Doctoral thesis submitted to
the Faculty of Behavioural and Cultural Studies
Heidelberg University
in partial fulfillment of the requirements of the degree of
Doctor of Philosophy (Dr. phil.)
in Psychology

Title of the publication-based thesis

Infant Processing of Emotional Faces and Bodies: Insights from Event-related Potentials and Asymmetrical Frontal Brain Activity

presented by
M.A. Erziehungswissenschaft,
Manuela Missana

year of submission
2015

Dean: Prof. Dr. Klaus Fiedler
Advisor: Prof. Dr. Tobias Grossmann

Acknowledgments

This thesis is the result of the time I spent at the Max Planck Institute for Human Cognitive and Brain Sciences. There are many people to whom I am very thankful, who helped and supported me throughout my PhD time.

First of all, I would like to thank Tobias Grossmann for giving me the opportunity to carry out this project and for being a great supervisor and collaborator. Thank you for all the new and exciting things I was able to learn in the past years, for your encouragement and excellent advice. Thank you for always having the time and being helpful for all the smaller and bigger problems during my PhD time.

Second, I would like to thank my "Early Social Development" Group members: Caterina, Purva, Katie, Nicole, Sarah and Merle. Thank you for all the interesting discussions, scientific as well as non-scientific, and all the fun we had!

Thank you to my wonderful colleagues at the MPI, in particular Katja Kirsche, Hyeon-Ae Jeon, Charlotte Grosse Wiesmann, Tanja Poulain, Anna Strotseva, and Florence Ruby. My special thanks go to Christian Obermeier and Douglas Weinbrenner, who welcomed me so warmly.

Thank you to Caterina Böttcher and Heike Böthel for helping me with the data acquisition. Thanks to Kerstin Flake, Andrea Gast-Sandmann, and Stephan Liebig for their support in creating the stimuli for the experiments and creating graphical illustrations.

Last but not least, I am deeply grateful to my friends and family. Thank you Johannes for always believing in me, for your support and for all your love. Noah, you are such a wonderful little boy. I am so proud of you.

TABLE OF CONTENTS

List of Scientific Publications for the Publication-based Thesis

I. Schrift

Missana, Manuela, Grigutsch, Maren, & Grossmann, Tobias (2014). Developmental and individual differences in the neural processing of dynamic expressions of pain and anger. *Plos One, 9,* e93728.

II. Schrift

Missana, Manuela, Atkinson, Anthony P., & Grossmann, Tobias (2015). Tuning the developing brain to emotional body expressions. *Developmental Science*, *18*(2), 243-253.

III. Schrift

Missana*, Manuela, Rajhans*, Purva, Atkinson, Anthony P., & Grossmann, Tobias (2014). Discrimination of fearful and happy body postures in 8-month-old infants: An event-related potential study. *Frontiers in Human Neuroscience*, *8*: 531.
* = both authors contributed equally.

IV. Schrift

Missana, Manuela & Grossmann, Tobias (2015). Infants' emerging sensitivity to emotional body expressions: Insights from asymmetrical frontal brain activity. *Developmental Psychology, 51*(2), 151-160.

List of Figures

List of Tables

Abbreviations

ACC = anterior cingulate cortex

Ag/AgCl = silver-silver chloride

AI = anterior insula

cm = centimeter

EBA = extrastriate body area

EEG = electroencephalography

e.g. = example given

EOG = electrooculography

EPN = early posterior negativity

ERP = event-related brain potential

FBA = fusiform body area

FFA = fusiform face area

fMRI = functional magnetic resonance imaging

fNIRS = functional near-infrared spectroscopy

g = gram

Hz = Hertz

IBQ-R = Infant Behavior Questionnaire – Revised

IC = independent component

ICA = independent component analysis

i.e. = in example

IRI = Interpersonal Reactivity Index

kΩ = kiloΩ

LPP = late positive potential

ms = milliseconds

mPFC = medial prefrontal cortex

Nc = negative component

μV = micro Volt

OFC = orbito-frontal cortex

Pb = positive before

Pc = positive component

PLD = point-light displays

ROI = regions of interest

s = second

SAM = Self-Assessment Manikin

SPF = Saarbrücker Persönlichkeitsfragebogen

STS = superior temporal sulcus

Part I

Introduction

1 General Introduction

1.1 Emotion Perception in Infancy

Communication is one of the most important aspects of the social human life. Through communication we share our thoughts, intentions and feelings with others. In our daily interactions we communicate through spoken language but also heavily rely on other verbal and nonverbal signals when conveying information to another person. For example, our words are accompanied by emotional vocal expressions and non-verbal signals such as facial and body expressions. In general, the expression of emotions is highly adaptive as it provides a rich source of information regarding one's own intentions and feelings (Darwin, 2009/1872). The ability to then recognize those inner states is an essential social skill that allows us to adequately respond to others' needs (Frith, 2009; Izard, 1977), thus contributing to our social relationships.

From birth, infants are interested in the social world and have a high preference to orient towards social signals, such as faces and voices (Ecklund-Flores & Turkewitz, 1996; Johnson, Dziurawiec, Ellis, & Morton, 1991). Within the first year infants not only show various emotional expressions themselves, but also develop the ability to detect and distinguish between emotions expressed by others (see de Haan & Matheson, 2009 for review). A host of behavioral studies has been conducted to study infants' emerging sensitivity to emotional signals. In particular, infants' ability to discriminate, categorize, and recognize emotions has been investigated (see Walker-Andrews, 1997 for review). More recently work has begun to focus on the brain processes that underlie emotion perception in infancy. For example, infant neural responses to a variety of emotional facial and vocal expressions were investigated in order to extend behavioral findings (de Haan & Matheson, 2009; Grossmann, 2013a). While previous research has provided important insights into how infants process emotions, there are several remaining questions. Past research on infants' emotion perception mainly used samples of the basic emotions, such as happiness, anger and fear (LaBarbera, Izard, Vietze, & Parisi, 1976; Nelson & de Haan, 1996; Nelson & Dolgin, 1985; Peltola, Leppänen, Mäki, & Hietanen, 2009; Soken & Pick, 1992). However, very little is known about other emotions, or whether infants can discriminate between negative emotional expressions. For example, it is currently unclear how infants process facial expressions of pain and whether they can distinguish them from other negative expressions. Previous research with infants and toddlers in the second year of life focused on behavioral responses to others in distress (expressing pain) (Bandstra, Chambers, McGrath, & Moore, 2011; Young, Fox, & Zahn-Waxler, 1999; Zahn-Waxler, Radke-Yarrow, Wagner, & Chapman, 1992). However, whether infants in the first year of life are able to discriminate pain from other facial expressions and how this process manifests itself in the brain has yet to be studied. Furthermore, studies investigating emotion perception focused on the perception of facial and vocal expressions. However, in our daily interactions we do not express emotions only via the face and the voice but use our body movements and postures to communicate emotional states. While there is recent behavioral work examining the perception of emotions from body expressions (Zieber, Kangas, Hock, & Bhatt, 2014b), its neural correlates are yet to be determined. Moreover, the majority of previous infant studies mostly used static displays to investigate emotion perception. The perception of emotion from dynamic expressions is an important extension of this work, because it provides a way to present infants with more ecologically valid emotional stimuli (Hess & Blairy, 2001; Kilts, Egan, Gideon, Ely, & Hoffman, 2003).

The next sections aim to describe infants' developing ability to perceive emotions from facial expressions (1.2) and from body expressions (1.3) by reviewing empirical behavioral and neural evidence. In the following section (1.4) the research questions are formulated with respect to the previous findings. In Chapter 2 the method is described with an introduction to EEG/ERP as well as frontal EEG asymmetry in the alpha frequency band. The following empirical Chapters 3 to 6 contain the studies that contributed to this thesis. In Chapter 7, the current findings are summarized and discussed in the context of previous neurophysiological and behavioral studies on emotion perception in infancy.

1.2 Emotion Perception from Faces

Research on infants' emotion perception from faces has a long tradition (see Nelson, 1987 for review). More generally, perception can be defined as a process to obtain information about our environment, making inferences about what we see and hear in order to understand the situation and allowing us to interact in the social world (Gibson, 1988; Gordon, 2004). With respect to infant research on emotion perception, studies mainly investigated whether infants are able to discriminate, categorize, and recognize emotional expressions (see Walker-Andrews, 1997). Discrimination can be defined as the ability to perceive differences between two or more stimuli, while categorization refers to the ability to recognize that certain stimuli belong to the same group even if they are expressed in different ways or by different people, e.g. different variants of expressing happiness in the face all belong to the group of happy expressions (de Haan & Nelson, 1997a; Quinn & Slater, 2003). Emotion recognition refers to the capacity of identifying emotions in others, including the understanding of the meaning of the expression (Walker-Andrews, 1997). This in turn, provides us with information about others' intentions and inner states during social interactions (Bornstein & Arterberry, 2003; Frijda, 1969). For example, viewing a person expressing fear in response to an object or event signals that this stimulus might be harmful and should therefore be avoided (L. J. Carver & Cornew, 2009).

Infant research made use of a variety of methods to approach emotion perception including behavioral techniques, such as familiarization, visual preference tasks, or habituation paradigms (Nelson & Dolgin, 1985; Nelson, Morse, & Leavitt, 1979; Walker-Andrews, 1997). In contrast to the behavioral measurement of emotion perception event-related-brain potentials (ERPs), which offer a good temporal resolution, are examined in order to study the neural processes involved in emotion perception (e.g., de Haan & Matheson, 2009; de Haan & Nelson, 1997a). Most recently functional near-infrared spectroscopy (fNIRS), which offer a good spatial resolution, has been used to investigate the activation of brain areas during various tasks by measuring hemodynamic responses in the infant brain (Aslin & Mehler, 2005; Lloyd-Fox, Blasi, & Elwell, 2010).

Facial expressions are one of the most important means to convey social signals and providing cues to guide our behavior during social interactions (Frith, 2009; Izard, 1977, 2007). Facial communication is also thought to serve as a vital basis for early mother and child attachment and bonding (Bowlby, 1969). Within hours after birth infants preferentially orient to faces (Goren, Sarty, & Wu, 1974; Johnson et al., 1991) and despite newborns’ low visual acuity, at close distance, newborn infants are able to detect salient facial features such as eyes, nose and mouth (Ramsey-Rennels & Langlois, 2007). Newborns’ face preferences suggest that their perception is tuned to the characteristic structural configuration of faces (Johnson, 2005; Morton & Johnson, 1991). Within the first days infants also preferentially attend to their mothers face over a strangers face (Bushnell, 2001; Bushnell, Sai, & Mullin, 1989; Walker-Andrews & Dickson, 1997). However, this early recognition of their mother’s face appears to be based on information from the outer contour of the head and the hairline, in addition to the internal configuration of eyes, nose and mouth (Bushnell et al., 1989). Only by the age of 6 months, when visual acuity and contrast sensitivity improves significantly and reaches adult-like levels (Gwiazda, Bauer, & Held, 1989), infants ability to discern fine detail, such as distances between eyes and eyebrows, develops, which is important to detect differences between facial expressions (Hainline & Abramov, 1992).

1.2.1 Emotion Perception from Faces – Behavioral Evidence

There is some evidence to suggest that shortly after birth newborns are able to discriminate between some facial expressions, such as happy, sad or surprised faces (Field, Woodson, Greenberg, & Cohen, 1982). However, subsequent work has failed to replicate these findings (Kaitz, Meschulach-Sarfaty, Auerbach, & Eidelman, 1988). This is in line with the host of behavioral studies indicating that the ability to detect and discriminate emotional facial expressions develops during the first year of life (Barrera & Maurer, 1981; LaBarbera et al., 1976; Schwartz, Izard, & Ansul, 1985; Young-Browne, Rosenfeld, & Horowitz, 1977). For example, 3-month-old infants discriminated smiling (happy) from frowning (angry) faces (Barrera & Maurer, 1981), happy from surprised faces and happy from sad expressions (Young-Browne et al., 1977). Moreover, Schwartz and colleagues (1985) showed that some 5-month-old infants can visually discriminate angry, sad and fearful facial expressions. In a study by LaBarbera and colleagues (1976) 4- to 6-month-old infants looked longer to a happy face than to an angry or neutral expression, indicating that they discriminate happy expressions from the other expressions. With the age of 6 months infants reliably also distinguish between varying intensities of sad and happy facial expressions (Striano, Brennan, & Vanman, 2002). By 7 months of age, infants look longer at fearful expressions than at happy expressions as shown in a visual preference test (Nelson & Dolgin, 1985).

That infants can discriminate between various facial expressions does not necessarily imply that they are able to categorize facial expressions. Infants need to grasp that a particular emotional facial expression belongs to the same category, independent of the individual who shows it and regardless of the intensity of the expression. In studies that investigate these categorization abilities, multiple exemplars of the same category are presented and infants are tested with a new exemplar of the familiarized category or a new exemplar from a different category (Bornstein & Arterberry, 2003; de Haan & Nelson, 1998; Walker-Andrews, 1997). Although both stimuli are novel to the infants, it is assumed that, if infants have formed a category of the expression, the time they spent looking at the stimulus should only increase to the new exemplar of the novel category (de Haan & Nelson, 1998). For example, in a study by Nelson and colleagues (1979), 7-month-old infants were familiarized with happy expressions posed by two actresses. After the familiarization phase infants were shown a new actress posing either a happy or a fearful facial expression. In this study, infants looked longer to the fearful expression than to the happy expressions, indicating that they represent emotional information at the categorical level. However, when infants were first familiarized with fearful expressions they did not show this categorization ability (Nelson et al., 1979), suggesting that they can categorize happy but not fearful expressions at this age. That 7-month-old infants can recognize the similarity of happy facial expressions over changing identities has been further demonstrated in a study by Kestenbaum and Nelson (1990). In another study, 7-month-old infants showed also the ability to categorize happy facial expressions of varying intensity (Kotsoni, de Haan, & Johnson, 2001). To summarize these results, infants at the age of 7 months rely on categorical information when perceiving happy facial expressions.

Towards the end of the first year, when infants start to locomote and explore the environment they begin to use others' expressions which later on will guide their behavior (Moses, Baldwin, Rosicky, & Tidball, 2001; Mumme, Fernald, & Herrera, 1996). This is the best evidence to suggest that, beyond discriminating and categorizing emotions, infants begin to grasp the meaning of facial expressions. The phenomenon that infants use others' emotional expressions is referred to as *social referencing* (Campos & Stenberg, 1981;

Klinnert, Campos, Sorce, Emde, & Svejda, 1983). For example, in a study by Mumme and Fernald (2003) 12-month-old infants were shown an experimenter on a television screen expressing happy, fear, or neutral facial and vocal signs towards a novel toy (target) while another novel toy was ignored. Then, these novel toys were presented to the infants, and infants' interactions with the toys were examined. No differences in interactions with the target were found when comparing happy and neutral conditions, whereas in the fear condition infants avoided the target more often when compared with the neutral condition (Mumme & Fernald, 2003). More evidence for infants being able to recognize facial expressions around this age comes from behavioral work showing that infants can integrate emotional information across modalities (face and voice) (Walker-Andrews, 1997).

1.2.2 Emotion Perception from Faces – Neural Evidence

From a neuroscience perspective, neuroimaging studies using functional magnetic resonance imaging (fMRI) with adults have identified a face sensitive region in the fusiform gyrus, the fusiform face area (FFA), which is activated more strongly by passive viewing of faces compared to objects (Kanwisher, McDermott, & Chun, 1997; Kanwisher & Yovel, 2006). In addition to the FFA, the superior temporal sulcus (STS) and the inferior and middle occipital gyri show selective activations during face processing (Haxby et al., 1999; Kanwisher et al., 1997). FFA and STS are sensitive to durable characteristics of a face and changeable (dynamic) aspects of faces, respectively (Haxby et al., 1999).With respect to detecting emotional information from faces, adult research has demonstrated selective activation in the medial prefrontal cortex (mPFC), orbito-frontal cortex (OFC), the insula, and the amygdala, especially in response to fearful facial expressions (Adolphs, 2002; Hornak, Rolls, & Wade, 1996; Vuilleumier, Armony, Driver, & Dolan, 2001).

The use of functional neuroimaging techniques such as fMRI is limited for studying emotion perception in infancy, because they require the participant not to move and expose them to a fairly noisy environment. However, EEG and fNIRS are methods well suited to study the neural correlates of emotion perception in infancy, because they do not suffer from these limiting factors. There is evidence to suggest that cortical processes involved in face and emotion perception are functional during infancy (Grossmann & Johnson, 2007). With respect to emotion perception, infant ERP studies provide neural evidence for infants' ability to discriminate between various emotional facial expressions (Grossmann, Striano, & Friederici, 2007a; Kobiella, Grossmann, Reid, & Striano, 2008; Nelson & de Haan, 1996). For example, in a study by Nelson and de Haan (1996), 7-month-old infants' ERPs were measured in response to happy and fearful facial expressions. Fearful facial expressions elicited an enhanced negative component (Nc) at 370 to 680 ms when compared to happy expressions (Nelson & de Haan, 1996). The Nc is a negative deflection that has its maximum at frontal and central electrode sites and has been associated with greater orientation and increased attention allocation to the stimulus (Reynolds & Richards, 2005). On this basis Nelson and de Haan (1996) concluded that infants allocate more attention towards fearful facial expressions compared to happy facial expressions. Moreover, the results of this study showed that happy facial expressions elicited a larger positivity (Pc) during a later time window of 680 to 1280 ms at frontal, central and parietal electrodes when compared to fearful expressions. This enhanced late positive component evoked by viewing happy facial expressions is thought to reflect processes associated with recognition memory for happy facial expressions (Nelson & de Haan, 1996).

Building on this prior study, Peltola and colleagues (2009) measured ERPs in 5- and 7-month-old infants when infants were presented with happy and fearful facial expressions in order to investigate when sensitive responding to fearful facial expressions emerges. Critically, only in 7-month-old infants, but not in 5-month-old infants, fearful facial expressions elicited an increased Nc between 350 to 600 ms compared to happy expressions. This suggests that infants' increased attention to fearful faces emerges between 5 and 7 months of age (Peltola et al., 2009). This is indicative of an important change in infants' emotion perception skills during the first year (see Grossmann, Striano, & Friederici, 2007, for evidence how the perception of angry faces follows a different time course in infancy).

There is also evidence that infants at the age of 7 months can distinguish between different negative facial expressions. Specifically, in a study by Kobiella and colleagues (2008), 7-month-old infants were presented with angry and fearful facial expressions and ERPs were measured. Angry facial expression elicited a larger Nc at fronto-central electrodes between 300 to 600 ms indicating greater attention allocation to angry when compared to fearful expressions (Kobiella et al., 2008).

To summarize, these findings demonstrate that around the age of 7 months, infants' ERP responses differ between various emotional facial expressions. This is in congruence with prior results from behavioral research. The research reviewed here suggests that, by the age of 7 months, infants (a) can discriminate between positive and negative emotions (i.e., happy and fearful facial expressions), as well as between some negative expressions (i.e., angry and fearful expressions) as reflected in the Nc and (b) recognize positive facial expressions as reflected in the Pc.

1.3 Emotion Perception from Bodies

Similar to facial expressions, body expressions provide an important means of communicating information regarding the intentions and emotional states of a person (Argyle, 1988; de Gelder, 2009; Walk & Homan, 1984). From an evolutionary point of view, body expressions are argued to be the most immediate and phylogenetically preserved way of expressing emotions essential to communicating affect, especially over larger distances when one cannot see the precise expression in the face (de Gelder, 2009). Adults are able to readily detect various emotions from body expressions (Coulson, 2004; Shaarani & Romano, 2007). This has also been shown in studies using point-light displays (PLDs)[1] of body expressions that only provide little information about the body shape (Atkinson, Dittrich, Gemmell, & Young, 2004; Atkinson, Tunstall, & Dittrich, 2007; Atkinson, Vuong, & Smithson, 2012).

Similar to what is known about the perception of faces, fMRI studies with adults show that the perception of human bodies is associated with specific brain areas. For example, the extrastriate body area (EBA) is more strongly activated during the perception of human bodies and body parts compared to other objects including faces (Downing, Jiang, Shuman, & Kanwisher, 2001). Another brain area that was identified to be sensitive to the human body is the fusiform body area (FBA). Specifically, the FBA is more activated to the whole body form than only to parts of the body (Taylor, Wiggett, & Downing, 2007) and plays a role when distinguishing between familiar and unfamiliar bodies (Hodzic, Kaas, Muckli, Stirn, & Singer, 2009). This work suggests that faces and bodies are processed in adjacent and overlapping but distinct networks that are part of the fusiform gyrus (Peelen & Downing, 2005).

Emotional body expressions have been found to elicit increased amygdala activation when participants were presented with fearful, angry or neutral bodies (Hadjikhani & de Gelder, 2003; Pichon, de Gelder, & Grèzes, 2008, 2009; van de Riet, Grèzes, & de Gelder, 2009). Brain imaging studies with patients and healthy adults showed that the ability to recognize emotions from body expressions relies on specific brain processes in the right hemisphere, such as right temporo-parietal junctions, right temporal pole and lateral orbital cortex (Grèzes, Pichon, & de Gelder, 2007; Heberlein, Adolphs, Tranel, & Damasio, 2004;

---

[1] Point-light displays (PLDs) are illuminated moving dots that reflect the motion of the major key joints of a moving character. PLDs were first invented and described by Gunnar Johansson in 1973.

Heberlein & Saxe, 2005). Furthermore, areas that have been associated with structural encoding of bodies (EBA and FBA) are modulated by emotional body expressions (Peelen, Atkinson, Andersson, & Vuilleumier, 2007).

From a developmental perspective, infant research on body expressions primarily focused on infants' perception of biological motion but not on the perception of emotional information. In behavioral studies, it has been shown that from very early on in development infants prefer biological motion (i.e., a walking hen), over non-biological (i.e., randomly drifting dots) (Johansson, 1973; Simion et al., 2008). This preference for biological motion is also orientation specific as newborns prefer upright over inverted biological motion (see Bertenthal, 1993 for reviews; Simion et al., 2008).

Infants' perception of biological motion has also been examined in ERP studies (Hirai & Hiraki, 2005; Reid, Hoehl, & Striano, 2006). In a study by Hirai and Hiraki (2005), 8-month-old infants were presented with biological and scrambled motion displays. The results of this study showed that the amplitude in response to biological motion was more negative at right hemisphere occipito-temporal electrodes after 200 to 300 ms compared to scrambled motion displays (Hirai & Hiraki, 2005). In another study by Reid and colleagues (2006), 8-month-old infants were shown upright and inverted PLDs depicting human movement. In response to upright presented PLDs a larger positive amplitude was observed at right parietal electrodes between 200 and 300 ms when compared to inverted PLDs (Reid et al., 2006). Although the ERP responses differed with respect to the direction of the amplitude modulation (positive vs. negative deflection), the results generally indicate that the infant brain develops brain processes that are specialized in detecting upright body expressions that involve the structural information typical for the human body. In addition, these ERP results support the notion that the processing of body movement is lateralized to the right hemisphere.

With regard to infants' perception of emotions from bodies so far only one behavioral study has addressed the discrimination of emotions when viewing body expressions (Zieber et al., 2014b). In this study, a paired-comparison looking procedure was applied in order to test 6.5-month-old infants looking behavior when they viewed videos of upright and inverted happy and neutral full-light body expressions (Zieber et al., 2014b). Infants preferred the happy expressions over the neutral expressions but only when they were presented in an upright orientation. In a second experiment, 6.5-month-old infants heard either a happy or an angry vocalization (i.e., laughing or grunting) while viewing videos of upright and inverted happy and angry full-light body expressions. The results indicated that infants were able to match happy and angry body expressions to the corresponding vocalization when the expressions were presented in an upright orientation but not when they were inverted. These findings suggest that 6.5-month-old infants are sensitive to bodily expressed emotions and are able to match them to corresponding affective vocalizations (Zieber et al., 2014b). However, to the best of our knowledge, hitherto no study has investigated the neural underpinnings of emotional body processing.

1.4 Present Studies/ Research Questions

The major aim of this dissertation was to contribute to the understanding of how the infant brain processes emotional signals. Specifically, the focus was on investigating the neural bases of infants' emotion perception from others' emotional facial and body expressions using EEG. Based on and expanding upon the existing work reviewed in the introduction, I will present four empirical studies examining infants' processing of emotional facial (*Study 1*) and body expressions (*Studies 2, 3* and *4*). The research questions addressed in these four studies will now be briefly outlined.

Study 1: Facial expressions. Much work has addressed infants' perception of emotional facial expressions at both behavioral and neural levels. These studies approached infants' perception of positive and negative expressions by relying on basic emotions, such as the expression of happiness, sadness, fear or anger. However, one facial expression that has been greatly neglected in infant research is the facial expression of pain. Pain is not considered to be a basic emotion, but nonetheless constitutes an unpleasant affective state that is associated with a facial expression distinct from other basic emotions (Williams, 2002). From a developmental perspective the perception of pain in others has mainly been assessed in studies on the development of empathic responding in the second year of life (Eisenberg, 2000; Eisenberg, Fabes, & Spinrad, 2006; Zahn-Waxler et al., 1992). But how infants in the first year of life process the facial expression of pain and whether they are able to discriminate it from other negative emotional expressions, such as anger, has not been studied so far. Moreover, how does the neural processing of pain and anger facial expressions compare between infants and adults? And, how do individual differences, especially infant temperament and adult dispositional empathy impact the brain responses to these expressions? In order to address these questions a multi-measure approach was applied by combining EEG/ERPs, frontal EEG alpha asymmetry and the assessment of individual differences through questionnaires. Specifically, in the first study of this dissertation, 8-month-old infants' processing of pain and anger facial expressions was examined by measuring infants' ERP responses. In order to compare infants' brain responses to the mature processing in adults, ERPs were examined in adults in response to the same expressions. To assess individual differences we obtained information about dispositional empathy in adults and infant temperament using questionnaires. As opposed to previous studies that mainly used static displays of emotional facial expressions, in the present study, dynamic facial expressions were presented, which provide a more naturalistic representation of these emotions.

In addition, we examined whether the perception of pain and anger facial expressions would elicit brain processes that are linked to motivational processes. Previous studies with adults and infants measuring asymmetrical frontal brain activity in the alpha frequency band suggest that the lateralization of frontal cortical activity can be seen as an index of the experience of certain motivational states, namely, approach and withdrawal tendencies (Davidson, 1984; Davidson & Fox, 1982; Harmon-Jones, 2003). Furthermore, studies have demonstrated that frontal EEG asymmetry might be involved in moderating emotional experiencing and perception (Coan & Allen, 2004; Davidson, 1992; Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Harmon-Jones & Allen, 1998; Harmon-Jones, Gable, & Peterson, 2010). The question arises whether the observation of emotional facial expressions is associated with changes in asymmetrical frontal brain activity?

Study 2: Body expressions (dynamic displays). In the second study, we investigated at what point during development the infant brain becomes tuned to emotional body expressions. Reading others' emotional body expressions is an essential social skill and adults are readily able to recognize emotions from body movements and postures (Atkinson, 2013; Atkinson et al., 2004; de Gelder, 2009). However, it is unclear when in development the infant brain becomes sensitive to bodily expressed emotions. Hitherto, only one behavioral study has examined whether infants are able to distinguish between emotional body expressions. Namely, Zieber and colleagues (2014b) have shown that 6.5-month-old infants discriminate happy dynamic body expressions from neutral expressions and are able to match happy and angry body expressions to corresponding vocalizations. However, the underlying neural correlates that contribute to this ability have not been studied so far. Furthermore, it is unclear whether (a) infants are to able to discriminate between other emotional body expressions such as happy and fearful bodies, (b) when during development this ability arises, and (c) whether the perception of emotional body expressions is specifically tuned to upright bodies.

Therefore, in the second study of this dissertation, ERPs were measured in 4-and 8-month-old infants in response to happy and fearful body expressions using PLDs presented in two orientations, upright and inverted. On the basis of prior work on facial expressions processing in infancy (Leppänen et al., 2009), we predicted that 8-month-old infants, but not 4-month-old infants, would show distinct brain responses to emotional body expressions. We also predicted that infants' discrimination between emotions would mainly be evident in the upright condition but not in the inverted condition, because prior work with adults and infants has demonstrated that the perception of body expressions is impaired by stimulus inversion (Atkinson et al., 2007; Stekelenburg & de Gelder, 2004; Zieber et al., 2014b).

Study 3: Body expressions (static displays). In the third study, we addressed the question whether infants are able to discriminate between static emotional body expressions as an extension of *Study 2*. It is unknown whether infants at the age of 8-months are able to detect differences between emotional body expressions in the absence of motion cues as it has been shown in adults (Atkinson et al., 2004). Therefore, 8-month-old infants were presented with static happy and fearful full-light body expressions in two orientations, upright and inverted. We predicted that, similar to *Study 2*, 8-month-old infants would be able to discriminate between static emotional body expressions. However, since in *Study 3* static displays as compared to *Study 2* (dynamic displays; PLDs) were presented, we predicted that the neural correlates might differ in timing and topography when compared between studies.

Study 4: Body expressions (dynamic displays) and frontal EEG alpha asymmetry. After assessing the perception of emotional information, specifically the discrimination between emotional expressions through faces and bodies (*Study 1, 2*, and *3*), in the fourth study, we examined whether the observation of emotional body expressions elicits brain responses that are associated with motivational processes (*Study 4*). In *Study 4*, the dataset of 4- and 8-month-old infants who participated in *Study 2* was used in order to examine frontal EEG alpha asymmetry in response to upright and inverted happy and fearful dynamic body expressions. We predicted that only for the group of the 8- month-old infants' frontal EEG alpha asymmetry patterns would differ in response to emotional body expressions. Furthermore, EEG asymmetry patterns would differ in the upright but not in the inverted condition, as the detection of emotions is impaired when body expressions are inverted.

In the concluding chapter (Chapter 7), findings from all four studies will be discussed in relation to each other as well as to other research in this area. Furthermore, based on the empirical findings presented in this dissertation, implications and directions for future work will be formulated.

2 Methods

2.1 Electroencephalography (EEG)

To approach neuroscientific questions in infant research the possible measures are limited. One measure that is most frequently used to study different processes in the infant brain is electroencephalography (EEG). The human brain constantly produces electrical activity that is associated with different brain states, such as states of activation and rest, and is associated with specific sensory, cognitive, and motor events (Luck, 2005). The EEG is an adequate method to capture this electrical activity and to study cognitive development in the preverbal infant because responses to events can be measured even though more explicit behavioral responses are not yet in the infant's behavioral repertoire or verbal instruction of the infant participant as sued with adults and older children is not an option. The EEG measurement in infant research represents an option of using a non-invasive and child-friendly technique to investigate brain processes in early development.

2.2 From EEG to ERP - Recording and Processing

Every process in the brain is accompanied by electric activity. This electric brain activity originates from action potentials at the axons of a neuron and postsynaptic potentials occurring during the changes in the membrane potential of the postsynaptic cell (for more detailed information see Creutzfeld & Houchin, 1974). The postsynaptic potentials can last up to hundreds of milliseconds, allowing the potentials from large groups of neurons that are active in synchrony and are aligned in parallel orientation, to sum (Luck, 2005). These changes in the postsynaptic potentials are measurable with the EEG. The EEG measures brain activity by offering a high temporal resolution in the range of milliseconds. Because the recorded brain activity at the scalp reflects activity that originates from many sources of the brain, the spatial resolution of the EEG is poor so that conclusions about source locations are limited (Luck, 2005).

The EEG measures the ongoing electric activity in the brain, whereas event-related potentials (ERPs) reflect time-locked changes of brain activity in response to a discrete event (DeBoer, Scott, & Nelson, 2005). The EEG signal is recorded via electrodes that are placed on the scalp at defined positions. The international 10-20 system of electrode placement is a commonly used layout (Jasper, 1958; Sharbrough et al., 1991). In this layout, the electrodes are positioned at relative distances of either 10 or 20 % from each other along an anterior and posterior and a lateral axis. In order to decrease the impedances, a conductive gel maximizing the skin conductance is applied to the head at the electrode positions. The recorded EEG measures the voltage fluctuations that originate from the differences in potentials between the electrodes that record the signal and a reference electrode (Luck, 2005).

Before the EEG data can be analyzed several preprocessing steps are applied. After recording the EEG signal, the data is filtered and artifact rejection can be applied to remove artifacts, which are unrelated to brain processes such as eye blinks and head movement. Various filters can be applied in order to minimize the effects of noise, drifts, and spontaneously occuring activity unrelated to the processing of the stimulus (Luck, 2005; Spencer, 2005).

The changes in potential are usually too small in order to be detected in a single trial against the ongoing background activity and to that effect the *signal-to-noise ratio* in a single trial is low. That is why a stimulus must be presented repeatedly and the EEG waves are averaged over large number of trials (Luck, 2005). Following the preprocessing steps, time-locked epochs (i.e., a defined time window in the EEG data related to the onset of a stimulus/condition) are extracted and averaged separately for each condition. With this process the *signal-to-noise ratio* is increased and the specific ERPs, consisting of positive and negative deflections that represent the average processing of a stimulus over a time period, can be observed (Luck, 2005).

2.3 Event-related Brain Potentials (ERPs)

ERP components (deflections in the averaged signal) are usually labeled according to their latency (the point in time at which the ERP component peaks relative to the onset of a stimulus) and by the direction of their deflection (positive or negative). ERP components with a negative polarity are labeled by giving an N for negative polarity and a P for positive polarity (Luck, 2005). The number following the N or P indicates the latency in relation to stimulus onset. For example, the N170 observed in adults indexes a negative deflection peaking around 170 ms after stimulus onset. Besides latency and deflection, ERP components can be distinguished with regard to their distribution on the scalp (topography). With respect to infant ERP work, it should be mentioned that ERP components tend to vary considerably in terms of polarity, latency, and topography in comparison to known adult ERP components (de Haan, 2007; DeBoer et al., 2005; McCulloch, 2007). In the following sections, two ERP components that are commonly observed during infancy and were of main interest in the experiments described later on will be briefly introduced.

2.3.1 Negative Component (Nc)

The negative component (Nc) is one of the most well-studied component in infant ERP research. The Nc is a negative deflection that typically occurs in the time range of 400 to 800 ms post stimulus onset and is most prominent over frontal and central electrodes (de Haan, Johnson, & Halit, 2003). In several studies using a visual oddball paradigm the Nc has been found to be larger to infrequently than to frequently presented stimuli (Ackles & Cook, 1998; Karrer & Ackles, 1987; Karrer & Monti, 1995). With regard to these findings, the Nc is thought to reflect infants' allocation of attention, with greater negative deflection to the infrequently presented stimulus indicating greater allocation of attention to the novel or unexpected event (Courchesne, Ganz, & Norcia, 1981; Nelson, 1994). Furthermore, the Nc might also reflect arousal that is elicited by novel or infrequent stimuli (Richards, 2002, 2003). The Nc has also been discussed in relation to recognition processes, because the Nc amplitude is modulated by the familiarity of a stimulus (de Haan & Nelson, 1997b, 1999). For example, at 6 months of age, the Nc amplitude is greater in response to a mother's than to a stranger's face (de Haan & Nelson, 1997b) or to familiar toys than novel toys (de Haan & Nelson, 1999). Moreover, the Nc has been shown to be sensitive to emotional information displayed in faces (Nelson & de Haan, 1996). In a longitudinal study by Webb and colleagues (2005) the Nc was shown to decrease in latency and increase in amplitude towards the end of the first life, indicating that the properties of this component undergo change during infancy (Webb, Long, & Nelson, 2005). In summary, these empirical findings indicate that the Nc reflects attentional processes affected by the expectancy, familiarity and emotional content of the stimulus.

