ORIGINS OF EMPATHY DEVELOPMENT IN INFANCY

By

Maria M. Crespo Llado

A thesis submitted to the Psychology Department of

Lancaster University for the degree of

DOCTOR OF PHILOSOPHY

LANCASTER UNIVERSITY

September 2017

Declaration

I declare that this thesis is my own work, and has not been submitted in substantially the same form for the award of a higher degree elsewhere.

Signature

Date

Abstract

The current thesis examined the processes involved in the generation of empathy in infancy. This thesis endorses the combination of developmental and cognitive neuroscience techniques for a more comprehensive understanding of empathy. In support of this view, the current work has adopted a multi-method approach in which neuroimaging, psychophysiological and behavioral techniques have been used to examine the cognitive and affective aspects of empathy in infancy. Through a series of experimental studies, this thesis has addressed intertwined yet different aspects of the experience of empathy.

Paper 1 investigated individual differences in 8-month-old infants' neural responses to peers' emotional non-verbal vocalizations by using event-related potential (ERP) method and parental reports of infants' temperament. Results showed that infants responded differently to peers' laughing and crying vocalizations, as indexed by modulations in the N100, P200 and late positive component (LPC). Of special interest, individual differences in negative emotionality were related to amplitude variations in the P200 and LPC components. Paper 2 expands on the previous results by examining frontal asymmetry patterns linked to infants' affective and behavioral responses to a peer crying and a peer laughing. Eight-month-old infants underwent two assessment sessions on separate days, in which electroencephalography (EEG) and behavioral measures were respectively recorded in each day. EEG analysis showed that distinct neural patterns were related to the observation of a peer laughing and a peer crying, with greater right frontal activation being associated with the observation of a peer crying. Furthermore, correlational analysis suggested a positive relation between left frontal cortical activation and infants' attempts to approach a peer crying or infants' attempts to engage with a peer laughing.

Following on from it, Paper 3 and 4 investigated potential neurocognitive mechanisms underlying affective and cognitive aspects of empathy. Paper 3 examined the role of motor mimicry and affective evaluation processes in infants' facial matching responses to others' emotional facial expressions by measuring spontaneous facial reactions (SFRs). In particular, 4- and 7-month old infants were presented with facial expressions of happiness, anger, and fear. Electromyography (EMG) was used to measure activation in muscles relevant for forming these expressions: zygomaticus major (smiling), corrugator (frowning), and frontalis (forehead raising). Results indicated no selective activation of the facial muscles for the expressions in 4-month-old infants. For 7-month-old infants, evidence for selective facial reactions was found especially for happy faces and fearful faces, while angry faces did not show a clear differential response.

Paper 4 goes on to explore the ontogeneis of cognitive aspects of empathy by examining the neural correlates underlying false belief (FB) processing in 15-month-old infants. Using a passive non-verbal FB task, 15-month-old infants were presented with sequences of images depicting a character acting congruently (FBc) or incongruently (FBi) to her false belief about an object's location, while EEG was continuously recorded. ERPs analysis revealed differences between conditions at frontal locations, as indexed by modulations in the N400 component. Specifically, a more negative N400 waveform was recorded for FBi as compared to FBc trials.

Acknowledgements

I would like to thank Dr Elena Geangu, for being a constructive supervisor and mentor. Her strong support and encouragement has kept me going in this difficult journey. I would also like to thank Prof Gavin Bremner for his helpful feedback on my thesis writing. I would also like to express my gratitude to Dr Gloria Garcia de la Banda and Dr Eugenio Parise for their inspiration, support, and advice. Importantly, I would also like to thank all those families who participated in my studies, without their time and contribution the current thesis would have not been possible.

I am also grateful to all the wonderful people with who I have shared my time in Lancaster. In particular, thanks to Beth Armstrong, James Brand, Francesca Citron, Matt Hilton, Christiana Iordanou, Claire Kelly, Sally Linkenauger, Szilvia Linnert, Alison May, Neil McLatchie, Steven Nicholson, Sana Alsarghali and James West for being wonderful and filling my life with joy. My officemates and friends Han Ke and Christian Kliesch deserve a special mention since they have been the ones who have endured the most with my daily frustrations. I would also like to express my gratitude to Jared Piazza for his endless patience and support during the last years. Thanks for holding my hand during the darkest moments and being my sun. Finally, I would like to express my gratitude to my family for all the support received, in spite of the distance I have always felt that they were there for me.

Dedication

For mum and dad

Statement of Authorship

Authorship contributions

Paper 1: INDIVIDUAL DIFFERENCES IN INFANTS' NEURAL RESPONSES TO THEIR PEERS' CRY AND LAUGHTER

Conception and design of study: **Maria M. Crespo Llado**, Elena Geangu

Acquisition of data: **Maria M. Crespo Llado**

Analysis and/or interpretation of data: **Maria M. Crespo Llado**, Ross E. Vanderwert

Drafting manuscript: **Maria M. Crespo Llado**, Elena Geangu

Revising the manuscript critically for important intellectual content: **Maria M. Crespo Llado**, Elena Geangu, Ross E. Vanderwert

Paper 2: FRONTAL ASYMMETRY PATTERNS AND INFANTS' RESPONSES TO THEIR PEERS' POSITIVE AND NEGATIVE EMOTIONS

Conception and design of study: **Maria M. Crespo Llado**, Elena Geangu

Acquisition of data: **Maria M. Crespo Llado**

Analysis and/or interpretation of data: **Maria M. Crespo Llado**, Elisa Roberti, Ross E. Vanderwert

Drafting manuscript: **Maria M. Crespo Llado**, Elena Geangu

Revising the manuscript critically for important intellectual content: **Maria M. Crespo Llado**, Elena Geangu, Ross E. Vanderwert

Paper 3: THE DEVELOPMENT OF SPONTANEOUS FACIAL RESPONSES TO OTHERS' EMOTIONS IN INFANCY. AN EMG STUDY

Conception and design of study: **Maria M. Crespo Llado**, Elena Geangu, Jakob Kaiser, Chiara Turati

Acquisition of data: **Maria M. Crespo Llado**, Jakob Kaiser

Analysis and/or interpretation of data: **Maria M. Crespo Llado**, Jakob Kaiser

Drafting manuscript: **Maria M. Crespo Llado**, Elena Geangu, Jakob Kaiser

Revising the manuscript critically for important intellectual content: **Maria M. Crespo Llado**, Elena Geangu, Jakob Kaiser, Chiara Turati

Paper 4: INFANTS' NEURAL RESPONSES DURING A NON-VERBAL FALSE BELIEF TASK. AN EVENT-RELATED POTENTIAL STUDY

Conception and design of study: **Maria M. Crespo Llado**, Elena Geangu

Acquisition of data: **Maria M. Crespo Llado**

Analysis and/or interpretation of data: **Maria M. Crespo Llado**

Drafting manuscript: **Maria M. Crespo Llado**, Elena Geangu

Revising the manuscript critically for important intellectual content: **Maria M. Crespo Llado**, Elena Geangu

Table of Contents

PAPER 1: Individual Differences in Infants' Neural Responses to their Peers' Cry and Laughter………………………………………………………109

Epigraph

Caminante, son tus huellas
el camino y nada más;
Caminante, no hay camino,
se hace camino al andar.
Al andar se hace el camino,
y al vovler la vista atrás
se ve la senda que nunca
se ha de volver a pisar.
Caminante no hay camino
sino estelas en la mar.

