 4-month-old infants, discriminated between fearful and happy body movements. Missana et al. (2014) further showed that infants discriminate emotions from static body postures, suggesting that infants at this age flexibly detect emotion from body posture and motion.

Given that facial and body expressions play a crucial role in conveying emotional information, an important question that arises is, whether and how face and body impact each other. In adults, it has been shown that when body and face convey conflicting emotional information emotion recognition is biased into the direction of the body expressions (Aviezer et al., 2012; De Gelder, 2006; Meeren et al., 2005). These findings indicate that emotional faces are interpreted in the context of body expressions. Similarly, researchers have shown that, in adults, body expressions bias the recognition of emotions from vocal cues (Righart & De Gelder, 2007). In summary, body expressions provide a powerful context when processing facial and vocal emotional cues.

1.2.3 Culture-based context effects: The role of culture in emotion perception

Whether emotion perception is universal or culture specific has been a debate among psychologists for decades. The dominating view in this area of research is that emotions are universally expressed and recognized across human cultures (Ekman & Friesen, 1971; Frijda & Mesquita, 1994; Izard, 1980). Contrary to this argument, more recent evidence suggests that while some aspects of emotion perception are shared across cultures, there are also important differences in the way in which emotions are recognized (Jack, Blais, Scheepers, Schyns, & Caldara, 2009; Marsh, Elfenbein, & Ambady, 2003; Moriguchi et al., 2005).

More specifically, (Marsh et al., 2003) reported behavioral findings that indicated the presence of subtle differences in identification of facial expressions of emotions across cultures. Furthermore, Moriguchi et al. (2005) used neuroimaging techniques and showed that different brain regions are activated in East Asian (Japanese) and Western

(US) adults when viewing the same facial expressions of emotions. Moreover, adults in the US showed brain activation in the posterior cingulate (PCC), supplementary motor cortex and amygdala whereas the Japanese showed brain activation in the right inferior frontal, premotor cortex and left insula while viewing fearful faces. Activation in the PCC is generally associated with perception of threat related stimuli (Maddock & Buonocore, 1997) and activation in the IFG is associated with processing of facial emotions where perceivers match the perceived facial emotions to templates of facial emotions in the brain (Nakamura et al., 1999). According to Morguichi et al. (2005), Caucasians perceive fearful faces in a more direct manner by attaching emotional valence to the stimuli whereas the activation of the insular regions in Japanese people suggests that they recruit the mirror neuron system and thus utilize a template matching method while viewing fearful faces. In doing so, the Japanese do not attach emotional valence to emotional stimuli. Furthermore, Morguichi and colleagues also argued that these differences between Caucasian and Japanese subjects were controlled for and were not associated with differences in their visual processing patterns. In conclusion, Morguichi and colleagues have suggested that culture plays a role in the perception of emotions.

Critically, people from Eastern and Western societies have been shown to differ more generally in the way in which they perceive the world. Specifically, on the basis of comparisons between Asians and North Americans, Nisbett. (2010) argued that adults from Western cultures tend to employ more context-independent and analytical perceptual processes (focus on foreground object in a visual scene) when viewing a visual scene, whereas adults from the Eastern societies utilize more context-sensitive and holistic perceptual processes (focus on both foreground and background objects in as visual scene) (Nisbett & Miyamoto, 2005). Additionally, Nisbett & Miyamoto. (2005)

presented developmental evidence, which suggests that such cultural differences in visual processing tendencies begin at around 5 years of age. Surprisingly, developmental research on cultural differences in children has not considered how such differences in perceptual processing contribute to emotion processing. Thus, it is important to examine whether children from different cultures differ in the way they attend to context when processing visual emotional information.

In summary, basic emotions, to some degree might be expressed and perceived similarly across cultures, but cross-cultural differences may exist in how emotions are processed, especially when considering the context in which emotional information is presented.

1.3 Research Questions

Based on the literature reviewed in the introduction it is clear that the way humans respond to and perceive emotions cannot be fully accounted for unless context is taken into consideration. Perceivers, stimuli, and culture are crucial contextual parameters that contribute to the way in which one perceives and responds to emotions. However, the developmental origins of these context-based effects remain largely unspecified. Thus, the major aim of this dissertation is to test these three types of context effects within a developmental framework. To systematically tackle this issue, in this current thesis, I will present three empirical studies examining perceiver-based context effects in infancy (Study 1), stimulus-based context effects in infancy (Study 2), and culture-based context effects in early childhood (Study 3). The following section will briefly outline the research questions addressed in each of the three empirical studies.

Study 1: Perceiver-based context effect in infancy. During the first year of life, infants develop the ability to detect and discriminate between emotional expressions in others (Leppänen & Nelson, 2009). Despite the well-mapped developmental emergence of emotion perception in infancy, very little is known about how infants differ in their neural sensitivity to emotional signals and what factors contribute to such differences. So far, only one study has examined whether infant temperament might influence the neural processing of happy and fearful facial expressions (Martinos et al., 2012). However, it is not known whether associations between infant temperament and individual differences in emotion processing are specific to facial expressions or can also be observed in response to emotional information from other relevant sources such as emotional body expressions. Thus, in the first study, we examined the role of infant temperament (approach, fearfulness) in the neural processing of happy and fearful emotional body expressions in 8-month old infants by measuring event related brain potentials (ERPs).

Study 2: Stimulus-based context effects in infancy. As mentioned earlier, body expressions are considered to be the most evolutionarily conserved and immediate means of communicating emotional information and are known to exert strong contextual effects on perception of facial emotions in adults (Aviezer et al., 2012; De Gelder, 2006; Meeren et al., 2005). To our knowledge, the developmental origins of the neural processes involved in emotion perception across body and face remain unclear. Thus, in the second study, we examined whether body expressions impact and possibly hamper the processing of emotional facial expressions in 8-month old infants with the help of ERPs.

Study 3: Culture-based context effects in early childhood. As discussed in the introduction, the role of culture in perceptual processes has been studied with children between the ages of 4-5 years (Nisbett & Miyamoto, 2005). However, it remains unclear whether these cultural differences between Easterners and Westerners in context sensitivity extend to emotional stimuli. Therefore, in the third study, we examined the relation between emotional responsiveness (using eye-tracking) and altruistic behavior (using the Dictator Game) in 4 to 5-year-old children across cultures (India and Germany).

Part 2

Methods

2 Methods

2.1 Electroencephalograhy (EEG) and Event Related potentials (ERPs)

Brain processes are characterized by electrical activity. Electrical activity originates in the brain when a signal propagates from one neuron to the other by changes in membrane potential. The changes in membrane potential at the post-synaptic neuron can last up to a hundred milliseconds thus allowing a summation of signals from a large group of neurons. The signal is recorded via specialized electrodes and is measured with EEG. This electrical brain activity is often associated with different brain states correlated with cognition, emotions, and perceptions. EEG is the most frequently used methodology to study the aforementioned brain states (Luck, 2005).

The EEG signal is recorded via electrodes that are placed on the scalp at predefined positions according to anatomical landmarks. The most commonly used setup is the 10-20 system (Sharbrough et al., 1991). In this setup, the EEG is recorded by measuring the difference in voltages that occur between the recording and the reference electrode. A conductive gel is applied at electrode sides in order to decrease impedances (Luck, 2005). After recording the EEG signal, the data is filtered and artifacts that are unrelated to the brain processes (such as eye blinks, head movement) are rejected. EEG waves are averaged over a large number of trials by repeatedly presenting the stimulus because the changes in potential with respect to one trial are too small in order to be detected and thus measured (Luck, 2005).

Event-related potentials (ERPs) can be defined as the change in potential that is elicited with respect to an external or internal event (Otten & Rugg, 2005). The ERPs consist of positive or negative deflections that arise from averaging multiple trials over a period of time. ERP components are classified on the basis of their latency (the peak of the ERP component with respect to stimulus onset), polarity (direction of the peak) and topography (distribution of the components on the scalp). When the deflection is negative, the ERP component is labeled N and is given a negative polarity and when the deflection is positive, the ERP component is labeled P and is given a positive polarity. In infancy research, the negative component (Nc) is one of the most commonly studied ERP component. Nc is considered to measure the infants' allocation of attention to a particular stimulus. A higher negative deflection represents a greater allocation of attention to that stimulus (Courchesne, Ganz, & Norcia, 1981).

In terms of advantages, the ERP method offers a high temporal resolution in the range of milliseconds, thus providing accurate information concerning the timing of cortical responses. Due to various methodological constraints, other methods such as functional magnetic resonance imaging (fMRI) are of limited use for infants. However, the ERP method is a viable, child friendly, and a non-invasive option that can be used in order to examine brain processes in infancy (Hoehl & Wahl, 2012). While there are advantages when using ERP methods, researchers should also need to consider certain limitations such as the low spatial resolution associated with using this methodology. ERPs, mainly record the brain activity from the scalp thus offering poor conclusions about the sources in the brain from where the electrical activity has originated (Luck, 2005). When working with a population of infants who are pre-verbal and have short attention spans, the ERP experiments are required to work without instructions and have to be short in duration. Despite the aforementioned limitations, the ERP method is a highly valuable tool when measuring brain activity in infants when compared to other neuro-imaging technologies that suffer from many other constraints.

2.2 Eye-tracking

Eye-tracking is a non-invasive methodology used to assess looking behavior in humans as well as non-human primates (Karatekin, 2007). In the recent years, eye-tracking has presented a promising avenue to study looking behavior in non-verbal infants and young children, thus providing insights into the development of typical and atypical social and cognitive functioning (Gredebäck, Johnson, & von Hofsten, 2009; Karatekin, 2007).

Eye-trackers are either mounted on the participant's head or in-front of the participant, mounted below or built into the screen on which the stimulus is presented. The modern day eye-tracker works on the principle of reflection of infra-red light where the infra-red light (750 to 1400 nm) is reflected onto the eyes (cornea) and is captured by a camera thereby allowing tracking eye-movement. A calibration procedure is used in order to standardize the differences associated with the shape of the eyes and the angular relationship between the eye-tracker and the eye (Gredebäck et al., 2009). This is done by directing the participant's attention to several locations on the screen while the eye-tracker records the co-ordinates of the pupil. Developmental studies mostly rely on a 5-point calibration system due to low attention span of infants and young children.

When working with developmental populations, the eye-tracking method is considered to have several advantages. Firstly, the process is non-invasive and mainly relies on the child's looking patterns and does not require a manual or verbal response. Secondly, changes in looking behavior can be examined over time with respect to a particular stimulus set (Gredebäck et al., 2009). Additionally, eye-tracking is less-expensive when compared to neuroimaging methods. On the other hand, eye-tracking methodology also has some disadvantages. Firstly, eye-tracking cannot provide information regarding the underlying neural processes that are recruited while processing specific visual information. Secondly, differences in eye-colors and presence of glasses interfere during data collection and pose difficulties while assessing eye-tracking data. Thus, it is important to consider these pros and cons when designing an experiment that utilizes eye-tracking technology.

2.3 Priming

When past events or experiences implicitly influence a current event, the phenomenon is often referred to as priming (Graf & Schacter, 1985; Squire, 1992). Thus, priming is a technique that taps into an individuals' implicit memory (Schacter & Buckner, 1998). Research conducted using priming as a technique has relied on both verbal (words) as well as non-verbal stimuli (objects, faces, pictures) (Tulving & Schacter, 1990). The neural correlates of priming have been studied with the help the ERPs. For example, (Schweinberger, Pfütze, & Sommer, 1995) have identified the N250r at the frontal and temporal sites and the late positive potential (LPP) when investigating priming effects in the recognition of familiar faces in adults. Furthermore, (Werheid, Alpay, Jentzsch, & Sommer, 2005) examined the priming effects of emotional facial expressions with ERPs.

From a developmental perspective, priming is used in several studies with children. Moreover, priming effects have been studied from as early as infancy in development (Peykarjou, Pauen, & Hoehl, 2014a, 2014b). The presence of priming methods in the field of cognitive development overrides that in the field of social development (Stupica & Cassidy, 2014). Since Priming is a methodology that has been extensively used for examining mental representations drive thoughts, feelings and behaviors in adults, (Stupica & Cassidy, 2014)have proposed the idea of utilizing priming in social development research.

Part 3

Empirical Studies

Study 1

3 Study 1

The association of temperament and maternal empathy with individual differences in infants' neural responses to emotional body expressions

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We examined the role of infant temperament and maternal dispositional empathy in the neural processing of happy and fearful emotional body expressions in 8-month-old infants by measuring event-related brain potentials (ERPs). Our results revealed that infants' tendency to approach novel objects and people was positively correlated with the neural sensitivity (attention allocation) to fearful expressions, while infant fearfulness was negatively correlated to the neural sensitivity to fearful expressions. Maternal empathic concern was associated with infants' neural discrimination between happy and fearful expression, with infants of more empathetically concerned mothers showing greater neural sensitivity (attention allocation) to fearful compared to happy expressions. Critically, our results also revealed that individual differences in the sensitivity to emotional information are explained by an interaction between infant temperament and maternal empathic concern. Specifically, maternal empathy appears to impact infants' neural responses to emotional body expressions, depending on infant fearfulness. These findings support the notion that the way in which infants respond to emotional signals in the environment is fundamentally linked to their temperament and maternal empathic traits. This adds an early developmental neuroscience dimension to existing accounts of social-emotional functioning, suggesting a complex and integrative picture of why and how infants' emotional sensitivity varies.

Keywords: infancy, individual differences, emotion perception, temperament, empathy

3.1 Introduction

During interactions with the social environment, detecting and responding to emotional signals serves as an important ability that allows us to predict future behavior of others and coordinate our own behavior during such interactions (Frijda & Mesquita, 1994; Frith, 2009b). In the first year of life, infants develop the ability to detect and discriminate between emotional signals conveyed to them by others (Leppänen & Nelson, 2009; Vaish et al., 2008). This ability can also be traced at the neural level as the infant brain becomes tuned to distinguish between negative and positive emotional information from face, voice, and body cues during this period of development (Missana et al., 2015; Peltola, Leppänen, Mäki, & Hietanen, 2009). Despite the well-mapped developmental emergence of emotion perception in infancy, very little is known about how infants differ in their neural sensitivity to emotional signals and what factors contribute to such individual differences. In adults it has been shown that personality factors and psychiatric disorders are characterized by specific and marked differences regarding the behavioral and neural sensitivity to emotional expressions displayed by others (Canli, 2004; Leppänen, 2006). Thus, a better understanding of what contributes to individual differences in infants' emotional sensitivity can shed important light on how certain biases in emotional information processing, that might have long-term beneficial (protective) effects or detrimental effects for the individual, come about and develop (Fox, 1991; Sharot, 2011; Vaish et al., 2008).

The concept of temperament is considered to capture the nature of how individual infants' behavior differs in terms of their emotional reactions and the ability to regulate these reactions across situations and contexts (Martinos et al., 2012). It therefore seems very likely that individual differences in infant temperament may be systematically linked to differences in infants' brain responses to emotional expressions displayed by others. However, hitherto there have only been very few studies that have tried to examine whether and how infant temperament is linked to differences in the neural processing of emotions displayed by others. Prior ERP work with infants has focused on understanding the link between infant temperament and the neural processing of emotions by examining effects on the Negative component (Nc) (Martinos et al., 2012). The infant Nc is thought to be an index of attention allocation to a visual stimulus with a greater Nc reflecting a greater allocation of attention (Ackles & Cook, 1998; Richards, 2003; Vaughan & Kurtzberg, 1992). This work has revealed that infant temperament and in particular the infants' tendency to express and regulate their negative emotions is associated with differences in their allocation of attention to negative (fearful) facial expressions (De Haan et al., 2004; Grossmann et al., 2011; Martinos et al., 2012).

However, it is not known whether associations between infant temperament and individual differences in neural emotion processing are specific to facial expressions or can also be observed in response to emotional information from other relevant sources. In particular, body expressions have been argued to be the most evolutionarily preserved and immediate means of conveying emotional information (De Gelder, 2006) and there is evidence to suggest that body cues strongly impact adults' perception of emotions (Aviezer et al., 2012; Meeren et al., 2005). For example, it has been reported that when body and face convey conflicting information the emotion perception from the face is impeded (Meeren et al., 2005) or even biased into the direction of the body expression (Aviezer et al., 2012). This suggests that body expressions provide powerful emotions (Aviezer et al., 2012; Meeren et al., 2005). For example, it has been reported that when body and face convey conflicting information the emotion perception from the face is impeded (Meeren et al., 2005) or even biased into the direction of the body expression (Aviezer et al., 2012). This suggests that body expressions provide powerful emotional cues that greatly impact emotion perception in adults. Despite the importance of body expressions for the perception of emotions, research on infants' responses to emotional body expressions has only recently begun. This work shows that during the first year of life infants develop the ability to discriminate between emotional body expressions (Missana et al., 2015; Zieber, Kangas, Hock, & Bhatt, 2013). Specifically, 8-month-old infants, but not 4-month-old infants, discriminate between happy and fearful body expressions (Missana et al., 2015). Furthermore, at the age of 8 months, infants discriminate between fearful and happy body expressions regardless of whether they view moving bodies or body postures (Missana, Rajhans, Atkinson, & Grossmann, 2014). Thus, the current study's goal was to extend prior work by examining the link between infant temperament and the neural processing of emotional body expressions.