2.3.2 N290/ N170

The infant N290 is a negative-going deflection observed over posterior electrodes, whose peak latency decreases from 350 ms at 3 months of age to 290 ms at 12 months of age (Halit, de Haan, & Johnson, 2003). It has been suggested that the infant N290 is a precursor of the adult N170, a face-sensitive component seen in adults (Bentin, Allison, Puce, Perez, & McCarthy, 1996; de Haan et al., 2003). In particular, this component is thought to be related to the structural encoding of faces (Bentin & Deouell, 2000; Eimer, 2000). In other studies with infants and adults, ERPs were measured in response to upright and inverted human and monkey faces (de Haan, Pascalis, & Johnson, 2002; Halit et al., 2003). The findings of these studies indicate that, by the age of 12 months, infants show an adult-like pattern of responding: enhanced amplitude of the N290 to inverted human faces compared to upright human faces, but not to inverted monkey faces when compared to upright monkey faces (Halit et al., 2003). However, at an earlier stage at 3 and 6 months of age the stimulus inversion did not modulate the amplitude of the N290 (de Haan et al., 2002; Halit et al., 2003). These results suggests that the N290 becomes more sensitive to upright human faces with age, pointing to the development of face-sensitive processing during infancy (de Haan et al., 2002; Halit et al., 2003).

2.4 Frontal EEG Alpha Asymmetry

Using ERPs is the most common way to analyze EEG data, but they capture only one specific aspect of the information contained in the EEG signal that is highly synchronized and time-locked to a certain event (evoked changes). However, this leaves out any changes in the EEG that occur in response to an event but vary in latency (induced changes). These induced changes can be assessed by analyzing oscillatory brain activity (Herrmann, Grigutsch, & Busch, 2005). The EEG, like any other continuous signal, can be described as the sum of oscillating sine and cosine functions of different frequencies (Herrmann et al., 2005). Depending on the sampling rate and analysis technique the EEG can be decomposed into frequency components with varying resolutions. A time-frequency-analysis for example retains the time as well as the frequency information.

Traditionally, the EEG oscillatory components are grouped into five different frequency bands: delta (≤ 4 Hz), theta (4-8 Hz), alpha (8-12 Hz), beta (12-30 Hz), and gamma (≥ 30 Hz) (see Buzsáki, 2006; Herrmann et al., 2005 for defined frequency ranges in adult populations). One established method to study motivational processes evoked in response to emotional information is the analysis of frontal EEG asymmetry in the alpha frequency band (Coan & Allen, 2004; Davidson, 1992; Davidson et al., 1990; Fox, 1991). Specifically, Davidson (1994, 1998) proposed a model that links differential activation of the left and right frontal cortices in the alpha frequency range to different motivational tendencies (approach and withdrawal tendencies). With respect to the neural correlates of these motivational tendencies (Davidson, 1994, 1998), studies have demonstrated that approach motivation is associated with relatively greater left frontal cortical activation, whereas withdrawal motivation is associated with relatively greater right frontal cortical activation (Buss et al., 2003; Coan, Allen, & Harmon-Jones, 2001; Davidson, 1984, 1994, 1998; Davidson & Fox, 1982; Harmon-Jones, 2003). Approach motivation is associated with increased exploration of a stimulus, whereas withdrawal motivation is linked to inhibition of exploration or withdrawal from harmful stimuli (Fox, 1991).

Part II

Empirical Studies

3 Study 1

Developmental and individual differences in the neural processing of dynamic expressions of pain and anger

Manuela Missana[1], Maren Grigutsch[2], & Tobias Grossmann[1]

[1] Early Social Development Group, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

[2] Department of Neuropsychology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

We examined the processing of facial expressions of pain and anger in 8-month-old infants and adults by measuring event-related brain potentials (ERPs) and frontal EEG alpha asymmetry. The ERP results revealed that while adults showed a late positive potential (LPP) to emotional expressions that was enhanced to pain expressions, reflecting increased evaluation and emotional arousal to pain expressions, infants showed a negative component (Nc) to emotional expressions that was enhanced to angry expressions, reflecting increased allocation of attention to angry faces. Moreover, infants and adults showed opposite patterns in their frontal asymmetry responses to pain and anger, suggesting developmental differences in the motivational processes engendered by these facial expressions. These findings are discussed in the light of associated individual differences in infant temperament and adult dispositional empathy.

Keywords: emotion, face, ERPs, empathy, pain

3.1 Introduction

Facial expressions play an important role in communicating emotions and in providing cues that guide behavior during social interactions (Frith, 2009). Our ability to detect pain and anger in other people is likely to serve vital social and protective functions, enabling us to become aware of and respond appropriately to potentially harmful and dangerous situations. Observing someone expressing pain can convey harm and elicit empathic helping behavior, while observing someone expressing anger signals interpersonal threat and may result in readiness for aggression or a submissive flight response in the observer.

The facial expression that accompanies the experience of pain is highly specific and can be readily distinguished by observers from facial expressions of negative basic emotions such as anger and fear (Craig, Prkachin, & Grunau, 2001). Expressing pain through facial expression is characterized by the lowering of the eyebrows and narrowing/closing of the eyes, raising of the cheeks, raising the upper lips, or vertically stretching the mouth open (Craig et al., 2001; Prkachin & Craig, 1995).

The facial expression of anger is somewhat similar to the expression of pain as far as the eye regions are concerned, because it is also characterized by furrowed eyebrows and by staring eyes. However, in particular the mouth and cheek region differ across these two expressions, with angry expressions showing a closed mouth with tense lips (Ekman & Friesen, 1975).

The neural correlates of responding to pain in others have been studied extensively in adults (see Lamm, Decety, & Singer, 2011 for review). This work provides evidence for shared representations in the human brain that are active both when adults feel pain and when they observe others in pain. On the basis of these findings, it has been argued that these shared representations constitute the neural basis of empathy for pain (Singer & Lamm, 2009). Adults' brain responses to pain in others have been examined in various experimental contexts such as (a) by knowing that another person was receiving a painful stimulation to the hand as indexed by a symbolic (arrow) cue (Singer et al., 2004), (b) by viewing body parts of actors in painful situations (Jackson, Meltzoff, & Decety, 2005; Jackson, Rainville, & Decety, 2006; Morrison & Downing, 2007; Morrison, Lloyd, Pellegrino, & Roberts, 2004), and (c) by observing facial expressions of pain (Botvinick et al., 2005; Lamm, Batson, & Decety, 2007; Saarela et al., 2007; Simon, Craig, Miltner, & Rainville, 2006). Across these different contexts painful situations systematically resulted in activation of the anterior cingulate cortex (ACC) and the anterior insula (AI) (Lamm et al., 2011). The notion that brain activation in these regions is a neural correlate of empathy for pain receives support from findings showing that brain responses to pain in others vary as a function of individual differences in empathic abilities, with individuals that score higher in empathy showing greater activation in their brain responses to pain (Saarela et al., 2007; Singer et al., 2004). Furthermore, brain responses within these regions show a great level of specificity and indicate that adults discriminate between pain and other negative emotional states (Benuzzi, Lui, Duzzi, Nichelli, & Porro, 2008).

Adults' ability to discriminate between pain and other negative expressions has also been shown in recent event-related brain potential (ERP) studies (González-Roldan et al., 2011; Reicherts et al., 2012). The ERP method provides precise information concerning the timing of brain processes associated with emotion perception. In prior work a general distinction has been made between *early* processes related to emotional attention as reflected in an early posterior negativity (EPN) and *late* evaluative processes reflected in a late positive potential (LPP) (see Olofsson, Nordin, Sequeira, & Polich, 2008 for a review of the adult ERP literature on emotional processing from visual stimuli). More specifically, in previous ERP studies it was found that whereas seeing angry facial expressions resulted in an enhanced EPN indexing increased perceptual (visual) processing related to the rapid detection of threatening faces (Schupp, Junghöfer, Weike, & Hamm, 2003; Schupp et al., 2004), facial expressions of pain elicited an LPP response that was enhanced in its amplitude compared to angry and fearful facial expressions (González-Roldan et al., 2011; Reicherts et al., 2012). An enhanced LPP is thought to reflect increased evaluation of an emotionally arousing stimulus (Olofsson et al., 2008). These studies thus provide evidence that the adult brain not only distinguishes between negative facial expressions but also shows an increased sensitivity and arousal to facial expressions of pain as indexed by an enhanced LPP. Similar ERP effects were observed when adults watched others in painful situations (Fan & Han, 2008), supporting the notion that the neural processes reflected in this ERP component can be flexibly triggered by observing others in pain even in the absence of overt facial cues.

From a functional perspective it is important to add that, apart from eliciting empathic responses, painful expressions may also serve an adaptive alarm function leading to the facilitation of defensive responses in the observer (Goubert, Vervoort, & Crombez, 2009; Williams, 2002; Yamada & Decety, 2009). In line with this view, Yamada and Decety (2009) showed that pain detection was enhanced after subliminal priming with negative affective stimuli when compared to priming with positive affective stimuli. It has been argued that the perception of pain might therefore be associated with an activation of threat-related brain systems (Yamada & Decety, 2009). The notion that experiencing pain or observing pain in others evokes activity in threat-related brain systems has also been shown in fMRI studies that found increased activation of the amygdala in response to pain (Botvinick et al., 2005; Simon et al., 2006).

From a developmental perspective, it has been argued that it may be adaptive for humans to respond sensitively to emotional expressions from early on in development (Campos, Thein, & Owen, 2003; Darwin, 2009/1872; Walle & Campos, 2012). There is evidence from behavioral and neural studies showing that infants from around 7 months of age can reliably discriminate between a variety of affective facial expressions (Kotsoni et al., 2001; LaBarbera et al., 1976; Nelson & de Haan, 1996; Serrano, Iglesias, & Loeches, 1992). For example, findings from studies using ERPs demonstrate that infants at the age of 7 months discriminate happy from fearful and angry expressions (Grossmann, Striano, & Friederici, 2007; Peltola et al., 2009), as indexed by differences in a negative component (Nc) elicited over anterior brain regions between 300 and 600 ms. Critically, evidence for 7-month-old infants' ability to discriminate between different negative emotional expressions has been provided by Kobiella and colleagues (2008). In this study, infants were presented with static angry and fearful facial expressions. Angry compared to fearful facial expressions elicited a larger fronto-central negativity in the time range from 300 to 600 ms (Kobiella et al., 2008). An enhanced negativity over anterior brain regions in this time window is thought to reflect greater orientation and attention allocation to the stimulus (Richards, 2003), suggesting increased allocation of attentional resources to angry faces. Even though there is evidence that infants at the age of 7 months can discriminate between various facial expressions as reflected in amplitude modulations of the Nc, it is not well understood how the infant Nc component relates to the ERP components generally reported during emotion processing in adults (EPN and LPP) (see above). For example, there is evidence showing that although at the age of 7 months infants exhibit an enhanced Nc over anterior electrodes in response to angry faces, it is not until 12 months of age that infants, like adults, show an enhanced EPN over posterior (occipital) electrodes in response to angry faces (Grossmann et al., 2007). Moreover, very little is known about how infants respond to facial expressions of pain and its neural correlates. Closing this gap in our understanding of emotional responding during infancy by studying infants' brain responses to expressions of pain is particularly pertinent given the role that responding to pain in others has played in the investigation of empathy in general (de Vignemont & Singer, 2006; Decety, 2010; Jackson et al., 2006; Singer & Lamm, 2009) and its development in particular (Decety, Michalska, & Akitsuki, 2008; Eisenberg, Fabes, et al., 2006; Zahn-Waxler et al., 1992).

In light of the work discussed above, three main questions were addressed in this study: (a) How does the neural processing of dynamic facial expressions of pain and anger compare between infants and adults; (b) Can infants discriminate between facial expressions of pain and anger; (c) Whether and how individual differences in dispositional empathy (adults) and temperament (infants) impact brain responses to these emotional expressions, and if so, what can this tell us about the function of those specific brain processes under investigation?

In order to examine these questions, we measured ERPs in response to dynamic facial expressions of pain and anger in adults and 8-month-old infants. In the present study, dynamic facial expressions were used because: (a) prior work with adults suggests an improved performance across a range of face perception tasks including face identity recognition and facial emotion recognition (Ambadar, Schooler, & Cohn, 2005; Harwood, Hall, & Shinkfield, 1999), (b) dynamic facial expressions are thought to be more ecologically valid since this is how they are typically experienced during social interactions, and (c) infants may better attend to the dynamic presentations than watching static displays (Burnham, 1987; Burnham & Day, 1979; Wilcox & Clayton, 1968).

In addition, we assessed frontal EEG alpha power asymmetry to elucidate the motivational processes related to approach and withdrawal tendencies evoked by viewing these facial expressions. Approach and withdrawal are assumed to reflect basic motivational dimensions in human behavior (Schneirla, 1959). Specifically, while approach motivation is linked to increased exploration of the social and physical environment, withdrawal motivation is associated with inhibition of exploration and most frequently related to negative affect (Fox, 1991). With respect to the neural correlates of these motivational tendencies, Davidson

(Davidson, 1994, 1998) proposed a model that links frontal EEG asymmetry to motivational tendencies and affective styles. Asymmetrical frontal brain activity in the alpha frequency band in adults and infants suggests that the lateralization of cortical activity measured at frontal electrode sites is associated with different motivational tendencies and can be seen as an index of approach or withdrawal motivations (Buss et al., 2003; Davidson, 1984, 1994, 1998; Davidson & Fox, 1982; Harmon-Jones, 2003). These studies show that approach motivation is associated with relatively greater left frontal cortical activation whereas relatively greater right frontal cortical activation is associated with withdrawal motivation. Specifically, frontal EEG alpha asymmetry research suggests that anger, while being a negatively valenced emotion, is typically associated with approach motivation, eliciting greater relative left frontal activation during anger-evoking events (C. S. Carver & Harmon-Jones, 2009; Harmon-Jones et al., 2010).

Finally, in order to investigate individual (trait) differences in emotional sensitivity and its relation to the neural processing of pain and anger, we obtained information about adult dispositional empathy and infant temperament using questionnaires. This approach was informed by previous studies (a) with adults: demonstrating that individuals that score higher in empathy, as measured by an empathy questionnaire, exhibit greater activation in their brain responses to pain (Saarela et al., 2007; Singer et al., 2004), and (b) with infants: demonstrating that differences in emotion regulation abilities, as measured by a parental questionnaire (IBQ-R), were associated with differences in the brain responses to negative facial expressions (Martinos, Matheson, & de Haan, 2012). The temperament of the infants, in particular approach- and withdrawal-related traits as measured by a parental questionnaire (IBQ-R), was found to be related to general differences in frontal EEG alpha asymmetry patterns in 7- to 9-month-old infants (LoBue, Coan, Thrasher, & DeLoache, 2011). On the basis of these findings, we expected that infants' ERP and frontal EEG asymmetry responses to negative facial expressions would be similarly related to measures of infant temperament.

3.2 Materials and Methods

Adults

Participants: Twenty right-handed young adults aged between 21 and 28 years (10 female, *Median* age = 25.5 years, *Range* = 7 years) participated in the study. The participants had no prior history of psychiatric illness. Ethical approval was obtained from the Ethics Committee of the University of Leipzig. The participants provided written informed consent and were paid for their participation.

Stimuli: The stimulus material consisted of video clips of dynamic facial expressions of pain and anger as well as happy and neutral expressions displayed by two actresses. In keeping with the stimulus presentation protocols of prior infant facial emotion processing ERP studies (e.g., Peltola et al., 2009) each participant was presented with expressions of only one of the actresses. Happy and neutral facial expressions were presented but not used for analysis in order to avoid overwhelming the infants with negative expressions, thereby improving the testing atmosphere and reducing the dropout rate (ERP responses and frontal asymmetry responses to all four emotional expressions in infant and adults are provided in the supplementary information; see also supplementary Figures 3.7 and 3.8). Presenting negative expressions against a background of neutral and happy expressions also likely presents the infants with a more ecologically valid task, as in typical development they are thought to only infrequently encounter negative affect in daily interactions (see Vaish, Grossmann, & Woodward, 2008). All stimuli were taken from a previously published study by Simon and colleagues (Simon, Craig, Gosselin, Belin, & Rainville, 2008; Simon et al., 2006) and slightly modified (see Figure 3.1). The actresses provided written informed consent, transferring the copyright of the produced material to the research group (Simon et al., 2008). The original video clips had a duration of 1 s and were cut backward from the peak of expression in order to control for different lengths, variability of exposure to the visual stimuli, and to assure that the peak of expression was captured within the clip (Simon et al., 2008; Simon et al., 2006). In addition, we analyzed the motion onset and overall amount of motion across emotional expressions based on a procedure by Pichon and colleagues (2008). Critically, this analysis showed that there were no systematic differences in the onset and overall amount of motion between the facial expression videos. In order to focus the participants' attention on the facial expressions, the original clips were edited by cropping external features such as the shoulders. All video clips had a duration of 3 s. Each clip consisted of a 1-s static image displaying a neutral expression followed by a 1-s dynamic expression followed by another 1-s static image displaying the peak of expression. The first static image was taken from the first frame and the second static image was taken from the last frame of the dynamic expression.

Procedure: The participants sat in a dimly lit, sound-attenuated, and electrically-shielded room facing a computer screen. They were instructed to attentively view the stimuli but no task was given in order to ensure that the data could be compared between adults and infants. 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. Each participant was randomly assigned to one of the two actresses. The presentation of either actress was counterbalanced. Before each video clip started, an alert signal sounded. Then a fixation cross appeared (for 1000 ms) on the screen to draw participants' attention to the center of the screen. This was followed by a black screen (for 300 ms) and then by the stimuli (3000 ms). The stimuli were presented in a pseudo-randomized order. The randomization was such that no expression was repeated more than once in a row in the course of the experiment. Participants viewed 41 trials of each facial expression. After the session, the stimuli were shown again and participants were asked to rate the facial expressions for arousal using the Self-Assessment Manikin (SAM) self-report scale (Bradley & Lang, 1994).

Questionnaire: To assess individual differences in empathic abilities, participants filled out the self-report questionnaire Interpersonal Reactivity Index (IRI) (Davis, 1980, 1983; German version by Paulus, 2009). The questionnaire consists of four sub-scales that are related to empathy. 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 (Davis, 1980). Based on prior work with adults (Singer et al., 2004), we focused our analysis on only two subscales of the IRI, namely the empathic concern and the perspective-taking scales.

Figure 3.1. Examples of the stimuli. This figure shows representative examples of the stimuli. Single video frames of facial expressions of pain (top two rows) and anger (bottom two rows) for both actresses are shown.

EEG Measurement and ERP Analysis: The EEG was recorded from 63 Ag/AgCl electrodes attached to an elastic cap (*EasyCap GmbH*, *Germany*) using the 10-20 system of electrode placement. The data were online referenced to the left mastoid and offline re-referenced to the algebraic mean of the left and right mastoid electrode. The horizontal electrooculogram (EOG) was bipolarly recorded from two single electrodes placed at the outer canthi of both eyes and the vertical EOG from electrodes on the infra- and supraorbital ridges of the right eye. The EEG was amplified using a 72-channel REFA8 amplifier (Twente Medical Systems International) in the frequency band between DC and 67.5 Hz and digitized at a rate of 250 Hz. Electrode impedances were kept below 5 kΩ. Data processing for ERP analysis was performed using an in-house software package EEP, commercially available under the name EEProbe^{TM} (Advanced Neuro Technology, Enschede). The raw EEG data were bandpass filtered between 0.3 and 20 Hz, and the recordings were segmented into epochs time-locked to the stimulus onset, lasting from 200 ms before onset until the offset of the video clips (total duration 3200 ms). The epochs were baseline corrected by subtracting the average voltage in the 200-ms baseline period (prior to video onset) from each post-stimulus data point. Data epochs were rejected off-line whenever the standard deviation within a gliding window of 200 ms exceeded 60 µV in any of the two bipolar EOG channels and 50 µV at EEG electrodes (F3, Fz, F4, C3, Cz, C4, T7, T8, P3, Pz, P4, O1, O2). At each electrode, artifact-free epochs were averaged separately for angry and painful facial expressions to compute the ERPs. The average number of epochs included in the final analyses was 37.1 for angry facial expressions and 37 for painful expressions. Statistical analyses were based on the visual inspection of the ERP waveforms and prior work focusing on the EPN (González-Roldan et al., 2011; Schupp et al., 2003) and LPP (González-Roldan et al., 2011). On the basis of this information, mean amplitude effects were assessed over a posterior occipital region (O1, O2) during an early time window from 250 to 350 ms post movement onset (EPN) and at an anterior ROI comprising frontal and central electrodes (F3, FZ, F4, C3, CZ, C4) during a later time window from 400 to 500 ms post movement onset (LPP). Mean amplitude effects were compared between facial expressions using paired-sample *t*-tests.

EEG Measures of Asymmetrical Activation: Frequency analysis of the EEG data was performed using the *FieldTrip* software (http://fieldtrip.fcdonders.nl/; Oostenveld, Fries, Maris, & Schoffelen, 2011) in combination with custom-made MATLAB scripts. The raw EEG data were highpass filtered with a cut-off frequency of 1 Hz in order to reduce slow drifts and remove DC components. The recordings were segmented into epochs of 4000 ms duration, lasting from 1000 ms prior to stimulus onset until video offset. Epochs were visually inspected and excluded from further analyses if they were contaminated by large non-stereotyped artifacts (e.g., gross muscle activity or movement artifacts). Remaining stereotyped artifacts (originating e.g., from eye blinks or eye movements, tonic muscle activity, or pulse artifacts) were corrected using a signal processing procedure (Jung et al., 2000) based on Independent Component Analysis (ICA). The segmented EEG data were decomposed into 60 independent components (ICs) by application of the symmetric FastICA algorithm. ICs representing physiological or electrode artifacts were identified by visual inspection of the components' scalp topographies, frequency spectra, and single-trial time courses. They were removed from the data before back projection to the electrode space. For the analysis of event-related oscillations, time-frequency representations of artifact-cleaned single trials were computed using Morlet wavelets with a width of 5 cycles. Mean alpha power during the processing of facial expressions was estimated by averaging the squared magnitude of the complex wavelet transform coefficients across trials (separately for angry and painful facial expression), over time points during the presentation of the dynamic stimuli (0–1000 ms post movement onset) and frequency bins (8–13 Hz). Mean alpha power values were then log-transformed using the natural logarithm function (ln) to normalize their distribution. EEG alpha power asymmetry scores were calculated for the mid-frontal (F3, F4) and lateral frontal (F7, F8) regions. The scores were obtained by subtracting left log-transformed alpha power values from the corresponding right log-transformed values (ln(right) – ln(left)). It has been shown that increases in alpha power are associated with decreased cerebral activation and vice versa (Goldman, Stern, Engel Jr., & Cohen, 2002; Laufs et al., 2003). The asymmetry score reflects the power in one hemisphere relative to the power in the opposite hemisphere. Higher scores on this metric suggest relatively greater left activity

(Davidson, 1988). For comparison reasons, as in prior studies (Davidson & Fox, 1982), asymmetry scores were also computed for the central region (C3, C4) and the parietal region (P3, P4).

Infants

Participants: The final sample consisted of 20 8-month-old infants aged between 247 and 271 days (10 females, Median age = 259 days, Range = 24 days) and all came from a middle-class background in a medium-sized German city. The infants were born full term (between 37 and 41 weeks) and had a normal birth weight (> 2500 g). Twenty additional infants were tested but had to be excluded from the final sample due to fussiness (n = 6) or too many artifacts (n = 14). Ethical approval was obtained from the Ethics Committee of the University of Leipzig. All parents provided written informed consent prior to the study and were paid for their children's participation.

Stimuli: The stimuli were the same as those used in the adult experiment (see above).

Procedure: The infants sat on their parent's lap during testing. Parents were asked not to talk to or interact with their infant during the course of the experiment. Each participant was randomly assigned to one of the two actresses. The presentation of either actress was counterbalanced.

In order to attract infants' attention to the screen, each facial expression video was preceded by a sound and a fixation cross (1000 ms). This was followed by a black screen (300 ms) and then the stimuli (3000 ms). During the inter-stimulus interval infants were presented with an abstract screensaver for the purpose of keeping infants' attention. The inter-stimulus interval lasted at least 1000 ms and varied depending on infants' attentiveness, as stimulus presentation was controlled by an experimenter in such a way that stimuli were only presented when infants were looking at the screen. In order to control for infants' attention to the stimuli, infants' were video monitored throughout the EEG recording. The EEG session ended when the infant became restless or inattentive. The mean number of trials seen per condition was 15.08. The criterion for the minimum number of trials for inclusion in the final ERP average was 5 artifact-free trials per condition. The mean number of trials included in the ERP average per condition was 10.78. While the minimum number of trials and the mean number of trials to be included in the final analysis might appear lower than in previous studies, please note that we used dynamic video stimuli in the current design that were substantially longer (about 2 seconds longer) than those used in prior research with static facial displays of emotion and applied a strict criterion for inclusion, which required the entire trial epoch (3200 ms) to be artifact free (for a similar design using video material and similar analysis criteria, see Grossmann, Missana, Friederici, & Ghazanfar, 2012). This and the additional use of neutral and happy dynamic stimuli likely accounts for the smaller trial numbers in the current study.

Questionnaire: Parents were asked to fill out a temperament questionnaire (Infant Behavior Questionnaire in its revised form, IBQ-R, German version). The IBQ-R is the most commonly used questionnaire to assess differences in temperament in infants. The IBQ-R consists of 14 subscales that cover a wide range of temperamental traits: approach, vocal reactivity, high intensity pleasure, smiling and laughter, activity level, perceptual sensitivity, sadness, distress to limitations, fear, falling reactivity/rate of recovery from distress, low intensity pleasure, cuddliness, duration of orienting, soothability (Gartstein & Rothbart, 2003). In accordance with previous studies that investigated the influence of temperament on infants perception of emotions and frontal EEG alpha asymmetry (LoBue et al., 2011; Martinos et al., 2012), temperament analyses in the present study were limited to two dimensions of infant temperament, namely, 'negative emotionality' (as indexed by the subscales fear, sadness, distress to limitations, recovery from distress) and approach oriented temperament (as indexed by the subscales approach and duration of orienting).

EEG Measurement and 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 were online referenced to the CZ electrode and offline re-referenced to the algebraic mean of the left and right mastoid electrode. The horizontal electrooculogram (EOG) was recorded from two electrodes (F9, F10) which are part of the cap located at the outer canthi of both eyes. The vertical EOG was recorded from an electrode on the supraorbital ridge (Fp2) which is part of the cap and an additional single electrode on the infraorbital ridge of the right eye. The EEG was amplified using a Porti-32/M-REFA amplifier (Twente Medical Systems International) and digitized at a rate of 500 Hz. Electrode impedances were kept between 5 to 20 kΩ.

Further processing was done analogously to the adult data analyses with the exception that infant data epochs were rejected off-line whenever the standard deviation within a gliding window of 200 ms exceeded 100 µV in any of the two bipolar EOG channels and 80 µV at EEG electrodes (F3, Fz, F4, C3, Cz, C4, T7, T8, P3, Pz, P4, O1, O2). At each electrode, artifact-free epochs were averaged separately for angry and painful facial expressions to compute the ERPs.

Statistical analyses were based on the visual inspection of the ERP waveforms and prior work focusing on the Nc (Kobiella et al., 2008). On the basis of this information, mean amplitude effects were assessed at an anterior ROI comprising frontal and central electrodes (F3, FZ, F4, C3, CZ, C4) during a 500 to 600 ms time window post movement onset (Nc). Visual inspection of the infant ERP data revealed no clearly defined ERP components at occipital electrodes and no discernable amplitude differences between facial expressions at these electrodes. Mean amplitude effects were compared between facial expressions using paired-sample *t*-tests.

EEG Measures of Asymmetrical Activation: Analyses for measuring infant EEG alpha asymmetry was done, with some exceptions, analogously to adult data analyses. Because infant data contained 50-Hz notch noises, a 50-Hz notch filter was applied after segmentation of the data. For artifact correction using the ICA procedure (Jung et al., 2000) the segmented EEG data were decomposed into 24 independent components. Power values were obtained in the alpha frequency band from 6 to 9 Hz. The alpha frequency band is lower in infants than in adults, therefor, as suggested in previous work, we studied alpha power ranging from 6 to 9 Hz (Stroganova, Orekhova, & Posikera, 1999). The calculation of the EEG alpha power asymmetry scores was done analogously to the adult data.

3.3 Results

ERP Analysis

Adults. Our ERP analysis revealed a significant difference for the EPN in response to pain and anger facial expressions between 250 and 350 ms post movement onset at occipital electrodes, $t(19) = 3.62$, $p = .002$. Visual inspection of the ERP data indicated a difference in peak latency for the EPN in response to anger and pain expressions (see Figure 3.2). An additional analysis of peak latency effects during a 500 to 600 ms time window post movement onset revealed a significant difference in peak latency, $t(19) = -2.23$, $p = .037$, with the EPN to angry faces peaking earlier than the EPN to pain faces. Our ERP analysis further revealed a significant difference for the LPP in response to painful and angry facial expressions at fronto-central electrode sites between 400 and 500 ms after movement onset, $t(19) = -2.97$, $p = .008$. Specifically, the LPP elicited by facial expressions of pain was greater (more positive) in its amplitude ($M = 2.62$ µV; $SE = 0.61$) than the LPP elicited by facial expressions of anger ($M = 1.13$ µV; $SE = 0.60$) (see Figure 3.2). Behavioral arousal ratings obtained after the EEG measurement showed that there was a significant difference in arousal between pain and anger, with pain expressions (*M* = 3.45; *SE* = 0.153) rated as being more arousing than anger expressions (*M* = 2.85; *SE* = 0.182), *t*(19) = -2.69, *p* = .014. No significant correlations between the arousal ratings for facial expressions of pain and LPP responses to facial expressions of pain were found.

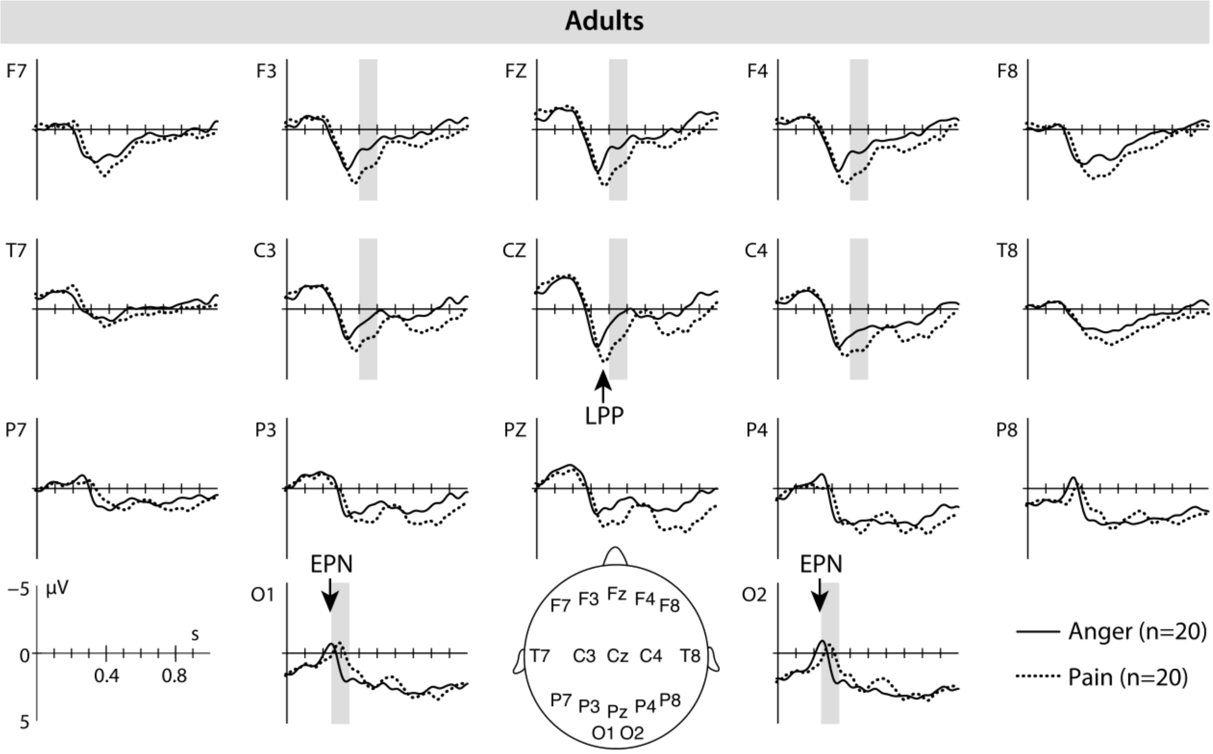


Figure 3.2. Adult ERP results. This figure shows the average event-related brain potentials (ERPs) time-locked to the movement onset in adults elicited by facial expressions of anger (solid line) and pain (dotted line) expressions. The time windows during which significant differences between the anger and pain condition were observed are marked in grey.

Empathy self-report questionnaire. Our analysis revealed a significant negative correlation between the ERP response to facial expressions of anger at fronto-central electrodes and the perspective-taking score as measured by the IRI (*r* = -.496, *p* = .026) (see Figure 3.3). The perspective-taking score is an index of a person’s ability and motivation to adopt another person's point of view (Davis, 1980). Specifically, the correlation was such that the higher adults rated themselves as possessing the ability and motivation to take another person's perspective, the smaller the amplitude of the LPP to angry expressions. There were no correlations between the ERPs in response to pain facial expressions and the IRI.

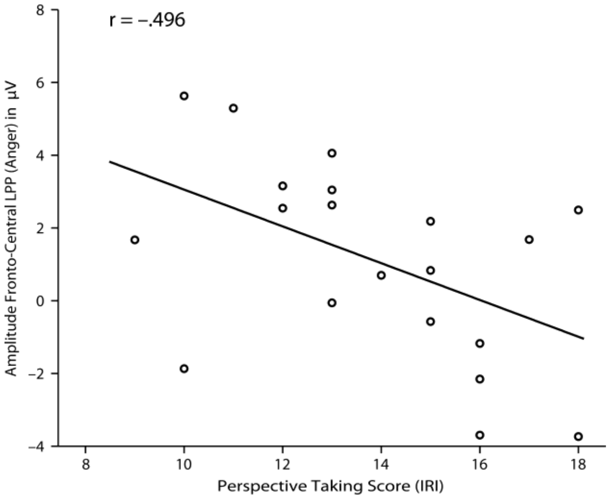


Figure 3.3. Correlation for adult ERP results. This figure shows the correlation between the amplitude of adults' brain responses to facial expressions of anger at fronto-central electrodes and individual perspective-taking scores as measured by the IRI (the correlation was significant on the $p < 0.05$ level).

Infants. Our ERP analysis revealed that, unlike adults, watching dynamic facial expressions of pain and anger resulted in a negativity elicited over anterior brain regions in infants that differed in its amplitude between facial expressions (see Figure 3.4). Specifically, infants discriminated between the two negative expressions as revealed by a significant difference between the ERP response to facial expressions of pain and anger between 500 and 600 ms after movement onset, $t(19) = -2.64$, $p = .016$. The ERP response to facial expressions of anger was more negative in its mean amplitude ($M = -8.19$ µV; $SE = 2.42$) than the ERP response to facial expressions of pain ($M = -1.89$ µV; $SE = 1.79$). No ERP differences between expressions were found at occipital electrodes.