Antonio Machado
Ext. Proverbios y Cantares (XXIX)

General Introduction

Maria M. Crespo Llado

Lancaster University

The ability to share and understand others' feelings is crucial to interact successfully in our social environment. Broadly defined as empathy, this complex affective state underlies some of the most meaningful human interactions from mother-child bonding to more complex prosocial behaviors towards others (Batson, 2009; Decety & Svetlova, 2012). In addition, empirical evidence from clinical research emphasizes the importance of such a complex emotion in the development of healthy social interactions (Blair, 2001, 2005). Indeed, deficits in empathy have been linked to the genesis of certain neurodevelopmental disorders such as psychopathy, autism spectrum disorder or disruptive behavior disorder (Blair, 2005; Decety & Meyer, 2008). Also, some researchers suggest that empathy contributes to the development of moral behaviors (e.g. Eisenberg, 2000; Eisenberg & Eggum, 2009; Hoffman, 2000). Given the potential negative implications that can result from an atypical development of empathy, it is crucial to elucidate the developmental mechanisms underlying empathic responses throughout infancy.

Although a substantial body of research has been conducted on empathy development in young children, only a modest number of studies have examined empathy during the first year of life. So far, what we know about empathy prior to the first birthday, it is that infants seem to be born with an innate ability to resonate with others' emotions (e.g., Hoffman, 1975; Sagi & Hoffman, 1976). For instance, few hours after birth infants display vocal and facial expressions of distress in response to another newborn cry (e.g., Simner, 1971; Sagi & Hoffman, 1976; Geangu, Benga, Stahl, & Striano, 2010). Similarly, by 10-12 weeks of age infants also show emotional resonance to adults' facial and vocal displays of happiness, sadness and anger (e.g., Haviland & Lelwilca, 1987; Serrano, Iglesias, & Loeches, 1995; Kahana-Kalman, & Walker-Andrews, 2001). These early signs of affect sharing are thought to be followed by more sophisticated other-oriented responses towards others in distress, which can already be observed during the second half of the first year in the form of modest signs of affective concern or simple attempts to approach the distressed victim (Hay, Nash, & Pedersen, 1981; Roth-Hanania, Davidov, & Zahn-Waxler, 2011). These precocious other-oriented empathic responses continue to increase gradually throughout childhood (e.g., Liew et al., 2011; Nichols, Svetlova, & Brownell, 2010; Svetlova, Nichols, & Brownell, 2010; Zahn-Waxler, Radke-Yarrow, Wagner, & Chapman, 1992) and are believed to constitute the precursor for later prosocial behaviors (Batson, 1991; Decety & Lamm, 2006; Hoffman, 1982; Knafo & Israel, 2012; Singer, 2006).

Although it is widely assumed that affect sharing is a likely precursor of empathy, this notion has never been directly tested in infants. We still do not have a clear understanding of the different mechanisms underlying infants' ability to share others' emotions and how they relate to the production of later empathic and prosocial responses. In adults, evidence suggests that several processes contribute to the experience of empathy, such as automatic motor mimicry, emotional appraisal, and cognitive perspective taking (e.g., Decety, 2010a; Decety & Jackson, 2004; Decety & Meyer, 2008). The extent to which these mechanisms are engaged in early empathy development is still not well understood. Behavioral research is limited in its ability to address this complex question given the many challenges involved in the study of empathy, or any other psychological construct, with preverbal infants. Notably, it is difficult to trigger and assess infants' empathic responses given the fact that they lack the ability to provide verbal responses and follow verbal instructions. Nonetheless, these inherent limitations can be partially overcome by using neuroimaging and psychophysiological techniques, which have the potential to help us to identify and understand the component processes that trigger empathy without the need to rely on introspective data. Taken together, the current thesis proposes a neuroscientific approach to examine the mechanisms of early empathy development due to its promising potential for the evaluation of developing populations.

The current work will selectively review empirical evidence from social neuroscience research on empathy. In particular, this thesis will use current neuroscientific models of empathy as a framework to describe this phenomenon as well as examine the main neural routes that lead to the experience of empathy. Next, this thesis will describe the two key components of empathy (i.e. affective and cognitive) along with their potential cognitive and neural mechanisms. For the affective component, special attention will be drawn towards current evidence from developmental and social neuroscience research on affect sharing and infant-oriented empathic responses. Additionally, this thesis will review neuroimaging research on infants' ability to process emotional cues from faces and voices, which is considered to be essential for affect sharing. For the cognitive component, theory of mind and emotion regulation processes will be discussed in relation to empathy and its development across time. Finally, some inter- and intra-personal factors that contribute to the modulation of empathy during its development will be reviewed.

Current Neurocognitive Developmental Models on Social Cognition

Before getting into specific details on empathy and its development, I would like to frame the study of empathy behaviours into wider contemporary developmental cognitive neuroscience models of social cognition which have been essential for the development of my doctoral studies. Social cognition is a complex cognitive phenomenon that covers a wide range of social processes such as perception of emotions, join attention, mentalizing, or empathy (Grossman & Johnson, 2007; Nelson, Jarcho, & Guyer, 2016). Thus, it is reasonable to think that the neural mechanisms underlying social behaviours do not rely on a unique brain network, but rather the combination of multiple neural circuits involved in dissociable yet related functional brain processes (Adolphs, 2002; Frith, 2007). Although the human brain is already tuned to social stimuli quite early in life (Grossman & Johnson, 2007), neuroimaging evidence suggests that these different neural networks are not fully functional at birth, and follow different developmental trajectories up to early adulthood (Kilford, Garrett, & Blackmore, 2016; Nelson et al., 2016).

For the last 10 years, multiple adolescent neurocognitive developmental models have started to map changes in social behaviours onto maturational changes across different brain areas. These models have mainly focused on the bi-directional interactions between cognitive-control and affective-motivational systems and their associated brain networks (Casey, Jones, & Hare, 2008; Ernst, 2014; Nelson et al., 2016; Steinberg, 2008). Cognitive control refers to a set of skills that allow the modulation of one's thoughts, feelings, or actions in the pursuit of short- and long- term goals. This set of processes, including inhibitory control, working memory, and selective attention, is mediated by the prefrontal cortex (PFC) and displays a protracted pattern of maturation that extends up to early adulthood (Casey et al., 2008; Giedd et al., 1999; Gotgay et al., 2004; Shaw et al., 2008). The protracted nature of this system is closely tied to increases in myelination and pruning in the PFC during adolescence (Huttenlocher & Dabholkar, 1997; Mills et al., 2016; Yakovlev & Lecours, 1976), processes that are sensitive to be shaped by experience (Leppanen & Nelson, 2009; Werker & Hensch, 2015). On the contrary, the affective system, which relies on subcortical areas such as the amygdala and the ventral striatum, follows an inverted U-shape developmental trajectory, with a peak in subcortical bran activation during adolescence followed by a subsequent decline in early adulthood (Casey, Jones, & Somerville, 2011; Somerville & Casey, 2010; Scherf, Smith, & Delgado, 2013).