Our proposal is that temperament, that is, the biologically predisposed tendencies of responding to the environment, fundamentally impacts the way in which the infant views and interacts with the environment and in particular other people's emotional expressions. Therefore, the current study was designed to examine whether individual differences in temperament as measured by parental report are linked to differences in the neural processing of emotions as measured by ERPs by focusing on two fundamental traits in infant temperament, namely, (1) infants' tendency to approach novelty and (2) infants' fearfulness. We chose to examine these two temperament traits because prior work has found that both approach of novelty and fearfulness critically contribute to infants' and children's emotional responses and experiences (Davidson, 1984; Fox & Davidson, 1984; Kinsbourne, 1978). Moreover, these temperament traits are of great significance for existing accounts of individual differences in socio-emotional functioning and personality also with respect to psychopathological models of anxiety, as approach to novelty is thought to be conceptually linked to the Behavioral Activation System (BAS) and as fearfulness is thought to be conceptually linked to the Behavioral Inhibition System (BIS) (Fox, 1991; Gray, 1982). More specifically, increased fearfulness and decreased approach to novelty in infancy and childhood have been identified as risk factors for developing anxiety disorders later in life (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, 2007; Kagan, 1997; Pérez-Edgar et al., 2011; Rosenbaum et al., 1993). Given the importance of these temperament traits for social development, it is vital to elucidate whether and how temperament is associated with the neural processing of emotional information in infancy. Moreover, to investigate individual differences in the neural processes that underpin emotion perception in infancy will help to gain insights into the mechanisms that may confer risk and result in resilience in early emotional development. In the following paragraphs we will outline the specific hypotheses that were tested in the current study.

First, we hypothesized that individual differences in both approach to novelty and fearfulness are associated with differences in responding to fearful expressions but not happy expressions because these temperament traits are most likely to impact the processing of novel or negative information (Hypothesis 1: *Emotional Selectivity*). This hypothesis is based on prior behavioral work discussed above (Davidson, 1984; Fox & Davidson, 1984; Kinsbourne, 1978), pointing into the direction of such a link. Second, we hypothesized that individual differences in approach to novelty and fearfulness represent independent temperamental dimensions (Fox, 1991), possibly resulting in opposing effects on processing fearful expressions (Hypothesis 2: *Differential Impact of Approach versus Fearfulness*). More specifically, fearful expressions are relatively novel to the infants when compared to happy expressions (Vaish et al., 2008) and might therefore be processed differently according to the approach tendency towards novelty displayed by the infant. Furthermore, individual differences in infants' own fearfulness are indicative of the frequency and intensity to which the infant experiences fear and possibly related to how much the infant avoids fear inducing and novel situations. Therefore, such differences in the experience of fear are likely to impact infants' neural responses to watching others in fear. While our study design allows for the investigation of the direction of the association between infant temperament and neural sensitivity (attention allocation), we had no specific predictions as to whether fearfulness or approach would systematically increase or decrease the neural sensitivity (attention allocation) to fear. This is because it is plausible that either approach, through its association with novelty processing, or fearfulness, through its association with heightened alertness to threat signals (Bar-Haim et al., 2007; Nakagawa & Sukigara, 2012; Pérez-Edgar et al., 2011), may sensitize the infant brain to fearful expressions.

In addition to studying how intrinsic factors such as infant temperament shape responding to others emotions, it is also important to elucidate how certain extrinsic (environmental) factors are linked to emotion perception and its neural underpinnings in infancy. Prior research has recognized the general importance of maternal behavior and care in the early development and programming of the mammalian offspring's brain (Kappeler & Meaney, 2010; Weaver et al., 2004). Among the maternal characteristics that have been investigated in humans, maternal empathy is a vital part of positive parenting and has been found to play a key role in early socio-emotional development (Feshbach, 1987). Specifically, maternal empathy and related attributes such as sympathy, understanding, and caring have positive effects on the development of the child, while a lack of or strongly reduced maternal empathy is related to psychopathological developments in the child (Cicchetti, 1987). We therefore decided to examine the association between maternal dispositional empathy and in particular maternal empathic concern, defined as the tendency to experience feelings of sympathy and compassion for unfortunate others (Davis, 1983), and the neural processing of emotional expressions in infants. We hypothesized that maternal empathic concern is positively associated with a greater neural sensitivity (attention allocation) to negative (fearful) as compared to positive (happy) expressions, because, either through social learning or through genetic association, mothers with greater empathic concern for others in distress (including fear) may have infants who are also more prone to sensitively respond to others in distress (fear) (Hypothesis 3: *Mother-Infant Shared Sensitivity*). This hypothesis is based on the idea that infants' and mothers' emotional responding is tightly linked and co-regulated (Fonagy, Gergely, & Target, 2007).

Moreover, we also assessed whether there were any interactions between maternal empathy and infant temperament on the neural responsiveness to emotional expressions. This is of importance because effects of maternal empathy on infants' neural processing of emotions might depend on (or be moderated by) the temperament of the infant. It is conceivable that infant temperament interacts with maternal empathy in shaping infants' brain responses to emotions. One possibility is that infants who are more fearful are also more sensitive to maternal empathic behaviors (especially those behaviors that concern emotional responding to distress as captured by maternal empathic concern), as fearful children have been shown to be more responsive to environmental variables more generally (Pluess & Belsky, 2010). Specifically, it has been argued that fearful individuals are more susceptible to both negative (risk-enhancing) and positive (development-enhancing) environmental conditions (Ellis, Boyce, Belsky, Bakermans-Kranenburg, & Van IJzendoorn, 2011). According to this scenario, variation in maternal empathy might impact the neural responses to emotions more strongly in infants that score high in fear when compared to infants that score low in fear (Hypothesis 4: *Temperament-based differential susceptibility to maternal empathy).* Whether this is the case and whether growing up with highly empathic mothers enhances or reduces neural responding to emotions in fearful infants was also assessed in the current study.

3.2 Methods

Participants

In the present study, the infants were recruited via the database of the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany. The final sample consisted of 27 eight-month-old infants, who came from middle-class German families and were between 243 and 261 days (13 females, *Median age* = 251, *Range* = 18 days). The infants were born full-term (between 37 and 41 weeks) and had a normal birth weight (> 2500 g). Note that this sample of infants also participated in a study that concerned the effects of duration of exclusive breastfeeding on emotional processing (Krol, Rajhans, Missana, & Grossmann, 2015)[1].An additional 11 eight-month old infantswere tested, but had to be excluded from the final sample due to missing

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[1] None of the breastfeeding measures were associated with any of the infant temperament or maternal empathy measures examined in the current study.

questionnaire data (*n* = 6), too many EEG artifacts (*n* = 3), and experimenter error (*n* = 2). All parents

provided informed consent prior to participation and were compensated with travel money and a toy for the infant.

Stimuli

The stimulus material consisted of full-light static body expressions displaying six different fearful and six different happy expressions in both upright and inverted orientations. Still frames of a previous dataset of dynamic body expressions were selected at the peak of emotional expression (A. P. Atkinson et al., 2004) (see Figure 1). From the original set of eight stimuli per condition, six were chosen for each emotion on the basis of recognition rate by a group of adult raters (A. P. Atkinson et al., 2004), indicating at least 40% average correct identification of the displayed emotion (chance level was 16.7%) (see Figure S1, in the the online only supplementary material for a complete set of the stimulus material used in the current study). In order to establish a link with the literature on facial expression processing, the current study utilized static displays of body expressions since most ERP work on infants' processing of emotional facial expressions has mainly focused on static but not dynamic expressions.

Figure 3.1. This figure shows an example of the stimuli used in the current study (happy and fearful body expressions).

Procedure

The infants were seated on their parent's lap in a dimly lit, sound attenuated and electrically shielded room during the experimental session. The stimuli were presented in the center of the screen on a black background, using a 70 Hz, 17-inch computer screen at a distance of 70 cm. In order to attract the infants' attention to the screen, each full-light body expression was preceded by an alerting sound and a fixation cross (1000 ms), followed by a black screen (400ms), followed by the stimuli (2000 ms). During the inter-stimulus interval infants were presented with an abstract screensaver for the purpose of keeping infants' attention. The stimuli were presented in a randomized order with the exception that no two stimuli with the same emotion and orientation combination were presented consecutively. The sessions were video recorded to control for infants' attention to the stimuli. The EEG session ended when the infant became fussy, or inattentive. The mean number of trials presented to the infants was 15.38. The mean number of trials included in the ERP average was 4.74 for the fearful upright condition, 5.93 for the happy upright condition, 4.58 for the fearful inverted condition and 5.71 for the happy inverted condition.

ERP analysis

The EEG was recorded from 27 Ag/AgCl electrodes attached to an elastic cap (EasyCap GmbH, Germany) using the 10–20 system of electrode placement. The data was online referenced to the CZ electrode and offline re-referenced to the algebraic mean of the left and right mastoid electrodes. The horizontal electrooculogram (EOG) was recorded from two electrodes (F9, F10) that are part of the cap located at the outer canthi of both eyes. The vertical EOG was recorded from an electrode on the supraorbital ridge (Fp2) that is part of the cap and an additional single electrode on the infraorbital ridge of the right eye. The EEG was amplified using a Porti-32/M-REFA amplifier (Twente Medical Systems International) and digitized at a rate of 500 Hz. Electrode impedances were kept between 5 and 20 kΩ. Data processing for ERP analysis was performed using an in-house software package EEP, commercially available under the name EEProbeTM (Advanced Neuro Technology, Enschede). The raw EEG data was bandpass filtered between 0.3 and 20 Hz. The recordings were segmented into epochs time-locked to the stimulus onset, lasting from 200 ms before onset until the offset of the frame (total duration 2200 ms). The epochs were baseline corrected by subtracting the average voltage in the 200 ms baseline period (prior to video or picture onset) from each post-stimulus data point. The baseline period contained a 200 ms black screen. Data epochs were rejected off-line whenever the standard deviation within a gliding window of 200 ms exceeded 80 µV in any of the two bipolar EOG channels and 60 µV at EEG electrodes. EEG data was also visually inspected offline for artifacts.

Questionnaire measures

Infant Temperament. Maternal assessment of infant temperament was obtained from the Infant Behavior Questionnaire-Revised, German version (IBQ-R). The IBQ-R includes the following subscales, approach, vocal reactivity, high intensity pleasure, smile and laughter, activity level, perceptual sensitivity, sadness, distress to limitations, fear, rate of recovery from distress, low intensity pleasure, cuddliness, duration of orienting, soothability. The items in this questionnaire ask the parents to report, on a 7-point scale the relative frequency of occurrence of specified infant reactions in concrete situations (with 1 being situations they think that are extremely untrue for their infant and 7 being situations extremely true for their infant), during the past two weeks. This format is used in order to minimize problems associated with recall (Gartstein & Rothbart, 2003). Temperament analyses in the present study were limited to two dimensions of infant temperament, namely, (1) infants' tendency to approach novelty and (2) infants' fearfulness because prior work has found that approach of novelty and fearfulness contribute to infants' and children's emotional responses and experiences. Additionally, increased fearfulness and reduced approach to novelty in these two temperamental traits has been often linked to psychopathological development relevant for anxiety disorders (Kagan, 1997; Rosenbaum et al., 1993). The scores were calculated by taking the average of scores reported by the parent for the specific questions that belonged to a temperament trait.

Maternal Empathy. To assess individual differences in empathic disposition, mothers filled out the self-report questionnaire Interpersonal Reactivity Index (IRI), German version (Davis, 1980; Davis, 1983; Paulus, 2009). The questionnaire consists of four sub-scales that are related to empathy. Each sub-scale contained 4 items and the mothers were asked to report their responses on a five-point scale. The two subscales empathic concern and personal distress are related to the emotional component of empathy. The perspective-taking subscale is related to the cognitive dimension of empathy, and the fantasy-empathy subscale represents the ability to identify with fictional characters in movies and novels. We focused our analysis on the emotional components (empathic concern) of empathy, as this seems most relevant for the current research questions. In particular, empathic concern (or sympathy), but not personal distress, has been linked with prosocial behaviors (helping) in adults (Eisenberg et al., 1989) and is therefore an important variable to assess in mothers in the current sample, as this might relate to how mothers react when their infants experience distress and may thus influence the infants' responses to emotionally arousing situations. Maternal empathic concern scores were calculated by taking the sum of the values of the four items relevant to the empathic concern scale (*Range* = 6 to 20).

Both the IBQ-R and the IRI were sent home with the parents after the experimental session and the completed versions were received within ten days of the visit to the laboratory.

Prior to the testing, we obtained information regarding birth-weight, gestational age and maternal education. This allowed us to rule out the possibility that these variables had an effect on the results presented in the current study.

Data analysis. For data analysis, a time window of 700 to 800 ms was selected at two ROIs over the right hemisphere (F4, C4, P4) and the left hemisphere (F3, C3, P3) in order to evaluate effects on the amplitude of the Nc. The selection of the time window and ROI was based on a prior analysis of the ERP correlates (including the Nc) of emotional body expression processing (Missana et al., 2014). The Nc can be seen as an index of attention allocation to a visual stimulus with greater negative amplitude indicating increased attention to that stimulus (Richards, 2003). To date, only one study has examined the neural correlates of emotion discrimination from static body expressions in infants. Missana et al. (2014) found evidence for discrimination of emotion at the late peak of the Nc, but not within the early peak of the Nc. We therefore chose to focus our analysis on the same time window (700-800 ms) as used in prior work (see Figure S2, included in the online only supplementary material, for the grand-average ERP responses and Table S1, in the online only supplementary material for the descriptive statistics, obtained in the current sample of 27 infants). The three main dependent variables used for statistical analysis were: (1) Nc amplitude to fearful body expressions, 2) Nc amplitude to happy body expressions and 3) difference between happy and fear calculated by subtracting fearful Nc amplitude from happy Nc amplitude, as an index of whether infants were biased (in their attention allocation) with respect to processing either fearful expression or happy expressions[2]. The relationship of the between-subjects variables, infant temperament and maternal empathy, to the aforementioned dependent variables was examined using Pearson correlations. This analysis was then followed up by independent *t*-tests using the between-subjects variables categorically based on a mean split[3] (high versus low) (maternal empathy: low M = 12.09, SD = 2.38; high M= 16.44, SD= 1.71; infant approach: low M = 4.74, SD= 0.44; high M = 5.96, SD = 0.50; infant fear: low M = 1.68, SD = 0.38; high M = 3.36 SD = 0.66)

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[2] Note that a positive score indexes a greater (relative) attention allocation to fearful expressions (fear bias), whereas a negative score indexes a greater (relative) attention allocation to happy expressions (happiness bias).

[3] Mean splits were used because the data were normally distributed; maternal empathy, $D(27) = 0.15, p = 0.117$; infant approach, $D(27) = 0.09, p = 0.2$; infant fear, $D(27) = 0.13, p = 0.2$.

3.3 Results

Infant Temperament

In line with our predictions (Hypothesis 1), our analysis revealed that both differences in infants' tendency to approach novelty and in infants' fearfulness correlated with differences in the brain response to fearful body expressions (see Figure 2). Specifically, a significant negative correlation was found between infants' tendency to approach and their ERP response (Nc) to fearful body expression (r = -.401, p = .038) but not to happy body expressions (r = -.202, p = .313), while a marginally significant positive correlation was found between infants' fearfulness and their ERP response (Nc) to fearful body expression (r = .359, p = .066) but not to happy body expressions (r = .02, p = .922), confirming our prediction of a differential impact of approach versus fearfulness (Hypothesis 2) (see Figure 2). Thus, infants who scored high on the approach scale showed brain responses (Nc) that showed a more negative ERP response (Nc) than infants who scored low on the approach scale, indexing greater attention allocation to fearful body expressions, whereas infants scoring high and low on the fearfulness scale showed the opposite pattern. The opposing effects of fearfulness and approach on the Nc are further supported by a significant difference obtained when comparing between the correlations of fearfulness and approach with the Nc to fearful bodies, z = 2.67, p = .008 (Lee & Preacher, 2013). It should be noted that while both approach and fearfulness were found to be significantly correlated only with the Nc to fearful bodies, when comparing correlations obtained for Nc to fearful bodies and Nc to happy bodies, neither infants' tendency to approach novelty nor infants' fearfulness resulted in significant differences between correlations (z = .77, p = 0.44 and z = -1.27, p = 0.21, respectively). Moreover, no association effects were observed when the difference between happy and fear, calculated by subtracting fearful Nc amplitude from happy Nc amplitude, was used as the dependent variable. The difference in the neural sensitivity to fearful body expressions between infants who show high approach scores when compared to those who show low approach scores was corroborated by an independent *t*-test comparing between high and low approach infants based on a mean split, $t(25) = 2.33$, $p = .028$ (see Figure 2). Conversely, infants who scored high on the fearfulness scale showed brain responses (Nc) that showed a more positive ERP response (Nc), indexing smaller attention allocation, to fearful body expressions than infants who scored low on the fearfulness scale. This difference in the neural sensitivity to fearful body expressions between infants who show high fearfulness scores when compared to those who show low fearfulness scores was corroborated by an independent *t*-test comparing between high and low fear infants based on a mean split, $t(25) = -2.34$, $p = .028$ (see Figure 2). Given that infant temperament traits of approach and fearfulness had opposite effects on the neural processing of fearful expressions, one may expect to find that these temperament traits are negatively correlated, however, there was no such correlation between the scores obtained for the approach scale and the fearfulness scale ($r = -.152$, $p = .45$, two-tailed) (see Table S2 in the online only supplementary material, for a correlation matrix providing information regarding the associations between infants temperament [fearfulness and approach to novelty] and maternal empathy [empathic concern] variables).