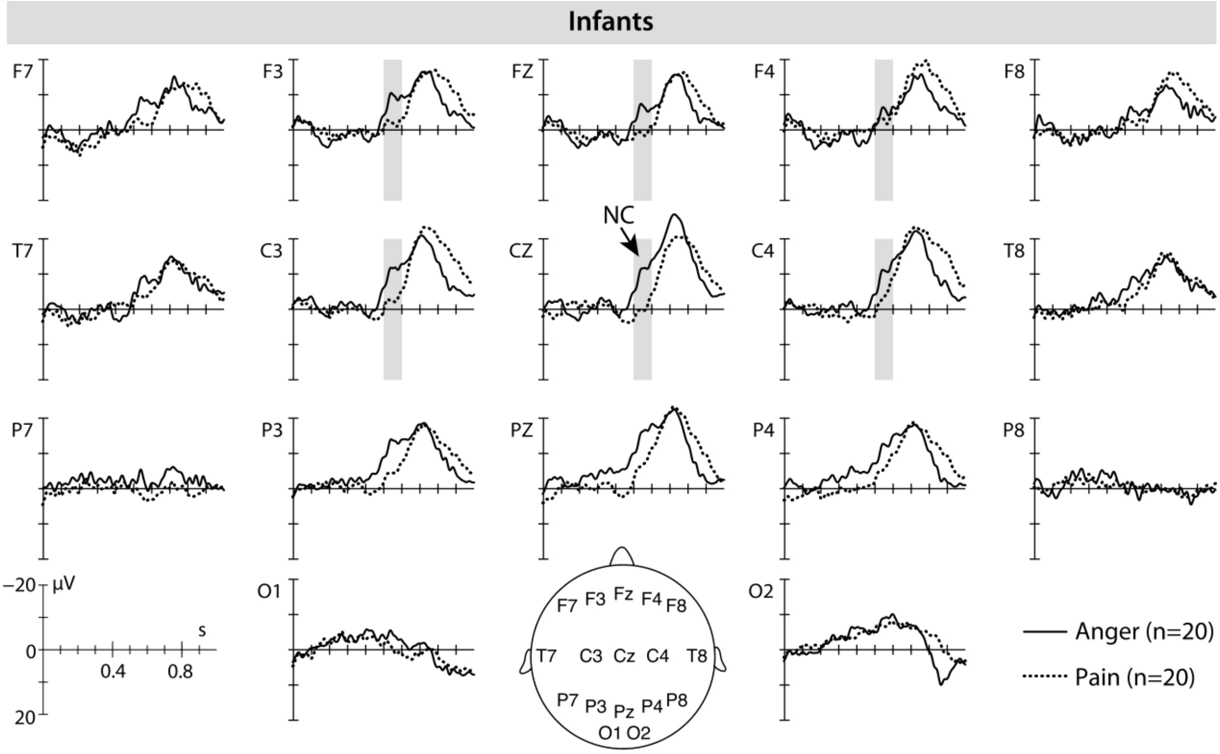


Figure 3.4. Infant ERP results. This figure shows the average event-related brain potentials (ERPs) time-locked to the movement onset in 8-month-old infants elicited by facial expressions of anger (solid line) and pain (dotted line). The time windows during which significant differences between the anger and pain condition were observed are marked in grey.

Infant temperament questionnaire. Our analysis revealed a significant negative correlation between the ERP response to facial expressions of anger and the recovery from distress score as measured by the IBQ-R, r = -.545, p = .013 (see Figure 3.5). The recovery from distress score reflects parents' ratings of their infants' ability to regulate emotions and regain calm after distress (Gartstein & Rothbart, 2003). Specifically, the correlation was such that the higher the parents rated their infants' ability to regulate and recover from distress, the more negative the amplitude of the ERP in response to angry expressions. Other subscales of the IBQ-R were not related to infants' ERP responses to anger and pain facial expressions.

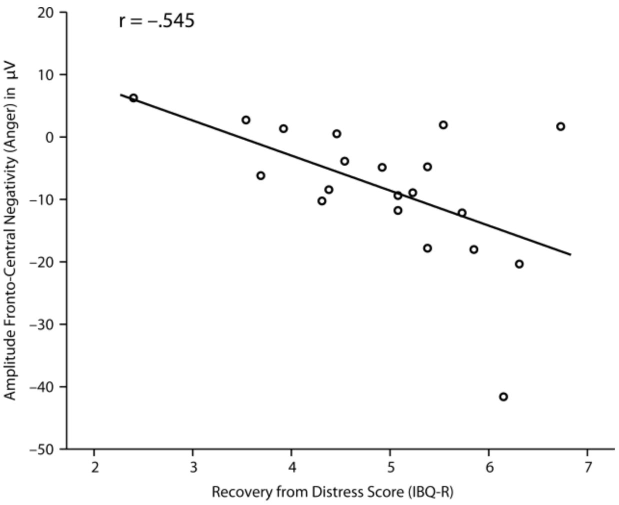


Figure 3.5. Correlation for infant ERP results. This figure shows the correlation between the amplitude of infants' brain responses to facial expressions of anger at fronto-central electrodes and individual recovery from distress scores as measured by the IBQ-R (the correlation was significant on the $p < 0.05$ level).

Frontal EEG alpha asymmetry analysis

Adults. Our analysis revealed a significant difference between the frontal EEG alpha asymmetry scores in response to facial expressions of anger and pain at lateral-frontal electrodes (F7, F8), $t(19) = 3.10$, $p = .006$. Facial expressions of anger were found to result in greater (positive) frontal EEG alpha asymmetry scores indicative of a greater relative left frontal activation, while facial expressions of pain were found to result in smaller (negative) frontal EEG alpha asymmetry scores indicative of greater relative right frontal activation (see Table 3.1). A similar effect with greater relative left frontal activation in response to anger as compared to greater relative right frontal activation to pain was also observed at mid-frontal electrodes (F3, F4) where the difference between the frontal EEG alpha asymmetry scores in response to facial expressions of anger and pain was marginally significant, $t(19) = 1.90$, $p = .072$ (see Table 3.1). For central (C3, C4) and parietal regions (P3, P4) there were no differences in EEG alpha asymmetry scores between expressions.

Empathy self-report questionnaire. Our results revealed a significant negative correlation between individuals' frontal EEG alpha asymmetry scores (F3, F4) in response to facial expressions of pain and empathic concern scores as measured by the IRI, $r = -.460$, $p = .041$ (see Figure 3.6). The empathic concern score refers to the individual's degree of participating in other people's emotions, and experiencing feelings of sympathy and concern for others (Davis, 1980, 1983). Specifically, the observed correlation was such that the higher adults rated themselves as possessing the ability and motivation to experience feelings of sympathy and concern for others, the more right lateralized their frontal EEG alpha asymmetry score, indexing a greater motivational tendency to withdraw.

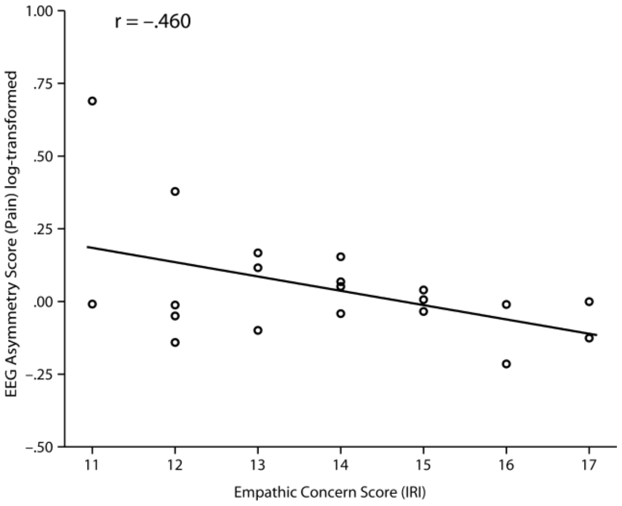


Figure 3.6. Correlation for adult frontal EEG alpha asymmetry results. This figure shows the correlation between frontal EEG alpha asymmetry observed in adults during the presentation of facial expressions of pain and individual empathic concern scores as measured by the IRI (the correlation was significant on the $p < 0.05$ level).

Infants. Our results revealed a significant difference between the frontal EEG alpha asymmetry scores in response to facial expressions of anger and pain at mid-frontal electrodes (F3, F4), $t(19) = -2.11$ $p = .048$ (see Table 3.1). Contrary to the results in adults reported above, in infants, viewing facial expressions of pain was associated with greater (positive) frontal EEG alpha asymmetry scores, while viewing facial expressions of anger was associated with smaller (negative) frontal EEG alpha asymmetry scores. This pattern reflects greater relative left frontal activation when processing pain, indexing the motivational tendency to approach and greater relative right hemisphere activation when processing anger, indexing the motivational tendency to withdraw. There were no differences between the EEG alpha asymmetry scores at the lateral-frontal electrodes (F7, F8), *t*(19) = .2 *p* = .841. Furthermore, EEG alpha asymmetry at central (C3, C4) and parietal (P3, P4) electrodes did not differ between expressions.

Infant temperament questionnaire. There were no correlations between frontal EEG alpha asymmetry scores in response to anger and pain and infant temperament scores as measured by the IBQ-R.

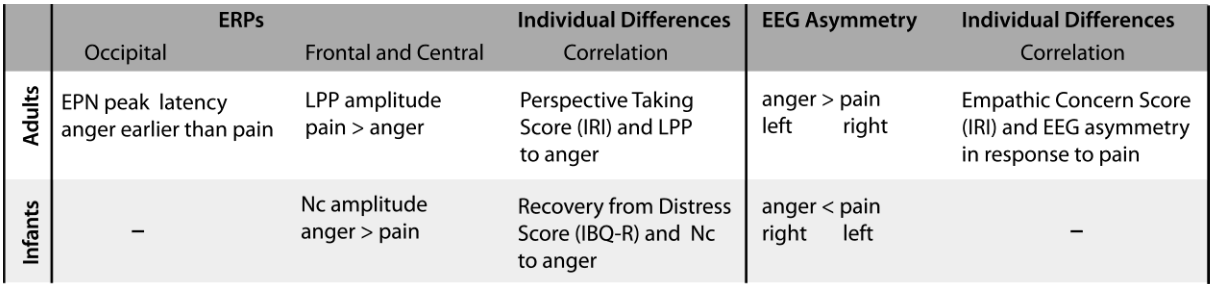
Table 3.1. Frontal EEG alpha asymmetry scores. This table shows the mean (± standard deviation) of the frontal EEG alpha asymmetry scores during the presentation of facial expressions of anger and pain. Please note that higher numbers indicate greater relative left-side activation. **p<.01.,*p<.05.,+p=marginal significant

			Condition			
	N	**Electrodes**	**Anger**	**Pain**	***t***	***p***
Adults	20	F7 / F8	- 0.013 ± 0.42	- 0.046 ± 0.41	3.102	0.006**
		F3 / F4	0.074 ± 0.17	0.047 ± 0.20	1.908	0.072+
Infants	20	F3 / F4	- 0.009 ± 0.13	0.054 ± 0.20	-2.111	0.048*

3.4 Discussion

The current study investigated the neurodevelopment of processing dynamic expressions of pain and anger. To our knowledge, this is the first study to compare infants' and adults' emotion processing by measuring both ERPs and frontal EEG alpha asymmetry in brain activation and linking differences in brain response to individual differences in infant temperament and adult dispositional empathy. Our study demonstrates that taking such a multi-measure (ERP, frontal EEG alpha asymmetry, temperament, empathy) and multi-method (EEG/ERPs and questionnaire methods) approach is very useful in investigating developmental differences between infants and adults and may contribute to a more comprehensive understanding of the development of emotion processing (see Table 3.2 for an overview of the ERP and frontal EEG alpha asymmetry findings in the current study).

Table 3.2. Overview of findings. This table provides an overview of the findings of the current study.



	ERPs		Individual Differences	EEG Asymmetry	Individual Differences
	Occipital	Frontal and Central	Correlation		Correlation
Adults	EPN peak latency anger earlier than pain	LPP amplitude pain > anger	Perspective Taking Score (IRI) and LPP to anger	anger > pain left right	Empathic Concern Score (IRI) and EEG asymmetry in response to pain
Infants	–	Nc amplitude anger > pain	Recovery from Distress Score (IBQ-R) and Nc to anger	anger < pain right left	–

The ERP results indicate that the brain processes elicited by expressions of pain and anger differ substantially between infants and adults. Our ERP data show that, in adults, facial expressions elicited an EPN at posterior (occipital) electrodes that peaked earlier in response to angry faces than to pain faces, suggesting that the perceptual (visual) processing was facilitated in response to angry faces. This facilitation effect evident in the response to angry faces is in line with prior work with adults showing that angry faces as evolutionary important signals of interpersonal threat are detected more readily than other facial expressions (Öhman, Lundqvist, & Esteves, 2001). This early ERP difference between processing anger and pain facial expressions is unlikely to be the result of differences in low-level motion properties between the two expressions, as motion onset and overall motion did not differ across expressions (see Method). Moreover, the early ERP differences between the facial expressions were not evident in the infant group even though they watched the same stimuli and at this age possess similar visual acuity to adults (Gwiazda et al., 1989). The absence of an EPN in 8-month-old infants is in line with prior work showing that it is not until 12 months of age that infants show an enhanced EPN over posterior (occipital) electrodes in response to angry faces (Grossmann et al., 2007).

Our analysis further revealed significant amplitude differences between processing dynamic expressions of pain and anger for the LPP at frontal and central electrodes in adults. Specifically, the LPP was enhanced in its amplitude in response to pain expressions when compared to anger expressions. This replicates prior adult ERP findings using static expressions of pain (González-Roldan et al., 2011) and suggests that adults show an increased evaluation and emotional arousal in response to seeing others in pain (Fan & Han, 2008). Supporting the notion that painful expressions evoked greater arousal in adults, subjective behavioral ratings of facial expressions revealed that pain faces are judged as being more arousing than angry faces. Taken together, these findings in adults are in agreement with other studies showing higher arousal ratings for pain faces compared to other negative expressions (e.g., anger and fear) (González-Roldan et al., 2011; Reicherts et al., 2012; Simon et al., 2006) and also correspond to ERP work indicating arousal modulation effects on the LPP with more arousing stimuli eliciting greater LPPs (see Olofsson et al., 2008).

Infants watching the same expressions showed ERP responses at frontal and central electrodes that were different from what was observed in adults. Specifically, angry expressions when compared to pain expressions elicited an enhanced negative component at frontal and central electrodes between 500 and 600 ms in 8-month-old infants. This finding is consistent with previous work in which 7-month-old infants showed a similar fronto-central ERP enhancement in response to static angry faces when compared to fearful faces (Kobiella et al., 2008). Thus, these ERP data demonstrate that infants at 8 months of age are able to discriminate between facial expressions of pain and anger, and seeing angry expressions results in a greater allocation of attentional resources than seeing expressions of pain. Such an early developing attentional sensitivity as indexed by the increased ERP sensitivity to anger might be particularly critical when it comes to detecting potential sources of aggression and threat (Campos et al., 2003; Darwin, 2009/1872; Walle & Campos, 2012). However, prior work suggests that only at around one year of age do infants begin to show adult-like neural processes that indicate threat detection from angry faces as reflected in the EPN (see Grossmann et al., 2007). Moreover, the observed differences in the infant and adult ERP responses to pain suggest that there is developmental change that occurs sometime after 8 months that sensitizes children to facial expressions of pain. This is in line with a host of behavioral work showing that empathic responding by helping and comforting others in pain only emerges later during ontogeny, namely, during the second year of life (Eisenberg, Fabes, et al., 2006; Zahn-Waxler et al., 1992). It might therefore be particularly important in the future to extend the current paradigm by testing infants in their second year of life.

Our analysis further revealed that the amplitude of the ERP responses to angry facial expressions at frontal and central electrodes in adults was negatively correlated with their self-reported perspective-taking score on the IRI. Specifically, the higher adults rated themselves as possessing the ability and motivation to relate to others and to understand others' perspectives, the smaller the LPP amplitude to angry expressions.

In infants the ERP response to angry expressions was negatively correlated with their recovery from distress on the IBQ-R. Specifically, the better the infants were able to self-regulate their emotions (distress) as judged by their parents, the greater the negative amplitude of the ERP response to angry expressions. Although we expected IBQ-R subscales representing negative emotionality to be related to infants' ERP responses to negative facial expressions, no associations between these measures were found. Our results are similar to the findings by Martinos and colleagues (Martinos et al., 2012) showing that only infants' self-regulation abilities but not infants' negative emotionality per se was associated with infants'

ERP responses to negative (fearful) emotional expressions. In line with our findings, Martinos and colleagues (Martinos et al., 2012) showed that infants that were better at self-regulation showed a larger Nc response to fearful facial expressions.

The finding that behavioral ratings of perspective-taking in adults and emotional self-regulation in infants correlated with the ERP response to angry faces suggests that sensitive responding to angry faces as a signal of interpersonal threat may afford specific self-regulatory mechanisms and that this ability to self-regulate/take the perspective of others may vary systematically across individuals. Moreover, it may further indicate that, in line with prior work (Decety & Jackson, 2004; Eisenberg, 2000; Eisenberg et al., 1994), there is a developmental link between emotion regulation in infancy and perspective-taking later in life. However, this possible link should be assessed more explicitly in future work employing a longitudinal design.

These findings are in line with theoretical proposals in the empathy literature that have postulated a link between emotion (self) regulation and perspective-taking (Eisenberg et al., 1994; Eisenberg, Smith, Sadovsky, & Spinrad, 2004) and with empirical findings with adults that show the influence of perspective-taking on anger regulation (Mohr, Howells, Gerace, Day, & Wharton, 2007). However, while these data may provide preliminary correlational evidence for this potential link, longitudinal work would be required to assess this association and its developmental trajectory systematically.

Infants and adults showed opposite patterns in their frontal EEG alpha asymmetry responses to pain and anger, suggesting developmental changes in the motivational processes engendered by the perception of these expressions. While pain resulted in greater relative left frontal activation in infants, indexing a motivational tendency to approach, adults showed a greater relative right frontal activation, indexing a motivational tendency to withdraw. Critically, in adults, greater relative right frontal activation to pain was correlated with a higher score of empathic concern. This might indicate a higher degree to which adults participate in other people’s emotions and experience feelings of sympathy or concern for others in pain or distress (Davis, 1980, 1983). In other words, adults who judged themselves as having higher dispositional empathic concern responded with greater withdrawal to expressions of pain, indicative of a vicarious experience of the aversiveness of another person’s pain (Eisenberg, Fabes, et al., 2006; Singer, 2006). This effect observed in adults is in line with a host of studies emphasizing the role of experiencing another person’s pain in empathic understanding (Goubert, Craig, & Buysse, 2009; Singer & Lamm, 2009). Another explanation for the observed greater relative right frontal activation during the observation of pain in the adult group is that, as suggested by prior work (Goubert, Vervoort, et al., 2009; Williams, 2002; Yamada & Decety, 2009), painful expressions might be perceived as threatening. Therefore, the resulting motivational tendency in adults might have been to withdraw from the painful expression.

In contrast to adults, 8-month-old infants showed greater relative left frontal activation, indicating a tendency to approach expressions of pain. This suggests that infants do not experience another person’s pain expression as aversive or negative but might rather be interested in the expression possibly to gather more information concerning the person’s situation. While prior work measuring infants’ behavioral responses to distress vocalizations and distress/pain simulations demonstrates that feelings of empathic concern already emerge in the first year of life (Geangu, Benga, Stahl, & Striano, 2010; Roth-Hanania, Davidov, & Zahn-Waxler, 2011), our data suggest that infants at 8 months of age do not yet respond empathically to facial expressions of pain. This might have something to do with differences between vocally and facially expressed emotions and signs of vocal distress, as witnessed by infants in prior studies (Geangu et al., 2010; Roth-Hanania et al., 2011), being a more direct and more powerful trigger of early forms of emotional and empathic responding (see Vaish &

Striano, 2004 for how vocal emotional cues are more powerful than facial cues in guiding infants' behavior). Nevertheless, the ability to differentiate facial expressions of pain from other emotional facial expressions forms a prerequisite for the further development of empathy-related responding.

For an infant to experience an approach tendency towards facial expressions of pain as suggested by the current frontal EEG alpha asymmetry findings might provide an important mechanism to gather further information concerning the person’s situation and may hence serve an important learning function.

The perception of angry faces resulted in greater relative left frontal activation in adults, indexing a motivational tendency to approach, while infants showed a greater relative right frontal activation to angry faces indexing a motivational tendency to withdraw. Our finding of greater relative left frontal activation in adults during the perception of angry faces is in line with prior work that obtained similar EEG asymmetry patterns when adults were experiencing anger themselves (Harmon-Jones, 2003; Harmon-Jones & Sigelman, 2001), suggesting that perceiving and expressing anger may result in approach behaviors. The opposite pattern, relatively greater right frontal activation during the perception of angry faces, was found in the infant group, pointing to a developmental difference in the motivational evaluation of angry faces between infants and adults. This developmental difference may be explained by the fact that adults might respond to seeing angry faces as conveying interpersonal threat that elicits aggressive (attack) tendencies resulting in approach tendencies, whereas infants might feel frightened by an adult looking at them angrily resulting in withdrawal tendencies.

The developmental differences between infants and adults evident in the frontal EEG alpha asymmetry findings are consistent with the current ERP findings that indicate similar differences across ages, pointing to a general developmental change in responding to emotional expressions of pain and anger. More specifically, our data suggest that between infancy and adulthood there is considerable change when it comes to (a) discriminating between pain and anger as evident in the ERP responses and (b) perceiving the significance of these emotions for motivational brain systems as evident in the frontal EEG alpha asymmetry. This suggests that only through extensive experience with these facial expressions and the associated situations can a deeper understanding of these emotions be achieved (Decety & Svetlova, 2012). As alluded to above, when exactly this development is achieved remains an open question and should be addressed in future studies with older infants or toddlers.

With regard to the expected correlation between infants' temperament measures and frontal EEG alpha asymmetry responses, no such correlations were found in the present study. This appears to be in contrast to a previous study by LoBue et al. (LoBue et al., 2011) that reported correlations between approach and withdrawal-related temperament traits and EEG alpha asymmetry in 7- to 9-month-old infants. However, LoBue and colleagues (LoBue et al., 2011) only found such correlations when they looked at frontal EEG asymmetry collapsed across emotion and neutral conditions but not when examining correlations for the experimental conditions separately, which were negative (e.g., threatening stimuli, such as snakes) and positive (e.g., non-threatening stimuli, such as giraffes) visual stimuli. Taken together, our findings and the findings from LoBue and colleagues (LoBue et al., 2011) therefore suggest that there are no emotion-specific associations between frontal EEG asymmetry patterns and infants' temperament.

There are a few limitations of this study that require discussion. First, it should be noted that in the current study behavior was not measured directly to assess approach and withdrawal tendencies in infants and adults. Therefore, the present findings are limited to neural indexes of motivational tendencies and future research is needed to examine to what extent the brain measures correlate with overt behavioral responses. Second, with respect to the correlational analysis it should be acknowledged that the sample size is relatively small for a study investigating individual differences in emotion processing and that the measures used rely on self-report in the case of the adults and parental report in the case of the infants, which are prone to reporting biases. It would thus be important to further investigate the obtained individual differences by including more direct measures of temperament and empathy and correlate them with emotion processing in a larger sample across development.

In summary, it can be concluded that exploring the neural processes that underpin infants' and adults' responses to pain and anger has provided important insights into the nature of emotion perception and particularly its developmental and individual differences. Our data suggest that processing expressions of pain and anger is shaped by developmental changes that occur in the context of individual differences in emotional sensitivity that can be detected already very early on in ontogeny. Furthermore, the current study demonstrates that it is critical to utilize novel methodological approaches using multiple methods and measures in order for developmental differences to be uncovered and better understood.

Acknowledgments

We would like to thank all participants and families who took part in this study. We also thank Heike Böthel for help with data collection, Kerstin Flake for assistance in preparing the figures, and Elizabeth Kelly for proofreading the manuscript.

3.5 Supporting Information

See the following pages for supplementary figures and tables to Study 1.

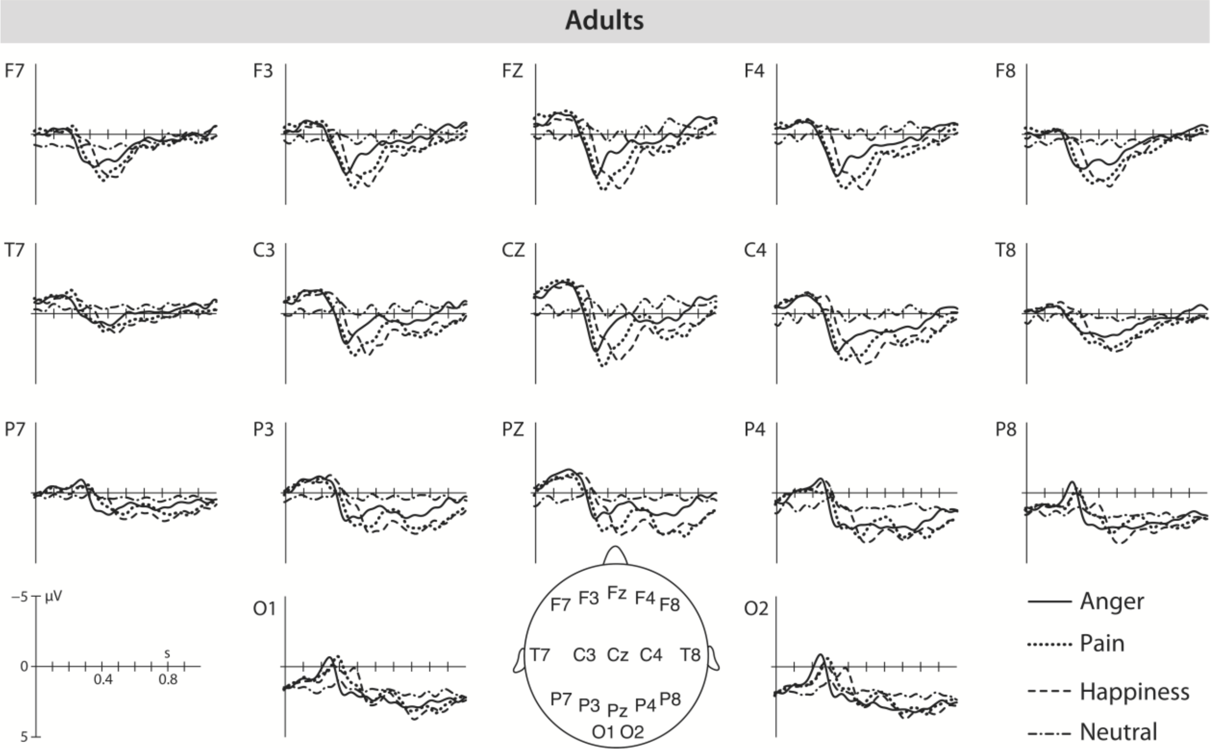


Figure 3.7. Adult event-related brain potentials. This figure shows the event-related potentials of adults in response to facial expressions.

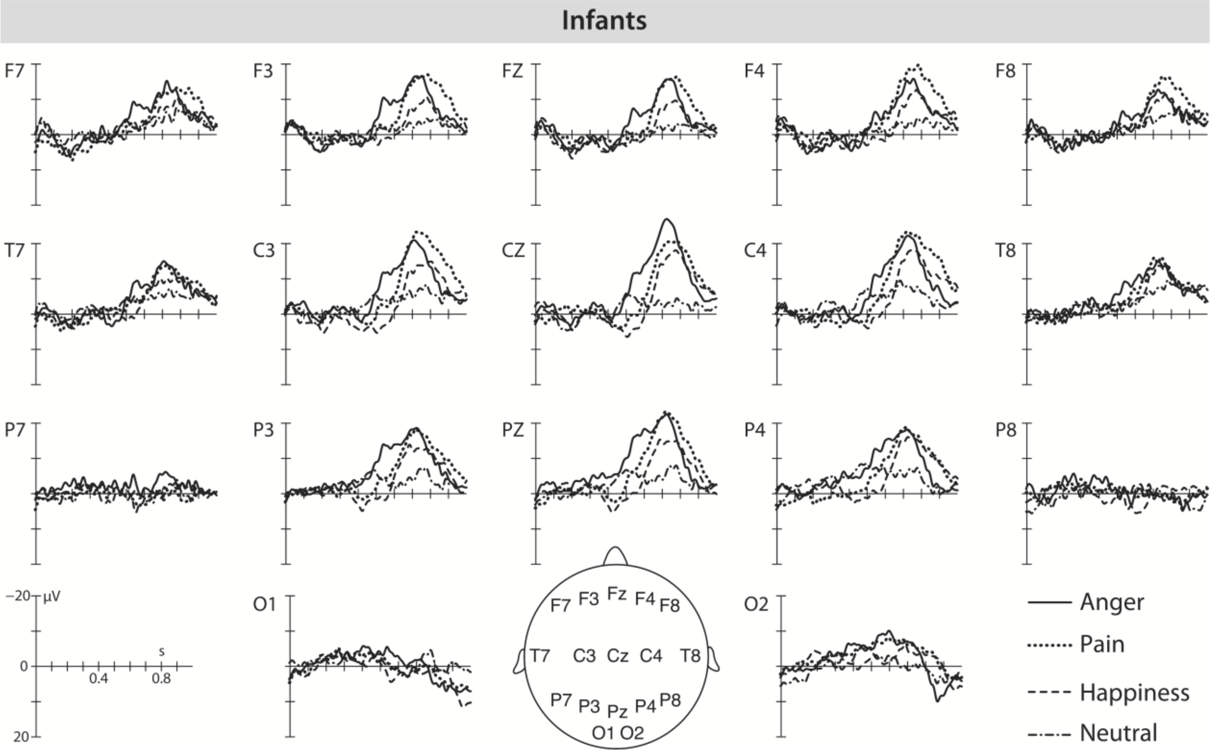


Figure 3.8. Infant event-related brain potentials. This figure shows the event-related potentials of infants in response to facial expressions.

Table 3.3. Means of adult amplitudes at occipital electrodes. Means of adult amplitudes in response to facial expressions in the time range of 250 to 350 ms at occipital electrodes (O1, O2).

Facial expression	*Mean (in μV)*	*SE*
Anger	1.00	.42
Pain	-.05	.42
Happy	.21	.38
Neutral	1.28	.36

Table 3.4. Means of adult amplitudes at fronto-central electrodes. Means of adult amplitudes in response to facial expressions in the time range of 400 to 500 ms at fronto-central electrodes (F3, Fz, F4, C3, Cz, C4).

Facial expression	*Mean (in μV)*	*SE*
Anger	1.13	.60
Pain	2.62	.61
Happy	3.13	.69
Neutral	-.02	.51

Table 3.5. Means of infant amplitudes at occipital electrodes. Means of infant amplitudes in response to facial expressions in the time range of 200 to 300 ms at occipital electrodes (O1, O2).

Facial expression	*Mean (in μV)*	*SE*
Anger	-2.64	1.82
Pain	-2.63	2.34
Happy	-2.42	1.86
Neutral	-.69	2.25

Table 3.6. Means of infant amplitudes at fronto-central electrodes. Means of infant amplitudes in response to facial expressions in the time range of 500 to 600 ms at fronto-central electrodes (F3, Fz, F4, C3, Cz, C4).

Facial expression	*Mean (in μV)*	*SE*
Anger	-8.19	2.42
Pain	-1.89	1.79
Happy	2.22	1.62
Neutral	-2.89	1.97

Table 3.7. Mean adult lateralization scores (log-transformed) in response to facial expressions.

	Lateralization scores			
Facial expression	F3/F4 *Mean (log-transformed)*	*SE*	F7/F8 *Mean (log-transformed)*	*SE*
Anger	.074	.04	.014	.09
Pain	.047	.04	-.046	.09
Happy	.050	.04	-.005	.09
Neutral	.063	.05	-.019	.10

Table 3.8. Mean infant lateralization scores (log-transformed) in response to facial expressions.

	Lateralization scores			
Facial expression	F3/F4 *Mean (log-transformed)*	*SE*	F7/F8 *Mean (log-transformed)*	*SE*
Anger	-.009	.03	-.003	.06
Pain	.054	.04	-.011	.05
Happy	.034	.03	-.014	.06
Neutral	.024	.04	-.117	.05

4 Study 2

Tuning the developing brain to emotional body expressions

Manuela Missana[1], Anthony P. Atkinson[2], & Tobias Grossmann[1]

[1] Early Social Development Group, Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstrasse 1a, 04103 Leipzig, Germany

[2] Department of Psychology, Durham University, South Road, Durham, DH1 3LE, United Kingdom

Research Highlights

- ERPs were measured in response to emotional body expressions in infants using point-light displays
- 8-month-old infants, but not 4-month-old infants, discriminated between the orientation (upright, inverted) and the emotion (fearful, happy) of bodies in motion
- neural evidence for the developmental emergence of emotion perception from body cues

Reading others' emotional body expressions is an essential social skill. Adults readily recognize emotions from body movements. However, it is unclear when in development infants become sensitive to bodily expressed emotions. We examined event-related brain potentials (ERPs) in 4- and 8-month-old infants in response to point-light displays (PLDs) of happy and fearful body expressions presented in two orientations (upright and inverted). The

ERP results revealed that 8-month-olds but not 4-month-olds respond sensitively to the orientation and the emotion of the dynamic expressions. Specifically, 8-month-olds showed (i) an early (200-400 ms) orientation-sensitive positivity over frontal and central electrodes, and (ii) a late (700-1100 ms) emotion-sensitive positivity over temporal and parietal electrodes in the right hemisphere. These findings suggest that orientation-sensitive and emotion-sensitive brain processes, distinct in timing and topography, develop between 4 and 8 months of age.

4.1 Introduction

Reading others' emotional expressions is a vital skill that helps us predict others' actions and guide our own behavior during social interactions (Frijda & Mesquita, 1994; Frith, 2009; Izard, 1977, 2007). Emotional communication is inherently multidimensional and multisensory in nature as emotional information can be gleaned from various sources such as the face, the voice and the body posture and motion of a person (Heberlein & Atkinson, 2009). The bulk of research investigating emotion expression perception has focused on facial and vocal expressions (Belin, Campanella, & Ethofer, 2012). Much less work has been dedicated to understanding the perception of emotional body expressions, even though body expressions may be the most evolutionarily preserved and immediate means of conveying emotional information (de Gelder, 2006). The work on emotional body expressions has revealed that adults are readily able to detect and recognize various emotions from body expressions (Atkinson, 2013; de Gelder, 2009). This ability to recognize emotions from body expressions relies on specific brain processes localized principally in the right hemisphere, including superior temporal, somatosensory and premotor cortices (Atkinson, 2013; de Gelder, 2006; Grèzes et al., 2007; Heberlein et al., 2004; Heberlein & Saxe, 2005).