For the purposes of this thesis, I would like to highlight three main neurocognitive models: the dual-system models (Casey et al., 2008; Steinberg, 2008; Luna & Wright, 2015), the triadic model (Ernst, Pine, & Hardin, 2006), and the social information processing model (Nelson, Leibenluft, McClure, & Pine, 2005). The main premise of the dual-system model is that brain areas critical to cognitive control develop later and more slowly than brain areas mediating affective and motivational behaviours. Nonetheless, it is possible to find several variations of this model regarding the developmental course of these systems. For example, while some authors propose that the affective system follows an inverted-U shape trajectory, with its maximum peak activity during adolescence (Luna & Wright, 2015; Steinberg, 2008), others defend that the activation of the affective-motivational system increases until mid-adolescence time when it reaches a plateau (Casey et al., 2008). Another point of contention refers to the cognitive system, with some dual-systems models defending a linear development through late adolescence and early adulthood, whereas others suggest that their development reaches a plateau in mid-adolescence. Figure 1 illustrates the resemblances and disparities between the distinct versions of the dual-system model. Expanding on these dual models, Ernst et al.' (2006) proposed a triadic model that adds a third neural system underlying responses to punishment (avoidance system) anchored in the amygdala. According to this model, the reward-related system matures earlier than the harm-avoidant system or the cognitive control system, which follows a more protracted development across adolescence.

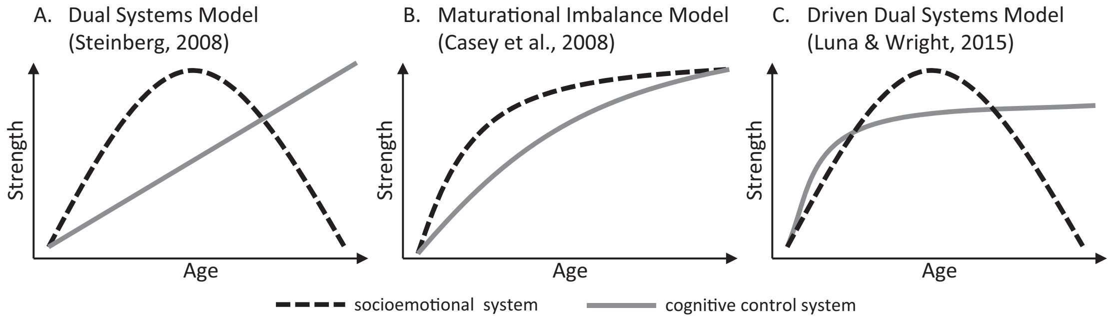


Figure 1. Schematic presentation of the three main dual-system models. Adapted from "The dual systems model: Review, reappraisal, and reaffirmation", by E. P. Shulman, A. R. Smith, K. Silva, G. Icenogle, N. Duell, J. Chein, and L. Steinberg , 2016, *Developmental Cognitive Neuroscience, 17*, p.105

Although the models mentioned above have been essential to increase our understanding of neurocognitive development, they posit some limitations linked to their lack of precision in their predictions, neural labels, inferences and applications (see Pfeifer & Allen, 2012, 2016 for review). As Pfeifer and Allen note, these models fail to provide precise predictions which in turn may explain the high number of studies supporting these models. Moreover, these models are not specific when labelling critical brain regions. They often use regional-based labels (e.g. prefrontal cortex) rather than network-based labels to describe underlying networks, which are imprecise as well as uninformative. This constrain closely links to their lack of precision in the specificity of neural inferences. The inferences of these models are based on one-to-many and many-to-one relationships, which can be misleading. Last, but not least, these models tend to explain a wide range of negative developmental outcomes.

A more refined approach is the social information processing model of adolescent development developed by Nelson and colleagues (2005, 2016). This model expands and updates the existing models by including more precise definitions and predictions of the social brain systems. This model identifies three functional systems:

the perceptual, the affective and the cognitive-regulatory system. According to this model, social stimuli are processed in the three nodes in a sequential manner, going from perceptual to affective to cognitive. Nonetheless, the model also emphasizes that the systems do not work independently but as an interactive network via feedback loops. In general this model posits that the three systems rely on different brain areas that follow differential developmental courses. Perceptual systems are inherently tuned to salient social stimuli early after birth, yet their response becomes increasingly more specialised and refined through at least late adolescence and early adulthood (Leppanen & Nelson, 2009; Nelson et al., 2016). In contrast, developmental changes in the affective system are characterized by phase-specific shifts in social salience and behavioural engagement patterns. Although there is not enough evidence, it is believed that these swings may be mediated by functional changes within subcortical regions (e.g. the amygdala, ventral striatum, septum, nucleus accumbens) related to rapid and drastic hormonal alterations at puberty. Finally, the cognitive system displays a particularly protracted pattern of maturation, experiencing a decrease in functional activity during socials tasks across the transition from adolescence to adulthood.

In summary, current developmental neurocognitive models of social cognition have begun to clarify the developmental course of social cognition and the associated brain areas across the lifespan. More importantly, these models provide a rich source of hypotheses that are testable using neuroimaging tools, while establish the basis for the study of more advanced levels of cognitive development, such as empathy. Yet, further research is needed to elucidate how the different systems interact and how individual and social environmental differences relate to variations in social behaviour.

Towards a Definition of Empathy

Empathy is a complex psychological phenomenon that has been defined in many ways by different academics working in the field, yet only social neuroscientists have provided a relatively specific construct for the purpose of research (McCall & Singer, 2013; Singer & Lamm, 2009). In plain words, when empathising with someone we vicariously experience what another person is feeling without confounding the feeling with one's own direct experience. For example, let us imagine a situation in which we encounter a close friend whose parents have died in a car accident. Clearly, she is very distressed as indexed by her facial and vocal expressions as well as body posture. Empathising with our friend will result in the immediate experience of feelings of distress in ourselves, yet to a lesser extent, which probably will be followed by active attempts to comfort or help her in order to reduce her suffering. During this process, commonly known as empathy, we have been able to vicariously experience our friend's distress, to understand how our friend must be feeling after the loss of her parents, to regulate our own emotions to avoid self-distress reactions, and to have the motivation to provide help. Nonetheless, we do not always empathise with others. For example, often we are confronted with the suffering of strangers when reading the newspaper or watching the TV news, yet those episodes do not always affect us, either because we do not connect with the victims, because we do not fully understand the situation or have certain negative beliefs about it, perhaps even because we do not have the time to pay attention to it or be bothered by it. Similarly, there are occasions where we may be exposed to our friends' happiness and instead of sharing their joy with them we may feel a hint of jealousy or even sadness. Additionally, empathy is not always followed by the motivation to assist, help or comfort the other person. For instance, we may feel sad for someone who has lost the custody of their children because that person has been found guilty of drug consumption, yet we may not have the motivation to help that person because we believe it is the best thing for the children. Together, these examples capture the complexity of empathy and illustrate that this phenomenon is not an all or none experience. On the contrary, its occurrence can be modulated by multiple factors such as characteristics of the empathic emotion, features of the empathizer, the relation between the empathizer and target, and the appraisal of the situation (e.g., de Vignemont & Singer, 2006; Hein & Singer, 2008).