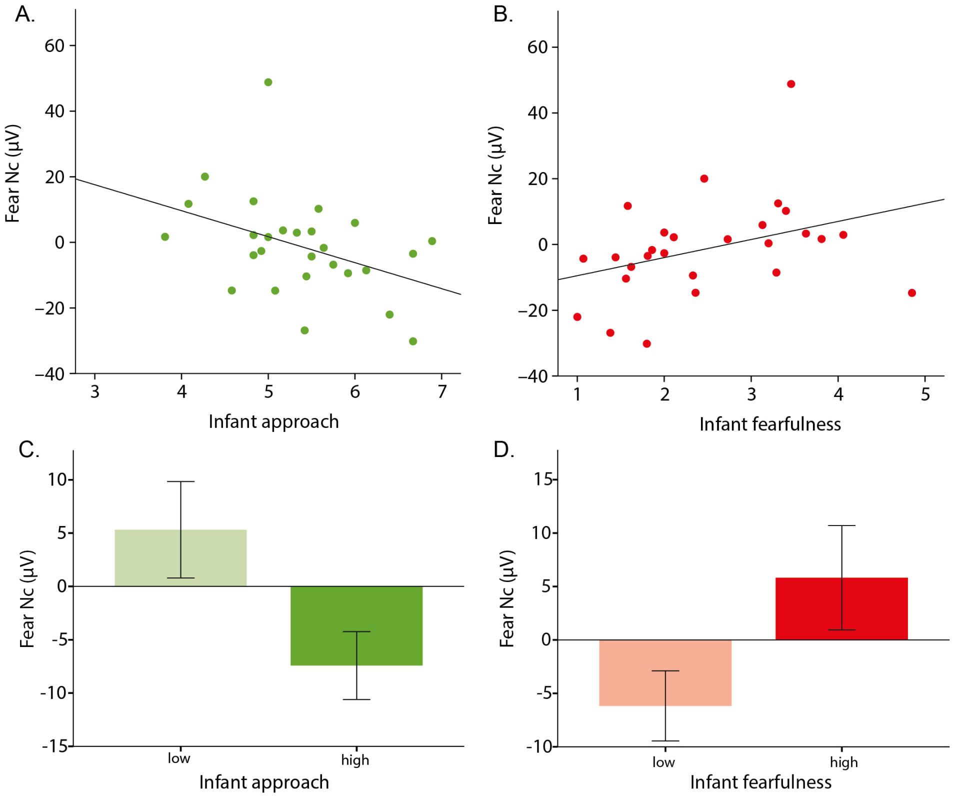

Figure 3.2. These graphs show that both infants' tendency to approach novelty and infants' fearfulness were associated with differences in the brain responses to fearful body expressions. A significant negative correlation was found between infants' tendency to approach and their ERP responses to fearful body expressions (A), while a marginally significant positive relationship was found between infant fearfulness and their ERP response to fearful body expressions (B). This figure further shows that the neural sensitivity to fearful expressions differed between infants scoring high and low in approach (C) and high and low in fearfulness (D).

Maternal Empathy

In line with our predictions (Hypothesis 3), our analysis revealed that differences in maternal empathic concern correlated with differences in the brain responses to fearful and happy body expressions (see Figure 3). Specifically, a significant positive correlation was found between maternal empathic concern and the difference score calculated by subtracting ERP response (Nc) to fearful body expression from the ERP response (Nc) to happy body expressions (*r*= .391, *p*= .044, two-tailed). Thus, infants whose mothers scored high on dispositional empathic concern showed a more negative ERP response (Nc) to fearful body expressions than happy body expressions, indexing greater attention allocation to fearful than happy expressions (negativity/novelty bias), while infants whose mothers scored low on dispositional empathic concern showed a more positive ERP response (Nc) to fearful body expressions than happy body expressions, indexing greater attention allocation to happy expressions than fearful expressions (positivity/familiarity bias). No significant associations were observed when the Nc to fearful or the Nc to happy body expressions was used as the dependent variable. Moreover, when maternal empathic concern was entered as a covariate into the analysis of the Nc (repeated measures ANOVA with emotion as within-subject factor), we did obtain a significant interaction between emotion and maternal empathic concern (*F* [1,25] = 4.502, *p* = .044). This confirms the correlational analysis presented above and shows that the exact modulation of the Nc by emotion depends on variation in maternal empathy. In addition, we performed a repeated measures ANOVA using empathic concern (high versus low based on a mean split) as a (categorical) between-subjects factor. However, this analysis did not reveal a significant interaction between empathic concern and emotion. This pattern of results indicates that the effect of maternal empathy is dimensional (continuous covariate) rather than categorical (two groups low versus high empathy) in nature.

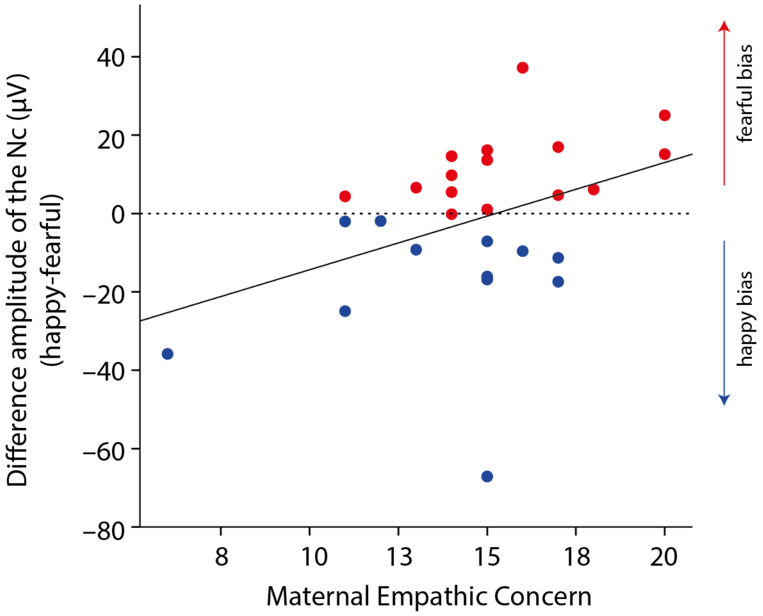

Figure 3.3. This graph shows that differences in maternal empathic concern correlated with differences in the brain responses to fearful compared to happy body expressions. We observed a significant positive correlation between maternal empathic concern and the ERP difference score calculated by subtracting ERP response (Nc) to fearful body expression from the ERP response to happy body expressions.

Interactions between infant temperament and maternal empathy

A repeated measures ANOVA revealed that there was a significant two-way interaction between the between-subjects factors infant fearfulness (high fearfulness versus low fearfulness) and maternal empathy (high empathic concern versus low empathic concern) regardless of the emotional body expression watched by the infants, $F(1, 19) = 6.52$, $p = .019$ (see Figure 4). Specifically, in line with our predictions (Hypothesis 4), we found that within the high fear group there were significant differences between infants with mothers high in empathic concern and low in empathic concern, *F*(1, 11) = 9.759, *p* = .01, whereas there were no such differences in the low fear group, *F*(1, 12) = .885, *p* = .365 (see Figure 4). This confirms the hypothesis that infants scoring high on fearfulness are more susceptible to maternal empathic responding. Moreover, while infants in the low fear group with mothers scoring high on empathic concern showed negative-going ERP responses (Nc), infants in the high fear group with mothers scoring high on empathic concern showed positive-going ERP responses (Nc), *F*(1, 15) = 9.063, *p* = .009. In contrast, infants with mothers scoring low on empathic concern did not show any differences in their ERP responses as a function of fearfulness, *F*(1, 15) = .067, *p* = .801 (see Figure 4).

Critically, all of the effects regarding our four main hypotheses described above were specific to upright presented emotional body expressions, as additional analysis performed on the ERP responses to inverted fearful and happy body expressions (body expression presented upside down) failed to reveal any significant effects.

Further analysis revealed that there were no differences in birth weight, gestation duration or in the years of maternal education between infants scoring low and high in fear (*F*[1,24] = .055, *p* = .533; *F*[1,24] = .027, *p* = .870; *F*[1,24] = .873, *p* = .359 respectively) and for infants scoring low and high in approach (*F*[1,24] = .025, *p* = .87; *F*[1,24] = .006, *p* = .940; *F*[1,24]= .075, *p* = .787 respectively). Neither were there any group differences in birth weight, gestation duration or years of maternal education for maternal empathy (*F*[1,24] = .401, *p* = .533; *F*[1,24] = .238, *p* = .630; *F*[1,24] = .011, *p*

= .919 respectively). Thus, none of the observed effects can be explained by birth weight, time of gestation or years of maternal education.[4]

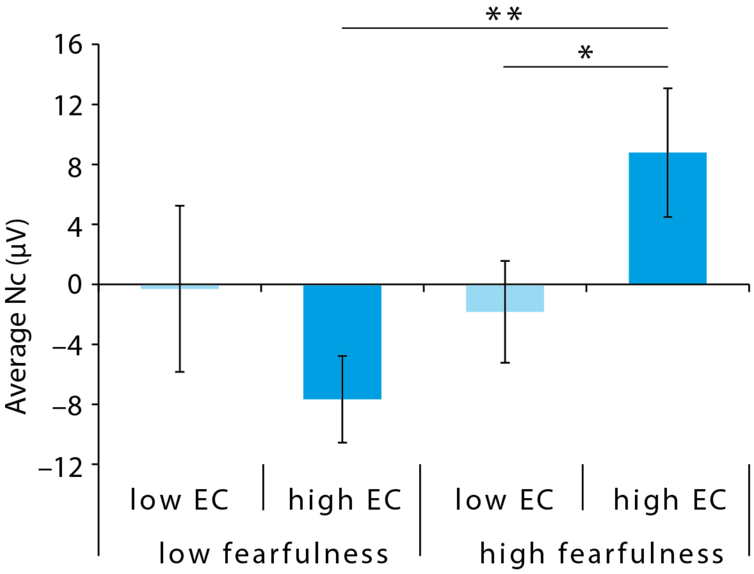

Figure 3.4. This graph depicts a significant interaction between infant fearfulness (high versus low fearfulness) and maternal empathy (high versus low empathic concern) regardless of the emotion being watched by the infant.

3.4 Discussion

The present study examined the role of infant temperament and maternal empathy in the neural processing of emotional body expressions in 8-month-old infants. Our results revealed that differences in both infant temperament and maternal empathy

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[4] Please note that due to failure to return the relevant questionnaire the information regarding birth weight, gestation duration and socio-economic status was missing for two of the participants included in the sample.

perception in the developing infant brain is best understood as a process that is sensitive to the context in which it occurs (Barrett et al., 2011; Mareschal et al., 2007).

With respect to the two traits of infant temperament considered, we found that both differences in (1) infants' tendency to approach novelty and (2) infants' fearfulness were linked to differences in their brain responses to fearful but not happy body expressions. This finding confirms our first hypothesis (emotion selectivity) according to which we had predicted to find that both temperament traits are linked to differences in the neural sensitivity to fearful (novel) stimuli. This suggests that the infant temperament traits examined in the current study are not associated with general differences in emotion perception but might be more specifically linked to the processing of negative (fearful) body expressions. However, future work is needed to further corroborate this finding, because our analysis did not reveal clear evidence for strict emotion specificity (comparing correlation coefficients between Nc to fearful bodies and Nc to happy bodies were not significantly different from each other for the two temperament traits, see results). Nevertheless, our data revealed that, in line with our second hypothesis (differential impact of fearfulness versus approach), there was positive association between infant fearfulness and the ERP response to fearful expressions, whereas there was a negative association between infant approach to novelty and the ERP response to fearful expressions.

low on the approach scale. This finding might be explained by the fact that infants at this age have relatively little experience with fearful expressions and might thus perceive them as novel stimuli, while happy expressions are highly familiar to them (Vaish et al., 2008). It is thus plausible that general differences in approaching novelty as reflected in the temperament measure impact the neural processing of specific emotions (particularly negative emotions) that are relatively novel to the infant. In light of this finding, it is interesting to note that in prior work with 7-month-olds, infants who, on the basis of their genotype (met carriers of the COMT gene [val158me]), are thought to have increased levels of dopamine in prefrontal cortex, showed greater neural sensitivity (attention allocation) to fearful facial expressions as indexed by a greater Nc (Grossmann et al., 2011). Increased levels of dopamine in turn have been associated with greater levels of approach and in particular novelty seeking in adults. Therefore, the current findings, in concert with prior work assessing genetic variation in the dopaminergic system (Grossmann et al., 2011), suggest that infants' sensitivity to fearful expressions is linked to individual differences in approach to novelty and this might be based on differences in dopaminergic function. This account is in agreement with existing accounts of individual differences in socio-emotional functioning and personality that have conceptually linked approach tendencies to novelty seeking and dopaminergic function (Goldberg & Weinberger, 2004; Kagan & Snidman, 2004).

Contrary to the findings regarding infant approach, concerning infant fearfulness, we found that infants who scored high on fearfulness showed brain responses (Nc) that were more positive in response to fearful expressions, indexing reduced allocation of attention to fearful body expressions than infants who scored low on fearfulness. This shows that, a fearful temperament, rather than increasing infants' neural responsiveness (increased attention) to fearful body expressions as commonly assumed, appears to decrease infants' neural responsiveness to fearful expressions. This is in contrast to work suggesting that there is a link between fearfulness and a heightened sensitivity to threatening signals (see Bar-Haim et al., 2007). However, it should be noted that the link between heightened sensitivity to threat and fearfulness in children and adults is relatively weak and might be moderated by factors not assessed in the current study (Pérez-Edgar et al., 2011). The current finding of a decreased attentional sensitivity to fearful bodies might be explained by a scenario, according to which fearful infants show decreased interest in (or even avoidance of) novel stimuli, including fearful body expressions. This explanation based on infants' differing sensitivity to novelty could also account for the finding that approach and fearfulness are associated with opposite effects on the neural processing of fearful expressions because greater fearfulness may reflect a greater avoidance of novelty, while greater approach may reflect greater interest in novelty. This explanatory framework is supported by a host of studies on infant temperament, demonstrating that infants systematically differ in their reactions to novelty and these differences in infants' sensitivity to novelty predict whether a child will show an inhibited or uninhibited temperament later in development (Kagan & Snidman, 2004). Negative emotions such as fear are less frequently encountered in daily life than positive emotions (in typical development), confounding novelty with negative expressions. Interestingly, it has been argued that novelty plays a critical role in guiding responses to negative emotions and help infants learn about negative emotional expressions (Vaish et al., 2008).

With respect to the role of maternal empathy in infants' neural sensitivity to emotions, our analysis revealed that differences in maternal empathic concern (defined as the tendency to experience feelings of sympathy and compassion for others in distress) correlated with differences in the brain responses to fearful and happy body expressions. Specifically, we found that infants whose mothers scored high on dispositional empathic concern showed a more negative ERP response (Nc) to fearful body expressions than to happy body expressions, indexing greater attention allocation to fearful than happy expressions (novelty /negativity bias), while infants whose mothers scored low on dispositional empathic concern showed a more positive ERP response (Nc) to fearful body expressions than happy body expressions, indexing greater attention allocation to happy expressions than fearful expressions (familiarity/positivity bias). This finding confirms our hypothesis that mothers with greater empathic concern for others in distress (fear) have infants who are also more prone to sensitively respond to others in distress (fear) and is in line with prior work emphasizing the role of maternal empathy in early socio-emotional development (Davis, 1983; Feshbach, 1987). From the current analysis, it is unclear whether this association between maternal empathic concern and infants' neural sensitivity to emotional expressions is genetic in nature or based on social learning. Prior work suggests that genetic factors contribute to children's emotional responses to others in distress as individual differences in empathic concern have been shown to be moderately heritable (0.25) (Knafo et al., 2009). Importantly, more recently, (Knafo & Uzefovsky, 2013) have shown that individual differences in empathic concern in children are explained by an interaction between maternal behavior and the genotype of the child. Namely, in that study, maternal negativity showed a negative association with empathic concern but only among children who carried the 7-repeat allele of the DRD 4 gene. It is thus particularly important to examine how the infants' predispositions (including temperament) interact with the maternal environment to understand how children's characteristics can influence the effects of the environment on them.

Indeed, our study revealed that individual differences in the neural responses to emotional information are explained by an interaction between maternal empathic concern (high and low empathic concern) and infant temperament (high and low fearfulness). In line with our prediction, we found that within the high fear group there were significant differences between infants with mothers high in empathic concern and low in empathic concern, whereas there were no such differences in the low fear group, suggesting that highly fearful infants are particularly sensitive to their caregivers' empathic concern. This is in line with differential susceptibility accounts that propose that fearful temperament is related to a greater sensitivity to environmental factors including maternal behaviors (Belsky, 2005; Ellis et al., 2011). The observed pattern of fearful infants with mothers scoring high on empathic concern showing reduced neural responsiveness to emotional body expressions and those with mothers scoring low on empathic concern showing increased neural responsiveness to emotional body expressions perhaps points to protective effects of maternal empathy on fearful infants' emotional reactivity. This is because reducing the sensitivity to emotional stimuli may help fearful infants to cope with emotionally arousing situations and thus represent an adaptive strategy. This strategy may be fostered in fearful infants in this context because highly empathic mothers are more responsive (or involved) during situations in which their infants become emotionally aroused, as adults scoring high on empathic concern/sympathy have been shown to be more inclined to help and intervene (Eisenberg et al., 1989). It is important to mention that all infants were tested in the presence of their mothers. Therefore, it is possible that this impacted the way in which infants responded to the emotional stimuli in the current study. It is probable that especially for fearful infants having a highly empathic (and presumably responsive) mother present during testing may have contributed to attenuating neural responses to emotional stimuli. The view that having a person that has a close relationship present during emotionally arousing and potentially threatening situations reduces emotional reactivity is supported by a host of studies in adults (Brown & Coan, in press; Coan & Maresh, in press). Interestingly, in adults it has also been shown that relationship quality matters in this context, as the reduction of the a person's response to threat was found to be strongest when the person being threatened was in close contact with a spouse rated high in marital quality (Coan, Schaefer, & Davidson, 2006). With respect to the current findings, it seems important for future work to more systematically investigate the possibility that maternal presence may have similar effects by obtaining information regarding relationship quality (attachment) and observing mother-infant interactions in a more naturalistic context in which emotions are elicited in the infant.