Already during the first year of life infants become sensitive to various facial and vocal expressions (Grossmann, 2013a). In particular, there is behavioral and neural evidence to suggest that infants begin to discriminate between positive and negative emotional expressions during the first year of life (Vaish et al., 2008). For example, 7-month-old infants but not 5-month-old infants showed longer looking times to fearful faces when compared to happy faces and differences in their event-related brain potentials (ERPs) during the processing of these facial expressions, indicating that infants' ability to discriminate between emotions emerges during the first year of life (Nelson & de Haan, 1996; Peltola et al., 2009). Specifically, a series of ERP components discriminate between fearful and happy expressions (early- latency: Positivity before [Pb], mid-latency: Negative component [Nc], and late-latency Positive component [Pc]) (Nelson & de Haan, 1996)**;** these components are thought to be associated with attentional/novelty (early Pb and mid-latency Nc) and recognition memory (late-latency Pc) processes engaged by infants during visual experiments (see Webb et al., 2005). Critically, ERP differences similar to those that discriminate between facial expressions have been described in 7-month-olds when angry voices were compared to happy and neutral voices (Grossmann, Oberecker, Koch, & Friederici, 2010; Grossmann, Striano, & Friederici, 2005), suggesting that the sensitivity to emotional information across face and voice emerges during the first year of life. Indeed, there is ERP evidence showing that 7-month-old infants can integrate emotional information across face and voice (Grossmann, Striano, & Friederici, 2006). Specifically, in this study, 7-month-olds showed an enhanced late-latency Pc, when emotional information matched across face and voice, indexing the recognition of common affect across modalities, while mismatching emotional information resulted in a greater mid-latency Nc, indexing greater allocation of attention to novelty. Despite the progress that has been made in understanding the ontogeny of emotion perception from face and voice, how the ability to perceive and respond to others' emotional body expressions develops during infancy is only poorly understood.

This is an important question because from very early in development infants have been shown to be sensitive to biological motion, serving as a foundation for detecting and interpreting body movements. Behavioral research using point-light displays (PLDs) (Johansson, 1973) suggests that, from birth, human infants prefer to look at biological motion (e.g., walking hen) over non-biological motion (e.g., randomly drifting dots), and they also show a preference for upright over inverted biological movement (for similar findings with 3-month-old infants using point-light walkers see Bertenthal, 1993; Simion et al., 2008). Infants have also been shown to detect distortions of body configuration at 3 months of age (Gliga & Dehaene-Lambertz, 2005) and perceive human point-light displays as solid forms at 5 months of age (Moore, Goodwin, George, Axelsson, & Braddick, 2007), suggesting that they are sensitive to form and form-from-motion information related to the configuration of body parts. These findings suggest that human infants possess an early developing system that allows for the detection of biological motion and human bodies.

This early perceptual sensitivity to biological motion can also be traced at the neural level. In one study, upright compared to inverted human point-light motion elicited a greater right posterior positivity (P290) at parietal sites in 8-month-old infants' ERPs (Reid et al., 2006). In another ERP study, 8-month-olds showed greater (more negative) amplitude ERPs at right parietal sites 200 to 300 ms post stimulus onset to upright motion in PLDs when compared to scrambled point-light motion (Hirai & Hiraki, 2005). Despite the inconsistencies concerning the direction of the modulation of the ERP component across these studies, these findings suggest that 8-month-olds' neural systems are able to detect human biological motion and this likely relies on posterior regions in the right hemisphere. In 5-month-old infants, the ERP effect discriminating between upright and scrambled motion was not lateralized to the right hemisphere as in 8-month-olds but observed at posterior electrode sites over both hemispheres (Marshall & Shipley, 2009). This suggests that the right hemisphere dominance in dealing with biological motion cues emerges only after 5 months of age.

Although much work has been concerned with infants' emerging abilities to make sense of bodies in motion, so far only one published study has addressed the development of the ability to sensitively respond to emotional information carried in body motion. Zieber and colleagues (2014b) examined infants' ability to discriminate between emotional body expressions in a series of behavioral experiments with 6.5-month-old infants (using video full-light body expressions taken from Atkinson et al., 2004; Atkinson et al., 2007). In this study, 6.5-month-olds showed a visual preference for happy over neutral body expressions and were shown to look longer at body-voice pairings that conveyed congruent emotional information (happiness or anger) than incongruent emotional information. Critically, these effects were specific to body expressions presented in an upright orientation, since infants did not show any difference in their looking responses when the body expression was presented upside-down (Zieber et al., 2014b). While these findings provide first insights into infants' perceptual ability to discriminate between emotional body expressions, there are a number of vital remaining questions that are addressed in the current study. In particular, it is not known: (a) what neural processes underpin the behaviorally expressed sensitivity, (b) whether the brain responses elicited by positive and negative bodily expressed emotions are similar to those elicited by facial and vocal expressions, and (c), at what age this (neural) sensitivity to bodily expressed emotions develops.

Therefore, the aim of our study was to investigate the developmental emergence of infants' neural sensitivity to emotional body expressions. We examined when the infant brain becomes tuned to emotional body expressions by presenting 4- and 8-month-olds with upright and inverted happy and fearful dynamic body expressions using PLDs. We used PLD stimuli because they provide very little static information and no information regarding the facial expression but contain the essential motion cues that allow adult observers to recognize emotions from body motion (Atkinson et al., 2004; Atkinson et al. 2007). We had three main predictions with respect to infants' developing ability to discriminate emotional body expressions. First, based on prior work using facial and vocal expressions (Grossmann et al., 2005; Nelson & de Haan, 1996; Peltola et al., 2009) we predicted that 8-month-olds, but not 4-month-olds, would be able to discriminate between emotional expressions conveyed through body movement. Second, based on prior work that has shown that body expression perception in adults is impaired (but not abolished) by stimulus inversion (Atkinson et al., 2007; Stekelenburg & de Gelder, 2004), we predicted that infants' discrimination between emotions would mainly be evident in the upright condition but not, or at least not as clearly, in the inverted condition (see Zieber et al., 2014b for behavioral evidence showing that infants' detect emotional information better in upright orientation). Third, given previous findings of right-hemisphere lateralization of emotional body-expression processing in adults (Grèzes et al., 2007; Heberlein et al., 2004; Heberlein & Saxe, 2005), we predicted that the brain responses indicating the ability to discriminate between emotional body expressions in infants will be observed mostly or only over the right hemisphere. In addition, with respect to infants' sensitivity to the orientation (upright or inverted) of body expression, we predicted a main effect of stimulus orientation similar in topography and timing to Reid and colleagues' (2006) ERP findings with 8-month-olds using upright and inverted walking and kicking movements. Given that the current study was the first to examine orientation effects using ERP measures in infants younger than 8 months, we did not have any specific predictions concerning development of the ERP responses to orientation of body movements. However, prior behavioral work suggests that infants younger than 8 months of age are sensitive to stimulus inversion as indexed by a looking preference for upright movement (Bertenthal, 1996; Simion et al., 2008).

4.2 Materials and Methods

Participants. The final sample consisted of 20 four-month-old infants aged between 123 and 137 days (10 females, *Median age* = 129 days, *Range* = 14 days) and 20 eight-month-old infants between 230 and 259 days (9 females, *Median age* = 251, *Range* = 29 days). An additional 15 four-month old infants and 20 eight-month-old infants were tested but were excluded from the final sample due to fussiness ($n = 5$) or too many artifacts ($n = 30$). The infants were born full-term (between 37 and 41 weeks) and had a normal birth weight (> 2500 g). All parents gave informed consent prior to the study. Ethical approval was obtained from the ethics committee of the University of Leipzig. All parents provided written informed consent prior to the study and were paid for their children's participation. The children were given a toy after the session.

Stimuli. The stimulus material consisted of 2-second clips of point-light body movements displaying eight different fearful and eight different happy expressions (from Atkinson et al., 2012), which were presented upright and inverted (see Figure 4.1). Stimulus inversion was achieved by creating vertical mirror duplicates of the upright stimuli. Stimulus motion was equated across the two emotion categories by selecting 8 expressions from the original set of 10 for each emotion, such that the differences in the means of 3 similar measures of stimulus motion were as small as possible. Stimulus motion was calculated as the sum of the distance, in pixels, traveled by the dots in each display (a) from one frame to the next across the length of the movie clip (fearful $M = 1212.50$, happy $M = 1329.00$), (b) across every two frames (fearful $M = 1157.75$, happy $M = 1296.88$) and (c) every three frames (fearful $M = 1140.25$, happy $M = 1237.13$). Pairwise comparisons revealed no differences between fearful and happy displays for any of the 3 measures (all ts < 0.9, all ps $\geq .4$).

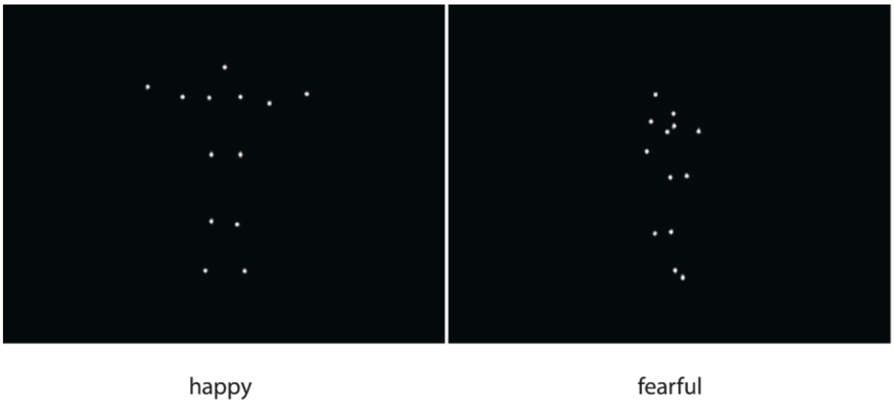


Figure 4.1. An example of the PLD stimuli. The figure shows two still frames taken at the maximum of the emotional expression.

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. Each trial began with an alerting sound and a fixation cross (1000 ms), in order to attract the infants' attention to the screen, followed by a black screen (400 ms) and then a point-light body expression movie clip (2000 ms). During the inter-trial interval infants were presented with an abstract screensaver for the purpose of keeping infants' attention. The inter-trial interval lasted at least 1000 ms and varied depending on the infants' attentiveness, as stimulus presentation was controlled by an experimenter in such a way that stimuli were only presented when infants were looking at the screen. 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. In addition, the sessions were video-recorded to off-line code for infants' attention to the stimulus. The EEG session ended when the infant became fussy, or inattentive.

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 were online referenced to the CZ electrode and offline re-referenced to the algebraic mean of the left and right mastoid 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. 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 were bandpass filtered between 0.3 and 20 Hz. The recordings were segmented into epochs time-locked to the start of the video clip. The video clips were cut in such a way that the video clip onset coincided with the movement onset of the PLD. 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 were also visually inspected offline for artifacts. At each electrode, artifact-free epochs were averaged separately for fearful upright, happy upright, fearful inverted and happy inverted body expressions to compute the ERPs. The criterion for the minimum number of trials for inclusion in the final ERP average was 7 artifact free trials per condition. For the 4-month-olds the mean number of trials seen per condition was 17.81. The mean number of trials included in the ERP average was 11.10 for the fearful upright condition, 11.40 for happy upright, 10.55 for fearful inverted and 10.30 for the happy inverted condition. The minimum number of trials was 7 and the maximum number of trials was 19. For the 8-month-olds the mean number of trials seen per condition was 19.98. The mean number of trials included in the ERP average was 11.45 for the fearful upright condition, 11.80 for the happy upright condition, 10.75 for fearful inverted and 12.10 for the happy inverted condition. The minimum number of trials was 7 and the maximum number of trials was 20. While the mean number of trials included in the final analysis might appear lower than in previous studies, note that we used dynamic video stimuli that were substantially longer in duration than in previous studies. Furthermore, we applied a strict criterion for inclusion in the analysis, which required the entire trial epoch (2200 ms) to be artifact free (for a similar design using video material and similar analysis criteria, see T. Grossmann et al., 2012). Decisions pertaining to the statistical analyses were informed by visual inspection of the ERP waveforms and by prior work focusing on infant facial expression processing (Nelson & de Haan, 1996; Peltola et al., 2009). Specifically, based on this information, three consecutive time-windows were selected to investigate effects of the experimental manipulations on the three ERP components (Pb: 200-400 ms, [early-latency component], Nc: 400-700ms, [mid-latency component], Pc: 700-1100ms [late-latency component]). To account for the longer latencies (approximately 100 ms longer) for the ERP components in the group of 4-month-old infants, the time windows for the ERP analyses were shifted by 100 ms for all three ERP components (Pb, Nc, and Pc). These components have been commonly studied in visual experiments in infants (Webb et al., 2005) and have been shown to be modulated by facial emotional information (happy versus fear) in prior work (Nelson & de Haan, 1996). The selection of regions of interest was informed by visual inspection of the ERP waveforms and prior work using point-light displays (Hirai & Hiraki, 2005; Reid et al., 2006) and happy and fearful emotional facial expressions (Nelson & de Haan, 1996; Peltola et al., 2009). Specifically, based on this information, ERP effects were examined for two regions of interest: (1) an anterior fronto-central region of interest including frontal and central electrodes (F3, F4, C3, C4) for analyzing the Pb, Nc, and Pc, and (2) a more posterior temporo-parietal region of interest including temporal and parietal electrodes (T3, T4, P3, P4) for analyzing the Pc. This latter region of interest was chosen because in prior work effects on the Pc were reported over both fronto-central and temporo-parietal regions (de Haan & Nelson, 1997b; Grossmann et al., 2006). In keeping with prior work (Leppänen et al., 2007), main statistical analyses were carried out separately for the two age groups. Mean amplitude ERP effects for these regions and time windows were assessed in repeated measures ANOVAs with the within-subject factors emotion (happy versus fear), orientation (upright versus inverted), and hemisphere (left versus right). Main statistical analyses were carried out separately for the two age groups because (a) it has been recommended not to combine ERPs for infants more than 1- to 2-months apart in age (DeBoer et al., 2005), and (b) prior work suggests that Pb, Nc and Pc undergo developmental change during this period of infancy (Webb et al., 2005) (see Figure 4.2). In addition, in order to examine potential age differences in our study the factor age was added as a between-subjects factor in supplementary analyses.

4.3 Results

Pb (200-400 ms). Our analysis for the Pb revealed a significant main effect of orientation at the anterior region of interest (frontal and central electrodes) in 8-month-old infants, $F(1, 19) = 4.788$, $p = 0.041$, $\eta^2 = 0.201$. In particular, inverted body expressions elicited a larger (more positive) Pb ($M = 7.588$ µV, $SE = 1.651$) than upright body expressions ($M = 4.083$ µV, $SE = 1.6$). No other main effects or interactions reached significance. No effects on the Pb were observed in the group of 4-month-old infants (all Fs < 1.301). Additional analysis comparing Pb responses across ages revealed no significant interactions with age (all Fs < 2.95).

Nc (400-700 ms). Our analysis for the Nc revealed that infants did not show any significant effects at either age or region. However, given that there was a significant main effect of the factor stimulus orientation in the group of 8-month-old infants during the early time window (Pb: 200-400 ms), we carried out a further analysis that assessed the effects of emotion separately for the two stimulus orientations (upright and inverted) at fronto-central electrodes. No significant effects or interactions reached significance (all Fs < 1.421). No effects on the Nc were observed in the group of 4-month-old infants (all Fs < 1.404). Additional analysis comparing Nc responses across ages revealed no significant interaction with age (all Fs < 1.155).

Pc (700-1100 ms). For the group of the 8-month-old infants the analysis revealed a significant effect for orientation at anterior electrodes, $F(1, 19) = 6.495$, $p = 0.020$, $\eta^2 = 0.255$. Inverted body expressions elicited a more positive amplitude ($M = 1.223$ µV, $SE = 1.171$) than upright body expressions ($M = -1.465$ µV, $SE = 1.264$). No other significant differences were found (all Fs < 1.726). No significant effects were observed in the group of 4-month-old infants (all $Fs < 3.689$; this F-value resulted from a marginally significant main effect of the factor hemisphere, $F(1, 19) = 3.689$, $p = 0.07$). Additional analysis comparing Pc responses across ages revealed no significant interaction with age (all Fs < 3.344; this F-value resulted from a marginally significant interaction between the factors orientation and age, $F(1, 19) = 3.344$, $p = 0.075$).

Our analysis for the Pc at the posterior region of interest (temporal and parietal electrodes) revealed a significant three-way interaction between the factors emotion, hemisphere and age, F $(1,38) = 4.746$, $p = 0.036$, partial $\eta^2 = 0.111$. In further analyses a significant interaction between emotion and hemisphere for the posterior region of interest in 8-month-old infants was found, $F(1, 19) = 8.05$, $p = 0.011$, $\eta^2 = .298$. For this posterior region mean amplitude during this time window differed between emotions only in the right hemisphere, *F*(1, 19) = 5.524, *p* = 0.03, η^2 = .225 (where happy body expressions elicited a larger (more positive) Pc [*M* = 1.349 µV, *SE* = 1.138] than fearful body expressions [*M* = - 0.688 µV, *SE* = 1.1]), but not in the left hemisphere. More specifically, this discrimination between emotions in the right hemisphere at posterior electrodes appeared to be driven by the upright condition, in which happy body expressions elicited a more positive Pc [*M* = 1.821 µV, *SE* = 1.415] than fearful body expressions [*M* = - 2.076 µV, *SE* = 1.341], *t* (19) = 2.551, *p* = 0.02, whereas no such differences were observed in the inverted condition, *t* (19) = 0.141, *p* = 0.889 (happy body expressions [*M* = 0.877 µV, *SE* = 1.393], fearful body expressions [*M* = - 0.7 µV, *SE* = 1.436]). We justified these separate analyses of the effects of emotions for the two stimulus orientations (upright and inverted) on the basis of the finding of a main effect of stimulus orientation during an early time window (Pb: 200-400 ms). No effects on the Pc were observed in the group of 4-month-old infants (all *F*s < 1.402).

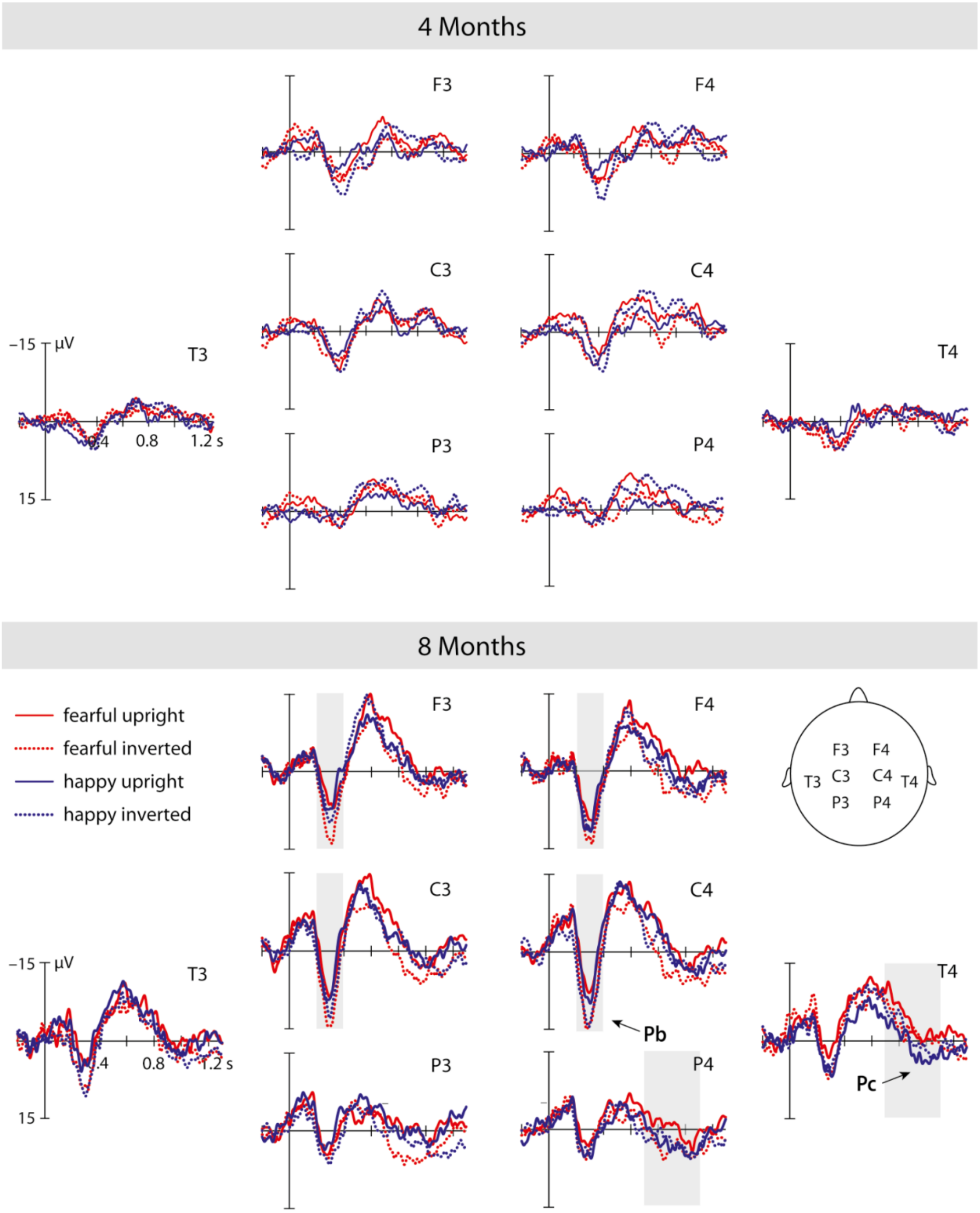


Figure 4.2. Infant ERP responses. The event-related potentials (ERPs) time-locked to the stimulus onset in 4- and 8-month-old infants elicited by fearful upright (red solid line), fearful inverted (red dotted line), happy upright (blue solid line) and happy inverted (blue dotted line) point-light body expressions. The time windows during which significant differences were observed are marked in grey.

4.4 Discussion

In this study, we examined ERPs in 4- and 8-month-old infants in response to dynamic displays of happy and fearful body expressions presented in two orientations (upright and inverted). Our ERP results revealed that 8-month-olds but not 4-month-olds respond sensitively to the orientation and the emotion of the dynamic body expressions. Specifically, 8-month-olds showed (i) an early (200-400 ms) orientation-sensitive Pb at frontal and central electrodes, and (ii) a late (700-1100 ms) emotion-sensitive Pc at temporal and parietal electrodes over the right hemisphere. These findings demonstrate that orientation-sensitive and emotion-sensitive brain processes, that are distinct in timing and topography, develop between 4 and 8 months of age. The ERP data therefore provide evidence that an important developmental transition in the neural processing of body expressions occurs between 4 and 8 months of age.

Our ERP results show that it is not until around the age of 8 months are infants' brains able to distinguish between upright and inverted body motion from PLDs. The current study was the first to examine orientation effects using ERP measures in infants younger than 8 months of age, and the ERP responses measured indicate that younger infants fail to distinguish between upright and inverted body movements. This might be seen as discrepant to prior behavioral work suggesting that younger infants (newborns and 3-month-olds) are sensitive to stimulus inversion as indexed by a looking preference for upright movement (Bertenthal, 1996; Simion et al., 2008). However, it should be noted that a similar dissociation between neural and behavioral measures is evident when examining the work investigating face inversion effects (de Haan et al., 2002; Farroni et al., 2005). This may have to do with the fact that in looking time studies stimuli are presented for much longer durations allowing for greater exploration by the infants, whereas in ERP studies stimuli are presented for much shorter durations required for the rapid detection of the relevant information. In any case, our data show an orientation-sensitive ERP response in 8-month-old infants during an early time window (between 200 and 400 ms). The timing of this ERP effect is in line with prior ERP work with 8-month-old infants using upright and inverted kicking and walking motion (Reid et al., 2006), suggesting that orientation of body motion is detected during early processing stages. However, while in the current study the orientation-sensitive ERP response (Pb) was found to be greater in amplitude to inverted body motion and observed at frontal and central electrodes, prior work found that *upright* body motion elicited larger positivity at posterior (parietal) electrodes, suggesting that topography and direction of modulation of the orientation-sensitive ERP response differ across studies. This difference might be explained by the fact that across these studies the PLD stimuli varied with respect to the kind of movement displayed. Namely, Reid and colleagues (2006) used walking and kicking movements that provide cues regarding the direction of biological motion in the horizontal plane to the infant, which may result in evoked activity in brain regions sensitive to such directional information (de Lussanet et al., 2008; Oram & Perrett, 1994; Vangeneugden et al., 2011). It is important to emphasize that, in Reid and colleagues (2006) study, the directional cues were in principal also available in the inverted condition, however, the coding of the direction of body movement may require for the body motion to be presented in the upright orientation (Gurnsey, Roddy, & Troje, 2010; Troje & Westhoff, 2006).

In the current study, no uniform direction of body movement was evident across the stimulus set or in many of the individual stimuli, suggesting that infants’ discrimination of upright and inverted body motion did not involve such directional cues but may have relied on more general brain processes detecting and discriminating familiar from unfamiliar visual events. Indeed, the current data show that the orientation-sensitive responding occurred for the Pb, which is an infant ERP component that has been found to be sensitive to the familiarity of a visual stimulus (Webb et al., 2005). Even though much less is known about the Pb than the Nc, prior work suggests that the response properties of the Pb are very similar to the Nc and may thus also reflect attentional resource allocation related to stimulus familiarity, whereby a smaller Pb is thought to reflect greater allocation of attention to a visual stimulus (Grossmann, 2013a; Hoehl, Wiese, & Striano, 2008). This suggests that 8-month-old infants dedicated increased attentional resources to processing upright body expressions. Increased attention to upright body expressions in 8-month-old infants may thus have an impact on later brain processes that follow the early orientation-sensitive ERP response.

Our analysis further revealed emotion-sensitive brain processing during a later time window (700-1100 ms). Critically, in line with our prediction based on prior work investigating facial and vocal emotion processing across infancy (Grossmann et al., 2010; Nelson & de Haan, 1996; Peltola et al., 2009), 8-month-old infants, but not 4-month-olds infants, distinguished between emotions. This supports the notion that brain processes associated with emotion detection and discrimination undergo some general development during this period of life (see Leppänen & Nelson, 2009). The finding that the ERP effect reflecting sensitive responding to emotional body expressions emerges between 4 and 8 months of age might be explained by a number of factors. One possibility is that the observation and own experience of emotional states plays a critical role in the emergence of these discrimination processes. In particular, it has been argued that towards the end of the first year of life, the frequent and repeated exposure to happy emotions in self and others shapes infants' responses to emotional information and their ability to distinguish between positive and negative emotions (Vaish et al., 2008). Another possibility is that infants develop a better grasp of emotions expressed by others as the result of more wide-ranging improvements in their social cognitive abilities that have been reported to occur towards the end of the first year of life, especially in relation to the sharing and understanding of the attention and intentions of others (Tomasello & Carpenter, 2007; Tomasello, Carpenter, Call, Behne, & Moll, 2005). Regardless of the exact mechanisms that underlie the developmental change observed between 4 and 8 months, our findings support the notion of an early ontogenetic emergence of the ability to respond sensitively to emotions displayed by others, thus providing a vital foundation for later emerging empathic and prosocial abilities in infancy.

More specifically, 8-month-olds showed an increased Pc in response to happy when compared to fearful body expressions. In prior work it has been shown that the Pc reflects neural processes associated with recognition memory. In particular, this work demonstrated that an increased Pc indexes the recognition of an item (Grossmann et al., 2006; Nelson, Thomas, de Haan, & Wewerka, 1998). Therefore, an increased Pc in response to happy body expressions as observed in the current data suggests that 8-month-old infants recognized the highly familiar (positive) expression and discriminated it from the less familiar (negative) expression. Furthermore, recognition reflected in the Pc might occur at the categorical level, as prior work has shown that a greater Pc is specifically evoked by new individual exemplars of a familiar visual category (Grossmann, Gliga, Johnson, & Mareschal, 2009). This appears likely given that infants in the current study were confronted with completely new and several different exemplars of happy body expressions. Importantly, this finding is in line with prior work showing a similar modulation of the Pc in response to happy when compared to fearful facial expressions (Nelson & de Haan, 1996), suggesting that recognizing positive emotional information is reflected in a neural signature common to face and body processing.

Contrary to prior work using facial expressions (Leppänen, Moulson, Vogel-Farley, & Nelson, 2007; Nelson & de Haan, 1996), we did not observe an effect of emotion for any of the earlier ERP components (Pb and Nc). This discrepancy might be explained by differences in the type of stimulus material used across studies. Notably, the stimuli differed not only regarding whether they provided bodily expressed or facially expressed emotions but also with respect to whether static or dynamic emotion displays were used. Importantly, in recent work, using ERPs we examined 8-month-old infants' processing of happy and fearful full-light static body expressions taken at the peak of the expression (Missana, Rajhans, Atkinson, & Grossmann, 2014) and found earlier emotion effects (N290 and Nc) than in the current study when using PLDs. This suggests that the discrimination of emotions from bodily expressions occurs faster for static displays than for dynamic displays, which is likely to do with the fact that in the dynamic context the emotional expression unfolds over time, whereas in the static context the peak of the expression is presented immediately.

Confirming our predictions, our findings further revealed that infant brain response sensitive to emotional body expressions (Pc) was lateralized to the right hemisphere. This finding is in agreement with prior work on biological motion processing with 8-month-old infants (Hirai & Hiraki, 2005; Reid et al., 2006) and emotional body expression processing with adults (Grèzes et al., 2007; Heberlein et al., 2004; Heberlein & Saxe, 2005) that has also shown a lateralization of the brain responses to the right hemisphere. It should also be noted that this finding is in line with prior infant ERP research on the Pc, suggesting that this ERP component is lateralized to the right hemisphere and can be localized to the temporal cortex (Nelson, 1996; Reynolds & Richards, 2005). This furthers the notion that right hemispheric processes play an important role in the perception of emotions from body movement. While this finding is in overall agreement with prior work concerning body movement processing, no lateralization in the ERP responses sensitive to facial and vocal expressions of emotions was reported in previous studies with infants (Grossmann et al., 2005; Peltola et al., 2009). This suggests that body expression processing during infancy might rely more exclusively on brain processes localized in the right hemisphere than facial and vocal expression processing. However, more work possessing better brain activation localization properties than ERPs such as functional near-infrared spectroscopy (fNIRS) with infants (for a review, see Lloyd-Fox, Blasi, & Elwell, 2010) is needed to obtain a clearer picture regarding the lateralization of infant brain responses.

With respect to the developmental change observed in the current ERP study one limitation should be discussed. Namely, in our additional analysis, we did not observe any interactions of the factor age (4 versus 8 months) with any of the ERP effects related to infants' discrimination of upright and inverted PLDs and happy and fearful PLDs. This indicates that, while our ERP data show that only at the age of 8 months, but not at 4 months, infants discriminate between the orientation and the emotion of a PLD, the ERP differences across age are not evident when directly assessed by including age as a between-subjects factor in our analyses. One possibility is that the age difference is not as strong as suggested by the results from the analyses carried out separately for the two ages, which might have to do with the fact that at least some of the 4-month-olds showed similar ERP responses to the 8-month-olds. In any case, it should be emphasized that the common way to assess development in infant perception research is by examining effects separately for different age groups as was done in the current study. Therefore, our analytical approach is in keeping with most prior work in this regard. Nonetheless, further work is needed to clarify the exact nature and time course of the identified developmental change.

This is the first study to use PLD body stimuli to display emotions to infants (previous behavioral work had relied on full-light displays of emotional expressions, Zieber et al., 2014). PLDs provide little static form information but contain the essential motion cues that allow adult observers to recognize emotions from body motion (Atkinson et al., 2004; Atkinson et al., 2007). Using PLDs we were able to show that 8-month-old infants can discriminate between emotional body expressions on the basis of motion cues. This finding critically extends prior work that has investigated infants' perception of biological motion from PLDs (Bertenthal, 1993; Hirai & Hiraki, 2005; Reid et al., 2006) by showing that infants can detect not only biological and human motion more generally but also extract specific information concerning the emotional state of the biological agent. Moreover, we observed that inversion of the body motion disrupts the discrimination of emotions, as indicated by the finding that the Pc did only differ between emotions in the upright context but not in the inverted context (note that, in our analysis we did not obtain an interaction between the factors emotion and orientation, but that this finding relies on separate comparisons between emotions performed for the two stimulus orientation). This suggests that 8-month-old infants require upright body motion to successfully extract emotional information. This effect is in agreement with (a) what has been reported in adults who show impaired recognition of dynamic body expressions when presented upside down (Atkinson et al., 2007) and (b) what has been shown in infants using behavioral looking time methods (Zieber et al., 2014b). The ERP differences between fearful and happy stimulus conditions are unlikely to be purely the result of differences in low-level motion properties between the two stimulus sets, however, for two reasons. First, we controlled for the amount of dot motion across the happy and fearful expressions. Second, the ERP differences between emotions were not evident for the inverted PLD stimuli, in which the available kinematic and dynamic information is identical to that available in the upright stimuli. Thus 8-month-olds are likely to be using higher-level motion cues, such as form-from-motion information or kinematics, to discriminate between the emotions.

Taken together, the findings presented in the current study have informed, at three levels, our understanding of how emotional body expressions are processed. First, at the developmental level, we have seen that over the course of the first year of life the human brain becomes tuned to emotional body expressions. The ontogenetic emergence of infants' ability to discriminate emotional body expressions occurs at a time in development when facial and vocal emotion processing capacities undergo similar change. These findings thus provide evidence for accounts that conceive of emotion perception as a unified ability that develops in concert across various processing channels (face, voice and body). Second, at the perceptual level, we have shown that for emotion discrimination processes to occur the infant requires to see the body motion in an upright orientation. This is similar to what is known from adults (Atkinson et al., 2007) and it is also in line with work investigating the effects of inversion on the perception of faces in the first year of life (de Haan et al., 2002). The disruption of emotion discrimination by body inversion can be seen as evidence for the developmental emergence of configural processing of body motion. That is, rather than relying on individual features of the body that are also present in the inverted stimulus, 8-month-olds require to see the configuration of body features in order for the discrimination process to take place. Third, at the neural level, we have shown that emotion discrimination from body expressions elicits brain responses that are lateralized to the right hemisphere. In agreement with prior work (Grèzes et al., 2007; Heberlein et al., 2004; Heberlein & Saxe, 2005), this suggests that the right hemisphere begins to play an important role in emotional body expression processing from early in ontogeny. All in all, the current data has shed new light on the developmental, perceptual and neural processes that underpin emotional body expressions thereby critically extending and informing accounts of emotion perception.

Acknowledgements

We would like to thank all participants and families who took part in this study. We also thank Caterina Böttcher for help with data collection and Kerstin Flake for assistance in preparing the figure.

5 Study 3

Discrimination of fearful and happy body postures in 8-month-old infants: An event-related potential study

Manuela Missana[1*], Purva Rajhans[1*], Anthony P. Atkinson[2], & Tobias Grossmann[1]

[1] Early Social Development Group, Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstrasse 1a, 04103 Leipzig, Germany

[2] Department of Psychology, Durham University, South Road, Durham, DH1 3LE, United Kingdom

*These authors contributed equally to this paper.

Responding to others' emotional body expressions is an essential social skill in humans. Adults readily detect emotions from body postures, but it is unclear whether infants are sensitive to emotional body postures. We examined 8-month-old infants' brain responses to emotional body postures by measuring event-related potentials (ERPs) to happy and fearful bodies. Our results revealed two emotion-sensitive ERP components: body postures evoked an early N290 at occipital electrodes and a later Nc at fronto-central electrodes that were enhanced in response to fearful (relative to happy) expressions. These findings demonstrate that, (a) 8-month-old infants discriminate between static emotional body postures, and (b) similar to infant emotional face perception, the sensitivity to emotional body postures is reflected in early perceptual (N290) and later attentional (Nc) neural processes. This provides evidence for an early developmental emergence of the neural processes involved in the discrimination of emotional body postures.