Although the concept of empathy has a complex nature, this should not be an excuse to work towards a more operational definition of empathy able to break this psychological construct into its different constitutive components. Though the perfect definition of empathy is still not available, current neuroscientific models have adopted a more successful approach aimed at mapping cognitive processes onto brain structures, illustrating precisely how these processes and underlying brain areas change over time, and how environmental factors modulate them. These models directly inform and motivate infant brain research and provide a rich source of hypothesis that can be assessed using neuroimaging tools (Crone & Ridderinkhof, 2011; Decety & Jackson, 2004; Engen & Singer, 2013; Kilford, Garrett, & Blakemore, 2016). Regardless of differences in terminology, they agree on three principal components (See Figure 2): (1) an affective response triggered by the observation or imagination of another person's emotion, which is isomorphic and modulated by the awareness that the other person is the source of one's own affective state; (2) a cognitive ability to understand other person's internal states; and (3) some regulatory mechanisms (Decety, 2007; Decety & Jackson, 2004; Decety & Meyer, 2008; de Vignemont & Singer, 2006; Engen & Singer, 2013). This definition has proven to be quite useful since it suggests that there are several groups of neurocognitive processes underlying the generation of an empathic response. Furthermore, this description enables us to distinguish empathy from other related phenomena such as mimicry, emotional contagion, compassion, sympathy, empathic concern or mentalizing (de Vignemont & Singer, 2006; Singer & Lamm, 2009; McCall & Singer, 2013).

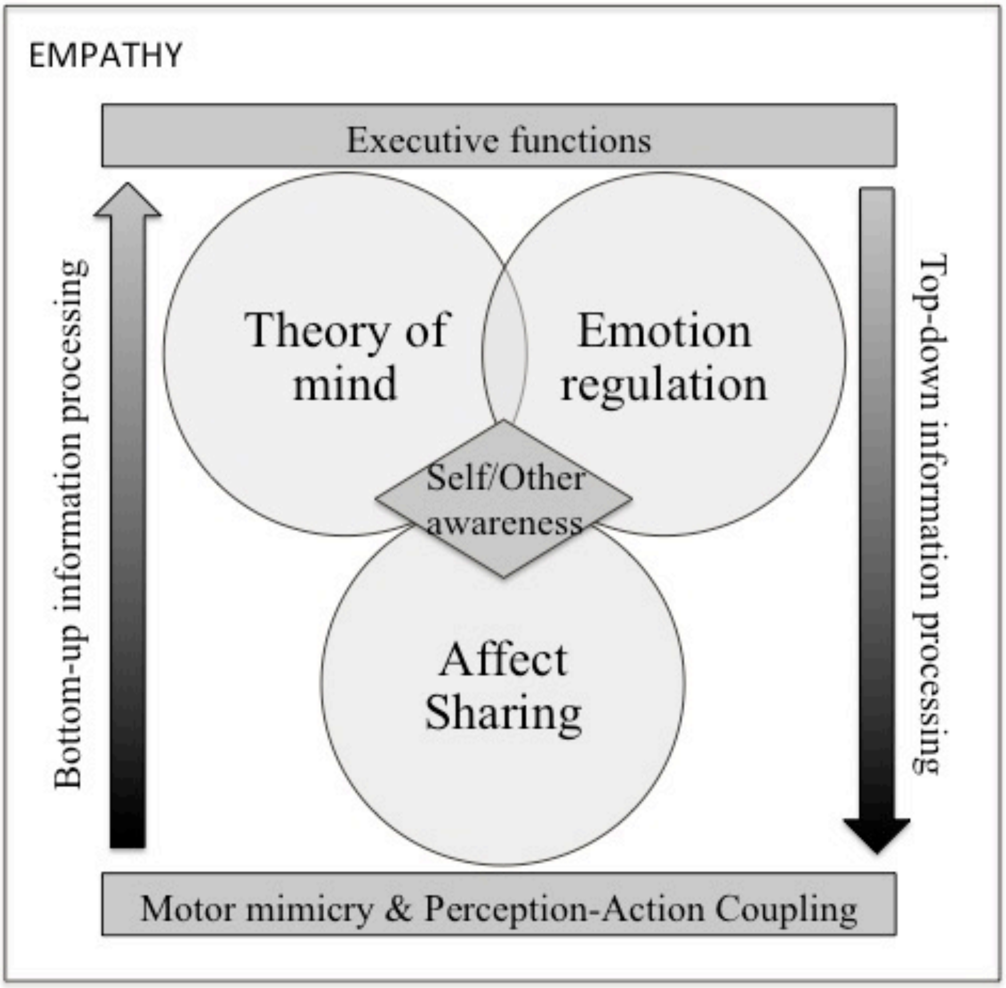


Figure 2. Schematic representation of current neuroscientific models of empathy depicting potential components involved in empathy, their interactions and their potential neural substrates.

The Generation of Empathy: A Two Components Tale

Current neuroscientific models of empathy have put forward the view that there are at least two different paths to generate empathic responses, which has lead to two main components of empathy being distinguished (Decety & Meyer, 2008; de Vignemont & Singer, 2006; Hein & Singer, 2008; Singer, 2006; Singer & Lamm, 2009; Zaki & Ochsner, 2013). Firstly, there is the perceptual-based route (affective component) based on bottom-up processes that account for the experience of affect sharing. At this low level the empathic response is triggered directly and automatically by perceptual information without the need of conscious or effortful processing of the other person's emotional state (Decety & Lamm, 2006; Decety & Meyer, 2008; Singer, 2006; Singer & Lamm, 2009). Secondly, there is the cognitive-based route (cognitive component) based on top-down processes responsible for generating second-order representation of others' feelings while regulating one's own emotional arousal to avoid personal distress. In this case, the empathic response is the result of high-order processes such as selective attention, perspective taking or self-regulation skills rather than mere perceptual input, which makes the person less dependent on external cues (Decety & Lamm, 2006; Decety & Meyer, 2008; Singer, 2006; Singer & Lamm, 2009). According to the model proposed by Decety and colleagues (Decety, 2005; Decety & Lamm, 2006; Decety & Meyer, 2008; Decety & Michalska, 2010), these two routes are intertwined and work together to generate and modulate empathy in humans. Both routes regulate each other through a feedback loop supplemented by top-down (mostly regulation and control) and bottom-up (sensory information and body response) information processes, adding cognitive flexibility and shaping the initial affective sharing response into a more other-oriented response, which may finally motivate the production of prosocial acts.