Moreover, we found that, regardless of the emotion being watched by the infants, infants in the low fear group with mothers scoring high in empathic concern showed negative-going ERP responses (Nc), while infants in the high fear group with mothers scoring high in empathic concern showed positive-going ERP responses (Nc). This demonstrates that, maternal empathy impacts infants' neural responses to emotional body expressions differently, depending on infant fearfulness. This finding further supports the notion that it is not enough to look at effects of maternal empathy in isolation but that it is important to examine how infant characteristics such as temperament influence (or interact with) the impact of the maternal environment. This is because our data suggest that the effects of maternal empathy depend on (reverse as a function of) infant temperament. As argued above, the reason why fearful infants with high empathy mothers showed attenuated neural responses to emotional body expressions might have to do with the fact that increased maternal empathy might help fearful infants to cope with emotionally arousing situations. Taken together, these findings are in general agreement with recent work highlighting the existence and importance of interactions between inherited traits and environmental factors in shaping socio-emotional functioning (Avinun & Knafo, 2013) and thus provides further evidence for how children's characteristics can influence the effects of the environment on them. Nonetheless, more work is needed to further examine this interaction between temperament and maternal empathy across development and across tasks to get a better understanding of its nature and its long-term effects on developmental outcomes.

Before we summarize the current findings, it is important to acknowledge the limitations of the current study. In particular, there are two main limiting factors that deserve attention. First, the sample size of the current study is relatively small, which is particularly problematic when investigating individual differences by dividing the sample into smaller groups, for example, infants low in fearfulness and high in fearfulness. This is why most of our results are based on correlational analysis that do not require for the sample to be divided and then followed up by independent *t*-tests using groups as a dichotomous between-subjects factor. However, our results concerning the interaction between infant temperament and maternal empathy rely on splitting the sample into four fairly small groups. These results should thus be seen as suggestive but not conclusive and be replicated in a larger sample of infants. Second, our measurement of infant temperament and maternal empathy rely on self-report measures by the mothers. While these measures are trusted and established instruments in this area of research, they might suffer from reporting biases and might not always directly map onto overtly expressed behavior. Therefore, in future work, it is critical to extend this work by examining infant temperament and maternal empathy using behavioral tasks.

In summary, the current study shows that infant temperament and maternal empathy, as well as the interaction of the two, play an important role in the development of infant brain functioning with respect to processing emotional information from body cues. In particular individual differences in the neural sensitivity reflecting the allocation of attention to visually presented emotions systematically vary as a function of intrinsic (temperament) and extrinsic factors (maternal empathy). Our results add an early developmental neuroscience dimension to existing accounts of socio-emotional functioning, suggesting a complex and integrative picture of how and why infants' emotional experiences might vary.

3.5 Future Directions for Translating Research on the Influential Child into Preventive Interventions

The present study, by informing our understanding of the nature of individual differences in emotional responding in typical development might have important implications for developmental processes involved in atypical development, as it points to potential sources which contribute to individual variation in emotional responsiveness that in extreme cases might be linked to psychopathological development.

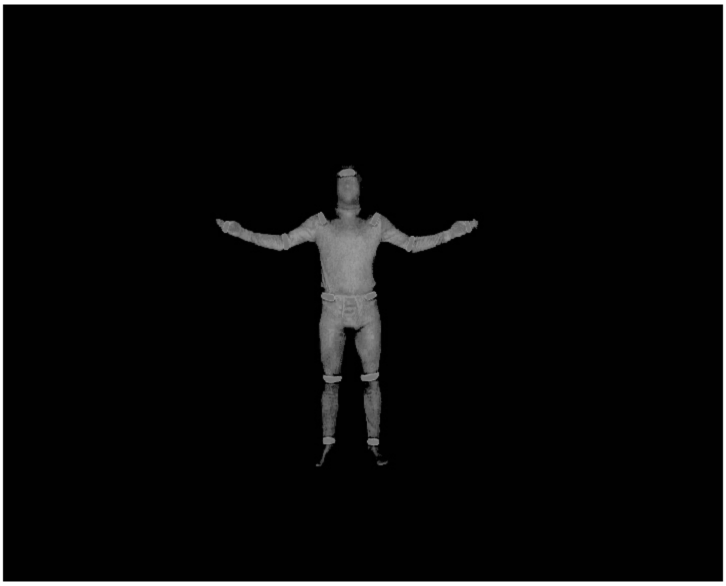
More specifically, infant fearfulness has been discussed as an early precursor to behavioral inhibition in childhood and might therefore be linked to anxiety disorders (Degnan & Fox, 2007). Given that our results suggest that infant fearful temperament interacts in critical ways with maternal empathy in shaping affective brain responding in infancy, it seems particularly important to take this interaction into account when considering factors contributing to risk and resilience in the development of anxiety disorders. In line with the idea of a differential susceptibility to environmental influences on children's socio-emotional development (Belsky, 2005), our data show that highly fearful infants are the most susceptible to environmental influences, namely, maternal empathic behavior. This suggests that in highly fearful infants, who are presumably at a higher risk for developing anxiety disorders, there might be a greater scope for change/plasticity resulting in the potential to improve mental health outcomes. Our findings may thus offer important implications with respect to the design and evaluation of particular preventative measures to tackle psychopathological issues related to anxiety disorders.

One way of translating the current research into preventive intervention would involve a two-step approach. First, it would be required to identify infants with an elevated risk of developing anxiety-related issues. This could be done by making parents aware of the fact that individual differences regarding fearful temperament exist and are associated with an increased risk for developing anxiety, but also by pointing out that this risk might be mitigated by the caregivers' empathic responsiveness. This first step could be achieved through various educational means including freely available online platforms. In addition, screening procedures should be put into place to allow parents to find out whether their infant has a fearful temperament (based on relevant IBQ-R items) and what their own empathic dispositions (based on relevant IRI items) are, which could be done through online temperament and empathy questionnaires. Second, once an infant has been identified as fearful and having a primary caregiver scoring low in empathic concern it would be important to offer the possibility to provide support. This support could consist of helping the parent to improve their empathic concern. How such training can be achieved is currently being heavily researched (Klimecki, Leiberg, Lamm, & Singer, 2013; Klimecki, Leiberg, Ricard, & Singer, 2013; Leiberg, Klimecki, & Singer, 2011). One promising avenue for training empathic concern (sympathy and compassion) is based on the concept of mindfulness and certain meditative practices rooted in the Buddhist tradition (Bornemann & Singer, 2013; Davidson et al., 2003; Siegel, 2007). However, there might also be more direct ways of improving this ability in caregivers that could be achieved through observation of free-play interactions between caregivers and their fearful infants by a therapist. This could provide the therapist with clues as to how to improve emotional communication between the caregiver and the infant through increases in the caregiver's empathic responding to their infant. To summarize, the suggested intervention might help the caregivers to identify whether their child is at a risk of developing anxiety disorders early on in infancy and provide information about necessary steps that may help prevent the onset of anxiety disorders during development. At the end we would like to add a cautionary note, because this should only be seen as a tentative proposal. Clearly, more systematic work following a larger sample of children across development is required to first establish that certain combinations of infant temperament and maternal empathy indeed pose a risk for developing anxiety related issues.

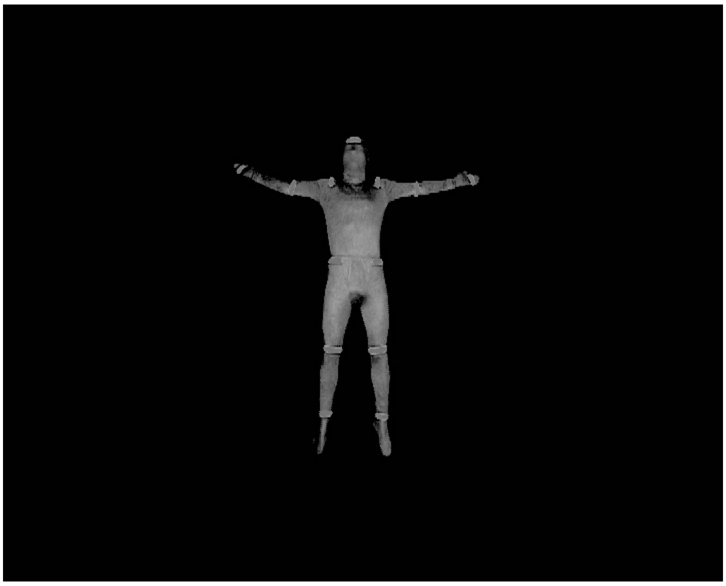
3.5 Supporting information

Figure S1. This figure provides images of the complete set of body posture stimuli used in the current study.

Happy body stimuli used in the current study

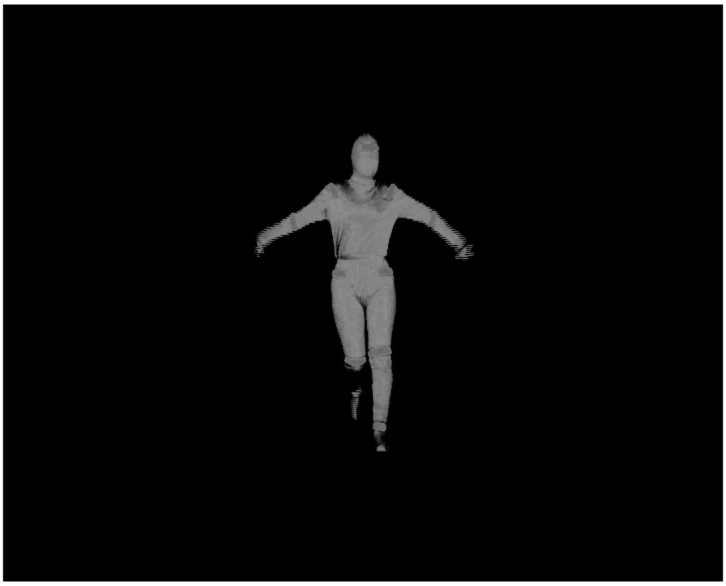


Happy#1

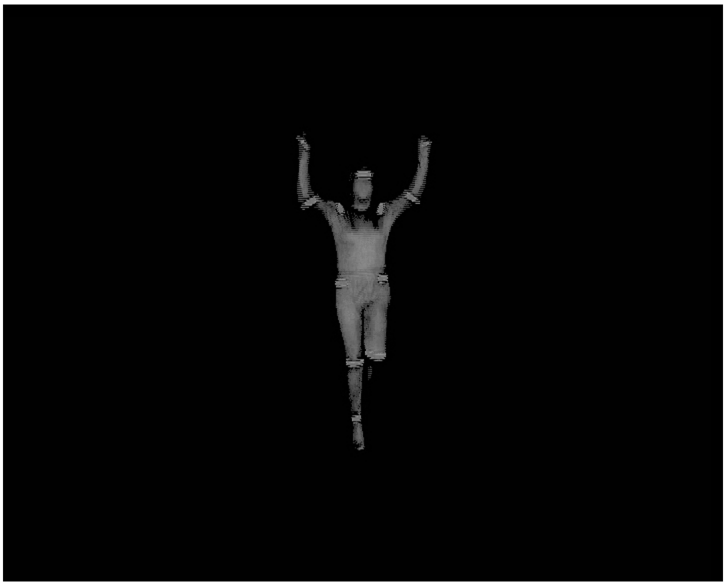


Happy #2

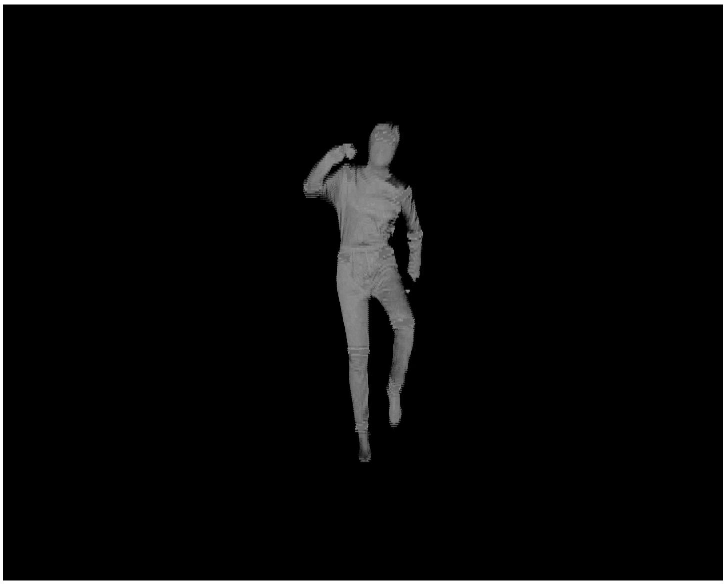
Happy #3



Happy #4



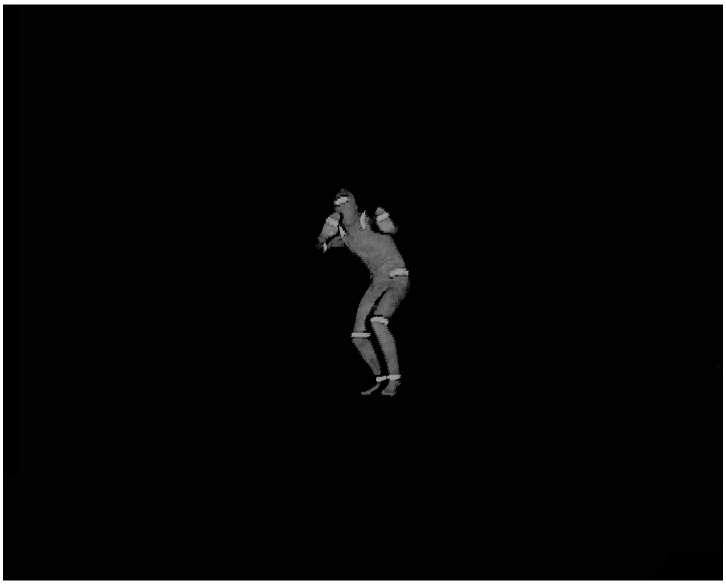
Happy #5



Happy #6

Fearful body stimuli used in the current study

Fearful#1



Fearful #2

Fearful #3

Fearful #4

Fearful #5

Fearful #6

Figure S2. This figures shows grand-average ERP responses to fearful and happy body expressions in the current sample of 8-month-old infants (N=27).

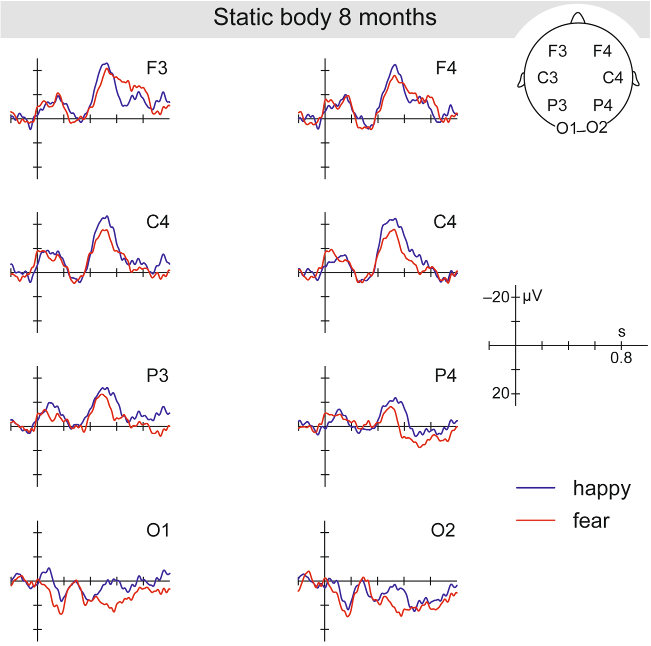


Table S1. This table provides the mean amplitudes (and standard errors) in µV for the late Nc (700-800 ms) over the left hemisphere (F3, C3, and P3) and the right hemisphere (F4, C4, and P4).

	Left Hemisphere	**Right Hemisphere**
Happy	-5.77(2.23)	-2.85(2.79)
Fearful	-1.28(2.95)	-5.60(2.74)

*Table S2.*Correlation matrix for maternal empathy and infant temperament (fearfulness and approach of novelty) in the current sample.

Correlation Matrix

		Approach	**Fear**	**Empathic Concern**
Approach (Infant)	Pearson Correlation	1	-.152	.451*
	Sig. (2-tailed)		.450	.018
	N	27	27	27
Fear (Infant)	Pearson Correlation	-.152	1	-.380
	Sig. (2-tailed)	.450		.050
	N	27	27	27
Empathic Concern (Mother)	Pearson Correlation	.451*	-.380	1
	Sig. (2-tailed)	.018	.050	
	N	27	27	27

*Correlation is significant at the 0.05 level (2-tailed).