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

5.1 Introduction

Reading others' emotional expressions is a vital skill that helps us predict others' actions and guide our own behavior during social interactions (Frith, 2009). Emotional communication is inherently multidimensional and multisensory in nature as emotional information can be gleaned from various sources such as the face, the voice, the body posture and motion of a person (Heberlein & Atkinson, 2009). The bulk of research investigating emotion expression perception has focused on facial and vocal expressions (Belin et al., 2012). Much less work has been dedicated to understanding the perception of emotional body expressions, even though body expressions may be the most evolutionarily preserved and immediate means of conveying emotional information (de Gelder, 2006). The work on emotional body expressions has revealed that adults are readily able to detect and recognize various emotions from body expressions (Atkinson, 2013; de Gelder, 2009) and that in some instances emotional body cues can even be detected in the absence of conscious awareness (see Tamietto & de Gelder, 2010). Furthermore, there is recent evidence to show relatively better discrimination between positive and negative emotions from body cues when compared to facial cues (Aviezer, Trope, & Todorov, 2012). This ability to recognize emotions from body expressions relies on specific brain processes localized principally in the right hemisphere, including superior temporal, somatosensory and premotor cortices (Atkinson, 2013; de Gelder, 2006; Grèzes et al., 2007; Heberlein et al., 2004; Heberlein & Saxe, 2005). Concerning the temporal dynamics of the brain processes involved in differential responding to emotional body expressions in adults, using event-related brain potentials (ERPs), it has been shown that fearful body postures evoke enhanced activity during early stages of visual processing (Van Heijnsbergen, Grèzes, & de Gelder, 2007) and further result in sustained activity over fronto-central brain regions during later processing stages (Stekelenburg & de Gelder, 2004).

Only recently, research has begun to examine how the ability to perceive and respond to others' emotional body expressions develops during infancy. Specifically, Zieber and colleagues (2014b) examined infants' sensitivity to emotional body expressions in a series of behavioral experiments with 6.5-month-old infants (using video full-light body expressions taken from Atkinson et al., 2004; Atkinson et al., 2007). In this study, 6.5-month-olds showed a visual preference for happy over neutral body expressions and were shown to look longer at body-voice pairings that conveyed congruent emotional information (happiness or anger) than incongruent emotional information. Critically, these effects were specific to body expressions presented in an upright orientation, since infants did not show any difference in their looking responses when the body expression was presented upside-down (Zieber et al., 2014b). While these findings provide first insights into infants' perceptual sensitivity to emotional body expressions, a number of vital remaining issues were addressed in a recent event-related brain potential (ERP) study (Missana, Atkinson, & Grossmann, 2015).

In this study Missana and colleagues (2015) investigated the developmental emergence of infants' neural sensitivity to emotional body expressions by presenting 4- and 8-month-olds with upright and inverted happy and fearful dynamic body expressions using point-light displays (PLDs). This ERP study yielded three main findings with respect to infants' developing sensitivity to emotional body expressions. First, similar to prior work using facial and vocal emotional expressions (Grossmann et al., 2005; Nelson & de Haan, 1996; Peltola et al., 2009) 8-month-olds, but not 4-month-olds, showed a neural discrimination between fearful and happy body movements, suggesting that the ability to process the emotional content of body movements develops during the first year of life. Second, in line with prior work that has shown that body expression perception in adults and infants is impaired by stimulus inversion (Atkinson, 2013; Zieber et al., 2014b), the differential ERP responses to fearful vs. happy expressions in 8-month-old infants was mainly evident in the upright condition but not in the inverted condition. Third, in agreement with previous findings of right-hemisphere lateralization of emotional body-expression processing in adults (Grèzes et al., 2007; Heberlein et al., 2004; Heberlein & Saxe, 2005), 8-month-old infants emotion-sensitive brain responses were lateralized to the right hemisphere.

Given what has been shown in recent work (Missana et al., 2015; Zieber et al., 2014b), another important question that arises is, once infants are sensitive to body expressions, how flexible are they in detecting them? Specifically, can infants discriminate between emotional body expressions in the absence of motion cues like adults can (Atkinson et al., 2004; Atkinson et al., 2012; de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Stekelenburg & de Gelder, 2004)? Such an extension of prior work is critical because (a) it provides a developmental perspective on emotional body expression processing by allowing for a comparison between prior ERP findings with adults (Stekelenburg & de Gelder, 2004; Van Heijnsbergen et al., 2007) and the current infant data, and (b) it establishes a link to the literature on facial expression processing since most prior ERP work on infants' processing of emotional facial expressions has been focused on static but not dynamic facial expressions (Missana, Grigutsch, & Grossmann, 2014).

In order to examine the question posed above, we conducted an experiment in which we presented a group of 8-month-old infants with static photographs of upright and inverted happy and fearful body expressions while measuring their ERPs. We hypothesized that if 8-month-olds are sensitive to emotional information conveyed through the body even in the absence of motion cues, then they would show evidence for discriminating between fearful and happy emotional body postures in their ERP responses. Regarding this hypothesis it is important to emphasize that from prior work with adults (Atkinson et al., 2004; Atkinson et al., 2007) we know that while inversion of body expressions impairs the recognition of emotion from body expressions, it does not completely abolish it. That is, adults' emotion recognition rates from inverted body expressions are still above chance. Similarly, in prior ERP work with infants (Missana et al., 2015) using dynamic body expressions, while there was a significant main effect of emotion (fearful, happy), no evidence for an interaction between the emotion and orientation (upright, inverted) was obtained, which is probably to do with the fact that ERP modulations occurred in a similar direction for upright and inverted displays of emotion. However, further analysis revealed that only in the upright condition did infants' neural responses discriminate between emotions (Missana et al., 2015). We hypothesized that neural evidence for emotion discrimination is related to the orientation of the body; however, given previous findings, we expected that this effect might not be directly reflected in a significant interaction between stimulus orientation and emotion. This hypothesis is also based on prior work that has shown that body expression perception in adults and in infants is impaired (but not completely abolished) by stimulus inversion (Atkinson et al., 2007; Missana et al., 2015; Stekelenburg & de Gelder, 2004; Zieber et al., 2014b). We therefore predicted that infants' discrimination between emotions would mainly be evident in the upright condition but not, or at least not as clearly, in the inverted condition. More specifically, we focused our investigation on infant ERP components linked to early visual processes (N290) at posterior sites, and later attentional processes (Nc) at anterior sites, which are reliability observed in response to visual stimuli and known to be modulated by emotional information (Grossmann et al., 2006; Kobiella et al., 2008; Peltola et al., 2009). Based on prior work (Missana et al., 2015), we had also planned to assess effects on a late ERP component referred to as the Pc, evoked at temporal and parietal electrodes, that has been found to be modulated by dynamic emotional body expressions. However, already at the level of the visual inspection of the ERP data there was no discernible Pc observed in the ERPs, which prevented us from studying this component further. This approach also allowed us (a) to assess potential differences between statically (current study) and dynamically presented body expressions (Missana et al., 2015) and (b) to examine whether the body inversion effects and hemispheric lateralization of the ERP responses observed in prior work using PLDs (Missana et al., 2015) could be replicated with a different group of 8-month-infants using static body expressions.

5.2 Methods and Materials

Participants. The final sample consisted of 15 eight-month-old infants aged between 243 and 261 days (10 females, *Median age* = 251, *Range* = 18 days). An additional 23 eight-month-old infants were tested, but were excluded from the final sample due to fussiness (*n* = 5), too many artifacts (*n* = 16) and experimenter error (*n* =2). Note that an attrition rate at this level is within the normal range for an infant ERP study (DeBoer et al., 2005). The infants were born full-term (between 37 and 41 weeks) and had a normal birth weight (> 2500 g). Ethical approval was obtained from the ethics committee of the Medical School at the University of Leipzig. All parents gave written informed consent prior to the study and were paid for their children's participation. The children were given a toy after the session.

Stimuli. The stimulus material consisted of full-light static body expressions displaying six different fearful and six different happy expressions (from Atkinson et al., 2004). These expressions were taken from the same actors posing the same emotions as in a previous ERPs study (Missana et al., 2015) by selecting still frames of the full-light version of the body expression recording at the peak of the expression (see Figure 5.1A). From the original set of 8 stimuli per condition used in Missana et al.'s (2015) study, 6 stimuli for each emotion were selected on the basis of their recognition rate by a group of adults (Atkinson et al., 2004) (at least 40 % mean percentage correct identification of the emotion displayed; chance level was 16.7 %). The stimuli had a mean height of 11.9 cm subtending a visual angle of 9.74° (SD = 3.5 cm) and a mean width of 6.5 cm subtending a visual angle of 5.4° (SD 3.1 cm).

Procedure. The infants were seated on their parent's lap in a dimly lit, sound-attenuated and electrically shielded room during testing. In order to rule out that the parents influenced the infants' responses to the stimuli we asked the parents not to talk or interact with their infant during the course of the experiment (Kobiella et al., 2008). Furthermore, we instructed the parents to look down at the infant but not at the screen and the sessions were video-recorded so that trials during which the parent interacted with the infant could be excluded from the analysis. The stimuli were presented in the center of the screen on a black background, using a 70-Hz, 17-inch computer screen at a distance of 70 cm. Each trial began with an alerting sound and a fixation cross (1000 ms), in order to attract the infants' attention to the screen, followed by a black screen (400 ms), followed by the full-light static expression (2000 ms). During the inter-trial interval infants were presented with an abstract screensaver for the purpose of keeping infants' attention. The inter-trial interval lasted at least 1000 ms and varied depending on the infants' attentiveness, as stimulus presentation was controlled by an experimenter such that stimuli were only presented when infants were looking at the screen. 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. In addition, the sessions were video-recorded to allow for off-line coding of infants' attention to the screen. The EEG session ended when the infant became fussy, or inattentive.

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. At each electrode, artifact-free epochs were averaged separately for fearful upright, happy upright, fearful inverted and happy inverted body expressions to compute the ERPs. The mean number of trials presented within each condition was 17.18. The mean number of trials included in the ERP average was 6.60 (*SE* = .73) for the fearful upright condition, 7.80 (*SE* = 1.15) for the happy upright condition, 5.93 (*SE* = .53) for the fearful inverted condition and 7.60 (*SE* = 1.05) for the happy inverted condition. The criterion for inclusion was a minimum of 4 trials per condition. The mean number of trials is somewhat lower than in prior infant ERP studies but this is likely to do with the fact that the current design consisted of four conditions, which is more than in prior studies. We note that the low trial number can be seen as a limitation of the current study but want to stress that, (a) in order to allow for comparisons, our procedure and analysis were closely matched to previous work that used dynamic displays of emotional body expressions (Missana et al., 2015), and (b) conservative rejection criteria were applied so that only artifact-free trials were included in the analysis. In this context it is also important to mention that the Nc, as one of the main components examined in this study, is a rather large deflection, discernible and present in individual infants even when a relatively small number of trials is used (see Hoehl & Wahl, 2012, recent methods paper that provides extensive information regarding ERP measurement and analysis standards for infants and present data from individual infants demonstrating that 5 trials are sufficient to evoke clear Nc responses)**.** Based on prior ERP work (Kobiella et al., 2008; Leppänen et al., 2007; Missana et al., 2015; Peltola et al., 2009) and the visual inspection of the ERP data three ERP components distinct in timing (early and late) and topography (occipital and fronto-central) were analyzed. First, to assess ERP effects on the N290 over visual cortex at occipital electrodes (O1, O2), ERPs were statistically analyzed during an early time window of 250 to 350 ms after stimulus onset. Second, to assess ERP effects on the Nc over frontal cortex at frontal and central electrodes (F3, F4, C3, C4), ERPs were statistically analyzed during a late time window of 700 to 800 ms after stimulus onset. Note that the onset and exact timing of the Nc has been shown to vary considerably across studies and might depend on the stimulus duration and other characteristics of the presentation protocol (de Haan et al., 2003; Grossmann et al., 2007; Leppänen et al., 2007; Luyster, Powell, Tager-Flusberg, & Nelson, 2014; Missana, Grigutsch, et al., 2014). Mean amplitude ERP effects for these regions and time windows were assessed in repeated measures ANOVAs with the within-subject factors emotion (happy versus fear), orientation (upright versus inverted), and hemisphere (left versus right). As prior work indicates that emotion-sensitive ERP response were lateralized to the right hemisphere and specific to the upright orientation (Missana et al., 2015), in addition to the repeated measures ANOVAs, we conducted paired samples *t*-Tests to evaluate the orientation specificity and lateralization of the ERP responses.

5.3 Results

N290. Our analysis revealed a significant main effect of emotion at occipital electrodes from 250 to 350 ms, $F(1, 14) = 7.02$, $p = 0.019$, $\eta^2 = 0.334$, where fearful body expressions (M = -1.58 µV, SE= 2.59) elicited a more negative N290 than happy body expressions (M = 6.14 µV, SE = 3.34). Further analysis showed that this effect of emotion was driven by differences in the upright orientation, as upright fearful body expressions (M = -2.23 µV, SE = 3.04) elicited ERPs that were significantly more negative in their mean amplitude than ERPs elicited by upright happy body expressions (M = 6.42 µV, SE = 3.42) during this time window, t [14] = 2.22, $p = 0.043$ (uncorrected) (see Figure 5.1B and Table 5.1), whereas no significant differences between emotions were observed for this component when the stimuli were inverted, t [14] = 1.39, $p = 0.196$. Note that our analysis showed no significant interaction between the factors emotion, orientation and hemisphere, $F(1, 14) = 2.49$, $p = 0.137$, $\eta^2 = 0.151$.

Nc. Our analysis revealed a significant main effect of emotion at frontal and central electrodes from 700 to 800 ms, $F(1, 14) = 5.03$, $p = 0.042$, $\eta^2 = 0.264$, where fearful body expressions (M= -8.12 µV, SE= 2.15) elicited a more negative Nc than happy body expressions (M = -1.56 µV, SE = 1.79). Further analysis showed that this effect of emotion on the Nc was driven by differences over the right hemisphere for the upright orientation. Specifically, at the right-hemisphere fronto-central electrodes ERPs to upright fearful body expressions were significantly more negative in their mean amplitude (M = -9.19 µV, SE = 2.64) than ERPs elicited by upright happy expressions (M = -0.14 µV, SE = 2.78), t [14] =

2.79, $p = 0.014$ (uncorrected) (see Figure 5.1B and Table 5.1), whereas no significant differences were observed at the right-hemisphere fronto-central electrodes when the stimuli were inverted, t [14] = 1.53, $p = 0.147$, or at the left-hemisphere fronto-central electrodes when the stimuli were presented upright, t [14] = 1.52, $p = 0.150$ or inverted, t [14] = 1.43, $p = 0.174$. Note that our analysis showed no significant interaction between the factors emotion, orientation and hemisphere, $F(1, 14) = 0.389$, $p = 0.543$, $\eta^2 = 0.027$.

Note that reported p-values for pairwise-comparisons are uncorrected. The p-value for the Nc survives a Bonferroni correction but for the N290 the p-value does not survive a Bonferroni correction threshold at $p < 0.025$.

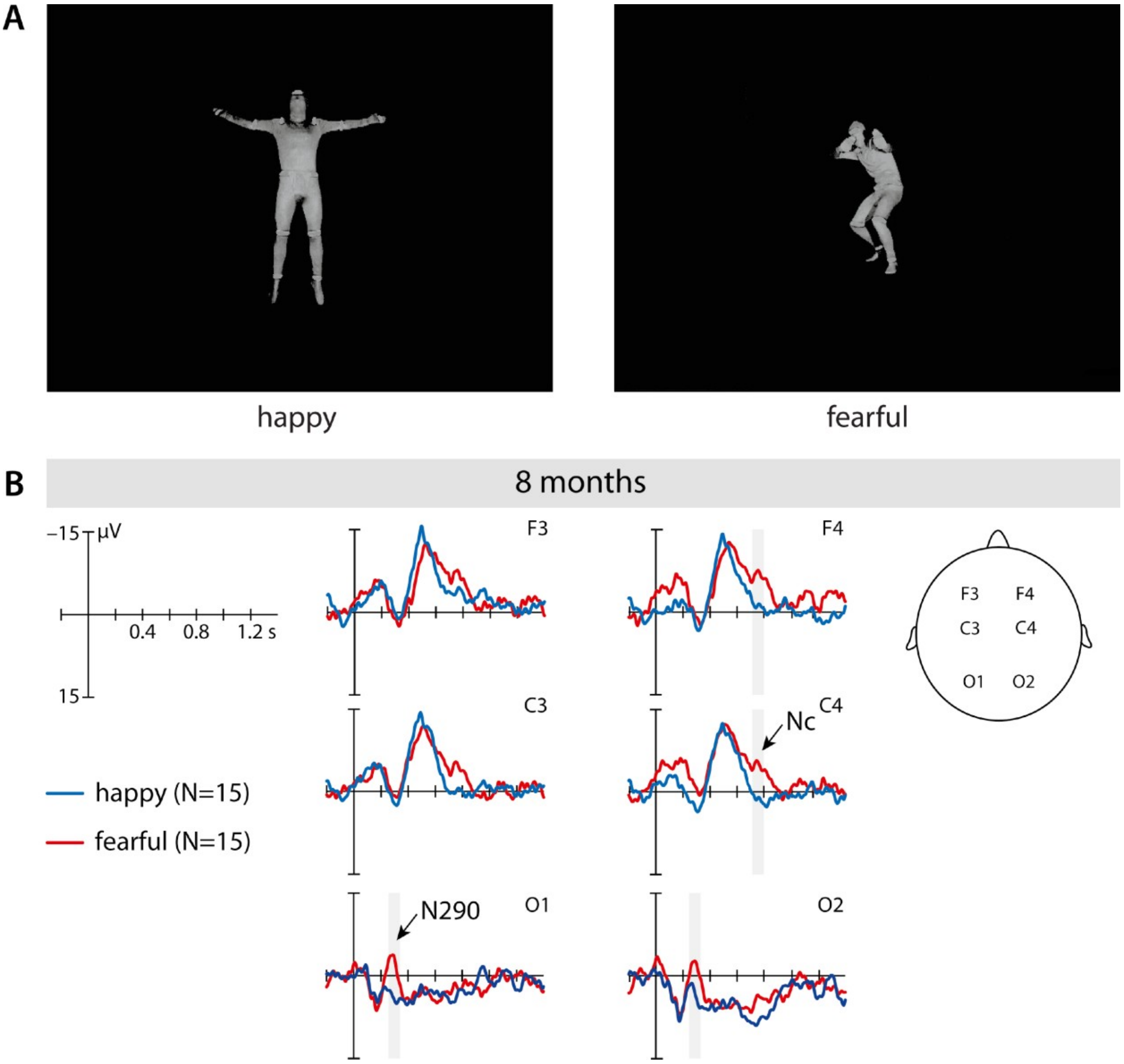


Figure 5.1. Examples of the stimuli and ERPs. A) These are examples of the static full-light body expression stimuli (upright) used in the study. B) This shows the event-related brain potentials (ERPs) at fronto-central and occipital electrodes time-locked to the stimulus onset in 8-month-old infants elicited by fearful upright (red) and happy upright (blue) static full-light body expressions. The time windows during which significant differences between fearful and happy body expressions were observed are marked in grey. Note that negativity is plotted upward.

Table 5.1. Means (SD) of ERPs in microvolt. This table shows the means (standard deviations) of ERPs in microvolt for happy upright, fearful upright, happy inverted, and fearful inverted body expressions at occipital and frontal and central electrodes.

		Early visual processing		**Attention allocation**		
		N290: 250 - 350 ms		***Nc: 700 - 800 ms***		
		Occipital		**Frontal and Central**		
		O1/O2		**F3/ C3**	**F4/ C4**	
happy upright	Mean (SD) µV	6.42 (13.42)	*	-3.08 (11.70)	-0.14 (10.78)	*
fearful upright	Mean (SD) µV	-2.23 (11.79)		-8.88 (9.02)	-9.19 (10.24)	
happy inverted	Mean (SD) µV	5.86 (17.06)		-2.46 (6.52)	-0.55 (6.24)	
fearful inverted	Mean (SD) µV	-0.94 (14.35)		-7.65 (12.58)	-6.77 (11.10)	

* $p < .05$

5.4 Discussion

The current study examined how infants process emotional information from body postures by investigating the neural correlates of discriminating between fearful and happy body expressions. Our results revealed two emotion-sensitive ERP responses (N290 and Nc) distinct in timing and topography. Namely, we found that 8-month-old infants discriminated between emotions as reflected in ERP differences for (a) the N290 at occipital electrodes during an early time window (250-350 ms), and (b) the Nc at frontal and central electrodes during a late time window (700-800 ms).

More specifically, the pattern of ERP findings indicates that this ability relies on early visual processes (N290, Kobiella et al., 2008) as revealed by the ERP difference observed at occipital electrodes and later attentional processes (Nc, Nelson & de Haan, 1996; Peltola et al., 2009) as indexed by the ERP difference observed at frontal and central electrodes. The early ERP effect on the N290, with an enhanced N290 elicited by fearful body expressions when compared to happy body expressions, is in line with prior work showing that the N290 varies as a function of emotional facial expressions (Kobiella et al., 2008). This suggests that emotional information affects early visual (posterior) processing likely related to the structural encoding of both bodies and faces (Gliga & Dehaene-Lambertz, 2005; Halit, Csibra, Volein, & Johnson, 2004). Critically, the early occipital ERP effect appears to be specific to the discrimination processes elicited by static emotional body expressions, because it was only observed in the current study but not in prior ERP work using emotional PLDs (Missana et al., 2015). This might have to do with the fact that in the current study the ERP response was measured in response to discrete emotional body postures (taken at the apex of the expression) enabling fast detection of differences in expression, while for the dynamic stimuli changes in body posture unfold more slowly over time and might thus be harder to detect for the infants. The later ERP effect on the Nc, with an enhanced Nc elicited by fearful body expressions when compared to happy body expressions, is in general agreement with prior work showing a similar effect on the Nc in response to fearful and happy facial expressions (Nelson & de Haan, 1996; Peltola et al., 2009). Interestingly, the enhanced Nc response to fearful expressions in infants is similar to a fronto-central response observed in prior work with adults (Stekelenburg & de Gelder, 2004), suggesting that both infants and adults possess neural processes associated with increased allocation of attention to fearful bodies. This speaks to the importance of fear signals in directing attention (Vuilleumier, 2005). The results indicate that by the age of 8-months the infant brain distinguishes between bodily expressions of emotion, even in static displays, which is consistent with previous research showing similar results in topography in adults' brains. However, further research is required to directly compare and contrast the timing and topography of these responses (and ultimately, of the underlying neural processing) across infants and adults.

With respect to this finding concerning the Nc response it is important to note that the ERP difference observed for body expressions occurred somewhat later than the ERP difference commonly reported for facial expressions, suggesting that it might take infants longer to extract emotional information from bodies than from faces. Why this might be the case should be examined in future work that directly compares emotion processing from faces and bodies. Irrespective of these timing differences, the current data on body expression processing and prior work on facial expressions processing suggest that the detection of emotional information affects later anterior processing related to differential attention allocation to bodies and faces. Furthermore, this finding indicates that fearful expressions regardless of whether they are presented in the face or through body posture evoke a greater allocation of attention as indexed by the Nc. That the perception of signals of fear in others would result in such an effect possibly serves a critical adaptive function because it may allow infants from early in life to pay attention and learn from others in dangerous and threatening situations.

It is important to mention that, although not obtaining an interaction between orientation (upright, inverted) and emotion (fearful, happy), detailed analyses of the N290 and the Nc revealed that ERPs differed between emotions, specifically in the upright condition. This suggests that emotion effects were mainly driven by body posture seen in an upright orientation. This is similar to what is known from behavioral and ERP studies with adults (Atkinson et al., 2007; Stekelenburg & de Gelder, 2004) and infants (Missana et al., 2015; Zieber et al., 2014b) regarding emotional perception from body expressions. Critically, the disruption of emotion discrimination by body inversion can be seen as evidence for configural processing of body posture. That is, rather than relying on individual features of the body that are also present in the inverted stimulus, 8-month-olds require to see the familiar configuration of body features in order for the emotion discrimination process to take place.

In this context, it is important to emphasize that this is one of the first infant ERP studies that investigated the effects of stimulus inversion on visual emotion processing (see Missana et al., 2015, for the only other ERP study that used this kind of manipulation). Clearly, more work is needed to further specify the exact nature of orientation effects on visual emotion processing. However, it should be noted that using inverted stimuli as control stimuli yields an advantage over studies that used a neutral condition or no control condition because the low level visual information is kept identical across orientations, whereas neutral conditions generally differ with respect to low level visual features from the emotional conditions. Thus, the use of inverted stimuli can be seen as a strength of the current study.

Moreover, although we did not obtain an interaction between the factors hemisphere (left, right) and emotion (fearful, happy), we observed that for the Nc ERPs differed between fearful and happy body expressions only over the right hemisphere. This is similar to what has been shown in prior work using dynamic body expressions (Missana et al., 2015), indicating that similar lateralization of the brain response can be observed for dynamic and static stimuli. In line with prior adult work (Grèzes et al., 2007; Heberlein et al., 2004; Heberlein & Saxe, 2005), this may suggest that the right hemisphere begins to play an important role in emotional body expression processing from early in ontogeny. Taken together, these results provide corroborating evidence for the laterality and orientation specificity of the brain processes employed by infants at the age of 8 months when perceiving emotional body expressions.

However, it should also be noted that the timing and the topography of the emotion-sensitive ERP effects varied between prior work using dynamic stimuli (Missana et al., 2015) and the current study. These dissimilarities provide insights into how the processing of dynamic and static body expressions differs. As discussed above, the N290 effect appears to be unique to static presentation of emotional bodies. Furthermore, the current data showed a modulation for the Nc at frontal and central electrodes, whereas prior work using dynamic stimuli elicited later effects on the Pc at temporal and parietal electrodes. This suggests brain processes distinct in timing and region are engaged when discriminating between emotional body expressions on the basis of motion cues (Missana et al., 2015) and posture cues (current study). Importantly, that dynamic and static presentation of emotional expressions evokes distinct processes in the human brain has been repeatedly shown in adults (Kessler, Doyen-Waldecker, Hofer, Traue, & Abler, 2011; Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004), suggesting that it is of critical importance to study the emergence of these differences in development. This is a topic that has been greatly neglected as far as the neuroscience of emotion perception in infancy is concerned. Clearly, future work is needed that directly compares emotion processing from static and dynamic body cues within the same infants in order to better describe and understand the nature of these differences.

As mentioned in the methods section, we took several precautionary measures to control that the parents did not influence infants' responses to the stimuli. We asked the parents not to attend to the screen, not to talk or interact with their infant during the course of the experiment. We further video-recorded the sessions so that trials during which the parent interfered with the procedure could be excluded from the analysis. Despite of all of these measures taken, we still cannot completely rule out the possibility that parents unintentionally cued the infants. This limitation applies to all infant studies in which the infants sit on their parents' lap and might be addressed in future studies by placing the infant in a seat that prevents direct contact between the infant and the parent (e.g., Fairhurst, Löken, & Grossmann, 2014).

In summary, the current findings have informed three main aspects of our understanding of how emotional body expressions are processed. First, as far as the developmental perspective is concerned, we have seen that 8-month-old infants detect emotional information from body postures, providing evidence that at this age they sensitively respond to emotional information from bodies. This sensitivity to emotional body expressions is manifested at a time in development when a similar sensitivity to facial and vocal emotional cues has developed (Grossmann, 2013a; Peltola et al., 2009). In conjunction with prior work, these findings thus provide evidence for accounts that conceive of emotion perception as a unified ability that is reflected across various processing channels (face, voice and body). Second, with respect to the neurodynamics of body expression processing, we have seen that emotional body posture discrimination is reflected in early perceptual (visual) and later attentional neural processes, suggesting that emotion discrimination is multifaceted and relies on perceptual processes that occur before differential attention is allocated to emotional stimuli. Third, at the hemispheric level, we have provided evidence that emotion discrimination from body expressions elicits brain responses (Nc) that are more prominent in the right hemisphere. In agreement with prior work (Grèzes et al., 2007; Heberlein et al., 2004; Heberlein & Saxe, 2005), this suggests that the right hemisphere begins to play an important role in emotional body expression processing from early in ontogeny. All in all, the current data has shed new light on emotional body expression processing in infancy thereby critically extending and informing accounts of emotion understanding.

Acknowledgements

We would like to thank all participants and families who took part in this study. We also thank Caterina Böttcher for help with data collection and Kerstin Flake for assistance in

6 Study 4

Infants' emerging sensitivity to emotional body expressions: Insights from asymmetrical frontal brain activity

Manuela Missana[1] & Tobias Grossmann[1,2]

[1] Early Social Development Group, Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstrasse 1a, 04103 Leipzig, Germany

[2] Department of Psychology, University of Virginia, 102 Gilmer Hall, Charlottesville, VA 22904, U.S.A.

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

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

6.1 Introduction

Understanding others' emotional expressions is a vital skill that helps us predict others' actions and guide our own behavior during social interactions (Frith, 2009). Emotional communication is inherently multidimensional and multisensory in nature as emotional information can be gleaned from various sources such as the face, the voice, and the body posture and motion of a person (Heberlein & Atkinson, 2009). The bulk of research investigating emotion expression perception has focused on facial and vocal expressions (Belin et al., 2012). Much less work has been dedicated to understanding the perception of emotional body expressions, even though body expressions may be the most evolutionarily preserved and immediate means of conveying emotional information (de Gelder, 2006). The work on emotional body expressions has revealed that adults are readily able to detect and recognize various emotions from body expressions (Atkinson, 2013; de Gelder, 2009). This ability to recognize emotions from body expressions relies on specific brain processes localized principally in the right hemisphere, including superior temporal, somatosensory, and premotor cortices (Atkinson, 2013; de Gelder, 2006; Grèzes et al., 2007; Heberlein et al., 2004; Heberlein & Saxe, 2005).

From a developmental perspective it has been shown that already during the first year of life infants' brains become sensitive to various facial and vocal expressions (for review, see

Grossmann, 2013a). Despite the progress that has been made in understanding the ontogeny of emotion perception from face and voice by studying its neural correlates using event-related brain potentials (ERPs), how the ability to perceive and respond to others' emotional body expressions develops during infancy has only recently been investigated. Namely, Missana and colleagues (2015) examined ERPs in response to dynamic happy and fearful body expressions in 4- and 8-month-old infants using point-light displays (PLDs) (Atkinson et al., 2012) presented in an upright and inverted orientation. The ERP results of this study revealed that 8-month-olds but not 4-month-olds showed an emotion-sensitive responding as reflected in an increased positive component (Pc) from 700 to 1100 ms to happy relative to fearful expressions when presented in an upright orientation (Missana et al., 2015). The Pc is taken to reflect recognition memory processes and a greater (more positive) Pc indexes the recognition of an item or event (Grossmann et al., 2006; Nelson & de Haan, 1996; Nelson et al., 1998; Webb et al., 2005). The ERP results from this study therefore suggest that (a) the infant brain becomes tuned to emotional body expressions between 4 and 8 months of age and (b) that at 8 months of age infants recognize positive body expressions. This is in line with work demonstrating that infants' perception of facial and vocal expressions of emotion undergoes similar developmental tuning during this period (Grossmann et al., 2005; Peltola et al., 2009).

Critically, the developmental emergence of infants' ability to detect fear in others and discriminate it from happy expressions occurs at a time in development when infants begin to express fear themselves (Campos, Kermoian, & Zumbahlen, 1992). For example, it has been shown that at 8 months of age, but not at 4 months of age, infants show increased anxiety towards strangers (Braungart-Rieker, Hill-Soderlund, & Karrass, 2010). This developmental change in infants' emotional responding has been linked to a sensitive period in infants' socio-emotional development related to the onset of independent locomotion (Campos et al.,

2000) and maturation of the amygdala and connected brain structures (see Tottenham, 2012, for a discussion). The occurrence of such developmental changes in early socio-emotional development related to fear responding has been extensively studied in other altricial species such as rodents (Moriceau, Roth, & Sullivan, 2010) and monkeys (Bauman & Amaral, 2008). This pattern is thought to serve important adaptive functions with respect to bonding with the caregiver during the earliest stages of postnatal development by increasing approach through the reduction of fear (Tottenham, 2012). This may therefore be seen as a highly preserved developmental mechanism in altricial species. Although infants' expression and perception of fear in comparison to happiness has been assigned such a critical role in early socio-emotional development, to date it is not known whether and when the perception of body expressions in others evokes sensitive responses linked to motivational brain processes in infants.

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

Frontal EEG alpha asymmetry has also been examined in early development. For example, in a study by Davidson and Fox (1982) frontal EEG alpha asymmetry was examined in 10-month-old infants who were presented with happy and sad facial expressions. In line with the notion that the perception of emotional expressions results in different motivational tendencies in the perceiver, in this study, happy facial expressions elicited greater relative left frontal activation than sad facial expressions that elicited greater relative right frontal activation (Davidson & Fox, 1982). Moreover, in infants it has been shown that the experience of particular emotional states is associated with systematic differences in frontal EEG alpha asymmetry. Specifically, expressing withdrawal-related behaviors in 6-month-old infants was associated with greater relative right frontal EEG asymmetry (Buss et al., 2003), while exhibiting approach-related behaviors (smiling) resulted in greater relative left frontal EEG asymmetry in 10-month-old infants (Fox & Davidson, 1988). This indicates that the perception of emotions in others and the experience of emotional states are reflected in systematic changes in frontal EEG alpha asymmetry in infants.

The aim of the current study was to extend previous ERP findings (Missana et al., 2015) regarding infants' emerging sensitivity to emotional body expressions by investigating the effects of perceiving dynamic fearful and happy body expressions on frontal EEG alpha asymmetry patterns in 4- and 8-month-old infants. Based on the prior work reviewed above, we had three main predictions. First, we predicted that 8-month-old infants, but not 4-month-old infants, show differential responding to emotional body expressions (developmental hypothesis). Second, we predicted that 8-month-old infants' frontal EEG alpha asymmetry patterns only differ when the emotional body expressions are presented in an upright orientation (orientation specificity hypothesis). Third, in terms of the asymmetry patterns, we predicted that 8-month-olds show (a) greater right frontal EEG asymmetry to fearful expressions, indexing a tendency to withdraw, and (b) greater left frontal EEG asymmetry to happy expressions, indexing a tendency to approach (emotion sensitivity hypothesis).

6.2 Materials and Methods

Participants. The experiment was based on EEG data collected from a previous study with 4- and 8-month-old infants (Missana et al., 2015). The sample consisted of 20 4-month-old infants aged between 123 and 137 days (10 females, *Median age* = 129 days, *Range* = 14 days) and 20 8-month-old infants between 230 and 259 days (9 females, *Median age* = 251, *Range* = 29 days). An additional 15 4-month old infants aged between 122 and 138 days (8 females, *Median age* = 133 days, *Range* = 16 days) and 20 8-month-old infants aged between 230 and 259 days (10 females, *Median age* = 251 days, *Range* = 29 days) were tested but were excluded from the final sample due to fussiness (*n* = 5) or too many artifacts (*n* = 30). Infants excluded from the final analysis did not systematically differ in gender, age, or maternal education from the included infants. Note that an attrition rate at this level is within the normal range for an infant ERP study (DeBoer et al., 2005). The infants were born full-term (between 37 and 41 weeks) and had a normal birth weight (> 2500 g). All infants came from a middle-class background in a medium-sized German city. Maternal education was assessed by obtaining information regarding the mother’s final school degree. Maternal education was scored by using a ranking from 1 (lowest possible school degree in Germany) to 3 (highest possible school degree in Germany). For our sample the mean for maternal education was 2.67 (*SD* = .56).