The theoretical distinction between a perception-based route and a more cognitive-based route in the generation of empathic reactions is consistent with several fMRI studies on empathy for pain with adult participants (see for reviews: Fan, Duncan, de Greck, & Northoff, 2010; Lamm, Decety, & Singer, 2010). In brief, these studies have shown that the generation of empathy via direct perceptual input (picture-based paradigms) is associated with the activation of brain areas previously involved in *action-perception decoupling* such as the somatosensory cortex, the premotor cortex, the inferior frontal cortex (IFC) and the inferior parietal cortex (IPC) (Engen & Singer, 2012; Zaki & Ochsner, 2013) as well as areas involved in automatic generation of emotions, including the anterior insula (AI), the anterior cingulate cortex (ACC) for pain and disgust, and the amygdala for fear (Engen & Singer, 2012; Singer, 2006; Singer & Lamm, 2009). On the other hand, the induction of empathy via the employment of perspective taking skills (cue-based paradigms) has been associated with the activation of regions underlying Theory of Mind representations, such as the ventro-medial prefrontal cortex (mPFC), temporo-parietal junction (TPJ), posterior cingulate cortex (PCC), temporal poles (TP) and superior temporal sulcus (STS) (Brunet, Sarfati, Hardy-Bayle, & Decety, 2000; Castelli, Happe, Frith, & Frith, 2000; Engen & Singer, 2012; Singer, 2006; Vogeley et al., 2001; Zaki & Ochsner, 2013).

Additionally, this division between routes has been supported by empirical evidence from clinical studies with patients suffering from different types of empathy deficits such as autistic spectrum disorder (ASD) and psychopathy (Blair, 2008; Dziobeck et al., 2008; Rogers, Viding, Blair, Frith, & Happe, 2006). Findings from these studies suggest that while children with ASD have deficits in cognitive empathy (cognitive-based route), children with psychopathic tendencies show deficits in emotional empathy (perceptual-based route) (see Blair, 2005 for a review). For instance, although individuals with psychopathic tendencies do not show theory of mind impairments (Blair et al., 1996; Dolan & Fullam, 2004; Richell et al., 2003), they show deficits in their ability to recognize emotions from facial expressions (Blair, Colledge, Murray, & Mitchell, 2001; Blair et al., 2004; Hastings, Tangney, & Stuewig, 2007). In contrast, while individuals with ASD have deficits in cognitive perspective taking (e.g., Baron-Cohen, Leslie, & Frith, 1985; Castelli, Frith, Happe, & Frith, 2002; Happe et al., 1996; Hill & Frith, 2003), they do not show impairments on emotional facial recognition tasks (Adolphs, Sears, & Piven, 2001; Ozonoff, Pennington, & Rogers, 1990; Prior, Dahlstrom, & Squires, 1990). Therefore, there is evidence for a double dissociation, with the disruption of the affective component not necessarily affecting the functioning of cognitive component, and vice versa.

There is also extensive behavioral evidence suggesting that these two routes follow different developmental pathways, with the affective component developing earlier than the cognitive one (e.g., Decety & Michalska, 2010; Decety & Svetlova, 2012). Thus, while infants are able to respond emotionally to others' emotions as early as few hours after birth (e.g., Sagi & Hoffman, 1976; Simner, 1971), it is not until the age of 15-18 months when they show some rudimentary abilities for ToM computations (e.g., Onishi & Baillargeon, 2005; Scott & Baillargeon, 2009; Song, Onishi, Baillargeon & Fisher, 2008; Träuble, Marinović, & Pauen, 2010). This early form of ToM continues to develop throughout adolescence into more complex forms (e.g., Apperly & Butterfill, 2009; Blackmore, 2008, 2012). Congruently, the timeline in which affect sharing and perspective taking emerge parallels the maturation of the cortical structures underlying them, with the limbic, para-limbic and somatosensory regions developing earlier than the prefrontal cortex, which mature later (Giedd et al., 1999; Gogtay, et al., 2004; Raz et al., 2005; Singer, 2006; Sowell et al., 2003).

In summary, there is substantial empirical evidence from developmental, clinical, and neuroscientific research that support the theoretical distinction between components in the generation and modulation of empathy. This model has important consequences for the study of the mechanisms underlying empathy, suggesting the presence of dissociable systems with distinct neural bases, having different developmental trajectories and serving different functions. Next, this thesis will provide a deeper description of the affective and cognitive components of empathy and their nominated mechanisms.

Emotional Component: Affect Sharing

Precursor of Empathy

Affect sharing refers to the tendency to resonate with the affective response produced by another person without the need to acknowledge that the other is the source of one's own emotion (Batson, 2011; de Vignemont & Singer, 2006; McCall & Singer, 2013; Singer & Lamm, 2009). This emotional resonance response tends to translate into the synchronization of another's person affective facial expressions, vocalizations or body postures (Hatfield, Cacioppo, & Rapson, 1994). Although there is a strong conceptual overlapping between mimicry and emotional resonance, it is worth mentioning that they are not the same process. Motor mimicry does not always involve an affective dimension, while affect sharing does not always involve motor mimicry for its occurrence since one can simply "catch" other people's emotions without the need to mimic an affective expression (Singer & Lamm, 2009).

Nowadays it is widely assumed that affect sharing is a likely precursor of empathy, even though this assumption has not yet been directly tested (Decety & Lamm, 2006; Decety & Mischalska, 2010; Hatfield, Rapson & Le, 2009; Knafo & Israel, 2012; Knafo & Uzefovsky, 2013; Simner, 1971; Singer, 2006; Singer & Lamm, 2009; McCall & Singer, 2013). This notion was first supported by empirical evidence from behavioral studies on contagious crying with neonates, which illustrates that as early as few hours after birth newborns are more inclined to cry when exposed to the crying of another newborn (Dondi, Simion & Caltran, 1999; Field, Diego, Hernandez-Reif & Fernandez, 2007; Geangu et al., 2010; Martin & Clark, 1982; Sagi & Hoffman, 1976; Simner, 1971). Throughout the first year of life, infants continue to respond with facial and vocal distress to the crying sounds of their peers (Geangu et al., 2010), and this increase in arousal persists throughout toddlerhood, although with lesser intensity (Nichols, Svetlova, & Brownell, 2009, 2015). When jointly presented with the corresponding facial expressions, these overt responses elicited by peer emotional vocalizations are accompanied by autonomic arousal changes as indexed by modifications in pupil dilation (Geangu, Hauf, Bharwaj, & Bentz, 2011; Upshaw, Kaiser, & Sommerville, 2015).