Study 2

4 Study 2

Putting the face in context: Body expressions impact facial emotion processing in human infants

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Body expressions exert strong contextual effects on facial emotion perception in adults. Specifically, conflicting body cues hamper the recognition of emotion from faces, as evident on both the behavioral and neural level. We examined the developmental origins of the neural processes involved in emotion perception across body and face in 8-month-old infants by measuring event-related brain potentials (ERPs). We primed infants with body postures (fearful, happy) that were followed by either congruent or incongruent facial expressions. Our results revealed that body expressions impact facial emotion processing and that incongruent body cues impair the neural discrimination of emotional facial expressions. Priming effects were associated with attentional and recognition memory processes, as reflected in a modulation of the Nc and Pc evoked at anterior electrodes. These findings demonstrate that 8-month-old infants possess neural mechanisms that allow for the integration of emotion across body and face, providing evidence for the early developmental emergence of context-sensitive facial emotion perception.

Keywords: emotion, infants, body expressions, priming, ERP

4.1 Introduction

Responding to others' emotional expressions is a vital skill that helps us predict others' actions and guide our own behavior during social interactions (Nico Frijda & Batja. Mesquita, 1994; Frith, 2009a; Izard, 2007). The bulk of research investigating emotion perception has focused on facial expressions presented in isolation and been based on the standard view that specific facial patterns directly code for a set of basic emotions (Barrett et al., 2011). However, emotional face perception naturally occurs in context because during social interactions emotional information can be gleaned from multiple sources, including the body expression of a person (De Gelder, 2006; Heberlein & Atkinson, 2009; Van den Stock, van de Riet, Righart, & De Gelder, 2008). Body expressions have been argued to be the most evolutionarily preserved and immediate means of conveying emotional information (De Gelder, 2006) and may provide potent contextual cues when viewing facial expressions during social interactions. For example, when body and face convey conflicting information then emotion recognition from the face is biased into the direction of the body expressions (Aviezer et al., 2012; De Gelder, 2006; Meeren et al., 2005). These findings indicate that emotional faces are interpreted in the context of body expressions. More generally, the notion that context plays an important role in the interpretation of facial expressions adds to the growing body of research which challenges predominant views that emphasize the encapsulated and independent nature of facial expression processing (for discussion, see Feldman Barrett, Mesquita, & Gendron, 2011).

With respect to the neural processes that underlie the impact of body expression on emotional face processing in adults, using face-body compound stimuli Meeren and colleagues (2005) presented evidence for a very rapid influence of emotional incongruence between face and body. Specifically, in this ERP study, incongruent compared to congruent body-face pairings evoked an enhanced P1 at occipital electrodes, suggesting that emotional incongruence between body and face affected the earliest stages of visual processing. The P1 is enhanced when attention is directed towards a certain stimulus location and has been shown to be generated in extrastriate visual areas (Clark & Hillyard, 1996; Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Hillyard & Anllo-Vento, 1998). This is in line with an increasing body of evidence suggesting that context influences early stages of visual processing. Importantly, Meeren and colleagues (2005) also found that brain processes related to the structural encoding of faces as reflected in the N170 at electrodes over posterior temporal regions were not modulated by congruency between faces and bodies.

Critically, the existing work with adults leaves unclear whether the neural processes involved in emotion integration across body and face emerge early in human ontogeny and can therefore be considered a key feature of human social perceptual functioning. In the current study we thus examined the neural processing of emotional information across bodies and faces in infancy using ERPs. Similar to adults the main focus of emotion perception research in infancy has been on facial expressions (Leppänen & C. A. Nelson, 2009). This work has shown that (a) beginning around 7 months of age infants discriminate between positive and negative emotions (especially fear) and (b) at that age, emotional facial expressions modulate neural processes associated with the perceptual encoding of faces (N290 and P400) and the allocation of attentional resources (Nc) and recognition of stimulus (Pc) (Leppänen, Moulson, Vogel-Farley, & Nelson, 2007; Nelson & De Haan, 1996; Nelson, Morse, & Leavitt, 1979; Peltola, Leppänen, Mäki, & Hietanen, 2009a; Webb, Long, & Nelson, 2005). Only recently, research has begun to examine how the neural correlates of the ability to perceive and respond to others' emotional body expressions develops during infancy. In a first study, using dynamic point-light displays (PLD) of emotional body expressions Missana, Atkinson, & Grossmann. (2015), reported that 8-month-olds, but not 4-month-olds, showed brain responses that distinguished between fearful and happy body expressions, suggesting that the ability to discriminate emotional body expressions develops during the first year of life. Furthermore, Missana, Rajhans, Atkinson and Grossmann. (2014) extended this line of work by showing that infants' ERP responses also distinguished between fearful and happy static emotional body postures at the age of 8 months.

Another line of work has looked at the neural correlates of infants' ability to integrate emotional information across modalities using ERPs. This work has shown that infants are able to match emotional information across face and voice (Grossmann et al., 2006; Vogel, Monesson, & Scott, 2012). Specifically, in 7-month-old infants detecting incongruent face-voice pairings resulted in an enhancement of the Nc component, indexing a greater allocation of attention, whereas detecting congruent face-voice pairings elicited an enhanced Pc, reflecting recognition of common emotion across face and voice (Grossmann et al., 2006). While this work has provided insights into the early development of cross-modal emotional integration processes, to date, the neural processes of integrating emotional information across body and face have not been studied in infancy.

The two main goals of the current study were (a) to test whether body expressions impact and possibly hamper the processing of emotional facial expressions, and (b) to elucidate the neural correlates of detecting and integrating emotional information across body and face in infancy. In order to investigate these issues, we used a priming design in which we presented 8-month-old infants with emotional body expressions (fearful and happy) that were followed either by a matching or a mismatching facial expression. Priming has been shown to be a powerful method to elucidate implicit influences of context on social information processing in adults and children (see Stupica & Cassidy, 2014). However, despite its tremendous potential in studying how social information is represented in the brain of preverbal infants, to date there are only relatively few studies that have used priming designs to investigate the neural correlates of social information processing in infancy (Gliga & Dehaene-Lambertz, 2007; Peykarjou et al., 2014a). Furthermore, 8-month-old infants were chosen because at this age infants have been shown to reliably detect and discriminate between fearful and happy expressions from faces (Nelson et al., 1979; Peltola et al., 2009b) but also from bodies(Missana, Atkinson, & Grossmann, 2014 a; Missana, Rajhans, Atkinson, & Grossmann, 2014 b), which is an important prerequisite for the detection of congruency across body and face. We predicted that if infants are indeed sensitive to the congruency between body and facial expressions then their ERPs would show priming effects on components shown to reflect early visual processes similar to those identified in prior work with adults (Meeren et al., 2005). In addition, we expected priming effects on later attentional processes and recognition memory processes (Nc and Pc) similar to the effects identified in prior infant work on face-voice emotion matching (Grossmann et al., 2006). Furthermore, we hypothesized that, similar to what has been shown in prior work with adults (Aviezer et al., 2012; Meeren et al., 2005) viewing mismatching body expressions might hamper emotion detection from facial expressions in infants. We therefore examined whether infants' neural discrimination between emotional facial expressions (happy and fear) is impaired when they previously saw a mismatching body expression. Specifically, we predicted that ERPs (especially the Nc and Pc) would differ between facial expressions of emotion only when presented in the context of a congruent body expression but not when presented in the context of an incongruent body expression.

4.2 Methods and Materials

Participants. In the present study, the infants were recruited via the database of the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany. The final sample consisted of 32 eight-month-old infants aged between 229 and 258 days (16 females, *Median age* = 245, *Range* = 29 days). An additional 18 eight-month-old infants were tested, but were excluded from the final sample due to fussiness (*n* = 12) or too many artifacts (*n* = 6). Note that an attrition rate at this level is within the normal range for an infant ERP study (DeBoer, Scott, & Nelson, 2007). The infants were born full-term (between 38 and 42 weeks) and had a normal birth weight (> 2800 g). All parents provided informed consent prior to the study and were compensated financially for participation. The children were given a toy as a present after the session.

Stimuli. For the emotional body stimuli, we used full-light static body displays taken from previously validated stimulus set by Atkinson et al. (2004), see Figure 1. For each emotion we presented body postures from 4 different actors (selected on the basis of high recognition rates) shown for these stimuli by a group of adults (Atkinson et al., 2004). The facial expressions that followed the emotional body postures were color photographs of happy and fearful facial expressions taken from the previously validated FACES database (Ebner, Riediger, & Lindenberger, 2010). We selected photographs from four actresses (age 19 to 30, ID-numbers 54, 63, 85, 134). These actresses were selected on the basis of high recognition rates shown by a group of adult raters (Ebner et al., 2010). In order to keep the stimulus presentation protocol comparable with previous infant studies, we decided to include only pictures of women (Grossmann et al., 2007; Kobiella, Grossmann, Reid, & Striano, 2008; Leppänen et al., 2007). The photographs were cropped so that only the face was visible within an oval shape. The body stimuli had a mean height of 12.52 cm and a mean width of 5.37 cm and the face stimuli had a mean height of 12 cm and a mean width of 9.3 cm.

Design. We employed a priming design in which emotional bodies served as a primes and emotional faces as targets. Specifically, we presented infants with emotional body expressions (fearful and happy) as primes that were followed either by a matching (congruent) or a mismatching (incongruent) facial expression as targets (see Figure 1). All possible pairings between body and face stimuli (from 4 actors) were used for stimulus presentation, leading to 16 possible combinations per condition (i.e., 16 combinations for a happy face preceded by a happy body) and 64 combinations in total for the four conditions. Each specific combination was included in the presentation list four times, leading to a maximum number of 256 trials. Each trial began with the presentation of a fixation star on a black background (450 ms), followed by the full-light static body expression which was presented for 1000 ms. This was followed by an inter-stimulus interval which varied randomly between 200 and 300 ms, during which a fixation star was presented on a black background. Following the inter-stimulus interval, the facial expression was presented for 1000 ms. This was followed by an inter-trial interval where a black screen was presented for a duration that randomly varied between 500 and 1000 ms. Stimuli were presented in a pseudo-randomized order and a newly randomized order was generated for each infant. We ensured that trials from the same condition did not occur twice in a row.

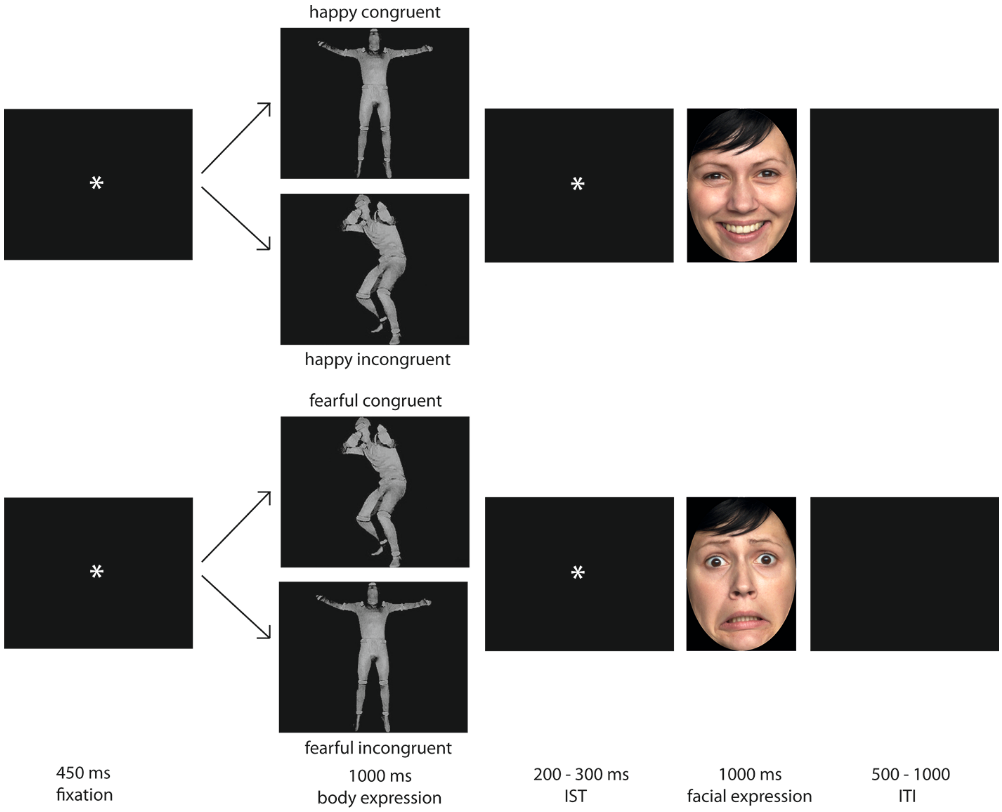

Figure 4.1 This figure shows an example of the stimuli and the design of the priming paradigm used in the current study.

Procedure. The infants were seated on their parent's lap in a dimly lit, sound-attenuated and electrically shielded room during testing. The stimuli were presented in the center of the screen on a black background, using a 70-Hz, 17-inch computer screen at a distance of 70 cm. The stimulus presentation was continuous but simultaneously controlled by the experimenter, who was able to stop the presentation, if required, and use attention getting videos including sounds in order to reorient the infant to the screen.

EEG measurement. The EEG was recorded from 27 Ag/AgCl electrodes attached to an elastic cap (EasyCap GmbH, Germany) using the 10-20 system of electrode placement. The data was online referenced to the CZ electrode. The horizontal electrooculogram (EOG) was recorded from two electrodes (F9, F10) that are part of the cap located at the outer canthi of both eyes. The vertical EOG was recorded from an electrode on the supraorbital ridge (FP2) that is part of the cap and an additional single electrode on the infraorbital ridge of the right eye. The EEG was amplified using a Porti-32/M-REFA amplifier (Twente Medical Systems International) and digitized at a rate of 500 Hz. Electrode impedances were kept between 5 and 20 kΩ. In addition, the sessions were video-recorded to off-line code for infants' attention to the screen. The EEG session ended when the infant became fussy, or inattentive.

ERP analysis. Data processing for ERP analysis was performed using an in-house software package EEP, commercially available under the name EEProbeTM (Advanced Neuro Technology, Enschede). The raw EEG data was re-referenced to the algebraic mean of the left and right mastoid electrode and we used a 0.3 - 20 Hz bandpass finite impulse response filter (length: 1501 points; Hamming window; half-power [–3 dB] points of 0.37 Hz and 19.93 Hz). The recordings were segmented into epochs time-locked to the target onset, lasting from 100 ms before onset until the offset of the frame (total duration 1100 ms). The epochs were baseline corrected by subtracting the average voltage in the 100 ms baseline period (prior to picture onset) from each post-stimulus data point. During the baseline period a black screen with a white fixation star was presented. Data epochs were rejected off-line whenever the standard deviation within a gliding window of 200 ms exceeded 80 μV in any of the two bipolar EOG channels and 60 μV at EEG electrodes. Following the automated rejection procedure, EEG data was also visually inspected offline for remaining artifacts, and trials that contained artifacts were rejected from analysis. Furthermore, trials in which the infant did not attend to the screen during either prime or target presentation were excluded from further analysis. At each electrode, artifact-free epochs were averaged separately for happy-match, happy-mismatch, fearful-match and fearful-mismatch facial expressions to compute the ERPs. The mean number of trials included in the ERP average was 19.75 (*SD* =7.85) for the happy congruent condition, 19.22 (*SD* =7.15) for the happy incongruent condition, 19.41 (*SD* =6.77) for the fear congruent condition, and 19.25 (*SD* =8.67) for the fear incongruent condition.

Based on prior ERP work (De Haan, Johnson, & Halit, 2003; Kobiella et al., 2008; Leppänen et al., 2007; Meeren et al., 2005; Missana et al., 2014 a; Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Webb et al., 2005) and visual inspection of the data (see supplementary Figure 1), our ERP analysis focused on the following ERP components: (A) early visual processing over posterior (occipital) regions (O1, O2) (P1 [100-200 ms]); (B) face-sensitive processing over posterior (occipital) regions (O1, O2) (N290 [200-300 ms], P400 [300-500 ms]); (C) later processes related to attention allocation (Nc [400-600 ms]) and recognition memory (Pc [600-800 ms]) over anterior regions (F3, F4, C3, C4, T7, T8). For these time windows and regions mean amplitude ERP effects were assessed in repeated measures ANOVAs with the within-subject factors emotion (happy versus fear), congruency (congruent versus incongruent), and hemisphere (left [F3, C3, T7] versus right [F4, C4, T8]).

4.3 Results

Early visual processing at posterior electrodes

P1. Our analysis did not reveal any congruency effects on the P1 from 100 to 200 ms at O1 and O2, $F(1, 31) = 0.393$, $p = 0.535$. Additionally, there was no significant main effect of emotion, $F(1,31) = 0.898$, $p = 0.351$, and there was no significant interaction between congruency and emotion, $F(1, 31) = 2.83$, $p = .102$, during this time window at occipital electrodes.

Face-sensitive processing at posterior electrodes

N290. Our analysis did not reveal any congruency effects on the N290 from 200 to 300 ms at O1 and O2, $F(1,31) = 0.10$, $p = 0.920$. Furthermore, there was no significant main effect of emotion, $F(1,31) = 1.902$, $p = 0.178$, and there was no significant interaction between congruency and emotion, $F(1,31) = 1.764$, $p = 0.194$, during this time window at occipital electrodes.