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

Stimuli. The stimulus material consisted of 2-s clips of point-light body movements displaying eight different fearful and eight different happy expressions (from Atkinson et al., 2012), which were presented upright and inverted (see Figure 6.1). Stimulus motion was equated across the two emotion categories by selecting 8 expressions from the original set of 10 for each emotion, such that the differences in the means of 3 similar measures of stimulus motion were as small as possible.

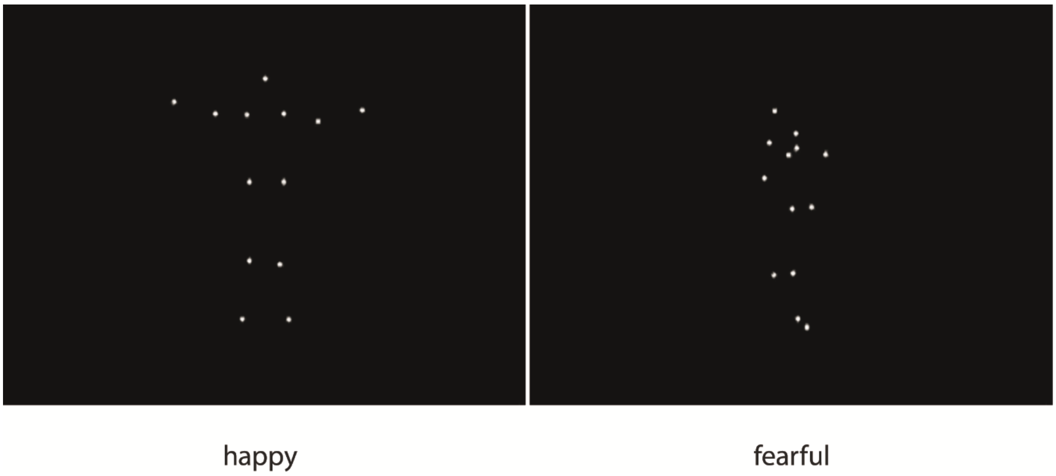


Figure 6.1. An example of the PLD stimuli. This figure provides an example of the PLD stimuli. The figure shows two still frames taken at the maximum of the emotional expression. Reprinted from "Tuning the developing brain to emotional body expressions" by Missana et al.,, 2014, Developmental Science. Reprinted with permission.

Procedure. The infants were seated on their parent's lap in a dimly lit, sound-attenuated and electrically shielded room during testing. In order to rule out the possibility that the parents influence the infants' responses to the stimuli, we asked the parents not to talk to or interact with their infant during the course of the experiment. Furthermore, we instructed the parents to look at the infant but not at the screen and the sessions were video-recorded so that trials during which the parent interacted with the infant could be excluded from the analysis. The stimuli were presented in the center of the screen on a black background, using a 70-Hz, 17-inch computer screen at a distance of 70 cm. In order to attract the infants' attention to the screen, each point-light body expression clip was preceded by an alerting sound and a fixation cross (1000 ms), followed by a black screen (400 ms), followed by the stimuli (2000 ms). During the inter-trial 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 screen. The EEG session ended when the infant became fussy or inattentive.

EEG measurement. The EEG was recorded from 27 Ag/AgCl electrodes attached to an elastic cap (EasyCap GmbH, Herrsching, Germany) using the 10-20 system of electrode placement. The data were online referenced to the CZ electrode and offline re-referenced to the algebraic mean of the left and right mastoid electrode. The horizontal electrooculogram (EOG) was recorded from two electrodes (F9, F10), which are part of the cap located at the outer canthi of both eyes. The vertical EOG was recorded from an electrode on the supraorbital ridge (Fp2), which is part of the cap and an additional single electrode on the infraorbital ridge of the right eye. The EEG was amplified using a Porti-32/M-REFA amplifier (Twente Medical Systems International, EJ Oldenzaal, Netherlands) and digitized at a rate of 500 Hz. Electrode impedances were kept between 5 and 20 kΩ.

EEG measures of asymmetrical activation. Frequency analysis of the EEG data was performed using the *FieldTrip* software (http://fieldtrip.fcdonders.nl/; Oostenveld et al., 2011) in combination with custom-made MATLAB scripts. The raw EEG data were high-pass filtered with a cut-off frequency of 3 Hz in order to reduce slow drifts and removing DC components. The recordings were segmented into epochs of 4000 ms duration, lasting from 1000 ms prior stimulus onset until 1000 ms post video offset. Epochs were visually inspected and excluded from further analyses if they were contaminated by large non-stereotyped artifacts (e.g., gross muscle activity or movement artifacts). Remaining stereotyped artifacts (originating e.g., from eye blinks or eye movements, tonic muscle activity, or pulse artifacts) were corrected using a signal processing procedure (Jung et al., 2000) based on Independent Component Analysis (ICA). The segmented EEG data were decomposed into 24 independent components (ICs) by application of the symmetric FastICA algorithm. ICs representing physiological or electrode artifacts were identified by visual inspection of the components' scalp topographies, frequency spectra, and single-trial time courses. They were removed from the data before back projection to the electrode space. For the analysis of event-related oscillations, time-frequency representations of artifact-cleaned single trials were computed using Morlet wavelets with a width of 5 cycles. The mean alpha power during the processing of point-light body expressions was estimated by averaging the squared magnitude of the complex wavelet transform coefficients across trials (separately for happy upright, happy inverted, fearful upright, and fearful inverted body expressions), over time points and frequency bins. Power values were obtained in the alpha frequency band from 4 to 8 Hz where the majority of power was localized. It has been shown that the alpha frequency range changes with development and is generally lower in infants and children than in adults (Marshall, Bar-Haim, & Fox, 2002; Stroganova et al., 1999). Prior work shows that peaks of alpha power were observed in the frequency range of 6–9 Hz in infants, suggesting that this range is most suitable for studying alpha power in infancy (Bell & Fox, 1994; Marshall et al., 2002). Because even lower frequency ranges were used in other work with infants (Fox & Davidson, 1987, 1988; Henderson, Fox, & Rubin, 2001), we decided to visually inspect our data to determine the appropriate frequency range. This visual inspection of the data revealed that in our infant groups the maximum power was found in the range of 4 to 8 Hz and we therefore focused our analysis on this range. Mean alpha power values were log-transformed using the natural logarithm function (ln) to normalize their distribution. EEG alpha power asymmetry scores were calculated for mid-frontal (F3, F4) electrodes during a time window of 700 to 1100 ms post stimulus onset. The selection of electrodes for our analysis was based on prior infant and children studies that examined frontal EEG asymmetry responses (Davidson & Fox, 1982; Fox & Davidson, 1988; Missana, Grigutsch, et al., 2014; Pickens, Field, & Nawrocki, 2001). We chose the time window for our analysis based on prior work using ERPs (Missana et al., 2015). For this purpose, it is important to keep in mind that we used dynamic stimuli that changed from a neutral display (the actor standing in a neutral position) to the expression of the respective emotion. In this dynamic context the emotional expression unfolds over time and the detection of differences between emotions does not occur before 700 ms, as demonstrated in previous work using ERPs (Missana et al., 2015). Our time window for the frontal EEG alpha asymmetry analysis therefore only started at 700 ms after movement onset. The time window chosen is shorter than in prior studies, but still long enough to fully capture oscillations within the frequency range of interest for our analysis (4–8 Hz). Specifically, at 6 Hz, a time window of 400 ms, as used in the current analysis, is more than twice as long as a cycle of the alpha oscillation which is at $T = 167$ ms (calculation based on the formula $T = 1/f$). The scores were obtained by subtracting left log-transformed alpha power values from the corresponding right log-transformed values (ln(right) – ln(left)). It has been shown that increases in alpha power are associated with decreased cerebral activation and vice versa (Goldman et al., 2002; Laufs et al., 2003). The asymmetry score reflects the power in one hemisphere relative to the power in the opposite hemisphere. Higher scores on this metric suggest relatively greater left activity (Davidson, 1988).

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

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

6.3 Results

Our analysis revealed a significant three-way interaction between the factors emotion, orientation, and age, F (1,38) = 7.125, $p = 0.011$, partial $\eta^2 = 0.158$. Given that the factor age interacts with the experimental manipulation, further analyses were conducted for the two age groups separately in order to resolve this three-way interaction. Specifically, in agreement with our predictions (*developmental hypothesis*), we found that for the group of 8-month-old infants there was a significant interaction between the factors emotion and orientation (F [1,19] = 5.735, $p = 0.027$, partial $\eta^2 = 0.232$), while no such interaction was observed in the group of 4-month-old infants. An additional analysis for a longer time window of 700 to 2000 ms revealed no significant interaction between the factors emotion, orientation, and age, F (1,38) = 1.031, $p = 0.316$, suggesting that the effect is limited to the time window examined above (see Figure 6.2 for time-frequency plots of the EEG data from the 8- and 4-month-old infants, respectively). In addition, we controlled for effects of maternal education by conducting a repeated measures ANOVA with the same factors (emotion, orientation, and age) as specified above and including maternal education as a covariate. This analysis revealed no main effects of maternal education or interactions with maternal education. Moreover, the emotion x orientation x age interaction remained significant when controlling for maternal education, $F\ (1,30) = 4.804$, $p = 0.036$.

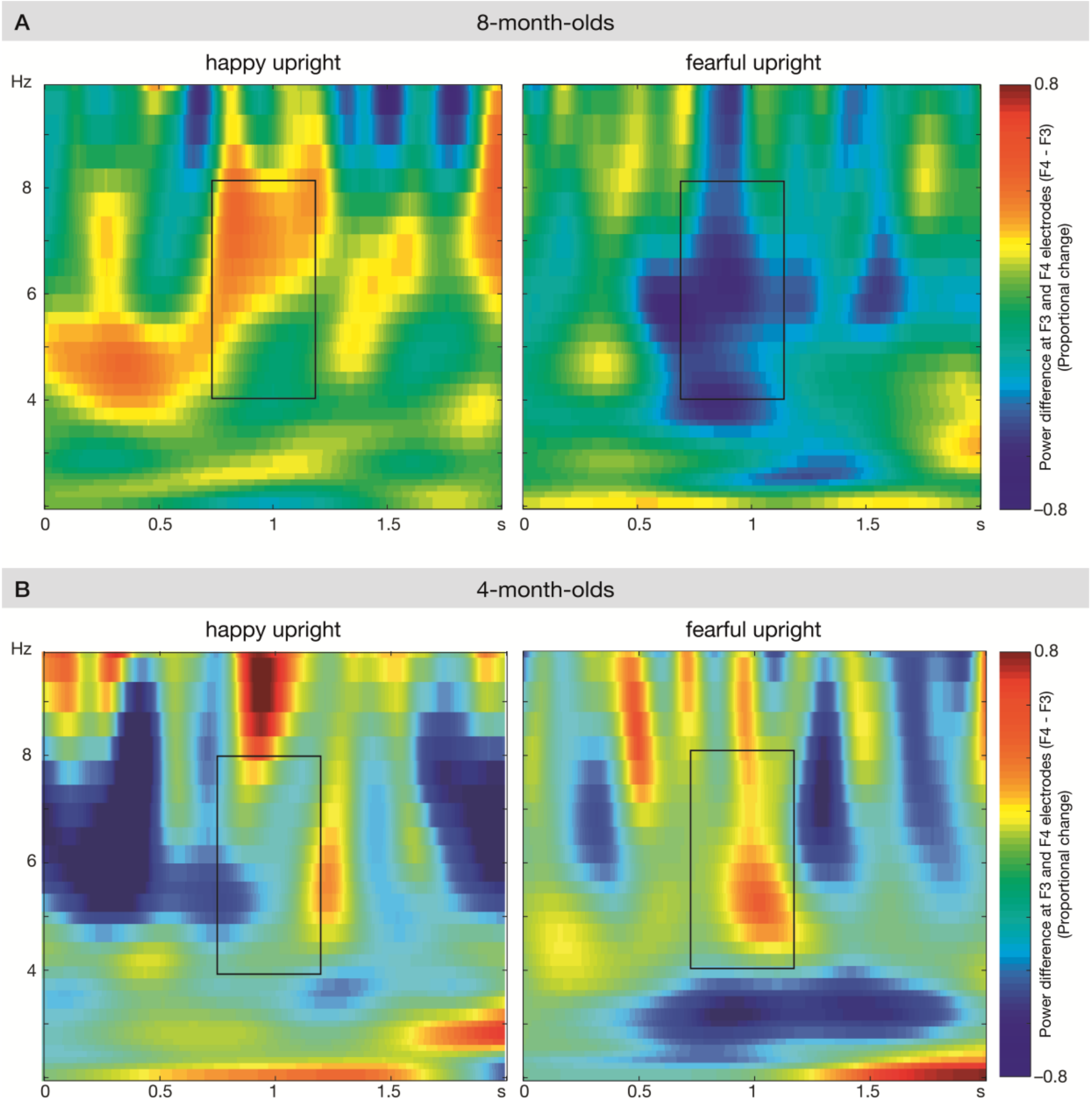


Figure 6.2. Figure of power changes. This figure shows the power changes relative to baseline for 2 s after stimulus onset and in the frequency range of 2 to 10 Hz in A) 8-month-old infants and B) 4-month-old infants. Each plot depicts the difference power at F4 and F3 electrode sites for happy and fearful upright body expressions. The rectangles represent the analyzed time window and frequency range.

Further analysis using paired-sample *t*-tests revealed a significant difference between the frontal EEG alpha asymmetry scores in 8-month-old infants in response to fearful expressions compared to happy expression in the upright orientation, $t\ (19) = 3.249$, $p = 0.004$.

Critically, in line with our predictions (*orientation specificity hypothesis*), this effect was specific to the upright orientation as no significant differences in the EEG alpha asymmetry scores were found between the response to inverted fearful expressions and happy body expressions in the inverted orientation, t (19) = - 0.348, p = 0.732.

As shown in Figure 6.3, fearful body expressions presented in an upright orientation were found to result in negative frontal EEG alpha asymmetry scores (M = - 0.087, SD = 0.19), reflecting greater relative right frontal activation indicative of a motivational tendency to withdraw from fearful body expressions. Additionally, as shown in Figure 6.3, happy expressions presented in an upright orientation were found to result in greater (positive) EEG alpha asymmetry scores (M = 0.008, SD = 0.20), reflecting greater relative left frontal activation indicative of a motivational tendency to approach happy body expressions. The pattern of results concerning the asymmetry responses evoked by fearful and happy expressions confirms our *emotion sensitivity hypothesis*. Note, however, that while the EEG alpha asymmetry score in response to upright happy expressions is positive, the value is very close to zero, implying that the asymmetry across hemispheres is rather small, speaking for a virtually symmetrical activation during this condition (see Table 6.1).

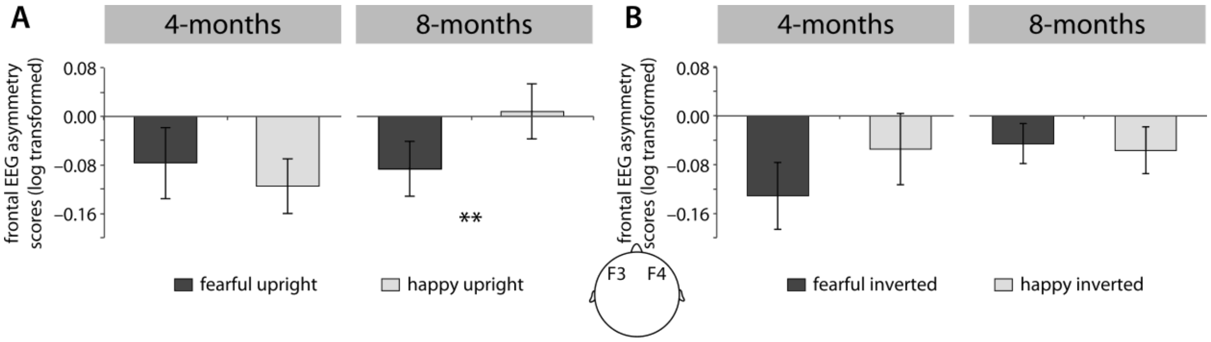


Figure 6.3. Frontal EEG alpha asymmetry scores. This figure shows 4- and 8-month-old infants' frontal EEG alpha asymmetry scores (log transformed) in response to fearful and happy upright (A) and inverted (B) presented body expressions. ** p < = .01

Table 6.1. Frontal EEG asymmetry scores (log-transformed). This table shows frontal EEG alpha asymmetry scores for 4- and 8-month-old infants in response to happy upright, happy inverted, fearful upright, and fearful inverted presented body expressions.

			asymmetry scores (Mean ± SD)			
	N	electrodes	happy upright	fearful upright	happy inverted	fearful inverted
4-month-olds	20	F3/F4	-0.115 ± 0.20	-0.077 ± 0.23	-0.055 ± 0.26	-0.131 ± 0.25
8-month-olds	20	F3/F4	0.008 ± 0.20	-0.087 ± 0.19	-0.057 ± 0.17	-0.046 ± 0.15

In additional analyses, t-tests were performed to test whether asymmetry scores differed from zero within the conditions. For both age groups no significant differences were found, all *p*-values > .019 (*p*-value threshold adjusted for multiple comparisons using Bonferroni correction) (Supplementary Table 6.4).

We conducted an additional analysis in which we compared the frontal EEG asymmetry scores across the two age groups separately for happy and fearful expressions (upright orientation). This was done in order to find out whether the developmental difference across ages reported above is due to a change in the way in which 8-month-old infants respond to a specific emotion. Critically, this analysis revealed that EEG alpha asymmetry scores only differed across ages for the happy expression, t (19) = -2.367, p = 0.029 but not for the fearful expression, t (19) = 0.189, p = 0.852. Specifically, for the happy expressions, in the group of the 4-month-olds, we observed a negative EEG alpha asymmetry score (M = -0.1148, SD = 0.20), indexing right frontal activation, whereas, in the group of the 8-month-olds, we observed a positive EEG alpha asymmetry score (M = 0.008, SD = 0.20) indexing left (or symmetrical) frontal activation.

Importantly, no effects were found at central electrodes, F (1,38) = 0.396, p = 0.533 and at parietal electrodes, F (1,38) = 1.218, p = 0.277. This is indicative of the specific involvement of the frontal region compared to central and parietal regions (Davidson & Fox, 1982).

Non-parametric tests (chi-square and binomial sign tests) were conducted to further examine potential differences in the number of infants showing particular frontal EEG asymmetry responses during the experimental conditions. Specifically, this analysis revealed a significant difference in the lateralization patterns (left versus right) when comparing between ages (4 versus 8 months) for upright happy expressions, χ^2 (1, N = 40) = 4.912, p = .027, but not for upright fearful expressions, χ^2 (1, N = 40) = .921, p = .337 (see Table 6.2). This corroborates the results obtained from our parametric analysis presented above by showing that only for the happy condition significantly more 8-month-old infants exhibited a lateralization to the left hemisphere in their frontal EEG asymmetry response.

Table 6.2. Frontal EEG alpha asymmetry patterns. This table shows the differences in frontal EEG alpha asymmetry patterns (left versus right) when comparing between ages (4 versus 8 months) for upright presented bodies (χ^2 -values and p-values).

		frontal asymmetry							
		happy upright				fearful upright			
	N	**left**	**right**	***χ²***	***p***	**left**	**right**	***χ²***	***p***
4-month-olds	20	6	14	4.912	.027	10	10	.921	.337
8-month-olds	20	13	7			7	13		

In addition, only for the group of the 8-month-old infants we found a marginally significant difference in the lateralization patterns (left versus right) when comparing between emotions (happy versus fearful), χ^2 (1, N = 20) = 3.6, p = .058 (see Table 6.3). No such difference in the lateralization patterns across emotions was observed in the group of 4-month-old infants, χ^2 (1, N = 20) = 1.667, p = .197 (see Table 6.3). This corroborates the results obtained from our parametric analysis presented above by showing that differences in lateralization patterns across emotions were found only for the 8-month-old infants.

Table 6.3. Differences in frontal EEG alpha asymmetry patterns. This table shows the differences in frontal EEG alpha asymmetry patterns (left versus right) when comparing between emotions (happy versus fearful) for upright presented bodies (χ^2 -values and p-values).

		frontal asymmetry							
		8-month-olds				4-month-olds			
	N	**left**	**right**	***χ²***	***p***	**left**	**right**	***χ²***	***p***
happy upright	20	13	7	3.6	.058	6	14	1.667	.197
fearful upright	20	7	13			10	10		

Moreover, our data show that 17 out of 20 8-month-old infants (85%) exhibited higher asymmetry scores to happy upright bodies indicative of a relative shift of frontal asymmetry patterns from right to left in response to happy body expressions, and a binomial sign test revealed that this is a significant difference in terms of the lateralization patterns, *p* = .003. Similar to the prior analysis, for the group of 4-month-old infants no such difference was obtained, *p* = .503, because only 8 out of 20 4-month-old infants (40%) showed higher asymmetry scores to happy upright bodies.

6.4 Discussion

The current study investigated the early development of the neural sensitivity to emotional body expressions by measuring frontal EEG alpha asymmetry patterns in response to dynamic fearful and happy body expressions in 4- and 8-month-old infants. Our results revealed that 8-month-old infants, but not 4-month-old infants, showed differences in their frontal EEG alpha asymmetry patterns distinguishing between fearful and happy body expressions. This finding is in line with prior ERP work showing that over the course of the first year of life the human brain becomes tuned to emotional body expressions (Missana et al., 2015). More generally, the ontogenetic emergence of the neural sensitivity to emotional body expressions, evident in our results, occurs at a time in development when facial and vocal emotion processing capacities undergo similar change (Grossmann et al., 2010; Peltola et al., 2009). The current findings therefore provide further evidence for accounts that regard emotion perception as a unified ability that develops in concert across various processing channels (face, voice, and body) (Heberlein & Atkinson, 2009).

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

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

The frontal EEG alpha asymmetry differences between fearful and happy stimulus conditions are unlikely to be the result of differences in low-level motion properties between the two stimulus sets. This is because, firstly, we controlled for the amount of dot motion across the happy and fearful expressions and, secondly, the frontal EEG alpha asymmetry differences between emotions were not observed for the inverted stimuli, in which the available dynamic information is identical to that available in the upright stimuli. Thus, 8-

month-olds are likely to be using higher-level motion cues to discriminate between the emotions (see Atkinson et al., 2007).

The frontal EEG alpha asymmetry patterns in response to the individual emotions observed in the current study confirmed our prediction regarding infants' emerging emotion sensitivity. Specifically, we found that 8-month-olds show greater relative right frontal EEG asymmetry to fearful expressions, indexing a tendency to withdraw, and greater relative left frontal EEG asymmetry to happy expressions, indexing a tendency to approach. These results are in line with previous findings indicating that (a) the perception and experience of happy expressions elicited greater relative left frontal activation associated with approach tendencies (Davidson & Fox, 1982; Fox & Davidson, 1988) and (b) the perception and experience of fear is related to withdrawal-related motivational tendencies and is associated with greater right frontal activation (Buss et al., 2003; Coan & Allen, 2003; Coan et al., 2001; Tomarken et al., 1990). Our findings support the general notion that the frontal cortex plays a role in processing emotional information and that this can already be traced in infancy (Fox, 1991; Grossmann, 2013b). More specifically, extending prior work with 10-month-old infants based on using facial expressions of emotion (Davidson & Fox, 1982), this finding provides evidence for specific changes in the motivational tendencies that are associated with perceiving emotional body cues. This suggests that perceiving others' emotional expressions engenders basic motivational processes in 8-month-old infants. Having such brain processes in place early in development might serve as a vital basis for guiding social behavior in terms of informing decisions as to whom (or what) to approach or avoid (Hamlin, Wynn, & Bloom, 2007). Clearly, future work with infants is needed to examine a possible link between the neural responses, similar to those measured in the current study, and overt social behavior.

With respect to infants' emerging neural sensitivity to emotional body expressions, it is also important to discuss that our results revealed that frontal EEG alpha asymmetry scores only differed across ages in response to the happy expressions but not in response to the fearful expressions. This suggests that the developmental change that takes places between 4 and 8 months mainly affects the processing of happy body expressions. The finding that developmental changes occur for processing happy body expressions stands in contrast to prior ERP work on infant facial expression processing, showing developmental changes with respect to processing fearful expressions (e.g., Peltola et al., 2009). This might point to potential differences in infants' perception of emotion from bodies and faces but is more likely to be explained by differences in using dynamic when compared to static expressions. This is because recent work with 8-month-old infants shows that using static body postures results in similar ERP responses (enhanced Nc) to fearful bodies as seen for fearful faces (Missana, Rajhans, et al., 2014). This discrepancy between dynamic and static displays of body expressions might have something to do with the fact that the dynamic stimuli used in the current study to portray happiness are perceived as 'infant-directed action' or as 'motionese' by the infants. Specifically, parents have been shown to modify their bodily movements in a variety of ways when interacting with infants (Brand, Baldwin, & Ashburn, 2002) and infants display strong preferences for 'motionese' when compared to adult-directed movements (Brand & Shallcross, 2008). Critically, for the current study 'motionese' is characterized by exaggerated positive affect in body movement similar to the happy body movement portrayed in our point-light displays. Therefore, it is possible that infants' responses to happy body expressions are related to their preference for 'motionese'. Regardless of this issue, our finding is in line with previous work on emotional body expression processing using ERPs (Missana et al., 2015). Specifically, prior work reported that infant ERP responses (in particular the Positive Component) changed in its amplitude between 4 and 8 months of age in response to happy expressions (more positive in older infants), indexing the recognition of positive expressions. Note that these EEG measures have been shown to tap into distinct processes that differ in their functional relevance (Missana, Grigutsch, et al., 2014): as the ERP measure (Pc) is a neural correlate of recognition memory (Grossmann et al., 2006; Nelson et al., 1998) while the frontal EEG alpha asymmetry measure is a neural correlate of motivational tendencies (Davidson, 1984; Davidson & Fox, 1982; Harmon-Jones, 2003). We therefore propose that the current findings in conjunction with the prior ERP work (Missana et al., 2015) are best interpreted as supporting the notion of a developmental transition in infants' emotion perception from body motion cues characterized by changes in recognition memory and motivational brain processes. These changes are likely to represent highly interdependent processes, as recognition of an emotion is required for motivational responses to occur.

Indeed, our analysis also revealed that the observed effects were limited to a time window of 700 to 1100 ms after movement onset. This is the same time window during which 8-month-old infants' ERP responses differed between fearful and happy dynamic body expressions (Missana et al., 2015). In this context, it is important to mention that while the frontal EEG alpha asymmetry effects were observed at frontal electrodes, the ERP differences in prior work were seen at temporal and parietal electrodes. The differential topography of effects suggests that the discrimination (as indexed by ERPs) and motivational evaluation of body expressions (as indexed by frontal asymmetry) occur at similar points in time, but rely on spatially distinct brain processes. The fact that frontal EEG alpha asymmetry patterns and ERP responses tap into distinct brain processes is in line with recent work using dynamic emotional facial expressions in 8-month-old-infants (see Missana, Grigutsch, et al., 2014). Nonetheless, in future studies, in order to better understand the nature of the brain processes elicited by viewing emotional expressions, it will be important to further investigate how ERP and frontal EEG alpha asymmetry effects interrelate and contribute to the perception of emotion. This points to a general need in understanding infants' perception of emotion as a complex emerging ability reflected in various psychologically relevant brain processes.

Finally, it is important to discuss the limitations of the current study by suggesting ways of how to address remaining issues in future studies. First, the current paradigm should be extended to other ages (beyond infancy) in order to further investigate the developmental trajectory of the perception of emotional body expressions. In particular, prior work has shown that there are considerable differences between 8-month-old infants and adults in their frontal EEG alpha asymmetry patterns observed in response to emotional facial expressions (Missana, Grigutsch, et al., 2014). This indicates that older infants' responses are not yet adult-like but development occurs beyond infancy with respect to the motivational processes evoked by viewing facial expression and this may generalize to viewing body expressions. Second, future work with infants is needed to assess whether there is a link between the neural responses, similar to those measured in the current study, and approach and withdrawal behaviors in response to emotional body expressions. Specifically, one possibility is to combine EEG measurements with behavioral preference tests as used in prior work with infants (Hamlin et al., 2007) to test whether, during the viewing of the expression, frontal EEG asymmetry patterns of a person are associated with approach of or withdrawal from that person during a preference test. Third, in order to better understand the developmental process that underpins emotion perception from body cues, future work is needed to systematically examine what factors contribute to individual differences in emotional body expression processing in infancy. In the current study we controlled for effects of maternal education. However, prior work with 8-month-old infants shows that other maternal variables such as maternal empathic concern and duration of exclusive breastfeeding, as well as infant temperament, are associated with marked differences in infants' ERP responses to static emotional body postures (Krol, Rajhans, Missana, & Grossmann, 2015; Rajhans, Missana, Krol, & Grossmann, under review). It is thus important to examine whether these factors are also linked to individual differences in frontal EEG alpha asymmetry.

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

Acknowledgements

We would like to thank all participants and families who took part in this study. We also thank Caterina Böttcher for help with data collection and Kerstin Flake for assistance in preparing the figure.

6.5 Supporting Information

Table 6.4. Table for *t*-values and *p*-values for *t*-tests for asymmetry scores. This table shows t-values and p-values for t-tests against zero for 4- and 8-month-old infants' frontal EEG alpha asymmetry scores in response to happy upright, happy inverted, fearful upright and fearful inverted presented body expressions.

	4-month-olds		**8-month-olds**	
	t	*p**	*t*	*p**
happy upright	-2.553	.019	.177	.862
happy inverted	-.928	.365	-1.473	.157
fearful upright	-1.520	.145	-1.937	.068
fearful inverted	-2.388	.027	-1.401	.177

*p** uncorrected p-value

Part III

Discussion

7 Discussion and Outlook

7.1 Summary of Empirical Studies

The aim of the current thesis was to investigate the development of emotion perception in the first year of life. In particular, the focus was on the examination of the neural correlates of infants' perception of others' emotional facial and body expressions. For this purpose, four EEG studies were conducted with 4- and 8-month-old infants. The experimental paradigm was comparable for all four studies in that participants were presented with video clips or static displays showing emotional expressions. In *Study 1* infants' processing of dynamic emotional facial expressions was assessed and compared to the processing in adults; in *Study 2* infants' processing of emotional dynamic body expressions was examined; in *Study 3* infants' processing of emotional static body postures was assessed; and in *Study 4* it was examined whether the perception of emotional body expressions elicits distinct brain responses that are associated with motivational processes.

The results from *Study 1* revealed that the neural responses elicited by pain and anger facial expressions differ substantially between infants and adults. The adult ERP data showed that facial expressions elicited an enhanced EPN (250 - 350 ms) at occipital electrodes that peaked earlier in response to anger faces as compared to pain faces. This difference at early processing stages was not evident in the infant group. Further analysis indicated a difference between the processing of pain and anger facial expressions for the LPP (400 - 500 ms) at frontal and central electrodes in adults. Specifically, the LPP was more pronounced (larger positive amplitude) in response to pain facial expressions. In contrast, the ERP responses in infants revealed a larger Nc (500 - 600 ms) to angry faces at frontal and central electrodes. Furthermore, infants and adults showed opposite patterns in their frontal EEG alpha asymmetry responses to pain and anger facial expressions. Specifically, in adults, anger facial expressions were associated with greater relative left frontal activation, whereas pain facial expressions were associated with greater relative right frontal activation. In contrast, the results of the infant group showed that pain facial expressions were associated with greater relative left frontal activation, whereas anger facial expressions were associated with greater relative right frontal activation.

The results from *Study 2* revealed that 8-month-old infants, but not 4-month-old infants, responded sensitively to the orientation and the emotion of body expressions. Specifically, 8-month-old infants showed an early orientation-sensitive Pb (200 - 400 ms) at frontal and central electrodes, such that upright emotional body expressions elicited a smaller Pb than inverted expressions. The ERP results further showed a later emotion-sensitive Pc (700 - 1100 ms) at temporal and parietal electrodes over the right hemisphere. Happy body expressions elicited larger (more positive) amplitudes when compared to fearful body expressions. These differences between the processing of emotional body expressions were found only when the bodies were presented upright.

The results from *Study 3* showed that infants discriminated not only between dynamic emotional body expressions, but also between static emotional body postures. Fearful body postures elicited a larger N290 (250 – 350 ms) at occipital electrodes when compared to happy body postures. Moreover, fearful body postures elicited a larger Nc (700 – 800 ms) at right frontal and central electrodes when compared to happy body postures. These findings were specific to the upright orientation of the body postures as no differences between the processing of emotions were found when the bodies were presented inverted.

The results from *Study 4* revealed that 8-month-old, but not 4-month-old, infants showed differences in their frontal EEG alpha asymmetry in response to fearful and happy dynamic body expressions. In 8-month-old infants, happy body expressions elicited a greater lateralization to the left hemisphere, whereas fearful expressions elicited a greater lateralization to the right hemisphere. These differences were only found when the body expressions were presented upright.

In summary, the findings of this thesis demonstrate that infant sensitivity to others' emotional signals, conveyed through face and body, develops during the first year of life. In particular, the current set of studies demonstrates that emotion perception is a complex process that involves the development of early sensory processes (N290) and later attentional (Pb and Nc), mnemonic (Pc), and motivational processes (frontal EEG alpha asymmetry) in the human brain. The current thesis shows that all of these processes undergo development during infancy and beyond. The following sections will discuss the developmental and neural aspects of infants' emerging emotion processing skills in turn.

7.2 Developmental Considerations

The results presented in *Study 1* demonstrate that adults' and infants' processing of pain and anger faces greatly differs. This suggests that, beyond infancy, major changes take place in the way in which the human brain responds to facial emotional information. Adults showed an enhanced processing of pain facial expressions indicating increased evaluation processes in response to others' expressions of pain (Fan & Han, 2008; Reicherts et al., 2012), whereas infants showed an enhanced processing of anger faces suggesting increased attention allocation in response to anger expressions (Grossmann et al., 2007). These differences between the processing of pain and anger facial expressions in adults and infants presumably reflect developmental changes in the perception of these expressions that occur sometime after 8 months of age. While our data show that infants at the age of 8 months are clearly able to discriminate between pain and anger from faces, it is possible that they are not yet able to empathically respond to the social signal value of pain facial expressions as indexing another person's distress. There is some evidence that infants show behavioral responses to distress vocalization (crying) and pain (distress) simulations that include vocal expressions, suggesting that feelings of empathic concern emerge in the first year of life (Geangu et al., 2010; Goubert, Vervoort, et al., 2009). However, our results indicate that 8-month-old infants might not be able to experience empathic concern for others solely on the basis of facial signs of distress (pain). With respect to the bulk of behavioral work, it is not until the second year of life that infants begin to show reliable and overt signs of empathic responding to others in distress (see Eisenberg, Fabes, et al., 2006). In these studies, children between the ages of 13 to 25 months start to exhibit empathy-related responding for others in pain in the form of helping, comforting, and sharing in order to alleviate others' distress (Eisenberg, 2000; Eisenberg, Fabes, et al., 2006; Zahn-Waxler et al., 1992). During this time in development, infants also start to differentiate between self and other and begin to take over others' affective perspectives (Eisenberg, 1991; Hoffmann, 1984). The developmental emergence of these skills has been argued to help children become more sensitive to others' needs and to respond empathically to distressed others (Eisenberg, Spinrad, & Sadovsky, 2006; Vaish, Carpenter, & Tomasello, 2009). It is thus possible that the 8-month-old infants tested in our study still lack these more sophisticated skills in interpreting and responding to facial signs of distress in others. In support of this notion of a still developing ability to interpret facial signs of distress, there are also considerable differences in the frontal EEG asymmetry responses reflecting motivational tendencies (approach of pain in infants, withdrawal from pain in adults). Presumably, 8-month-old infants' own experience of pain and with observing facial expressions of pain in others is still relatively rare. Therefore, to find neural signs of approach to pain might reflect infants' naivety with that particular expression and further indicate infants' tendency to explore a novel expression in order to gather more information.