Interestingly, these overt emotional responses seem to be modulated by the acoustical properties of the cry-like sounds, such that infants cry significantly more often when exposed to the sound of another infant crying as opposed to a synthetic cry (Sagi & Hoffman, 1976; Simner, 1971), to an infant chimpanzee cry (Martin & Clark, 1982), or to the sound of their own cry (Dondi et al., 1999; Martin & Clark, 1982). Likewise, the intensity of the distress stimulus has also proven to be a crucial feature, together with infants' ability to regulate their emotions, in the generation of affect sharing. For instance, those studies in which infants were observed to exhibit strong self-distress responses used long and intense stimuli of cry, increasing the likelihood of over-arousal and emotional dysregulation (e.g., Geangu et al., 2010; Simner, 1971). In contrast, infants rarely became distress themselves (as indexed by the occurrence of distress vocalizations) in those studies where shorter and milder distress stimuli were used (Hay et al., 1981; Roth-Hanania et al., 2011). Taken together, this pattern of results suggests that milder negative stimuli may have enabled infants to regulate their arousal in a more effective way and remain other-focused, yet this hypothesis remains untested. It is thus important to control the affective intensity of the cry stimuli in order to account for variability in distress reactions and physiological measures (Stevenson & James, 2008).

Child-caretaker interactions also offer a unique framework for infants to experience affect sharing. Behavioral studies examining affective responsiveness suggest that by 10 - 12 weeks of age infants already show emotional resonance to their own mothers' facial and vocal displays of happiness, sadness, and anger in similar degree (Fernald et al., 1989; Field, Pickens, Fox, Gonzalez & Nawrocki, 1998; Haviland & Lelwica, 1987; Kahana- Kalman & Walker-Andrews, 2001; Vaish, Grossmann & Woodward, 2008). This resonance response seems to be true in those cases where infant-mother dyads are characterized by positive affective synchrony, where mothers are likely to imitate infants' emotional expressions –mostly joy and interest –while avoiding to display of negative emotions toward their baby (Malatesta & Haviland, 1982; Stern, 1985; Trevarthen, 1979).

Critically, in reviewing the evidence gathered so far on emotional resonance, attention is drawn to the lack of studies on affect sharing for positive emotions. Our little knowledge is limited to a small number of studies accentuating the presence of an asymmetry in the way infants process positive versus negative affective cues, displaying stronger physiological responses towards negative rather than positive stimuli (Geangu et al., 2011; Upshaw et al., 2015). This trend is partially supported by social referencing studies showing that negative cues from a caregiver or experimenter are quite effective in inhibiting infants' interactions with a novel toy while positive cues do not increase the interaction with that novel target (e.g., Hornik, Risenhoover & Gunnar, 1987; Mumme & Fernald, 2003; Mumme, Fernald & Herrera, 1996). Infant ERP studies on emotion processing also provide indirect evidence for this asymmetry by showing that at the age of 7 months infants exhibit greater attentional preference towards fearful faces, as shown by the generation of a larger fronto-central Nc component for fearful faces, in comparison to happy and neutral facial expressions (de Haan, Belsky, Reid, Volein & Johnson, 2004; Leppänen, Moulson, Vogel-Farley, & Nelson 2007; Nelson & de Haan, 1996; Peltola, Leppänen, Mäki, & Hietanen,, 2009). Likewise, at the age of 7 months infants' brain shows greater attentional preference (i.e. enhanced early negativity) for angry voices in comparison to happy or neutral prosody (Grossmann, Striano, & Friederici, 2005). Together, these findings support the notion that affect sharing may undergo a negative bias by the end of the first year of life (Vaish et al., 2008).

In summary, the developmental data suggest that infants are sensitive to others' emotions soon after birth, which is seen by some authors as a direct evidence for an inborn empathetic distress reaction. The reviewed evidence also suggests that there is some degree of self-other distinction already functioning after birth. Nonetheless, multiple relevant questions remain unanswered in this field of research. Undoubtedly, more infant studies are needed to examine whether infants resonate to positive emotions, whether negative emotions are more contagious than positive ones, and ultimately which ontogenetic mechanisms account for infants' emotional resonance emergence. Regarding the mechanisms, there is still debate about the automaticity of the affect sharing response, with some theorists claiming that this early contagious response is primarily rooted in automatic mimicry processes while others argue that affect sharing requires certain emotional information appraisal. This debate will be further described in the next section.

Motor Mimicry and the Perception-Action Model: Evidence for and against

Previously considered as a “primitive form of sympathy” (Hatfield et al., 2009; Smith, 1976; Spencer, 1870), emotional resonance is thought to rely on two entwined mechanisms hypothetically implemented by motor neurons: motor mimicry and perception-action coupling (Decety, 2010a, 2010b; Decety & Lamm, 2006; Decety & Michalska, 2010; Decety & Meyer, 2008; Preston & de Waal, 2002). This idea is in line with the theoretical account of the automatic transmission of emotions, which argues that humans tend to automatically mimic others’ facial, vocal or postural expressions of emotions and that such motor mimicry evokes the same emotions in the observer through perception-action matching (e.g. de Waal, 2009; Hatfield et al., 1994; Lipps, 1907).

Neurophysiological evidence for this perception – action mechanism comes from empirical research on mirror neurons in monkeys using single cell electrophysiological recordings, which report a cluster of neurons that are selectively active during the execution of a specific motor action and during the observation of another person performing the same action (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fogassi, & Gallese, 2001). Evidence for the existence of these neurons in humans is more indirect, and primarily has derived from functional magnetic resonance imaging (fMRI) studies showing an overlap in the activation of the neural networks involved in action execution and action observation (e.g., Blackmore & Decety, 2001; Decety & Grezes, 2006). Remarkably, these overlapping regions are homologous to the brain areas activated in the monkey brain, including the inferior frontal gyrus, the ventral premotor cortex or the inferior parietal lobe. Further evidence comes from transcranial magnetic stimulation (TMS) which show that transient disruptions to the motor cortex result in impairments in the ability to recognize and anticipate others' actions (Michael et al., 2014; Stadler et al., 2012). Similarly, electroencephalographic (EEG) studies have also reported desynchronization of the mu rhythm over central sites corresponding to the location of the sensoriomotor cortex during action observation (Leocani, Toro, Manganotti, Zhuang, & Hallett, 1997; Toro et al., 1994). Traditionally the mu rhythm (8-13 Hz) has been linked to activity in the sensoriomotor cortex and its desynchronization (i.e., reduction of amplitude) during overt movements and action observation is believed to index the activation of shared action-perception representations (see Marshall & Meltzoff, 2011 for a review).