P400. Our analysis did not reveal any congruency effects on the P400 from 400 to 600 ms at O1 and O2 $F(1,31) = 0.008$, $p = 0.930$. Additionally, there was no significant main effect of emotion, $F(1,31) = 1.225$, $p = 0.277$, and there was no significant interaction between congruency and emotion, $F(1,31) = 0.003$, $p = 0.959$, during this time window at occipital electrodes.

Later processes related to attention allocation (Nc) and recognition memory (Pc)

Nc. Our analysis revealed a significant interaction between the factors congruency, emotion and hemisphere at anterior electrodes (F3, F4, C3, C4, T7, T8) between 400 and 600 ms, $F(1,31) = 4.16$, $p = 0.05$ (see Figure 2). Further analysis showed that the Nc differed between the emotions only over the left hemisphere in the congruent condition, $t(31) = 2.81$, $p = 0.009$, with fearful facial expressions primed with congruent body expressions being significantly more negative (*M* = -15.61 µV, *SE* = 1.35) than happy facial expressions primed with congruent body expressions (*M* = -11.70 µV, *SE* = 1.58) (see Figure 2 and Table 1). No significant differences between happy and fearful facial expressions were observed at the left hemisphere in the incongruent condition *t*(31) = 0.18, *p* = 0.856. Furthermore, there were no significant differences between emotions neither in the congruent condition *t*(31) = 1.00, *p* = 0.324 nor in the incongruent condition, *t* (31) =0.88, *p* = 0.383 over the right hemisphere. Note that here we report uncorrected statistics for the paired comparisons using *t*-tests. However, the significant difference between emotions in the congruent conditions survives a conservative Bonferroni correction in which the *p*-value is adjusted for multiple comparisons (in our case by dividing it by 4, adjusted *p*-value is *p* = 0.0125).We did not observe a main effect of emotion at left anterior electrodes between 400 and 600 ms, *F*(1,31) = 3.572, *p* = 0.068.

Pc. Our analysis revealed a significant interaction between the factors congruency, emotion and hemisphere at anterior electrodes (F3, F4, C3, C4, T7, T8) between 600 to 800 ms, *F*(1,31) = 6.06, *p* = 0.02 (see Figure 2). Further analysis showed that the Pc differed between the emotions only at left hemispheric electrodes for the congruent condition, *t*(31) = 3.67, *p* = 0.001, with fearful facial expressions primed with congruent body expressions being significantly more negative (*M* = -5.61µV, *SE*= 1.15) than happy facial expressions primed with congruent body expressions (*M* = -1.37µV, *SE* =1.12) (see Figure 2 and Table 1). No significant differences between happy and fearful facial expressions were observed at the left hemisphere when primed with incongruent body expressions, *t*(31) = 0.40, *p* = 0.692. Furthermore, there were no significant differences between emotion neither in the congruent *t*(31) =1.35, *p* = 0.186 nor in the incongruent condition $t(31) = 1.90$, $p = 0.066$ over the right hemisphere. Note that similar to the analysis for the Nc, we also report uncorrected statistics for the paired comparisons for the Pc. In addition, we observed a main effect of emotion at anterior electrodes between 600 and 800 ms, $F(1,31) = 9.45$, $p = 0.004$. However, this main effect on the Pc is difficult to interpret, because it needs to be qualified by the interaction effect reported above.

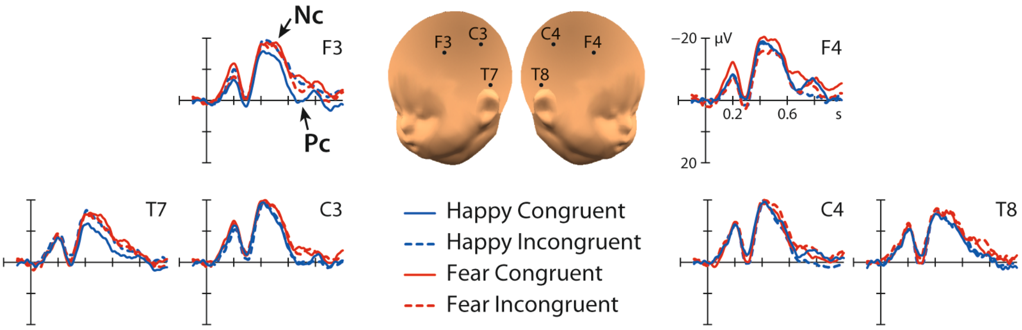

Figure 4.2. This figure shows 8-month-old infants' ERP responses at anterior electrodes to fearful and happy facial expressions primed congruently and incongruently by body expressions.

		Attention allocation and recognition memory					
		Nc: 400 -600 ms			*Pc: 600 - 800 ms*		
		F3/ C3/T7		F4/C4/T8	F3/ C3/T7		F4/C4/T8
happy congruent	Mean (SE) µV	-11.70 (1.58)	**	-14.28 (1.77)	-1.37 (1.12)	**	-4.14 (1.54)
fearful congruent	Mean (SE) µV	-15.61 (1.35)		-15.49 (1.60)	-5.61 (1.15)		-5.70 (1.19)
happy incongruent	Mean (SE) µV	-14.54 (1.67)		-14.10 (1.50)	-3.78 (1.63)		-2.60 (1.29)
fearful incongruent	Mean (SE) µV	-14.81 (1.44)		-15.42 (1.50)	-4.40 (1.57)		-5.61 (1.75)

** $p < 0.01$

Table 4.1. This table provides an overview of the ERP findings of the current study.

4.4 Discussion

The current study examined the impact that body expressions have on the processing of facial expressions in infancy by using an ERP priming paradigm. Our results show that body expressions affect the neural processing of facial expressions in 8-month-old infants. In particular, the ERP data demonstrate that viewing conflicting body expressions hampers the neural discrimination of facial expressions in infants. This finding suggests that early in development body expressions provide an important context in which facial expressions are processed. Furthermore, our results present developmental evidence for the view that emotion perception should be considered a context-sensitive and multi-determined process (Feldman Barrett et al., 2011). The finding that body cues play an important role when perceiving emotional facial expressions early in human ontogeny, suggests that context sensitivity during facial emotion perception can be considered a key feature of human social perceptual functioning.

With respect to the early visual processing at occipital electrodes, the results from the current study did not reveal any effects on the P1 (100-200 ms). Prior work with adults reported early ERP effects for the P1 at occipital electrodes related to detecting congruency of emotional information between body and face (Meeren et al., 2005). One possibility why we did not observe any such effects in our infant sample is that there might be developmental differences with respect to how infants and adults integrate emotions across body and face. It is plausible that only with development and more experience in seeing matching bodies and faces these early perceptual integration processes reflected in the P1 are established. Another possible explanation is related to the fact that there are methodological differences between prior work with adults and the current study with infants. Namely, we employed a priming design with infants, whereas

Meeren et al. (2005) used body-face compound stimuli in their study with adults. It is thus possible that for these early effects on the P1 to be observed, it is necessary that both body and face are visible simultaneously, as was the case for the compound stimuli in the adult work, but not for the priming stimuli in the current infant study. Future work is needed to explicitly test between these alternatives.

Critically, our results show that body context matters, because effects of body context on the processing of facial emotions were observed for later ERP components related to attention allocation (Nc, 400-600 ms) and recognition memory (Pc, 600-800 ms) at anterior electrodes. In particular, infants showed that only when presented with congruent body expressions, but not when presented with incongruent body expressions, the Nc and Pc discriminated between happy and fearful faces. This shows that conflicting body cues hamper discrimination between facial expressions during later stages of neural processing. Specifically, infants fail to dedicate differential attentional resources to fearful versus happy facial expressions as reflected in the absence of a relative enhancement of the Nc to fearful faces when compared to happy faces. This finding suggests that incongruent body cues impair what has been referred to as a fear bias (Leppänen & Nelson, 2009) in 7-month-old infants' attentional responding to facial expressions. In the context of conflicting body cues, infants also show an impairment of processes related to differential employment of recognition memory as reflected in the Pc. In particular, happy facial expressions did not elicit a greater Pc than fearful facial expressions in the incongruent context. This indicates that incongruent body cues impair the recognition of highly familiar (happy) facial expressions, because in the congruent body context happy facial expressions evoked an enhanced Pc, which is thought of as a neural marker of recognition memory (Nelson, Thomas, de Haan, & Wewerka, 1998).

It is important to mention that, in addition to the interaction effect, we also observed a main effect of emotion on this ERP component. This indicates that conflicting body cues, while having a detrimental effect on brain processes associated with recognition memory, do not completely abolish the differential employment of recognition memory processes triggered by viewing facial emotional expressions. Nevertheless, our analysis also revealed that only during the congruent body context, but not during the incongruent body context, the Pc amplitude differed between emotions, as shown in the post hoc comparisons using paired *t*-tests. Taken together, these findings regarding the Nc and Pc support the notion that context plays a critical role in triggering attentional and memory related processes associated with the perception of emotional facial expressions.

With respect to the nature of the observed context effects for the Nc and Pc, the current data suggest that incongruent emotional body context impedes the discrimination of emotional faces rather than congruent emotional body context bolstering the detection of emotional faces. This is because our data indicate that in the incongruent compared to the congruent body context, the Nc to fear faces and the Pc to happy faces are diminished in amplitude. While this pattern of results is indicative of a hampering in the incongruent context, future work should include an unprimed facial emotion condition in addition to the primed conditions in order to directly investigate whether congruent body context bolsters or incongruent body context indeed hampers the perception of facial emotion in infants, or both. Moreover, it seems critical to extend the current work by employing faces as primes and bodies as targets in order to find out whether these contextual effects occur independently of what serves as a prime or whether bodies are more potent in impacting the interpretation of emotional information than faces, as suggested by prior work with adults (Avizier et al., 2012).

Another point for discussion is that the context effects on the Nc and Pc observed in 8-month-old infants in the current study were lateralized to the left hemisphere. This, at first glance, might appear counterintuitive given previous work showing that both, emotion perception in general as well as facial and body perception in particular (Grèzes, Pichon, & De Gelder, 2007; Heberlein & Saxe, 2005; Missana et al., 2014) are lateralized to the right hemisphere. However, recent work using fMRI in adults shows that regions that categorically represent emotions regardless of modality (body or face) are lateralized to the left hemisphere (specifically to the left superior temporal sulcus) (Peelen, Atkinson, & Vuilleumier, 2010). The existence of such modality-independent representations of emotional information in the left hemisphere might also explain the lateralization of the ERP effects in the current infant sample. However, it should be stressed that the infant ERP data does not provide any information regarding the cortical sources that generate the observed ERP effects. It is therefore not possible to draw any direct comparisons between fMRI findings from adults and ERP findings from infants. Clearly, future work is needed to address this issue and functional near-infrared spectroscopy (fNIRS) (Lloyd-Fox, Blasi, & Elwell, 2010), which is particularly well suited to localize brain responses in infants and might provide a promising method to examine this question.

Finally, it is important to mention that no effects were observed for face-sensitive processing as reflected in the ERP components thought to be involved in face encoding in infants such as the N290 and the P400. This pattern is in line with prior work (Meeren et al., 2005), which also did not find any such effects in adults. However, prior work with 7-month-old infants shows that fearful faces elicit a larger P400 than happy faces (Leppänen et al., 2007). Therefore, the absence of any effects on face-sensitive ERP components in the current data may suggest that facial emotion does not impact face encoding when primed by bodies, regardless of whether those bodies provide congruent or incongruent emotional information. Alternatively, these differences between studies may also be explained by methodological differences (several electrodes placed at occipital sites and included in the analysis in prior work, only two occipital electrodes in the current study) or developmental differences (7 months of age in prior work, 8 months of age in the current study). Clearly, more work is needed that systematically compares across ages and ERP systems to further elucidate the exact nature of the priming effects obtained in the current study.

4.5 Conclusion

Taken together, the current findings demonstrate that infants put facial expressions into context. Our ERP data show that (a) body expressions impact the way in which infants attend to and retrieve information from memory about facial expressions, and (b) body expressions exert contextual effects on the facial emotion processing, with conflicting body cues hampering the neural discrimination of facial expressions. These results provide developmental evidence to an emerging body of work challenging the standard view of emotion perception, demonstrating that emotion perception from faces greatly depends on context.

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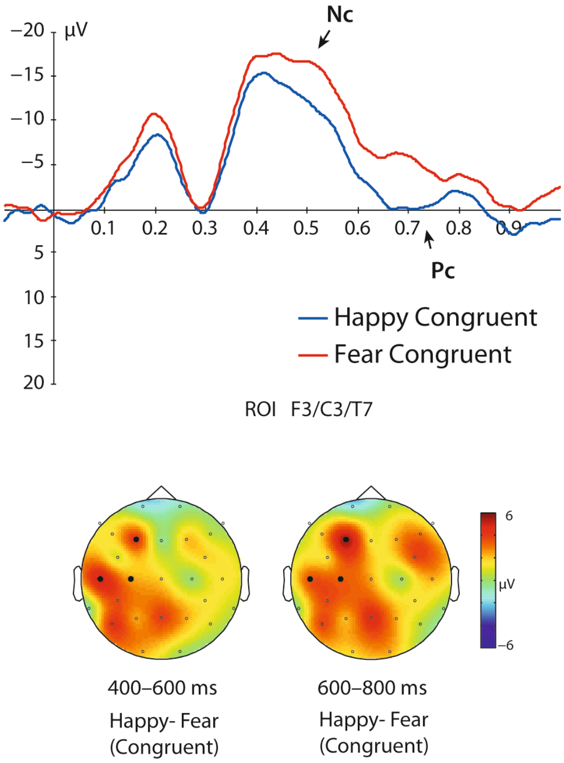
4.6 Supporting information



This figure shows the ERP response to fearful and happy facial expressions congruently primed by body expressions at the anterior region of interest and the scalp topographies of ERP components Nc (400-600 ms) and Pc (600-800 ms).

Study 3

5 Study 3

Children's altruistic behavior in context: The role of emotional responsiveness and culture

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Altruistic behavior in humans is thought to have deep biological roots. Nonetheless, there is also evidence for considerable variation in altruistic behaviors among individuals and across cultures. Variability in altruistic behavior in adults has recently been related to individual differences in emotional responsiveness to fear in others. The current study examined the relation between emotional responsiveness (using eye-tracking) and altruistic behavior (using the Dictator Game) in 4 to 5-year-old children (N = 96) across cultures (India and Germany). The results revealed that increased altruistic behavior was associated with a greater responsiveness to fear faces (faster fixation), but not happy faces, in both cultures. This suggests that altruistic behavior is linked to our responsiveness to others in distress across cultures. Additionally, only among Indian children greater altruistic behavior was associated with greater sensitivity to context when responding to fearful faces. These findings further our understanding of the origins of

altruism in humans by highlighting the importance of emotional processes and cultural context in the development of altruism.

5.1 Introduction

Why humans engage in costly acts of altruism towards genetically unrelated individuals has been one of the most enduring and puzzling questions in biology and psychology (Fehr & Fischbacher, 2003). The empirical work available now to address this question by tracing altruism's phylogenetic and ontogenetic origins provides compelling evidence that altruistic behavior is deeply rooted in our biology. From the phylogenetic perspective, altruistic behavior is not unique to humans but also found in other animals including our closest living relatives, the chimpanzees (Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Warneken & Tomasello, 2006). Furthermore, from the ontogenetic perspective, altruistic behavior emerges very early in development during infancy, before socialization can culturally shape this behavior. For example, already at the young age of 14 months, infants help others in need (Warneken & Tomasello, 2007). Based on these comparative and developmental data, it has been suggested that it is in our nature to be altruists (Warneken & Tomasello, 2009).

Nonetheless, the tendency of humans to engage in altruism varies greatly across individuals. Indeed, there exist extreme cases with regard to this tendency, ranging from extremely prosocial kidney donors to highly antisocial psychopaths (Blair, Mitchell, & Blair, 2005; Marsh et al., 2014). The study of these extreme cases not only informs the question of what contributes to individual differences in altruism but also sheds light on the basis of altruistic behavior more generally. In particular, emotional responsiveness to seeing others in distress (e.g., displaying fear or sadness) appears to be a key process related to altruistic tendencies, with kidney donors showing heightened and psychopaths showing decreased perceptual sensitivity to fear in others (Marsh & Blair, 2008; Marsh et al., 2014). At the neural level, the amygdala shows enhanced responding to fearful faces in highly altruistic kidney donors and blunted responding in psychopaths (Marsh et al., 2014). Critically, these effects are specific to fearful faces as no such differences are evident in response to other emotions such as anger (Marsh et al., 2014). This work indicates that perceptual sensitivity to distress cues in others is associated with differences in altruistic behavior, in line with the view that a basic form of empathic responding is linked to altruism (Batson, 2011). Indeed, from very early in development, empathic responding is a key affective ability underlying prosocial behavior (Hoffman, 2001).

Importantly, while altruism rather than self-interest dominates social behavior across cultures, the degree of altruism varies considerably across cultures (Henrich et al., 2005; Henrich, Heine, & Norenzayan, 2010). Studies of human altruism using economic games such as the dictator game – in which one person is allotted a divisible resource (usually money) and can then 'dictate' how much of that resource she is willing to give to another person – show that cultural differences in economic organization and the structure of social interactions explain a substantial portion of the behavioral variation in altruism across cultures (Henrich et al., 2005). Specifically, the greater the degree of market integration and the payoffs to cooperation with strangers in everyday life, the higher the level of altruism expressed in the dictator game. Interestingly, this is probably why, counter to intuition, altruistic behavior in such economic games is usually higher in individualistic than in collectivistic cultures (Henrich et al., 2005).