Although infants at 8 months of age might not be sensitive to facial signs of pain, the ability to discriminate facial expressions of pain from other emotional facial expressions is an important first step for the further development of empathy-related responding. To further extend our understanding of young infants' development of empathy for pain future studies should include older age groups that have been shown to be behaviorally sensitive to pain in others (i.e., infants in the second year of life). Moreover, other facial expressions associated with eliciting empathy-related responses such as sadness should be included in order to examine to what extent these processes are specific to pain or elicited by empathic concern more generally. For example, in a study by Bandstra and colleagues (2011) with 18- to 36-month-old infants more distress and prosocial behaviors to adults' expressions of sadness was found when compared to adults' expressions of pain. Critically, age differences were only observed in response to pain expressions with older infants showing more empathic concern than the younger infants (Bandstra et al., 2011). In line with the argument, this suggests that a more prolonged developmental trajectory is seen when infant responses to pain are examined. It is thus possible that these behavioral patterns are also reflected in the underlying brain processes. In addition, future studies should investigate possible associations of infants' processing of pain faces in the first year of life with empathic responding in the second year of life in order to assess whether individual differences in responding to others' emotion emerge early and are stable across development.

In *Studies 2, 3* and *4* the findings demonstrated that orientation-sensitive and emotion-sensitive brain processes develop between 4 and 8 months of age indicating that the human brain becomes tuned to emotional body expressions during that time of development. There are several aspects that might contribute to the development of the ability to discriminate between happy and fearful expressions. Previous studies have shown that infants around 7 months of age show increased neural sensitivity and attention towards facial signals of fear when compared to facial signals of happiness (Nelson & de Haan, 1996; Peltola et al., 2009). This points to the development of fear (or negativity) bias in the second half of the first year (Vaish et al., 2008). This heightened sensitivity to fearful expressions occurs during a time when infants begin to express fear themselves (Campos et al., 1992) and start to show increased anxiety towards strangers (Braungart-Rieker et al., 2010). These developmental changes in infants' emotional expression and responding have been linked to the onset of infants' independent locomotion, which leads to increased exploration and engagement with the environment (Campos et al., 2000; Campos et al., 1992). Moreover, towards the end of the first year infants also begin to rely on the cues provided by adults, and especially their caregivers, in order to determine which objects or situations to approach and avoid (*social referencing*; Campos, Barrett, Lamb, Goldsmith, & Stenberg, 1983; Campos & Stenberg, 1981; Sorce, Emde, Campos, & Klinnert, 1985).

Although the present studies provide initial evidence for the development of infants' ability to sensitively process emotional body expressions, much more work is needed to extend these findings. For example, as shown in *Study 1*, older infants are able to distinguish between different negative facial expressions (anger and pain) in spite of their overall perceptual similarities. With respect to body expressions such evidence for infants' ability to distinguish between different negative emotions is lacking. Furthermore it is not known whether infants are able to form categories of specific body expressions (e.g., happiness), and whether they are sensitive to varying intensities of these expressions. This ability has already been demonstrated for facial expressions (Kestenbaum & Nelson, 1990; Kotsoni et al., 2001; Nelson et al., 1979). Therefore, in future studies, these aspects of infants' responding to emotional expressions need to be scrutinized to achieve a better understanding of their skill set.

So far, the present findings were mainly discussed in light of general developmental differences. However, adults individuals have been shown to greatly vary in their responses to emotional stimuli, pointing to stable individual differences in emotion perception (Hamann & Canli, 2004). Importantly, individual differences in infants' responding to emotional information are much less studied and understood. Our results clearly show that infants differ in the way in which they perceive emotions. In *Study 1* we found that individual differences in infant temperament were associated with the neural responses to angry facial expressions. More specifically, infants' ERP responses to angry facial expressions were correlated with parent-rated emotional self-regulation, with those infants scoring higher on self-regulation showing attenuated ERP responses to anger. This shows that infants who are better at self-regulation are also more effective in coping with viewing signals of aggression in others (anger). This is in line with work demonstrating that infants develop strategies to regulate their arousal and cope with emotions within the first year of life by for example non-nutritive sucking during distressing events or gaze aversion when a stranger is approaching (Campos, 1989; Kopp, 1989; Sroufe, 1977). With respect to the current findings, it is thus likely that infants' capacity to regulate their own emotions has an influence on how they process and evaluate emotional expressions in others. Clearly, more work is needed that tracks these individual differences across development in a larger sample of infants in order to understand whether these are stable individual differences that impact emotional experiences beyond infancy.

With regard to infants' developing perceptual abilities, *Studies 2, 3* and *4* demonstrated that 8-month-old infants were sensitive to the orientation of emotional body expressions and discriminated between emotional body expressions only when the bodies were presented in an upright orientation. This suggests that rather than relying on individual features of the body, which are also present in inverted displays, the configuration of the body features is critical for the discrimination process to take place. This orientation sensitivity was not evident in the younger age group, which indicates that perceptual abilities change between 4 and 8 months of age. These findings are in line with results from a behavioral study showing that 6.5-month-old infants are able to discriminate emotional body expressions only when the bodies are presented in an upright version (Zieber et al., 2014b). An earlier study by Zieber and colleagues (2010) demonstrated that 9-month-old infants, but not 5-month-old infants, have a preference for intact bodies when compared to proportion-distorted bodies. Important for the current context, infants showed a preference for intact bodies only when presented upright (Zieber et al., 2010). This suggests that the older infants not only have knowledge about the proportion of the human body, but this ability relies on viewing the body in its canonical orientation. Together, these results indicate that infants become sensitive to orientation-specific information about the human body in the second half of the first year. This developmental course of infants' perception of emotional body expressions might be experience-driven as they naturally observe upright bodies. One possibility is that infants' developing sensitivity to upright bodies is related to their own ability to sit upright and crawl. Specifically, with increasing posture development and the onset of crawling, infants' visual perspective on their social world changes and they might have more opportunity to view upright movements of others (Zieber et al., 2010).

In the current studies infants' perception of emotion was investigated either from faces or from bodies. The findings suggest that infants are not only able to discriminate between various facial expressions, but can also discriminate between emotions conveyed through body motion and body postures. However, in daily life emotions are not presented in isolation, meaning that facial and body expressions usually provide corresponding and complimentary information. It has been argued that body expressions represent the most immediate means of communicating emotions and provide strong contextual cues when viewing facial expressions in real-life social interactions (de Gelder et al., 2006). For example, in research with adults, it has been shown that the perception of emotional facial expressions is strongly influenced by emotional body expressions (Aviezer et al., 2012; Meeren, van Heijnsbergen, & de Gelder, 2005) and that the recognition of emotional facial expressions is impaired when the face and body convey conflicting information (Meeren et al., 2005). From a developmental perspective, it is known that 7-month-old infants are able to match emotional information across face and voice (Grossmann et al., 2005; Vogel, Monesson, & Scott, 2012) and body and voice (Zieber, Kangas, Hock, & Bhatt, 2014a). However, it is not known whether infants are able to integrate emotional facial and body expressions and which neural processes are involved. In a new ERP study with 8-month-old infants, we investigated (Rajhans, Jessen, Missana, & Grossmann, under review) whether the perception of emotional body expressions impacts the processing of emotional facial expressions by elucidating the neural correlates involved in the detection and integration of emotional information across face and body. In this study, we employed a priming paradigm in which infants were presented with static emotional body postures (fearful and happy) that were followed by either a matching (congruent) or a mismatching (incongruent) static facial expression. Our results show that the integration across body and face was reflected in brain signatures related to attentional (Nc) and to recognition memory (Pc) processes. More specifically, this study demonstrated that 8-month-old infants are able to match facial expressions to the corresponding body expressions, and that priming with incongruent body expressions impaired the detection of emotional facial expressions (Rajhans, Jessen, et al., under review). However, this is only the first study that investigated the neural correlates involved in the perception of emotions across face and body. Therefore, much more work is needed to fully understand infants’ ability to match emotions from different sources (face, body, and voice). For example, important and interesting aspects would be to examine whether infants are able to match emotional body expressions with corresponding vocal expressions, and if so, what underlying brain processes are involved. Findings from face and voice matching studies suggest that infants are able to integrate facial and vocal expressions of the same emotion around the age of 7 months (Grossmann et al., 2006; Soken & Pick, 1992; Walker-Andrews, 1986). To the best of our knowledge, there are only two behavioral studies that investigated infants' integration of emotional body and vocal expressions (Zieber et al., 2014a, 2014b). However, the neural correlates of these processes remain to be studied.

Another aspect for discussion is the fact that the studies of this thesis focused on infant emotion processing by using cross-sectional samples. In cross-sectional studies only one group of individuals is observed (e.g., two age groups with different individuals in each group). This significantly limits the conclusions that can be drawn with respect to the actual processes that account for any given developmental trajectory (change). The study of the developmental trajectory would greatly benefit from a longitudinal approach in which the same group of infants is followed and their brain responses to emotion are measured over a specific time period during infancy. Currently, work is underway in our laboratory to examine the development of emotion perception during infancy longitudinally. In this large-scale study, 101 infants are followed from 4 months of age to 18 months of age. Different methods such as EEG/ERP, fNIRS, and behavioral measures are combined to shed light on infants' emerging emotion processing abilities. Another main aspect of this longitudinal study is to investigate what factors contribute to individual differences in infants' emotion perception by using genetic markers and parental questionnaires. We hope that this approach will broaden our understanding of the progression of the developmental processes at play in the early emergence of emotion perception (1st year) and later prosocial and empathic behaviors (2nd year).

Another important issue for discussion is that the focus of this thesis was on typically developing infants. However, in future research, it will be important to examine the processing of emotional signals in atypically developing infants, such as infants with an increased risk for developing autism spectrum disorders, infants with developmental delays, as well as in infants of depressed mothers. For example, children with autism show socially impaired behaviors, such as difficulties in understanding others' emotional and mental states and have profound difficulties in forming social relationships (Baron-Cohen, 1991; Baron-Cohen, Leslie, & Frith, 1985). More specifically, children with autism show impairments in their ability to detect and recognize emotional expressions from faces and voices (Bal et al., 2010; Capps, Yirmiya, & Sigman, 1992; Hobson, Ouston, & Lee, 1988). Critically, being able to detect and recognize emotions in others is seen as an important adaptive ability because it allows one to predict others' behavior and helps to regulate and adjust one's own behavior in social contexts (Izard, 1977; Izard et al., 2001). It is thus vital to identify early markers (differences) that help us to distinguish between typical and atypical responding to emotional information displayed by others. Brain measures might provide a sensitive tool that could be used to improve the early diagnosis of social impairments and may also help design early interventions by providing a more mechanistic understanding of what goes awry in neurodevelopmental disorders such as autism.

7.3 Brain Processes

In this section, I would like to focus the discussion on the specific brain processes revealed to be sensitive to emotional information in infancy. Generally one can distinguish between early (with respect to the time post-stimulus onset) perceptual brain processes and later brain processes related to attention and memory. With respect to early perceptual processing in the current studies, effects at the N290 (visual ERP component) were only found when infants were presented with static body postures. Specifically, a larger negativity at occipital sites was observed in response to static fearful body postures when compared to happy body postures. An enhanced negativity (N290) to fearful bodies might indicate a greater sensitivity to fearful body expressions during sensory processing in the visual cortices. However, this early sensory component was not observable when infants were presented with dynamic facial and body expressions. One possibility to explain this discrepancy is that when presenting static displays the emotion is presented immediately at its peak of expression, whereas in a dynamic context the emotional expression only unfolds over time. Therefore, in static displays the emotional expressions might be detected and processed faster than in dynamic displays. On the other hand, the absence of an emotional modulation of the N290 in 8-month-old infants is in line with previous work on the processing of emotional facial expressions, which demonstrated an enhanced N290 over occipital electrodes to specific facial expressions at 12 months of age (Grossmann et al., 2007). It might therefore be possible that older infants (above the age of 8 months) would show a modulation of the N290/ N170 in response to dynamic emotional expressions as well. Future work with older age groups is needed to clarify this issue.

Apart from sensory-specific ERP effects, the current studies also revealed ERP effects that were unrelated to the sensory processing but are associated with attention allocation (Nc) and recognition memory (Pc) (Nelson, 1996; Reynolds & Richards, 2005). In 8-month-old infants, dynamic facial expressions of anger elicited an Nc component that was larger when compared to dynamic pain facial expressions (*Study 1*). In response to dynamic emotional body expressions no differences for the Nc were observed. However, when body expressions were presented as static upright displays, fearful body expressions elicited a larger Nc compared to happy body expressions. The finding of an enhanced Nc in response to fearful body expressions is in line with prior work showing that fearful facial expressions elicited a larger Nc component than happy faces (Nelson & de Haan, 1996; Peltola et al., 2009). Therefore, although the timing of the Nc is slightly different in response to facial compared to bodily expressed emotions, our data suggest that the detection of emotional signals affects later processing stages that are related to the allocation of attention. Furthermore, upright dynamic body expressions elicited an emotion-sensitive Pc at right temporal and posterior electrodes in 8-month-old infants that was larger in response to happy body expressions than to fearful body expressions. In prior work, an enhanced Pc indexed the recognition of a stimulus from memory (Grossmann et al., 2006; Nelson et al., 1998). This suggests that 8-month-old infants recognize familiar happy expressions from the body movement.

With respect to the topography of the observed ERP components facial expressions elicited more widely distributed ERP components at frontal and central electrodes (*Study 1)*. This is in line with research showing that infants' ERP responses to emotional facial expressions are distributed over frontal and central electrode sites during later processing stages (Grossmann et al., 2007; Kobiella et al., 2008; Peltola et al., 2009). In *Studies 2* and *3,* ERP effects in response to emotional body expressions were lateralized to the right hemisphere as no differences between emotions were found in the left hemisphere. These findings are in line with prior adult research, demonstrating that the recognition of emotional body expressions relies on brain processes that are strongly lateralized to the right hemisphere (Grèzes et al., 2007; Heberlein et al., 2004; Heberlein & Saxe, 2005). Therefore, the current findings suggest that the right hemisphere might begin to play an important role during emotional body processing from early on in infancy. However, it should be pointed out that while the EEG offers a high temporal resolution of brain activity, it only provides little information on the spatial localization in the brain. Therefore, in future studies, it would be useful to further clarify the cortical sources that generated the ERP effects during the perception of emotional body expressions (i.e., the Pc). One possibility for source localization would be dipole modeling using high-density (64 or 128-channel) EEG systems (Hämäläinen, Ortiz-Mantilla, & Benasich, 2011; Reynolds & Richards, 2009). Another option would be to use fNIRS, which allows the measurement of activation in precise brain locations. This would help to gain more insights into the nature of the processes that underlie infants' sensitive responding to body expressions (Lloyd-Fox et al., 2010).

The findings from frontal EEG alpha asymmetry suggest that the perception of emotional facial and body expressions also triggered motivational processes in infants. The results indicate developmental differences in asymmetrical frontal brain activity between adults and 8-month-old infants during the processing of emotional faces and between 8- and 4-month-old infants during the processing of emotional body expressions. The observed differences in frontal EEG asymmetry patterns generally support the age differences found in the current ERP data, pointing to overall developmental changes in the perceptual, attentional and motivational processes. More generally, the results of frontal EEG asymmetry are in line with prior work demonstrating that the perception and experience of specific emotional states is associated with differences in frontal EEG alpha asymmetry (Buss et al., 2003; Davidson, 1992; Davidson & Fox, 1982; Harmon-Jones, 2003). However, as a limitation, it should be mentioned we did not investigate whether frontal EEG asymmetry responses are associated with infants' overt behavioral reactions, such as approach tendencies in response to someone expressing happiness or withdrawal tendencies when viewing someone expressing fear. In order to better understand the relation between frontal EEG asymmetry and behaviorally expressed motivational tendencies, future research should include behavioral measures to directly link frontal EEG asymmetry responses to motivational tendencies that arise when viewing emotional expressions. One possibility for combining frontal EEG asymmetry with behavioral outcomes in infants could be the usage of simple preference tasks or choice paradigms that indicate infants preference by their reaching behavior (Hamlin, Hallinan, &

Woodward, 2008; Hamlin et al., 2007). Furthermore, in the current thesis, frontal EEG alpha asymmetry was examined while infants were viewing emotional facial and body expressions. However, in our daily life we do not only perceive emotions through specific facial and body expressions but also through the voice. Therefore, future work should extend the present findings on frontal EEG asymmetry to the perception of emotional vocal expressions.

The current studies suggest that different brain processing stages (perceptual, attentional, mnemonic, and motivational) are involved in the perception of emotions from faces and bodies, however more research is needed to further clarify the relationship between the various processes and their role in early development. For example: What is the exact relationship between the brain processes identified? What role do experiential and genetic variables play in the development of these processes? How do these processes develop beyond infancy and how do they relate to measurable behavioral outcomes? The findings presented in the current thesis provide a rich foundation for which future work can precisely address these questions.

7.4 Conclusion Remarks

The aim of the current thesis was to investigate the electrophysiological bases of infants' processing of others' emotional facial and body expressions. Within the first year of life infants are already able to discriminate facial expressions of pain from anger, another negative facial expression. By 8 months of age, infants can discriminate emotions from dynamic body expressions as well as static body postures, even in the absence of any facial or vocal information. In addition, 8-month-old infants are sensitive to the orientation of a body, as they only discriminate between emotions presented in an upright orientation. Furthermore, frontal EEG alpha asymmetry results suggest that emotional facial and body expressions evoke distinct brain responses that are linked to the motivational brain systems. By using multiple measurements (EEG/ERP, frontal EEG alpha asymmetry and questionnaires) this work provides insights into how the human brain processes emotional information from faces and bodies early in development. It is my hope that this thesis stimulates future work to extend the current findings on all levels alluded to in the discussion.

References

Ackles, P. K., & Cook, K. G. (1998). Stimulus probability and event-related potentials of the brain in 6-month-old human infants: A parametric study. *International Journal of Psychophysiology, 29*(2), 115-143.

Adolphs, R. (2002). Neural systems for recognizing emotion. *Current Opinion in Neurobiology, 12*(2), 169-177.

Ambadar, Z., Schooler, J. W., & Cohn, J. F. (2005). Deciphering the enigmated face. *Psychological Science, 16*(5), 403-410.

Argyle, M. (1988). *Bodily communication* (2 ed.). Madison, CT: International Univ. Press.

Aslin, R. N., & Mehler, J. (2005). Near-infrared spectroscopy for functional studies of brain activity in human infants:Promise, prospects, and challenges. *Journal of Biomedical Optics, 10*(1), 011009-0110093.

Atkinson, A. P. (2013). Bodily expressions of emotion: Visual cues and neural mechanisms. In J. Armony & P. Vuilleumier (Eds.), *The cambridge handbook of human affective neuroscience* (pp. 198-222). New York: Cambridge University Press.

Atkinson, A. P., Dittrich, W. H., Gemmell, A. J., & Young, A. W. (2004). Emotion perception from dynamic and static body expressions in point-light and full-light displays. *Perception, 33*(6), 717-746.

Atkinson, A. P., Tunstall, M. L., & Dittrich, W. H. (2007). Evidence for distinct contributions of form and motion information to the recognition of emotions from body gestures. *Cognition, 104*(1), 59-72.

Atkinson, A. P., Vuong, Q. C., & Smithson, H. E. (2012). Modulation of the face- and body-selective visual regions by the motion and emotion of point-light face and body stimuli. *Neuroimage, 59*(2), 1700-1712.

Aviezer, H., Trope, Y., & Todorov, A. (2012). Body cues, not facial expressions, discriminate between intense positive and negative emotions. *Science, 338*(6111), 1225-1229.

Bal, E., Harden, E., Lamb, D., Van Hecke, A. V., Denver, J. W., & Porges, S. W. (2010). Emotion recognition in children with autism spectrum disorders: Relations to eye gaze and autonomic state. *Journal of Autism and Developmental Disorders, 40*(3), 358-370.

Bandstra, N. F., Chambers, C. T., McGrath, P. J., & Moore, C. (2011). The behavioural expression of empathy to others' pain versus others' sadness in young children. *Pain, 152*(5), 1074-1082.

Baron-Cohen, S. (1991). Do people with autism understand what causes emotion? *Child Development, 62*(2), 385-395.

Baron-Cohen, S., Leslie, A. M., & Frith, U. (1985). Does the autistic child have a “theory of mind”? *Cognition, 21*(1), 37-46.

Barrera, M. E., & Maurer, D. (1981). Recognition of mother's photographed face by the three-month-old infant. *Child Development, 52*(2), 714-716.

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

Belin, P., Campanella, S., & Ethofer, T. (2012). *Integrating face and voice in person perception*. New York: Springer.

Bell, M. A., & Fox, N. A. (1994). Brain development over the first year of life: Relations between electroencephalographic frequency and co-herence and cognitive and affective behaviors. In G. Dawson & K. Fisher (Eds.), *Human behavior and the developing brain*. New York: Guilford.

Bentin, S., Allison, T., Puce, A., Perez, A., & McCarthy, A. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience, 8*(6), 551-565.

Bentin, S., & Deouell, L. Y. (2000). Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cognitive Neuropsychology, 17*(1-3), 35-55.

Benuzzi, F., Lui, F., Duzzi, D., Nichelli, P. F., & Porro, C. A. (2008). Does it look painful or disgusting? Ask your parietal and cingulate cortex. *The Journal of Neuroscience, 28*(4), 923-931.

Bertenthal, B. I. (1993). Infants' perception of biomechanical motions: Intrinsic image and knowledge-based constraints. In C. E. Granrud (Ed.), *Visual perception and cognition in infancy* (pp. 175-214). Hillsdale, New Jersey: Lawrence Erlbaum Associates, Inc.

Bertenthal, B. I. (1996). Origins and early development of perception, action, and representation. *Annual Review of Psychology, 47*(1), 431-459.

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

Botvinick, M., Jha, A. P., Bylsma, L. M., Fabian, S. A., Solomon, P. E., & Prkachin, K. M. (2005). Viewing facial expressions of pain engages cortical areas involved in the direct experience of pain. *Neuroimage, 25*(1), 312-319.

Bowlby, J. (1969). *Attachement and loss. Vol. 1 Attachment*. New York: Basic Books.

Bradley, M., & Lang, P. J. (1994). Measuring emotion: The Self-Assessment Manikin and the semantic differential. *Journal of Behavior Therapy and Experimental Psychiatry, 25*(1), 49-59.

Brand, R. J., Baldwin, D. A., & Ashburn, L. A. (2002). Evidence for ‘motionese’: Modifications in mothers’ infant-directed action. *Developmental Science, 5*(1), 72-83.

Brand, R. J., & Shallcross, W. L. (2008). Infants prefer motionese to adult-directed action. *Developmental Science, 11*(6), 853-861.

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

Burnham, D. K. (1987). The role of movement in object perception by infants. In B. E. McKenzie & R. H. Day (Eds.), *Perceptual development in infancy: Problems and issues* (pp. 143-172). Hillsdale, New Jersey: Lawrence Erlbaum Associates, Inc.

Burnham, D. K., & Day, R. H. (1979). Detection of color in rotating objects by infants and its generalization over changes in velocity. *Journal of Experimental Child Psychology, 28*(2), 191-204.

Bushnell, I. W. R. (2001). Mother's face recognition in newborn infants: Learning and memory. *Infant and Child Development, 10*(1-2), 67-74.

Bushnell, I. W. R., Sai, F., & Mullin, J. T. (1989). Neonatal recognition of the mother's face. *British Journal of Developmental Psychology, 7*(1), 3-15.

Buss, K. A., Schumacher, J. R. M., Dolski, I., Kalin, N. H., Goldsmith, H. H., & Davidson, R. J. (2003). Right frontal brain activity, cortisol, and withdrawal behavior in 6-month-old infants. *Behavioral Neuroscience, 117*(1), 11-20.

Buzsáki, G. (2006). *Rhythms of the brain*. New York: Oxford University Press.

Campos, J. J. (1989). Soothing pain-elicited distress in infants with swaddling and pacifiers. *Child Development, 60*(40), 781-792.

Campos, J. J., Anderson, D. I., Barbu-Roth, M. A., Hubbard, E. M., Hertenstein, M. J., & Witherington, D. (2000). Travel broadens the mind. *Infancy, 1*(2), 149-219.

Campos, J. J., Barrett, K. C., Lamb, M. E., Goldsmith, H. H., & Stenberg, C. (1983). Socioemotional development. In M. M. Haith & J. J. Campos (Eds.), *Handbook of child psychology: Infancy and psychobiology* (Vol. 2, pp. 783-915). New York: Wiley.

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

Campos, J. J., & Stenberg, C. (1981). Perception, appraisal, and emotion: The onset of social referencing. In M. E. Lamb & L. R. Sherrod (Eds.), *Infant social cognition: Empirical and theoretical considerations* (pp. 273-314). Hillsdale, N.J.: Erlbaum.

Campos, J. J., Thein, S., & Owen, D. (2003). A Darwinian legacy to understanding human infancy: Emotional expressions as behavior regulators. In P. Ekman, J. J. Campos, R. J. Davidson & F. B. M. de Waal (Eds.), *Emotions inside out: 130 years after Darwin's the expression of the emotions in man and animals* (pp. 110-134). New York, N.Y.: New York University Press.

Capps, L., Yirmiya, N., & Sigman, M. (1992). Understanding of simple and complex emotions in non-retarded children with autism. *Journal of Child Psychology and Psychiatry, 33*(7), 1169-1182.

Carver, C. S., & Harmon-Jones, E. (2009). Anger is an approach-related affect: Evidence and implications. *Psychological Bulletin, 135*(2), 183-204.

Carver, L. J., & Cornew, L. (2009). The development of social information gathering in infantcy: A model of neural substrates and developmental mechanisms. In M. d. Haan & M. R. Gunnar (Eds.), *Handbook of developmental social neuroscience*. New York: The Guilford Press.

Coan, J. A., & Allen, J. J. (2003). Varieties of emotional experience during voluntary emotional facial expressions. *Annals of the New York Academy of Sciences, 1000*(1), 375-379.

Coan, J. A., & Allen, J. J. (2004). Frontal EEG asymmetry as a moderator and mediator of emotion. *Biological Psychology, 67*(1), 7-50.

Coan, J. A., Allen, J. J., & Harmon-Jones, E. (2001). Voluntary facial expression and hemispheric asymmetry over the frontal cortex. *Psychophysiology, 38*(6), 912-925.

Coulson, M. (2004). Attributing emotion to static body postures: Recognition accuracy, confusions, and viewpoint dependence. *Journal of Nonverbal Behavior, 28*(2), 117-139.

Courchesne, E., Ganz, L., & Norcia, M. E. (1981). Event-related brain potentials to human faces in infants. *Child Development, 52*(3), 804-811.

Craig, K. D., Prkachin, K. M., & Grunau, R. V. E. (2001). The facial expression of pain. In D. C. Turk & R. Melzack (Eds.), *Handbook of pain assessment* (2nd ed., pp. 153-169). New York: Guilford.

Creutzfeld, O., & Houchin, J. (1974). Neuronal basis of EEG waves. In A. Rémond (Ed.), *Handbook of Electroencephalography and Clinical Neurophysiology* (Vol. 2). Amsterdam, Netherlands: Elsevier.

Darwin, C. (2009/1872). *The expression of the emotions in man and animals*. Oxford: Oxford Univ. Press.

Davidson, R. J. (1984). Affect, cognition, and hemispheric specialization. In C. E. Izard, J. Kagan & R. B. Zajonc (Eds.), *Emotions, cognition, and behavior* (pp. 320-365). Cambridge: Cambridge University Press.

Davidson, R. J. (1988). EEG measures of cerebral asymmetry: Conceptual and methodological issues. *International Journal of Neuroscience, 39*(1-2), 71-89.

Davidson, R. J. (1992). Emotion and affective style: Hemispheric substrates. *Psychological Science, 3*(1), 39-43.

Davidson, R. J. (1994). Asymmetric brain function, affective style, and psychopathology: The role of early experience and plasticity. *Development and Psychopathology, 6*(4), 741-751.

Davidson, R. J. (1998). Affective style and affective disorders: Perspectives from affective neuroscience. *Cognition & Emotion, 12*(3), 307-330.

Davidson, R. J., Ekman, P., Saron, C. D., Senulis, J. A., & Friesen, W. V. (1990). Approach-withdrawal and cerebral asymmetry: Emotional expression and brain physiology: I. *Journal of Personality and Social Psychology, 58*(2), 330-341.

Davidson, R. J., & Fox, N. A. (1982). Asymmetrical brain activity discriminates between positive and affective stimuli in human infants. *Science, 218*(4578), 1235-1237.

Davis, M. H. (1980). A multidimensional approach to individual differences in empathy. *JSAS Catalog of Selected Documents in Psychology*.

Davis, M. H. (1983). Measuring individual differences in empathy: Evidence for a multidimensional approach. *Journal of Personality and Social Psychology, 44*(1), 113-126.

de Gelder, B. (2006). Towards the neurobiology of emotional body language. *Nature Reviews Neuroscience, 7*(3), 242-249.

de Gelder, B. (2009). Why bodies? Twelve reasons for including bodily expressions in affective neuroscience. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1535), 3475-3484.

de Gelder, B., Meeren, H. K., Righart, R., Van den Stock, J., Van de Riet, W. A. C., & Tamieto, M. (2006). Beyond the face: Exploring rapid influences of context on face processing. *Progress in Brain Research, 155*(Part B), 37-48.

de Gelder, B., Snyder, J., Greve, D., Gerard, G., & Hadjikhani, N. (2004). Fear fosters flight: A mechanism for fear contagion when perceiving emotion expressed by a whole body. *Proceedings of the National Academy of Sciences, 101*(47), 16701–16706.

de Haan, M. (2007). Current and future directions in infant electrophysiology. In M. d. Haan (Ed.), *Infant EEG and event-related potentials* (pp. 305-316). New York, NY: Psychology Press.

de Haan, M., Johnson, M. H., & Halit, H. (2003). Development of face-sensitive event-related potentials during infancy: A review. *International Journal of Psychophysiology, 51*(1), 45-58.

de Haan, M., & Matheson, A. (2009). The development and neural bases of processing emotion in faces and voices. In M. de Haan & M. R. Gunnar (Eds.), *Handbook of developmental social neurosciences*. New York: The Guilford Press.

de Haan, M., & Nelson, C. A. (1997a). Discrimination and categorization of facial expressions of emotion during infancy. In A. Slator (Ed.), *Perceptual Development* (pp. 287-309). Hove: Psychology Press.

de Haan, M., & Nelson, C. A. (1997b). Recognition of the mother's face by six-month-old infants: A neurobehavioral study. *Child Development, 68*(2), 187-210.

de Haan, M., & Nelson, C. A. (1998). Discrimination and categorization of facial expressions of emotion during infancy. In A. Slator (Ed.), *Perceptual development: Visual, auditory and speech perception in infancy,* (pp. 287-309). Hove, East Sussex: Psychology Press.

de Haan, M., & Nelson, C. A. (1999). Brain activity differentiates face and object processing by 6-month-old infants. *Developmental Psychology, 35*(4), 1114-1121.

de Haan, M., Pascalis, O., & Johnson, M. H. (2002). Specialization of neural mechanisms underlying face recognition in human infants. *Journal of Cognitive Neuroscience, 14*(2), 199-209.

de Lussanet, M. H. E., Fadiga, L., Michels, L., Seitz, R. J., Kleiser, R., & Lappe, M. (2008). Interaction of visual hemifield and body view in biological motion perception. *European Journal of Neuroscience, 27*(2), 514-522.

de Vignemont, F., & Singer, T. (2006). The empathic brain: How, when and why? *Trends in Cognitive Sciences, 10*(10), 435-441.

DeBoer, T., Scott, L. S., & Nelson, C. A. (2005). ERPs in developmental populations. In T. C. Handy (Ed.), *Event-related potentials. A methods handbook*. Cambridge, Massachusetts: The MIT Press.

Decety, J. (2010). The Neurodevelopment of Empathy in Humans. *Developmental Neuroscience, 32*(4), 257-267.

Decety, J., & Jackson, P. L. (2004). The functional architecture of human empathy. *Behavioral and Cognitive Neuroscience Reviews, 3*(2), 71-100.

Decety, J., Michalska, K. J., & Akitsuki, Y. (2008). Who caused the pain? An fMRI investigation of empathy and intentionality in children. *Neuropsychologia, 46*(11), 2607-2614.

Decety, J., & Svetlova, M. (2012). Putting together phylogenetic and ontogenetic perspectives on empathy. *Developmental Cognitive Neuroscience, 2*(1), 1-24.

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science, 293*(5539), 2470-2473.

Ecklund-Flores, L., & Turkewitz, G. (1996). Asymmetric headturning to speech and nonspeech in human newborns. *Developmental Psychobiology, 29*(3), 205-217.

Eimer, M. (2000). Effects of face inversion on the structural encoding and recognition of faces. Evidence from event-related brain potentials. *Cognitive Brain Research, 10*(1), 145-158.

Eisenberg, N. (1991). Meta-analytic contributions to the literature on prosocial behavior. *Personality and Social Psychology Bulletin, 17*(3), 273-282.

Eisenberg, N. (2000). Emotion, regulation, and moral development. *Annual Review of Psychology, 51*(1), 655-697.

Eisenberg, N., Fabes, R. A., Murphy, B., Karbon, M., Maszk, P., Smith, M., . . . Suh, K. (1994). The relations of emotionality and regulation to dispositional and situational empathy-related responding. *Journal of Personality and Social Psychology, 66*(4), 776-797.

Eisenberg, N., Fabes, R. A., & Spinrad, T. L. (2006). Prosocial development. In N. Eisenberg, W. Damon & R. M. Lerner (Eds.), *Handbook of child psychology* (Vol. 3: Social, emotional, and personality development, pp. 646-718). New Jersey: Wiley.

Eisenberg, N., Smith, C. L., Sadovsky, A., & Spinrad, T. L. (2004). Effortful control: Relations with emotion regulation, adjustment, and socialization in childhood. In R. F. Baumeister & K. D. Vohs (Eds.), *Handbook of self-regulation. Research, theory and applications* (pp. 259-282). New York: The Guilford Press.

Eisenberg, N., Spinrad, T. L., & Sadovsky, A. (2006). Empathy-related responding in children. In M. Killen & J. G. Smetana (Eds.), *Handbook of moral development* (pp. 517-549). Mahwah, New Jersey; London: Lawrence Erlbaum Associates, Inc.

Ekman, P., & Friesen, W. V. (1975). *Unmasking the face*. New Jersey: Prentice-Hall, Inc.

Fairhurst, M. T., Löken, L., & Grossmann, T. (2014). Physiological and behavioral responses reveal nine-month-old infants' sensitivity to pleasant touch. *Psychological Science, 25*(5), 1124-1131.

Fan, Y., & Han, S. (2008). Temporal dynamic of neural mechanisms involved in empathy for pain: An event-related brain potential study. *Neuropsychologia, 46*(1), 160-173.

Farroni, T., Johnson, M. H., Menon, E., Zulian, L., Faraguna, D., & Csibra, G. (2005). Newborns' preference for face-relevant stimuli: Effects of contrast polarity. *Proceedings of the National Academy of Sciences of the United States of America, 102*(47), 17245-17250.

Field, T., Woodson, R., Greenberg, R., & Cohen, D. (1982). Discrimination and imitation of facial expression by neonates. *Science, 218*(4568), 179-181.