The idea that perception-action matching mechanism is causally related in the generation of emotional contagion responses mostly comes from a series of studies exploring spontaneous facial responses (SFRs) by using facial electromyography (EMG). These SFRs, which are sometimes covert and not visible through direct observation (Cacioppo, Petty, Losch, & Kim, 1986; Tassinary & Cacioppo, 1992), are thought to play crucial roles in how we communicate and empathise with each other, as well as in establishing cohesive social groups (Hatfield et al., 1993; Hess & Fischer, 2013). Overall, this line of research suggests that adults and older children precisely and rapidly mimic the facial expressions displayed by the people with whom they interact (e.g., Dimberg, 1982; Dimberg, Thunberg, & Elmehed, 2000; Moody, McIntosh, Mann, & Weisser, 2007). At the neural levels, these findings converge with those reported by fMRI studies with adults showing that similar brain areas are activated during the observation and imitation of various emotional facial expressions (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Dapretto et al., 2006; Pfeifer, Iacoboni, Mazziotta, & Dapretto, 2008). There is also some direct evidence that participants' tendency to mimic facial expressions is linked to individual differences in dispositional empathy, with participants classified as high-empathizers producing greater facial mimicry (facial EMG) when exposed to static facial expression of anger and happiness than the low- empathizer participants (Sonnby-Borgstrom, Jonsson, & Svensson, 2003). Together, these studies have been interpreted as evidence supporting the hypothesis that perception-action coupling networks might be the mechanism underlying affect sharing

However, several findings are difficult to integrate with this perception-action matching proposal. On one hand, not all EMG studies find evidence that mimicry facilitates emotion recognition. In this respect, there are two well-known studies that failed to report evidence that emotion recognition accuracy or shared affect are mediated by mimicry (Blairy, Herrera, & Hess, 1999; Hess & Blairy, 2001). In these studies, mimicry and emotional resonance were not found to be related to each other. Nor was mimicry related to decoding accuracy. On the other hand, facial mimicry does not always occur. For example, Moody et al. (2007) and Beall et al. (2008) found that observing others' angry faces did not elicit matching EMG responses specific for anger but for fear. Only when angry individuals are perceived as physically weaker and threatening one's social status, their facial displays of anger elicit similar EMG responses in the observer (Hess, Adams, & Kleck, 2005; Soussignan et al., 2013). Finally, there are other studies that report counter-mimicry effects in competitive environments, responding with negative displays to their competitors' pleasure (Lanzetta & Englis, 1989; Likowski, Mühlberger, Seibt, Pauli, & Weyers, 2011). Overall, these findings are consistent with the idea that facial movements alone carry simple affective information and that the context needs to be jointly encoded to make more specific inference about individual's emotion (Barrett & Kensinger, 2010; Barrett, Mesquita, & Gendron, 2011). In all these examples, the facial responses converge with the meaning and the informative value for the observer of the emotional signals received from others, rather than its motor characteristics. Thus, mimicry may be somewhat less automatic and not always responsible of affect sharing.

To account for these additional findings, some researchers suggest that affect sharing is the result of early and quick evaluations of the emotional signal (Dezecache, Eskenazi, & Grèzes, 2016; Grèzes & Dezecache, 2014; Soussignan et al., 2013). Interestingly, the appraisal of emotional cues relies on neural mechanisms extending beyond shared action and emotion representations (Dezecache et al., 2016; Greèzes & Dezecache, 2014). Notably, processing emotional information relies on complex neural networks involving those that are part of the emotion-related brain circuits (e.g., the amygdala and the orbito-frontal cortex - Adolphs, 2002; Pessoa, 2017; Vuilleumier, Armony, Driver, & Dolan 2003; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004) and those functionally linked with motor preparation for action and estimating others' immediate intent for action (Balconi & Bartolotti, 2013; Baumgartner, Willi, & Jäncke, 2007; Coelho, Lipp, Marinovic, Wallis, & Riek, 2010; Coombes et al., 2009; Grèzes & Dezecache, 2014; Hamilton, 2015; Oliveri et al., 2003; Schutter, Hofman, & Van Honk, 2008). Of special interest, a growing body of fMRI studies have started to document functional links between systems that sustain emotional appraisal and those that underlie action preparation (e.g., Baconi & Bartolotti, 2013; Baumgartner et al., 2007; Conty, Dezecache, Hugueville, & Grèzes, 2012; Oliveri et al., 2003; Schutter et al., 2008), suggesting that the early evaluation of emotional cues is followed by the selection and execution of an optimal action for the immediate situation, which can be either congruent or incongruent with the observed emotional display. Functional links between systems that sustain emotional appraisal and shared motor representations have also been suggested (Dezecache et al., 2016; Hamilton, 2015; Kilner et al., 2007).

However, in this case the attributed role of the shared neural networks has more to do with the anticipation of others' behavior and intentions (Dezecache et al., 2016; Hamilton, 2015; Kilner, Friston, & Frith, 2007). Thus, this proposal emphasizes that our reactions to other's emotional displays are ultimately a result of an early emotional evaluation and estimation of other's intentions.

In summary, although there is some empirical evidence supporting the important role of motor mimicry and action-perception coupling mechanism in the generation of affect sharing, current findings suggest that this explanation is not sufficient to account for the whole phenomenon. On the other hand, although this mechanism has been well documented in adults and to a lesser degree in children, debates regarding its early ontogeny and the underlying neurocognitive mechanisms remain unexplored (Dezecache et al., 2016; Isomura & Nakano, 2016; Magnée, Stekelenburg, Kemner, & de Gelder, 2007; Oostenbroek et al., 2016). Thus, studies exploring facial mimicry in infancy are needed to shed light on the mechanisms underlying affect sharing.

Emotion Perception during Infancy

Closely link with the ability for two people to resonate with each other affectively, it is the ability to detect, discriminate and recognize others' emotional expressions through vocalizations, faces or body postures. This ability acquires special importance during the first year of life, prior to any cognitive understanding of emotions, when infants seem to depend on the perception of overt emotional cues to resonate with others (e.g., Geangu et al., 2011; Sagi & Hoffman, 1976; Simner, 1971). Developmental research suggests that as children develop, they are gradually less dependent on perceptual cues as they are able to use more complex and different types of information to infer emotions from others such as contextual cues or target's internal states (see Harris, 1994 for a review). In the domain of empathy, this ability is thought to be crucial for the development of empathy and children's interpersonal and social skills (e.g., Decety, 2015; Decety & Howard, 2013; Geangu, 2015; Hoffmann, 2001). Although infants' sensitivity to other's emotions may rely on their ability to extract emotional cues, this is not enough to explain the full experience of empathy. Other cognitive processes are needed into the "empathy" equation such as the ability to understand other's perspective or the ability to regulate own emotional arousal to avoid personal distress. In this line, current developmental models of social cognition agree to concieve the ability to detect and process information form social stimuli as the first stage of a chain of complex afective and cognitive processes (Grossmann & Johnson, 2007; Leppanen & Nelson, 2009; Nelson et al., 2005, 2016).