Furthermore, there is mounting evidence that perceptual processes are influenced by culture (Nisbett, 2010). One body of work suggests that when viewing a visual scene, Westerners generally engage in context-independent and analytic perceptual processes by selectively focusing on salient objects independently of their context, whereas Asians typically engage in context-dependent and holistic perceptual processes by attending to the relation between the object and the context in which the object is placed (Nisbett & Miyamoto, 2005). For example, Westerners focused on foreground objects faster than Asian adults, and then continued to look at the focal object for longer (Chua, Boland, &Nisbett, 2005). These cultural differences in visual perceptual processing between Asians and Westerners first develop around 5 years of age (Nisbett & Miyamoto, 2005), suggesting that cultural experience and learning play a role in the emergence of such biases. It is thus plausible that cultural learning may also play a role in whether and how context affects responsiveness to emotions in others.

Surprisingly, the link between altruism and perceptual sensitivity to fear in others has thus far only been examined in adults in Western cultures (Marsh et al., 2007). It is therefore unclear whether this link exists in children and how cultural factors affect this purportedly hard-wired link between perceptual sensitivity to others' distress and altruistic tendencies. Addressing these questions is particularly important because it can shed light on the psychology underlying altruistic behavior by allowing for a closer look at the emotional, developmental, and cultural origins of human prosociality.

In the current study, we therefore examined the relations between emotional responsiveness and altruistic behavior in 4- to 5-year-old children in India and Germany. Altruistic behavior was examined through the dictator game using stickers as resources. Prior to the dictator game, children participated in an eye-tracking task in which their responses to fearful and happy facial expressions, presented either in isolation or in the context of several neutral facial expressions, were examined. We tested three main hypotheses. First, if emotional responsiveness indeed plays an important role in accounting for differences in altruistic behavior, then an association between the two should exist already in childhood. More specifically, based on the prior work with adults, we predicted that the link should only occur with respect to responsiveness to fearful faces but not to other facial expressions, and that greater sensitivity to fearful faces as indexed by faster orienting in the eye-tracking task should be associated with greater altruism in the Dictator Game. Second, if the predicted link exists in childhood and can be considered a hallmark of human altruism, then it should be seen across cultures. Third, given the evidence for overall differences in perceptual processing between Westerners and Asians, there might also be culture-specific patterns such that Indian children may show a greater sensitivity to context when processing facial expressions and that this may in turn relate to their altruistic behavior.

5.2 Methods

Participants. The final sample consisted of 96 German and Indian children (mean age=4.55 years; females=43). An additional 10 preschool-aged children were also tested, but were excluded from the final sample due to insufficient eye-tracking and behavioral data. The German sample consisted of 43 children (mean age= 4.52 years; females= 20) recruited via a child research database. The Indian sample consisted of 53 children (mean age= 4.51 years; females=22) recruited from the junior kindergarten section of Shishuvan School, Matunga Central, a suburban school in Mumbai, India. In both samples, children came from middle-class families with largely comparable educational and economic backgrounds. All parents provided written informed consent prior to the study and the children were given a toy as a present after the session. The sample sizes in both countries were determined before testing and analysis as they depended on the availability of children within this particular and predefined age range for which we received informed consent from the parents. Note that the overall sample size and the sample size for each culture are considerably larger than in most experimental studies with children of that age.

Stimuli. In Task 1, we used color photographs of happy, fearful, and neutral facial expressions taken from the previously validated FACES database. We selected photographs from four actresses (age 19 to 30, ID-numbers 28, 48, 163, 182). These actresses were selected on the basis of high recognition rates shown by a group of adult raters (Ebner, Riediger, & Lindenberger, 2010a) and on the basis of their ethnicity. Two of the four actresses had a facial appearance, especially skin color, chosen to ethnically represent faces typically seen among South Asians. The remaining two actresses had a facial appearance, chosen to ethnically represent faces typically seen among Caucasians. The photographs were cropped such that only the face, but not the hair, and ears, was visible in order to focus children on the inner features (eyes, nose, and mouth) of the faces. The face stimuli had a mean height of 14.5 cm and a width of 11.5 cm. Regions of interest (ROIs) were created within Tobii Studio. ROIs comprised of the entire face region of the stimuli. Please note that, due to the privacy laws enforced by the FACES database, we are unable to show the stimuli (faces of actresses) presented in this study.

In Task 2, we used the same face stimuli as in Task 1. However, in contrast to Task 1, here emotional faces (happy or fearful) were presented in the context of eight neutral faces. The faces were presented in a 3 by 3 matrix, against a black background; with the emotional face (happy or fearful) appearing in any of eight locations in the 3 by 3 matrix expect the center location. The location at which the emotional face appeared in each trial was randomized and changed from one trial to the next. The matrix was 20 cm in height and 16 cm in width. Each individual facial stimulus in the matrix had a height of 5 cm and width of 3.5 cm. Regions of interest (ROIs) were created within Tobii Studio. ROIs comprised of the entire matrix and every individual facial stimuli in the matrix.

Eye-tracking procedure. The child sat on a chair approximately 60 cm away from a 17” laptop screen. The region behind the computer monitor was a blank white washed wall to prevent any distractions for the child. A Tobii X2-60 compact eye tracker was set up at the bottom of the laptop screen in order to record the child’s looking behavior. Stimuli were presented through Tobii Studio (Version 3.2). Prior to stimulus presentation, a five-point calibration procedure was administered in order to ensure appropriate tracking of the children’s eyes. The German children were tested by a German experimenter in a testing room at a research institute, and the Indian children were tested by an Indian experimenter in a similar-sized and furnished testing room at Shishuvan School, Mumbai, India. Children were instructed to look at the laptop screen and pay attention to faces but were not asked to detect any particular emotion. The main aim of this instruction was to investigate the implicit capture of attention by emotional faces without giving the child explicit instructions to pay attention to emotional faces. Thus, we investigated natural scanning behavior rather than instructing the children to look for and detect specific emotions. In order to keep children attentive and motivated throughout, they were given a wireless mouse and asked to press the button whenever they saw an animated animal on the screen. Note that the button presses to the animations were not recorded, as they were not relevant for the actual experiment.

In Task 1, children viewed 12 trials, such that each actress presented each emotion once. The trial order was pseudo-randomized such that the same emotion and same actress did not appear twice in a row. The emotional faces (stimuli) were presented for 2.5 s. Prior to the presentation of each face, a fixation item (asterisk) appeared at the center of the screen for 1.5 s in order to re-orient the child's attention to the center of the screen. Four animations, showing an animated chicken, cat, dog, or lion, appeared once at random in between the trials. The duration of these animated clips varied from 1 to 3 s.

Task 2 was conducted after the completion of Task 1. Each child was given the same instructions prior to the start of Task 2 as in Task 1. In Task 2, children viewed 16 trials. In each trial, children saw an emotional face (either happy or fearful) in one of the eight positions in a 3 by 3 matrix. The emotional face never appeared in the center of the screen (matrix) because every trial was preceded by a fixation item (asterisk) shown in the center of the screen for 1.5 s. Each 3 by 3 matrix was presented for 6 s.As in Task 1, stimulus presentation was pseudo-randomized such that the same actress or emotion did not appear twice in a row. Six animations, showing a chicken, cat, dog, lion, lobster, or rattle appeared once in between trials. The duration of these animated clips varied from 1 to 3 s.

For data analysis, we extracted information regarding the latency to the first fixation and duration of looking at the emotional face. We focused our analysis on the latency for the first fixation and total fixation duration as dependent variables, as prior work suggests that these are sensitive measures for detecting individual variation in emotion processing and cultural variation in visual perception (Chua et al., 2005; Nummenmaa, Hyönä, & Calvo, 2006). Because an initial analysis revealed no systematic effects for total fixation duration as a dependent variable, our analysis was focused on the latency for the first fixation measure. Critically, there were no differences in overall latency for the first fixation across cultures, indexing that there were no general differences in the way in which children in both cultures oriented towards the facial stimuli (see results section).

Dictator Game. The Dictator Game followed the eye-tracking task. The experimenter placed five stickers in front of the child. The child was told that he or she could have all five stickers. Then the experimenter told the child about an unfamiliar peer in the adjoining room (gender and age of the other child were matched to the participant child) who had no stickers. The child was then asked whether he or she would be willing to share stickers with the peer. If the child agreed to share with the peer the experimenter asked how many of the stickers the child would like to share. The child was then asked to put the stickers he or she wanted to share in a box on the table in front of them. The instructions were given to the children by a native experimenter in their native language. Note that the Indian children grow up multilingually and the primary language of instruction spoken at the school where the experiments were conducted is English. The native Indian experimenter therefore instructed the children in English.

Please also note that the review board at the Max Planck Institute approved the protocol for the study and it was carried out in accordance with the provisions of the World Medical Association Declaration of Helsinki.

5.3 Results

We conducted an omnibus repeated measures ANOVA for the latency to the first fixation on the emotional target face with emotion (happy, fearful) and context (without context [Task 1], with context [Task 2]) as within-subjects factors, and culture

(Germany, India) and altruistic behavior (low [0 or 1 sticker] versus high [2 or more stickers] based on a mean split: *Mean* = 1.33, *SE* = 0.12) as between-subjects factors. Critically, there was no main effect of culture as a between-subjects factors on the latency to the first fixation on the emotional target faces measure, *F* (1, 91) = 0.5, *p* = 0.48, allowing us to rule out that there were overall cultural differences in the way in which children orient to faces in these two experiments. This analysis revealed a four-way interaction between emotion, context, culture, and altruistic behavior: *F* (1, 91) = 7.64, *p* = 0.007. Follow-up repeated measures ANOVAs conducted separately for fear and happiness showed that a three-way interaction between context, culture, and altruistic behavior only existed for fear, *F* (1, 92) = 14.338, *p* = 0.0002, but not for happiness, *F* (1, 92) = 0.32, *p* = 0.859, suggesting that this interaction effect is specific to fear. Further analysis to examine this interaction carried out separately for the two cultures revealed that for both the Indian and the German children there was a main effect of altruistic behavior on children's processing of fearful facial expressions (Germany: *F* (1, 41) = 4.144, *p* = 0.048; India: *F* (1,51) = 9.605, *p* = 0.003). Specifically, as shown in Figure 1, children who were more altruistic were faster to fixate on fearful faces presented without context (Germany: [low altruistic behavior] *M* = 0.37 seconds, *SE* = 0.13, [high altruistic behavior] *M* = 0.24, *SE* = 0.11; India: [low altruistic behavior] *M* = 0.38, *SE* = 0.08, [high altruistic behavior] *M* = 0.17, *SE* = 0.11). Our analysis further revealed that only among Indian children there was an interaction between altruistic behavior and context, *F* (1, 51) =4.144, *p* = 0.048. Specifically, as shown in Figure 2, Indian children who were more altruistic were slower to fixate on fearful faces when these were presented in the context of neutral faces ([low altruistic behavior] *M* = 3.59, *SE* = 0.81, [high altruistic behavior] *M* = 8.38, *SE* = 1.17). In other words, Indian children who were more strongly influenced (slowed down) by context showed greater altruistic behavior.

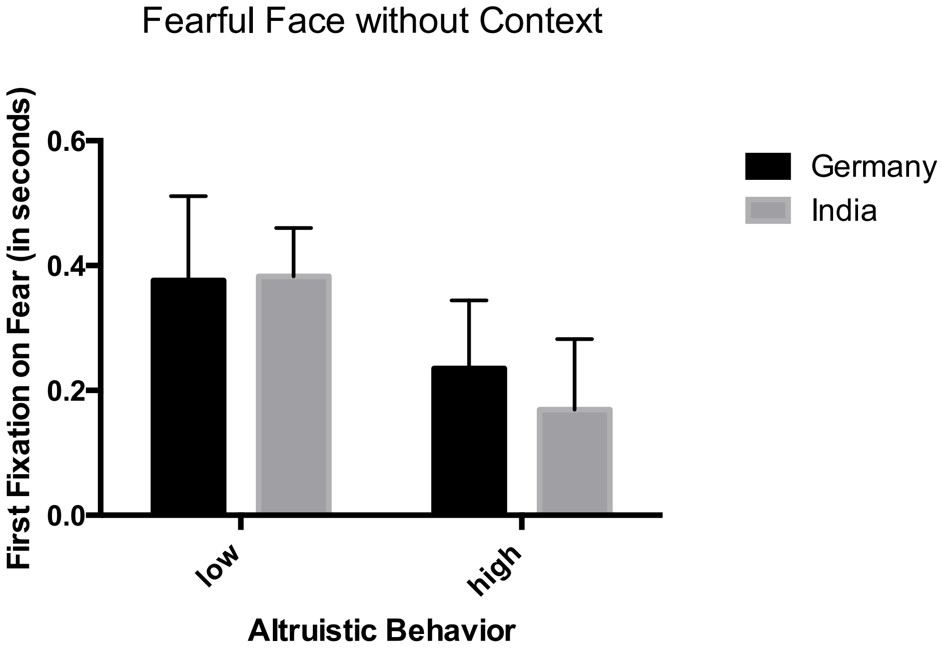

Figure 5.1. This figure shows the latency to the first fixation on fearful facial expressions in Task 1, where emotional faces were presented without a context, for children that show either low or high altruistic behavior in the Dictator Game separately for Germany and India.

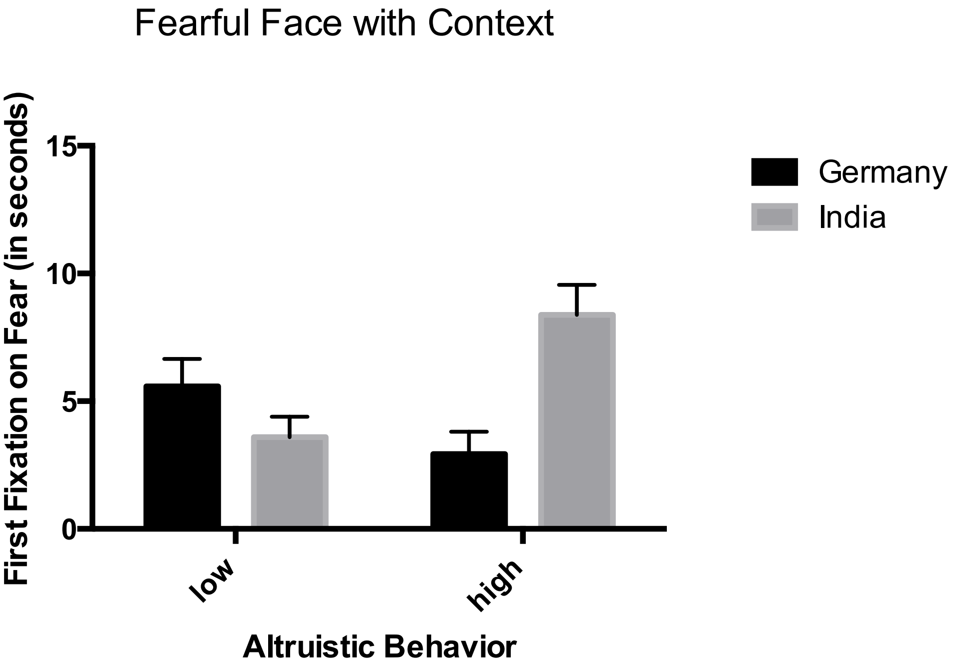

Figure 5.2. This figure shows the latency to the first fixation on fearful facial expressions in Task 2, where emotional faces were presented in the context of neutral facial expressions, for children that show either low or high altruistic behavior in the Dictator Game separately for Germany and India.

5.4 Discussion

We examined the relation between responsiveness to emotional faces (measured using eye-tracking) and altruistic behavior in the Dictator Game in children across cultures. Our results yielded three main findings. First, already in childhood, responsiveness to emotional faces is associated with differences in altruistic behavior. Specifically, similar to adults, children's selective responsiveness to fearful faces as indexed by faster orienting in the eye-tracking task was associated with greater altruism (sharing more stickers) in the Dictator Game. Second, this link between emotional responsiveness to fear and altruistic behavior existed in children of both cultures. Third, there were also culture-specific patterns, especially in children's processing of fearful faces in context. Namely, only among Indian children, those children who were slower to orient to fearful faces presented in the context of neutral faces (indexing a greater sensitivity to context) showed greater altruistic behavior in the Dictator Game. Taken together, our data suggest that across cultures and from early in development, altruistic behavior is tightly linked to our responsiveness to emotional signals of distress in others.

To our knowledge, the current findings are the first to provide direct developmental evidence for the existence of a link between emotional responsiveness to fear in others and altruistic tendencies. Such an extension of existing work with adults (Marsh & Blair, 2008) along a developmental dimension is important, because it suggests that responsiveness to fear in others might actually reflect a critical mechanism involved in the emergence of altruistic behavior. Furthermore, the current data point to emotional responsiveness to distress as a vital source for contributing to variability in the tendency of humans to engage in acts of altruism. Indeed, we may speculate based on these data that the striking differences in altruistic behavior observed between kidney donors on the one hand and psychopaths on the other hand in adulthood (Marsh et al., 2014) might have a strong developmental component rooted in differences in the responsiveness to others in distress (Davidov, Zahn-Waxler, Roth-Hanania, & Knafo, 2013; Hoffman, 2001). The current study provides a novel way to measure and link responsiveness to emotions in others to altruism, and may thus offer a new tool to examine and predict altruistic behavior in childhood and beyond.