Fox, N. A. (1991). If it's not left, it's right. Electroencephalograph asymmetry and the development of emotion. *American Psychologist, 46*(8), 863-872.

Fox, N. A., & Davidson, R. J. (1987). Electroencephalogram asymmetry in response to the approach of a stranger and maternal separation in 10-month-old infants. *Developmental Psychology, 23*(2), 233-240.

Fox, N. A., & Davidson, R. J. (1988). Patterns of brain electrical activity during facial signs of emotion in 10-month-old infants. *Developmental Psychology, 24*(2), 230-236.

Frijda, N. H. (1969). Recognition of emotion. In L. Berkowitz (Ed.), *Advances in experimental social psychology, 4,* (Vol. 4, pp. 167-223). New York: Academic Press.

Frijda, N. H., & Mesquita, B. (1994). The social roles and functions of emotions. In S. Kitayama & H. R. Markus (Eds.), *Emotion and culture: Empirical studies of mutual influence* (pp. 51-87). Washington, DC: American Psychological Association.

Frith, C. (2009). Role of facial expressions in social interactions. *Philosophical Transaction of the Royal Society B: Biological Sciences, 364*(1535), 3453–3458.

Gartstein, M. A., & Rothbart, M. K. (2003). Studying infant temperament via the Revised Infant Behavior Questionnaire. *Infant Behavior and Development, 26*(1), 64-86.

Geangu, E., Benga, O., Stahl, D., & Striano, T. (2010). Contagious crying beyond the first days of life. *Infant Behavior and Development, 33*(3), 279-288.

Gibson, E. J. (1988). Exploratory behavior in the development of perceiving, acting, and the acquiring of knowledge. In M. R. Rosenzweig & L. W. Porter (Eds.), *Annual review of psychology* (pp. 1-41). Palo Alto, CA: Annual Reviews.

Gliga, T., & Dehaene-Lambertz, G. (2005). Structural encoding of body and face in human infants and adults. *Journal of Cognitive Neuroscience, 17*(8), 1328-1340.

Goldman, R. I., Stern, J. M., Engel Jr., J., & Cohen, M. S. (2002). Simultaneous EEG and fMRI of the alpha rhythm. *Neuroreport, 13*(18), 2487-2492.

González-Roldan, A. M., Martinez-Jauand, M., Muñoz-García, M. A., Sitges, C., Cifre, I., & Montoya, P. (2011). Temporal dissociation in the brain processing of pain and anger faces with different intensities of emotional expression. *Pain, 152*(4), 853-859.

Gordon, I. E. (2004). *Theories of visual perception* (Vol. 3). Hove: Psychology Press.

Goren, C. C., Sarty, M., & Wu, P. Y. (1974). Visual following and pattern discrimination of face-like stimuli by newborn infants. *Pediatrics, 56*(4), 544-549.

Goubert, L., Craig, K. D., & Buysse, A. (2009). Perceiving others in pain: Experimental and clinical evidence on the role of empathy. In J. Decety & W. Ickes (Eds.), *Social neuroscience of empathy* (pp. 153-165). Cambridge, Mass.: The MIT Press.

Goubert, L., Vervoort, T., & Crombez, G. (2009). Pain demands attention from others: The approach/avoidance paradox. *Pain, 143*(1-2), 5-6.

Grèzes, J., Pichon, S., & de Gelder, B. (2007). Perceiving fear in dynamic body expressions. *Neuroimage, 35*(2), 959-967.

Grossmann, T. (2013a). The early development of processing emotions in face and voice. In P. Belin, S. Campanella & T. Ethofer (Eds.), *Integrating face and voice in person perception* (pp. 95-116). New York: Springer.

Grossmann, T. (2013b). The role of medial prefrontal cortex in early social cognition. *Frontiers in Human Neuroscience, 7*(340), 1-6.

Grossmann, T., Gliga, T., Johnson, M. H., & Mareschal, D. (2009). The neural basis of perceptual category learning in human infants. *Journal of Cognitive Neuroscience, 21*(12), 2276-2286.

Grossmann, T., & Johnson, M. H. (2007). The development of the social brain in human infancy. *European Journal of Neuroscience, 25*(4), 909-919.

Grossmann, T., Missana, M., Friederici, A. D., & Ghazanfar, A. A. (2012). Neural correlates of perceptual narrowing in cross-species face-voice matching. *Developmental Science, 15*(6), 830-839.

Grossmann, T., Oberecker, R., Koch, S. P., & Friederici, A. D. (2010). The developmental origins of voice processing in the human brain. *Neuron, 65*(6), 852-858.

Grossmann, T., Striano, T., & Friederici, A. D. (2005). Infants' electric brain responses to emotional prosody. *Neuroreport, 16*(16), 1825-1828.

Grossmann, T., Striano, T., & Friederici, A. D. (2006). Crossmodal integration of emotional information from face and voice in the infant brain. *Developmental Science, 9*(3), 309-315.

Grossmann, T., Striano, T., & Friederici, A. D. (2007). Developmental changes in infants' processing of happy and angy facial expressions: A neurobehavioral study. *Brain and Cognition, 64*(1), 30-41.

Gurnsey, R., Roddy, G., & Troje, N. F. (2010). Limits of peripheral direction discrimination of point-light walkers. *Journal of Vision, 10*(2), 1-17.

Gwiazda, J., Bauer, J., & Held, R. (1989). From visual acuity to hyperacuity: A 10-year update. *Canadian Journal of Psychology, 43*(2), 109-120.

Hadjikhani, N., & de Gelder, B. (2003). Seeing fearful body expressions activates the fusiform cortex and amygdala. *Current Biology, 13*(24), 2201-2205.

Hainline, L., & Abramov, I. (1992). Assessing visual development: Is infant vision good enough? In C. Rovee-Collier & L. P. Lipsitt (Eds.), *Advances in Infancy Research* (pp. 30-102). Norwood, NJ: Ablex.

Halit, H., Csibra, G., Volein, A., & Johnson, M. H. (2004). Face-sensitive cortical processing in early infancy. *Journal of Child Psychology and Psychiatry, 45*(7), 1228-1234.

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

Hämäläinen, J. A., Ortiz-Mantilla, S., & Benasich, A. A. (2011). Source localization of event-related potentials to pitch change mapped onto age-appropriate MRIs at 6months of age. *Neuroimage, 54*(3), 1910-1918.

Hamann, S., & Canli, T. (2004). Individual differences in emotion processing. *Current Opinion in Neurobiology, 14*(2), 233-238.

Hamlin, J. K., Hallinan, E. V., & Woodward, A. L. (2008). Do as I do: 7-month-old infants selectively reproduce others' goals. *Developmental Science, 11*(4), 487-494.

Hamlin, J. K., Wynn, K., & Bloom, P. (2007). Social evaluation by preverbal infants. *Nature, 450*(7169), 557-559.

Harmon-Jones, E. (2003). Clarifying the emotive functions of asymmetrical frontal cortical activity. *Psychophysiology, 40*(6), 838-848.

Harmon-Jones, E., & Allen, J. J. B. (1998). Anger and frontal brain activity: EEG asymmetry consistent with approach motivation despite negative affective valence. *Journal of Personality and Social Psychology, 74*(5), 1310-1316.

Harmon-Jones, E., Gable, P. A., & Peterson, C. K. (2010). The role of asymmetric frontal cortical activity in emotion-related phenomena: A review and update. *Biological Psychology, 84*(3), 451-462.

Harmon-Jones, E., & Sigelman, J. (2001). State anger and prefrontal brain activity: Evidence that insult-related relative left-prefrontal activation is associated with experienced anger and aggression. *Journal of Personality and Social Psychology, 80*(5), 797-803.

Harwood, N. K., Hall, L. J., & Shinkfield, A. J. (1999). Recognition of facial emotional expressions from moving and static displays by individuals with mental retardation. *American Journal on Mental Retardation, 104*(3), 270-278.

Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron, 22*(1), 189-199.

Heberlein, A. S., Adolphs, R., Tranel, D., & Damasio, H. (2004). Cortical regions for judgments of emotions and personality traits from point-light walkers. *Journal of Cognitive Neuroscience, 16*(7), 1143-1158.

Heberlein, A. S., & Atkinson, A. P. (2009). Neuroscientific evidence for simulation and shared substrates in emotion recognition: Beyond faces. *Emotion Review, 1*(2), 162-177.

Heberlein, A. S., & Saxe, R. R. (2005). Dissociation between emotion and personality judgments: Convergent evidence from functional neuroimaging. *Neuroimage, 28*(4), 770-777.

Henderson, H. A., Fox, N. A., & Rubin, K. H. (2001). Temperamental contributions to social behavior: The moderating roles of frontal EEG asymmetry and gender. *Journal of the American Academy of Child & Adolescent Psychiatry, 40*(1), 68-74.

Herrmann, C. S., Grigutsch, M., & Busch, N. A. (2005). EEG oscillations and wavelet analysis. In T. C. Handy (Ed.), *Event-related potentials: A methods handbook* (pp. 229-259). Cambridge, Massachusetts: The MIT Press.

Hess, U., & Blairy, S. (2001). Facial mimicry and emotional contagion to dynamic emotional facial expressions and their influence on decoding accuracy. *International Journal of Psychophysiology, 40*(2), 129-141.

Hirai, M., & Hiraki, K. (2005). An event-related potentials study of biological motion perception in human infants. *Cognitive Brain Research, 22*(2), 301-304.

Hobson, R. P., Ouston, J., & Lee, A. (1988). Emotion recognition in autism: Coordinating faces and voices. *Psychological Medicine, 18*(4), 911-923.

Hodzic, A., Kaas, A., Muckli, L., Stirn, A., & Singer, W. (2009). Distinct cortical networks for the detection and identification of human body. *Neuroimage, 45*(4), 1264-1271.

Hoehl, S., & Wahl, S. (2012). Recording infant ERP data for cognitive research. *Developmental Neuropsychology, 37*(3), 187-209.

Hoehl, S., Wiese, L., & Striano, T. (2008). Young infants' neural processing of objects is affected by eye gaze direction and emotional expression. *PLoS One, 3*(6), e2389.

Hoffmann, M. L. (1984). Interaction of affect and cognition in empathy. In C. E. Izard, J. Kagan & R. B. Zajonc (Eds.), *Emotions, cognition, and behavior* (pp. 103,131). Cambridge: Cambridge University Press.

Hornak, J., Rolls, E. T., & Wade, D. (1996). Face and voice expression identification in patients with emotional and behavioural changes following ventral frontal lobe damage. *Neuropsychologia, 34*(3), 247-261.

Izard, C. E. (1977). *Human Emotions*. New York: Plenum Press.

Izard, C. E. (2007). Basic emotions, natural kinds, emotion schemas, and a new paradigm. *Perspectives on Psychological Science, 2*(3), 260-280.

Izard, C. E., Fine, S., Schultz, D., Mostow, A., Ackerman, B., & Youngstrom, E. (2001). Emotion knowledge as a predictor of social behavior and academic competence in children at risk. *Psychological Science, 12*(1), 18-23.

Jackson, P. L., Meltzoff, A. N., & Decety, J. (2005). How do we perceive the pain of others? A window into the neural processes involved in empathy. *Neuroimage, 24*(3), 771-779.

Jackson, P. L., Rainville, P., & Decety, J. (2006). To what extent do we share the pain of others? Insight from the neural bases of pain empathy. *Pain, 125*(1), 5-9.

Jasper, H. (1958). The ten-twenty electrode system of the International Federation. *Electroencephalography and Clinical Neurophysiology, 10*, 371-375.

Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception and Psychophysics, 14*(2), 201-211.

Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience, 6*(10), 766-774.

Johnson, M. H., Dziurawiec, S., Ellis, H., & Morton, J. (1991). Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition, 40*(1), 1-19.

Jung, T., Makeig, S., Humphries, C., Lee, T. W., McKeown, M. J., Iragui, V., & Sejnowski, T. J. (2000). Removing electroencephalographic artifacts by blind source separation. *Psychophysiology, 37*(2), 163-178.

Kaitz, M., Meschulach-Sarfaty, O., Auerbach, J., & Eidelman, A. (1988). A reexamination of newborns' ability to imitate facial expressions. *Developmental Psychology, 24*(1), 3-7.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience, 17*(11), 4302-4311.

Kanwisher, N., & Yovel, G. (2006). The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society B: Biological Sciences, 361*(1476), 2109-2128.

Karrer, R., & Ackles, P. K. (1987). Visual event-related potentials of infants during a modified oddball procedure. *Electroencephalography and Clinical Neurophysiology, 40*(supplement), 603-608.

Karrer, R., & Monti, L. A. (1995). Event-related potentials of 4–7-week-old infants in a visual recognition memory task. *Electroencephalography and Clinical Neurophysiology, 94*(6), 414-424.

Kessler, H., Doyen-Waldecker, C., Hofer, H., Traue, H. C., & Abler, B. (2011). Neural correlates of the perception of dynamic versus static facial expressions of emotion. *GMS Psycho-Social-Medicine, 8:Doc03*, 1-8.

Kestenbaum, R., & Nelson, C. A. (1990). The recognition and categorization of upright and inverted emotional expressions by 7-month-old infants. *Infant Behavior and Development, 13*(4), 497-511.

Kilts, C. D., Egan, G., Gideon, D. A., Ely, T. D., & Hoffman, J. M. (2003). Dissociable neural pathways are involved in the recognition of emotion in static and dynamic facial expressions. *Neuroimage, 18*(1), 156-168.

Klinnert, M., Campos, J. J., Sorce, J., Emde, R. N., & Svejda, M. (1983). Emotions as behavior regulators: Social referencing in infancy. In R. Plutchik & H. Kellerman (Eds.), *Emotions in early development* (pp. 57-86). New York: Academic Press.

Kobiella, A., Grossmann, T., Reid, V. M., & Striano, T. (2008). The discrimination of angry and fearful facial expressions in 7-month-old infants: An event-related potential study. *Cognition and Emotion, 22*(1), 134-146.

Kopp, C. B. (1989). Regulation of distress and negative emotions: A developmental view. *Developmental Psychology, 25*(3), 343-354.

Kotsoni, E., de Haan, M., & Johnson, M. H. (2001). Categorical perception of facial expressions by 7-month-old infants. *Perception, 30*(9), 1115–1125.

Krol, K. M., Rajhans, P., Missana, M., & Grossmann, T. (2015). Duration of exclusive breastfeeding is associated with differences in infants' brain responses to emotional body expressions. *Frontiers in Behavioral Neuroscience, 8*, 459.

LaBarbera, J. D., Izard, C. E., Vietze, P., & Parisi, S. A. (1976). Four- and six-month-old infants' visual responses to joy, anger, and neutral expressions. *Child Development, 47*(2), 535-538.

Lamm, C., Batson, D. C., & Decety, J. (2007). The neural substrate of human empathy: Effects of perspective-taking and cognitive appraisal. *Journal of Cognitive Neuroscience, 19*(1), 42-58.

Lamm, C., Decety, J., & Singer, T. (2011). Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *Neuroimage, 54*(3), 2492-2502.

Laufs, H., Krakow, K., Sterzer, P., Eger, E., Beyerle, A., Salek-Haddadi, A., & Kleinschmidt, A. (2003). Electroencephalographic signatures of attentional and cognitive default modes in spontaneous brain activity fluctuations at rest. *Proceedings of the National Academy of Sciences of the United States of America, 100*(19), 11053-11058.

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

Leppänen, J. M., & Nelson, C. A. (2009). Tuning the developing brain to social signals of emotions. *Nature Reviews Neuroscience, 10*(1), 37-47.

Lloyd-Fox, S., Blasi, A., & Elwell, C. E. (2010). Illuminating the developing brain: The past, present and future of functional near infrared spectroscopy. *Neuroscience and Biobehavioral Reviews, 34*(3), 269-284.

LoBue, V., Coan, J. A., Thrasher, C., & DeLoache, J. S. (2011). Prefrontal asymmetry and parent-rated temperament in infants. *PLoS One, 6*, 1-10.

Luck, S. J. (2005). *An introduction to the event-related potential technique*. Cambridge, Massachusetts: MIT Press.

Luyster, R. J., Powell, C., Tager-Flusberg, H., & Nelson, C. A. (2014). Neural measures of social attention across the first years of life: Characterizing typical development and markers of autism risk. *Developmental Cognitive Neuroscience, 8*, 131-143.

Marshall, P. J., Bar-Haim, Y., & Fox, N. A. (2002). Development of the EEG from 5 months to 4 years of age. *Clinical Neurophysiology, 113*(8), 1199-1208.

Marshall, P. J., & Shipley, T. F. (2009). Event-related potentials to point-light displays of human actions in 5-month-old infants. *Developmental Neuropsychology, 34*(3), 368-377.

Martinos, M., Matheson, A., & de Haan, M. (2012). Links between infant temperament and neurophysiological measures of attention to happy and fearful faces. *Journal of Child Psychology and Psychiatry, 53*(11), 1118–1127.

McCulloch, D. L. (2007). Visual evoked potentials in infants. In M. d. Haan (Ed.), *Infant EEG and event-related potentials* (pp. 39-76). New York, NY: Psychology Press.

Meeren, H. K., van Heijnsbergen, C. C., & de Gelder, B. (2005). Rapid perceptual integration of facial expression and emotional body language. *Proceedings of the National Academy of Sciences of the United States of America, 102*(45), 16518-16523.

Missana, M., Atkinson, A. P., & Grossmann, T. (2015). Tuning the developing brain to emotional body expressions. *Developmental Science, 18*(2), 243–253.

Missana, M., Grigutsch, M., & Grossmann, T. (2014). Developmental and individual differences in the neural processing of dynamic expressions of pain and anger. *PLoS One,9,*e93728.

Missana, M., Rajhans, P., Atkinson, A. P., & Grossmann, T. (2014). Discrimination of fearful and happy body postures in 8-month-old infants: An event-related potential study. *Frontiers in human neuroscience, 8*(531), 531.

Mohr, P., Howells, K., Gerace, A., Day, A., & Wharton, M. (2007). The role of perspective taking in anger arousal. *Personality and Individual Differences, 43*, 507-517.

Moore, D. G., Goodwin, J. E., George, R., Axelsson, E. L., & Braddick, F. M. B. (2007). Infants perceive human point-light displays as solid forms. *Cognition, 104*(2), 377-396.

Moriceau, S., Roth, T. L., & Sullivan, R. M. (2010). Rodent model of infant attachment learning and stress. *Developmental Psychobiology, 52*(7), 651-660.

Morrison, I., & Downing, P. E. (2007). Organization of felt and seen pain responses in anterior cingulate cortex. *Neuroimage, 37*(2), 642-651.

Morrison, I., Lloyd, D., Pellegrino, G. D., & Roberts, N. (2004). Vicarious responses to pain in anterior cingulate cortex: Is empathy a multisensory issue? *Cognitive, Affective, and Behavioral Neuroscience, 4*(2), 270-278.

Morton, J., & Johnson, M. H. (1991). CONSPEC and CONLERN: A two-process theory of infant face recognition. *Psychological Review, 98*(2), 164-181.

Moses, L. J., Baldwin, D. A., Rosicky, J. G., & Tidball, G. (2001). Evidence for referential understanding in the emotions domain at twelve and eighteen months. *Child Development, 72*(3), 718-735.

Mumme, D. L., & Fernald, A. (2003). The infant as onlooker: Learning from emotional reactions observed in a television scenario. *Child Development, 74*(1), 221-237.

Mumme, D. L., Fernald, A., & Herrera, C. (1996). Infants' responses to facial and vocal emotional signals in a social referencing paradigm. *Child Development, 67*(6), 3219-3237.

Nelson, C. A. (1987). The recognition of facial expressions in the first two years of life: Mechanisms of development. *Child Development, 58*(4), 889-909

Nelson, C. A. (1994). Neural correlates of recognition memory in the first postnatal year of life. In G. Dawson & K. Fischer (Eds.), *Human development and the developing brain* (pp. 269-313). New York: Guilford Press.

Nelson, C. A. (1996). Electrophysiological correlates of memory development in the first year of life. In H. Reese & M. Franzen (Eds.), *Biological and neuropsychological mechanisms: Life span developmental psychology*. Hillsdale, NJ: Lawrence Erlbaum Associates Inc.

Nelson, C. A., & de Haan, M. (1996). Neural correlates of infants' visual responsiveness to facial expressions of emotion. *Developmental Psychobiology, 29*(7), 577–595.

Nelson, C. A., & Dolgin, K. (1985). The generalized discrimination of facial expressions by 7-month-old infants. *Child Development, 56*(1), 58-61.

Nelson, C. A., Morse, P. A., & Leavitt, L. A. (1979). Recognition of facial expressions by seven-month-old infants. *Child Development, 50*(4), 1239-1242.

Nelson, C. A., Thomas, K. M., de Haan, M., & Wewerka, S. S. (1998). Delayed recognition memory in infants and adults as revealed by event-related potentials. *International Journal of Psychophysiology, 29*(2), 145-165.

Öhman, A., Lundqvist, D., & Esteves, F. (2001). The face in the crowd revisited: A threat advantage with schematic stimuli. *Journal of Personality and Social Psychology, 80*(3), 381-396.

Olofsson, J. K., Nordin, S., Sequeira, H., & Polich, J. (2008). Affective picture processing: An integrative review of ERP findings. *Biological Psychology, 77*(3), 247-265.

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience, 2011*(1), 1-9.

Oram, M. W., & Perrett, D. I. (1994). Responses of anterior superior temporal polysensory (STPa) neurons to "biological motion" stimuli. *Journal of Cognitive Neuroscience, 6*(2), 99-116.

Paulus, C. (2009). Der Saarbrücker Persönlichkeitsfragebogen SPF(IRI) zur Messung von Empathy.

Peelen, M. V., Atkinson, A. P., Andersson, F., & Vuilleumier, P. (2007). Emotional modulation of body-selective visual areas. *Social Cognitive and Affective Neuroscience, 2*(4), 274-283.

Peelen, M. V., & Downing, P. E. (2005). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology, 93*(1), 603-608.

Peltola, M. J., Leppänen, J. M., Mäki, S., & Hietanen, J. K. (2009). Emergence of enhanced attention to fearful faces between 5 and 7 months of age. *Social Cognitive and Affective Neuroscience, 4*(2), 134-142.

Pichon, S., de Gelder, B., & Grèzes, J. (2008). Emotional modulation of visual and motor areas by dynamic body expressions of anger. *Social Neuroscience, 3*(3-4), 199-212.

Pichon, S., de Gelder, B., & Grèzes, J. (2009). Two different faces of threat. Comparing the neural systems for recognizing fear and anger in dynamic body expressions. *Neuroimage, 47*(4), 1873-1883.

Pickens, J., Field, T., & Nawrocki, T. (2001). Frontal EEG asymmetry in response to emotional vignettes in preschool age children. *International Journal of Behavioral Development, 25*(2), 105-112.

Prkachin, K. M., & Craig, K. D. (1995). Expressing pain: The communication and interpretation of facial pain signals. *Journal of Nonverbal Behavior, 19*(4), 191-205.

Quinn, P. C., & Slater, A. (2003). Face perception at birth and beyond. In O. Pascalis & A. Slater (Eds.), *The development of face processing in infancy and early childhood: Current perspectives* (pp. 3-12). New York: Nova Science.

Rajhans, P., Jessen, S., Missana, M., & Grossmann, T. (under review). Putting the face into context: Body expressions impact facial emotion processing in human infants.

Rajhans, P., Missana, M., Krol, K. M., & Grossmann, T. (under review). The association of temperament and maternal empathy with individual differences in infants' neural responses to emotional body expressions.

Ramsey-Rennels, J. L., & Langlois, J. H. (2007). How infants perceive and process faces. In A. Slater & M. Lewis (Eds.), *Introduction to infant development* (pp. 191-215). New York: Oxford University Press Inc.

Reicherts, P., Wieser, M. J., Gerdes, A. B. M., Likowski, K. U., Weyers, P., Mühlberger, A., & Pauli, P. (2012). Electrocortical evidence for preferential processing of dynamic pain expressions compared to other emotional expressions. *Pain, 153* (9), 1959–1964.

Reid, V. M., Hoehl, S., & Striano, T. (2006). The perception of biological motion by infants: An event-related potential study. *Neuroscience Letters, 395*(3), 211-214.

Reynolds, G. D., & Richards, J. E. (2005). Familiarization, attention, and recognition memory in infancy: An event-related potential and cortical source localization study. *Developmental Psychology, 41*(4), 598-615.

Reynolds, G. D., & Richards, J. E. (2009). Cortical source localization of infant cognition. *Developmental Neuropsychology, 34*(3), 312-329.

Richards, J. E. (2002). The development of visual attention and the brain. In M. d. Haan & M. Johnson (Eds.), *The cognitive neuroscience of development* (pp. 73-98). Hove, UK: Psychology Press.

Richards, J. E. (2003). Attention affects the recognition of briefly presented visual stimuli in infants: An ERP study. *Developmental Science, 6*(3), 312-328.

Roth-Hanania, R., Davidov, M., & Zahn-Waxler, C. (2011). Empathy development from 8 to 16 months: Early signs of concern for others. *Infant Behavior and Development, 34*(3), 447-458.

Saarela, M. V., Hlushchuk, Y., Williams, A. C. C., Schurmann, M., Kalso, E., & Hari, R. (2007). The compassionate brain: Humans detect intensity of pain from another's face. *Cerebral Cortex, 17*(1), 230-237.

Sato, W., Kochiyama, T., Yoshikawa, S., Naito, E., & Matsumura, M. (2004). Enhanced neural activity in response to dynamic facial expressions of emotion: An fMRI study. *Cognitive Brain Research, 20*(1), 81-91.

Schneirla, T. C. (1959). An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. In M. R. Jones (Ed.), *Nebraska symposium on motivation*. Lincoln, NE: University of Nebraska Press.

Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2003). Attention and emotion: An ERP analysis of facilitated emotional stimulus processing. *Neuroreport, 14*(8), 1107-1110.

Schupp, H. T., Ohman, A., Junghöfer, M., Weike, A. I., Stockburger, J., & Hamm, A. O. (2004). The facilitated processing of threatening faces: An ERP analysis. *Emotion, 4*(2), 189-200.

Schwartz, G. M., Izard, C. E., & Ansul, S. (1985). The 5-month-old's ability to discriminate facial expressions of emotion. *Infant Behavior and Development, 8*(1), 65-77.

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

Shaarani, A. S., & Romano, D. M. (2007). Perception of emotions from static postures. *Affective Computing and Intelligent Interaction, 4738*, 761-762.

Sharbrough, F., Chatrian, G., Lesser, R., Lüders, H., Nuwer, M., & Picton, T. (1991). American electroencephalographic society guidlines for standard electrode position nomenclature. *Journal of Clinical Neurophysiology, 8*(2), 202-202.

Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Sciences of the United States of America, 105*(2), 809 – 813.

Simon, D., Craig, K. D., Gosselin, F., Belin, P., & Rainville, P. (2008). Recognition and discrimination of prototypical dynamic expressions of pain and emotions. *Pain, 135*(1-2), 55-64.

Simon, D., Craig, K. D., Miltner, H. R., & Rainville, P. (2006). Brain responses to dynamic facial expressions of pain. *Pain, 126*(1), 309-318.

Singer, T. (2006). The neuronal basis and ontogeny of empathy and mind reading: Review of literature and implications for future research. *Neuroscience and Biobehavioral Reviews, 30*(6), 855-863.

Singer, T., & Lamm, C. (2009). The social neuroscience of empathy. *Annals of the New York Academy of Sciences, 1156*(1), 81-96.

Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science, 303*(5661), 1157-1162.

Soken, N. H., & Pick, A. D. (1992). Intermodal perception of happy and angry expressive behaviors by seven-month-old infants. *Child Development, 63*(4), 787-795.

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

Spencer, K. M. (2005). Averaging, detection, and classification of single-trial ERPs. In T. C. Handy (Ed.), *Event-related potentials: A methods handbook*. Cambridge, Massachusetts: The MIT Press.

Sroufe, L. A. (1977). Wariness of strangers and the study of infant development. *Child Development, 48*(3), 731-746.

Stekelenburg, J. J., & de Gelder, B. (2004). The neural correlates of perceiving human bodies: An ERP study on the body-inversion effect. *Neuroreport, 15*(5), 777-780.

Striano, T., Brennan, P. A., & Vanman, E. J. (2002). Maternal depressive symptoms and 6-month-old infants' sensitivity to facial expressions. *Infancy, 3*(1), 115-126.

Stroganova, T. A., Orekhova, E. V., & Posikera, I. N. (1999). EEG alpha rhythm in infants. *Clinical Neurophysiology, 110*(6), 997–1012.

Tamietto, M., & de Gelder, B. (2010). Neural bases of the non-conscious perception of emotional signals. *Nature Reviews Neuroscience, 11*(10), 697-709.

Taylor, J. C., Wiggett, A. J., & Downing, P. E. (2007). Functional MRI analysis of body and body part representations in the extrastriate and fusiform body areas. *Journal of Neurophysiology, 98*(3), 1626-1633.

Tomarken, A. J., Davidson, R. J., & Henriques, J. B. (1990). Resting frontal brain asymmetry predicts affective responses to films. *Journal of Personality and Social Psychology, 59*(4), 791-801.

Tomasello, M., & Carpenter, M. (2007). Shared intentionality. *Developmental Science, 10*(1), 121-125.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences, 28*(5), 675-691.

Tottenham, N. (2012). Human amygdala development in the absence of species-expected caregiving. *Developmental Psychobiology, 54*(6), 598-611.

Troje, N. F., & Westhoff, C. (2006). The inversion effect in biological motion perception: Evidence for a "life detector"? *Current Biology, 16*(8), 821-824.

Vaish, A., Carpenter, M., & Tomasello, M. (2009). Sympathy through affective perspective taking and its relation to prosocial behavior in toddlers. *Developmental Psychology, 45*(2), 534-543.

Vaish, A., Grossmann, T., & Woodward, A. (2008). Not all emotions are created equal: The negativity bias in social-emotional development. *Psychological Bulletin, 143*(3), 383-403.

Vaish, A., & Striano, T. (2004). Is visual reference necessary? Contributions of facial versus vocal cues in 12-month-old' social referencing behavior. *Developmental Science, 7*(3), 261-269.

van de Riet, W. A. C., Grèzes, J., & de Gelder, B. (2009). Specific and common brain regions involved in the perception of faces and bodies and the representation of their emotional expressions. *Social neuroscience, 4*(2), 101-120.

Van Heijnsbergen, C. C. R. J., Grèzes, J., & de Gelder, B. (2007). Rapid detection of fear in body expressions, an ERP study. *Brain Research, 1186*, 233-241.

Vangeneugden, J., de Maziere, P. A., Van Hulle, M. M., Jaeggli, T., Van Gool, L., & Vogels, R. (2011). Distinct mechanisms for coding of visual actions in macaque temporal cortex. *The Journal of Neuroscience, 31*(2), 385-401.

Vogel, M., Monesson, A., & Scott, L. S. (2012). Building biases in infancy: The influence of race on face and voice emotion matching. *Developmental Science, 15*(3), 359-372.

Vuilleumier, P. (2005). How brains beware: Neural mechanisms of emotional attention. *Trends in Cognitive Sciences, 9*(12), 585-594.

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2001). Effects of attention and emotion on face processing in the human brain. An event-related fMRI study. *Neuron, 30*(3), 829-841.

Walk, R. D., & Homan, C. P. (1984). Emotion and dance in dynamic light displays. *Bulletin of the Psychonomic Society, 22*(5), 437-440.

Walker-Andrews, A. S. (1986). Intermodal perception of expressive behaviors by human infants: Relation of eye and voice? *Developmental Psychology, 22*(3), 373-377.

Walker-Andrews, A. S. (1997). Infants' perception of expressive behaviors: Differentiation of multimodal information. *Psychological Bulletin, 121*(3), 437-456.

Walker-Andrews, A. S., & Dickson, L. R. (1997). Infants' understanding of affect. In S. Hala (Ed.), *The development of social cognition* (pp. 161-186). Hove: Psychology Press.

Walle, E. A., & Campos, J. J. (2012). Interpersonal responding to discrete emotions: A functionalist approach to the development of affect specificity. *Emotion Review, 4*(4), 413-422.

Webb, S. J., Long, J. D., & Nelson, C. A. (2005). A longitudinal investigation of visual event-related potentials in the first year of life. *Developmental Science, 8*(6), 605-616.

Wilcox, B. M., & Clayton, F. L. (1968). Infant visual fixation on motion pictures of the human face. *Journal of Experimental Child Psychology, 6*(1), 22-32.

Williams, A. C. C. (2002). Facial expression of pain: An evolutionary account. *Behavioral and Brain Sciences, 25*, 439-488.

Yamada, M., & Decety, J. (2009). Unconscious affective processing and empathy: An investigation of subliminal priming on the detection of painful facial expressions. *Pain, 143*(1), 71-75.

Young-Browne, G., Rosenfeld, H. M., & Horowitz, F. D. (1977). Infant discrimination of facial expressions. *Child Development, 48*(2), 555-562.

Young, S. K., Fox, N. A., & Zahn-Waxler, C. (1999). The relations between temperament and empathy in 2-year-olds. *Developmental Psychology, 35*(5), 1189-1197.

Zahn-Waxler, C., Radke-Yarrow, M., Wagner, E., & Chapman, M. (1992). Development of concern for others. *Developmental Psychology, 28*(1), 126-136.

Zieber, N., Bhatt, R. S., Hayden, A., Kangas, A., Collins, R., & Bada, H. (2010). Body representation in the first year of life. *Infancy, 15*(5), 534-544.

Zieber, N., Kangas, A., Hock, A., & Bhatt, R. S. (2014a). The development of intermodal emotion perception from bodies and voices. *Journal of Experimental Child Psychology, 126*, 68-79.

Zieber, N., Kangas, A., Hock, A., & Bhatt, R. S. (2014b). Infants' perception of emotion from body movements. *Child Development, 85*(2), 675-684.

Erklärung gemäß § 8 Abs. 1 Buchst. b) und c) der Promotionsordnung der Fakultät für Verhaltens- und Empirische Kulturwissenschaften

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

Promotionsausschuss der Fakultät für Verhaltens- und Empirische Kulturwissenschaften
der Ruprecht-Karls-Universität Heidelberg
Doctoral Committee of the Faculty of Behavioural and Cultural Studies, of Heidelberg University

Erklärung gemäß § 8 Abs. 1 Buchst. b) der Promotionsordnung der Universität Heidelberg
für die Fakultät für Verhaltens- und Empirische Kulturwissenschaften
Declaration in accordance to § 8 (1) b) and § 8 (1) c) of the doctoral degree regulation of Heidelberg University, Faculty of Behavioural and Cultural Studies

Ich erkläre, dass ich die vorgelegte Dissertation selbstständig angefertigt, nur die angegebenen Hilfsmittel benutzt und die Zitate gekennzeichnet habe.
I declare that I have made the submitted dissertation independently, using only the specified tools and have correctly marked all quotations.

Erklärung gemäß § 8 Abs. 1 Buchst. c) der Promotionsordnung
der Universität Heidelberg für die Fakultät für Verhaltens- und Empirische Kulturwissenschaften

Ich erkläre, dass ich die vorgelegte Dissertation in dieser oder einer anderen Form nicht anderweitig als Prüfungsarbeit verwendet oder einer anderen Fakultät als Dissertation vorgelegt habe.
I declare that I did not use the submitted dissertation in this or any other form as an examination paper until now and that I did not submit it in another faculty.

Vorname Nachname
First name Family name ____

Datum, Unterschrift
Date, Signature ____