Our data further revealed that increased altruistic behavior is associated with greater responsiveness (faster orienting) to fearful faces in Indian and German children.

This is in general agreement with prior cross-cultural work that has identified similar influences on and patterns of prosocial behavior in German and Indian children at 2 years of age (Kärtner, Keller, & Chaudhary, 2010). However, while Kärtner et al. (2010) found parents' socialization goals concerning interpersonal responsiveness (obedience) to play an important role in fostering prosocial behavior across cultures, our data indicate that intrinsic processes (such as the child's propensity to respond to distress cues in others) are also critical. This increased focus on intrinsic and culture-independent factors to explain the emergence and variability of prosocial behavior in childhood is in line with recent proposals that (a) view empathic concern as a key affective ability linked to prosocial responding that emerges early in development (Davidov et al., 2013) and (b) stipulate the presence of a prosocial temperament/personality factor that is largely explained by genetics (Knafo-Noam, Uzefovsky, Israel, Davidov, & Zahn-Waxler, 2015). From a developmental perspective, sensitive responding to fear in others can be traced back into the first year of life. By around 7 months of age, infants pay increased attention to fearful facial expressions as shown in behavioral and event-related potential studies (Leppänen & Nelson, 2012). Critically, this biased attention to fear in others has been shown to vary as a function of infant temperament (Rajhans, Missana, Krol, & Grossmann, 2015) and genetic variation within neurotransmitter systems (Grossmann et al., 2011). Together with the current findings, this raises the prospect that by measuring individual differences in responsiveness to fear in others during infancy, it might be possible to examine prosocial temperament/personality and predict altruistic behavior in children.

The current data also revealed fascinating culture-specific effects. As hypothesized on the basis of prior work(Nisbett & Miyamoto, 2005), Indian but not

German children showed a greater sensitivity to context when processing emotional facial expressions and this context sensitivity was related to their altruistic behavior. Specifically, among Indian children, those children who were slower to orient to the fearful face presented in the context of eight neutral faces (and were thus more sensitive to context) showed increased altruistic behavior in the Dictator Game. This is a surprising effect given that prior work with adults in Western societies (Marsh et al., 2007) reported a general association between increased altruistic behavior and greater responsiveness (faster orienting) to fearful faces. However, this effect is in agreement with work showing that Asians typically engage in greater context-dependent perceptual processes by attending to the relation between the object and the context in which the object is placed and are slower to fixate on a focal object in a visual scene than Westerners (Nisbett & Masuda, 2003). Interestingly, our data do not show that Indian children are generally more sensitive to context but rather that this increased sensitivity to context in Indian children is specific to fearful (but not happy) faces presented in context. This selective effect may suggest that particularly when attending to distress cues in others, context plays a greater role in Indian culture. More specifically, those Indian children who are more strongly affected (slowed down) by context when detecting fearful faces also show increased altruistic behavior. The reason why Indian children that behaved more altruistically were slowed down by context, rather than sped up, when detecting a fearful faces remains to be examined in future studies. Regardless of the direction of the context effect, the current finding points to a culture-specific association between context-sensitive fear processing and altruistic behavior that in Indian children operates in addition to the culture-independent association described above.

In summary, the current findings provide new insights into the developmental and cultural origins of altruism. In particular, our results demonstrate that across cultures, responsiveness to fear in others is linked to altruistic behavior in childhood. Moreover, the current data provide evidence for culture-specific patterns of context-sensitivity in these processes. These findings paint a rich picture emphasizing key affective, developmental, and cultural components that characterize the nature of altruism in humans.

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Part 4

Discussion

6 General Discussion

The aim of this dissertation was to investigate context based effects in emotion perception from a developmental perspective. For this purpose, three empirical studies were conducted that examined (1) perceiver-based context effects in infancy (Study 1), (2) stimulus-based context effects in infancy (Study 2), and culture-based context effects in early childhood (Study 3).

Specifically, Study 1 investigated perceiver-based context effects in infancy by focusing on the role that infant temperament plays in the neural processing of emotional body expressions in 8-month-old infants. Study2 focused on stimulus-based context effects in infancy by examining the early development of the neural processes involved in emotion perception across body and facial stimuli in 8-month-old infants with the help of event-related brain potentials (ERPs). Lastly, in order to assess culture-based context effects in early childhood, Study 3 examined the role of culture in children's context sensitivity when responding to emotional faces and its associations with altruistic behavior.

The results from Study 1 revealed that differences in infant temperament were systematically related to differences in the neural processing of emotional body expressions. More specifically, infants' tendency to approach novelty and infants' fearfulness were linked to differences in their brain responses to fearful but not happy body expressions. This suggests that specific infant temperament traits examined in Study 1 were specifically linked to the processing of fearful body expressions and not associated with general differences in emotion perception.

The results from Study 2 showed that body expressions impacted facial emotion processing and that incongruent body cues impaired the neural discrimination of emotional facial expressions in 8-month old infants. More specifically, effects of body context on the processing of facial emotions were observed for later ERP components related to attention allocation (Nc, 400-600 ms) and recognition memory (Pc, 600-800 ms) at anterior electrodes. The observed context effects for the Nc and Pc suggest that incongruent emotional body context impedes the discrimination of emotional faces, whereas congruent body context allowed for infants' successful discrimination of facial emotions as seen in the absence of body context in prior work (Dolan, 2002; Tracy & Robins, 2008).

The results from Study 3 revealed a relation between emotional responsiveness and altruistic behavior in 4 to 5-year-old children across cultures (India and Germany). Increased altruistic behavior was associated with a greater responsiveness to fearful faces, but not happy faces, in both cultures. Interestingly, only Indian children showed an effect, which indexes that context plays a role in contributing to the association between the detection of fearful faces and altruistic behavior. This suggests that altruistic behavior is generally linked to children's responsiveness to others in distress (fear) across cultures, but context plays an additional role in Indian, not German, children's responsiveness to fearful faces.

In summary, the findings of this dissertation indicate that emotion perception is a context-sensitive process which is in agreement with previous work (Barrett et al., 2011). The novelty of the current work rests upon the findings that context-sensitivity in emotion perception emerges early in development (Study 1 and 2) and also that cultural context during emotion processing plays a role in contributing to children's social behavior (Study 3). To the best of my knowledge, the evidence assembled in the current thesis from three studies represents the first attempt to systematically extend Feldman-Barrett et al.'s framework for conceptualizing context effects in emotion processing into the developmental domain. Therefore, the current thesis can be seen as a critical developmental extension of efforts challenging the prevailing view of emotion perception as being highly compartmentalized, conserved, and independent of context (Dolan, 2002; Tracy & Robins, 2008).

6.1 Decoding perceiver-based context effects in infancy

The results presented in Study 1 demonstrate that infant temperament critically shapes the way in which infants' brains responds to emotional information. More specifically, two traits of infant temperament assessed in this study, namely, infants' tendency to approach novelty and infants' fearfulness were associated with differences in their brain responses to fearful but not happy body expressions. This suggests that these two infant temperament traits are specifically associated with the processing of negative (fearful) body expressions. Given the argument that heightened sensitivity to negative emotions is a critical processing bias that might serve adaptive functions in alerting the individuals to potentially threatening or harmful situations which emerges in the second half the first year of postnatal life (Vaish et al., 2008), it is important to note that infant temperament contributes to variability in this processing bias. The next critical step would be to find out how enduring these individual differences in emotion processing biases are. There is compelling evidence that infant and child temperament is predictive of personality traits in adulthood (Buss & Plomin, 1984; Caspi & Silva, 1995; Rothbart, 1989). Furthermore, there is work to show that individual differences in adult personality traits impact emotion perception (Hamann & Canli, 2004). This suggests the possibility that individual differences in emotion processing bias seen in infants may continue to influence emotion processing beyond infancy. It will thus be critical to assess this possibility in longitudinal developmental studies. An extension of the current work along those lines would significantly advance our understanding of the role of perceiver-based context effects in emotion processing.

Another related point that requires attention is the fact that in Study 1,a sample of typically developing infants was studied. It would be beneficial to extend this approach to groups at risk for developmental disorders that have been associated with impaired emotion processing or to see how early developing differences in emotion processing can be used to predict developmental trajectories associated with atypical emotion processing. Specifically, it will be important to see whether it is possible to identify early markers of atypical emotion processing. For example, infant fearfulness has been discussed as an early precursor to behavioral inhibition in childhood and might be linked to anxiety disorders associated with particular emotion processing biases in adults (Degnan & Fox, 2007). Thus, it seems particularly important to consider temperamental traits such as infant fearfulness and approach as they might help researchers identify risk and resilience with respect to the development of anxiety-related issues.

In Study 1, only one dimension of negative emotionality, that is fearfulness, was assessed with respect to infant temperament. There is evidence to suggest that especially the expression of anger impacts temperament and behavior in 5- to 7-year-old-children (Solomon, O'Toole, Hong, & Dennis, 2014). However, it remains to be studied whether anger-related temperament effects have their origin in infancy. Extending the current line of research into studying effects of anger in the development of emotion processing appear to be of particular importance if we want to better understand the antecedents of aggressive behaviors in childhood (Fine, Trentacosta, Izard, Mostow, & Campbell, 2004).

In summary, the current findings critically suggest that individual differences in infant temperament might represent one aspect that is central to our understanding of perceiver-based context effects early in development.

6.2 Decoding stimulus-based context effects in infancy

The findings from Study 2 demonstrate that body expressions affect the neural processing of facial expressions in 8-month-old infants. By showing that body cues play an important role when perceiving emotional facial expressions early in life, the results from Study 2 provide developmental evidence for the notion that emotion perception is a context-sensitive process. So far, the investigation of the neural correlates of emotion processing in infancy has largely been focused on presenting facial expressions in isolation. However, in infants' daily lives, faces are not seen in isolation but perceived alongside body cues as well as vocal cues of emotion. To the best of my knowledge, this is the first study that investigated infants' integration of emotional body and facial expressions at a neural level. Therefore, this should be considered as a first step and much more research is needed to better inform our understanding of infants' ability to integrate emotional information from faces and bodies.

For example, it will be important to see whether the priming effects are also seen when faces serve as the primes and bodies as the target (the reverse of what we did in Study 2). In other words, do incongruent facial emotional information hamper the discrimination of emotional body expressions in infants? This is particularly important considering work with adults has suggested that body cues have a stronger impact on the recognition on facial cues then vice versa (Aviezer et al., 2012). If this were the case, then only or at least to a greater extent when bodies are presented as primes, as done in Study 2, we would expect to see an effect on infants' discrimination of emotional expressions. In future work it will also be important to address another issue related to using a priming design. Namely, during social interaction, facial and bodily cues are simultaneously accessible for infants, whereas in our priming design the body cue was not visible to the infants when having to discriminate between facial expressions. It will thus be important to use compound stimuli in which faces and bodies are arranged in congruent and incongruent manner to better probe infants' sensitivity to face-body correspondences, as done in previous adult studies (Meeren et al., 2005). In order to better understand what perceptual features infants use when integrating between face and body it will be informative to record face and body scanning patterns through eye tracking (Hunnius & Geuze, 2004). This will allow further study of contextual biases that contribute to emotion discrimination and integration, and has the potential to reveal undetected individual differences in emotion processing and how they affect these processes. In conclusion, Study 2 provides a starting point for the systematic study of stimulus-based context effects on facial emotion processing, highlighting the importance of body cues that contribute to this process.

6.3 Decoding culture-based context effects in childhood

The results from Study 3 have suggested that across cultures and early in development, altruistic behavior is associated with our responsiveness to emotional signals of distress (fear) in others. Interestingly, Indian but not German children showed a greater sensitivity to context when processing emotional facial expressions and this context sensitivity was related to their altruistic behavior. The results from Study 3 provide evidence for culture-specific patterns as another component of context-sensitivity during emotion processing. Furthermore, these findings not only indicate that emotion processing should be considered as context-sensitive but also that emotion perception itself serves as a context when guiding social behavior such as the sharing seen in the Dictator Game, which was influenced by the individual children's emotional processing biases. This proposed relation between emotion perception and overt social behavior goes beyond (Barrett et al., 2011) framework as it considers a critical additional piece in the puzzle of explaining emotion processing in humans. In particular, emotion perception needs to be understood in its functional context with respect to the question of what emotion processing and especially particular biases therein contribute to the way we behave towards others. The case has been made in prior work that emotional sensitivity and especially empathy might be tightly linked to altruistic behavior in humans (Eisenberg & Miller, 1987). It seems critical to consider possible functional implications of emotion processing with respect to the way it guides and influences social behavior.

Regarding differences observed between cultures in Study 3, it has been argued that culture-specific variation in visual processing of stimuli arises from differences in the societal structure and practices (Ji, Zhang, & Nisbett, 2004; Nisbett, 2010). More specifically, Eastern cultures' emphasis on the importance of interpersonal relationships and interdependence on other members of their society is thought to impact the way people with this culture perceive, think, and act. Westerners on the other hand have been described as more focused on independence with a greater focus on the self, resulting in a more individualistic approach to life. Based on these differences in societal practices and norms, it has been shown that Eastern cultures rely more on context (background when compared to foreground object) when observing a situation (visual scene) while

Westerners focus more on the foreground object (Nisbett & Masuda, 2003). Interestingly, the results from Study 3 did not show that Indian children are generally more sensitive to context, but rather that this increased sensitivity to context in Indian children was specific to fearful (but not happy) faces presented. This selective effect may suggest that particularly when attending to distress cues in others, context plays a greater role in Indian culture. More specifically, those Indian children who are more strongly affected (slowed down) by context when detecting fearful faces also show increased altruistic behavior. The reason why Indian children that behaved more altruistically were slowed down by context, rather than sped up, when detecting fearful faces remains to be examined in future studies. For example, it might be important to see whether this effect is specific to faces surrounding a fearful face or whether it extends beyond faces to non-social objects. With this extension, it would be possible to determine if it is social (facial) information in particular that slows down Indian children, as those faces may be used as a reference especially by those who are more other-oriented, prosocial and altruistic. In other words, children that see distress in one face surrounded by many neutral faces may 're-interpret' the distress signal based on the fact that the other faces indicate no distress. For happy faces surrounded by neutral faces it is likely that no such contrast arises as neutral and happy faces are both thought to signal safety (no distress or absence of threat) (Vaish et al., 2008).

Another aspect that should be taken into consideration is that prior cross-cultural work has reported general context effects in children from East Asia when compared to the U.S., whereas in our Study 3 we have assessed children from South Asia (India) and Germany (Europe). Although the Indian culture is thought to be very similar to that of East Asian cultures (Eastern) and German culture is considered to be similar to the US

(Western), it has been suggested that the societal practices, norms and values of Europeans are somewhat in-between that of East Asians and US Americans (Nisbett & Masuda, 2003). It therefore seems to be critical to extend the current approach to other Eastern countries and other Western countries in order to systematically examine cross-country (for example between the US and Germany or between India and Japan) and cross-cultural effects (between Eastern and Western cultures). As the current study relied on urban children in both countries, it will also be important to see whether there are any differences between rural and urban samples, as prior work suggests that there are such differences (Kärtner et al., 2010). Regardless of these outstanding questions, the data presented in Study 3 indicates that cultural context plays a role in how emotional processes are linked to social behavior, suggesting that this an important contextual variable that needs to be taken into account when studying the development of emotion processing.

6.4 Limitation

Apart from the need for future work related to the limitations mentioned above, it is important to acknowledge one general limitation regarding the empirical approach taken in this thesis. From a developmental perspective, a general limitation arises from the fact that in Studies 1 and 2 infants in their first year of life were tested, whereas in Study 3 children between the ages of 4 to 5 years were tested, all in independent cross-sectional studies. It is therefore not possible to draw conclusions regarding the question of how context-sensitive emotion processing develops from infancy to childhood. Future studies employing a longitudinal design will be required to address this important developmental question.

6.5 Conclusion

The major goal of this dissertation was to extend (Barrett et al., 2011) framework of context-sensitive emotion processing into early development. The findings from this dissertation critically extend this framework by providing first evidence for context-sensitivity in emotion processing into the developmental domain. Specifically, this dissertation shows that perceiver-based and stimulus-based context effects on emotion processing occur in infancy, before the onset of spoken language. In other words, these contexts appear to play a role already before spoken language can exert influences on emotion perception (Barrett, Lindquist, & Gendron, 2007). Furthermore, as shown in Study 3, the current thesis suggests that cultural contextual factors need to be taken into consideration when studying emotion processing in highly verbal4- to 5-year-old children that have been socialized into particular social practices and norms. Taken together, the current thesis represents a first stride into describing the role of different contexts in the early development of emotion processing. It is my hope that this dissertation will provide a foundation for further stimulating research within the novel conceptual framework of context-sensitive emotion processing.

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Erklärunggemäß § 8 Abs. 1 Buchst. b) und c) der Promotionsordnung derFakultätfürVerhaltens- und EmpirischeKulturwissenschaften

Declaration in accordance to § 8 (1) b) and § 8 (1) c) of the doctoral degree regulation of Heidelberg University, Faculty ofBehavioural andCultural Studies

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Promotionsausschuss der FakultätfürVerhaltens- und EmpirischeKulturwissenschaftender Ruprecht-Karls-Universität Heidelberg
Doctoral Committee of the Faculty ofBehavioural andCultural Studies of Heidelberg University

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