An extensive amount of behavioral studies suggest that infants are able to discriminate between emotions that differ in valence at 4 months if these are expressed multimodally (i.e. using the face and voice) (Flom & Bahrick, 2007; Montague & Walker-Andrews, 2001), at 5 months if they are expressed vocally (Fernald, 1993; Flom & Bahrick, 2007; Walker-Andrews & Grolnick, 1983; Walker- Andrews & Lennon, 1991), and at 7 months if they are communicated facially (Flom & Bahrick, 2007; Kestenbaum & Nelson, 1990; Nelson, Morse & Leavitt, 1979; Ludemann & Nelson, 1988). The field of social neuroscience has also shed some light on the infants' neural mechanisms underpinning the processing of emotional information conveyed in the form of faces or vocalizations (e.g., Grossmann et al., 2005; Grossman, Oberecker, Koch & Friederici, 2010; Leppänen et al., 2007; Peltola et al., 2009).

In particular, EEG-ERP work on face processing reveals that early during the first year of life infants process differently faces as compared to non-face objects as indexed by differences in the neural activity recorded over occipito-temporal regions (de Haan & Nelson, 1999; de Haan, Pascalis, & Johnson, 2002; Halit, Csibra, Volein, & Johnson, 2004; Halit, de Haan, & Johnson, 2003). These findings converge with additional neuroimaging evidence suggesting that the fusyform area and the superior temporal sulcus (regions linked to face processing in adults) are already tuned to faces in 2- to 8-month-old infants (Otsuka et al., 2007; Tzourio-Mazoyer et al., 2002). Conversely, ERP research on infants' processing of affective facial expressions suggests that certain components are modulated by the type of emotional expression. In brief, findings from these studies have shown that infants at the age of 7-months show a greater attentional preference toward fearful faces, as shown by the generation of a larger fronto-central Nc component for fearful faces as compared to happy and neutral facial expressions (de Haan et al., 2004; Leppänen et al., 2007; Nelson & de Haan, 1996; Peltola et al., 2009). The Nc component is known to reflect allocation of attentional resources (Courchesne, Ganz, & Norcia, 1981; Nelson, 1994; Richards, 2003). Besides cortical attention networks, fearful facial expressions also enhance activity in cortical face-sensitive networks. Specifically, 7-month-old infants seem to allocate more resources for the visual processing of fearful faces as indexed by a larger occipito-temporal P400 in response to fearful faces compared to both happy and neutral expressions (Leppänen et al., 2007), and greater for fearful compared to angry faces (Kobiella, Grossmann, Reid, & Striano, 2008). The P400 has been previously linked to perceptual processing of structural information from faces (de Haan, Johnson, & Halit, 2003; de Haan & Nelson, 1999; de Haan et al., 2002),

Fewer functional near-infrared spectroscopy (fNIRS) studies have also investigated the neural correlates underlying emotional face processing in infants (Fox, Wagner, Shrock, Tager-Flusberg, & Nelson, 2013; Minagawa-Kawai et al., 2009; Nakato, Otsuka, Kanazawa, Yamaguchi, & Kakigi, 2011). Taken together, these studies provide evidence for the presence of different hemodynamic patterns/responses to distinct types of facial expressions (happy and angry) over temporal and frontal regions. Specifically, Minagawa-Kawai et al. (2009) found an increase brain activity in the orbitofrontal cortex (OFC) in response to smiling as compared to neutral faces. Similarly, Fox et al. (2013) found greater activation of the right frontal cortex in response to smiling faces as opposed to neutral faces in 6- to 7-month-old infants. Further evidence is provided by Nakato et al. (2011) who observed an asymmetric pattern of activation within temporal areas, with the left hemisphere being more responsive to happy facial expressions and the right hemisphere being more responsive to angry facial expressions. Furthermore, this study revealed differences in the temporal course of the hemodynamic responses. The observation of happy faces elicited a gradual and sustained increase of the hemodynamic response even after the disappearance of the face whereas the neural response to angry faces peaked and decreased much more rapidly.

Although auditory information seems to be dominant over visual input early in development (Bugental, Kaswan, Love & Fox, 1970; Caron, Caron & MacLean, 1988; Flom & Bahrick, 2007; Gottlieb, 1971; Fernald, 1993; Lewkowicz, 1988a, 1988b), less attention has been paid to the neural correlates underlying infants' perception of emotional vocal expressions (see Grossmann, 2010; Walker-Andrews, 1997 for reviews). The few existing studies have provided converging evidence toward an early emergence of cerebral specialization for affective prosody during the first year of life (Cheng, Lee, Chen, Wang & Decety, 2012; Grossmann et al., 2005; Zhang et al., 2014), suggesting that at this age the discrimination is automatic, and possibly related to the activity of primary and non-primary auditory areas in the temporal cortex (Näätänen, Paavilainen, Rinne, & Alho, 2007). The available ERP evidence reveals that as early as few days after birth the infants' brain shows larger ERP responses (e.g., mismatch response – MMR –) for angry voices in comparison to happy, neutral (Cheng et al., 2012; Grossmann et al., 2005), and fearful voices (Zhang et al., 2014). Consistent with ERP studies on emotional face processing, these findings support the idea of enhanced sensitivity and greater allocation of attentional resources to negative emotional (angry) vocalizations. This pattern of results has been partially replicated by a recent fNIRS study with 7-month-old infants, in which negative emotional voices evoked greater activation in the superior temporal cortex as compared to positive and neutral voices, again stressing an enhanced sensitivity to negative emotional prosody in the infants' brain (Grossmann et al., 2010). Following the lack of infant studies, there is a huge gap in the literature on the neural correlates of vocal emotional processing during childhood. In typically developmental children, so far a single study developed by Chronaki et al. (2012) has found an effect of vocal emotion on the amplitudes of the N100 (90 – 180 ms) and N400 (380-500 ms) at posterior locations (Chronaki et al., 2012). An emerging body of research on atypical development have also reported effects of emotional vocalizations on N100 and P300 amplitudes in ADHD children (Chronaki, Benikos, Fairchild, & Sonuga-Barke, 2015) as well as on N100 latencies in children with autism during the performance of emotion recognition tasks using prosody (Lerner, McPartland, & Morris, 2013).

It is worth mentioning that all of the studies reviewed before used speech human vocalizations to examine the neural correlates underlying emotional processing from the voice. Little is known about the processing of emotional non-speech human vocalizations (e.g., laughter, crying), which is at most quite surprising taking into account that these type of signals are produced by pre-verbal infants from an early age and are thought to communicate pure, "raw" emotional states (Barr, Hopkins & Green, 2000; Sauter, Eisner, Ekman, & Scott, 2010; Scherer, 1995).

The importance of emotional non-verbal vocalizations. Non-verbal vocalizations of emotions such as laughter and crying are genuine signals produced already by pre-verbal infants that convey pure, and unambiguous information about own emotions (Barr, Hopkins & Green, 2000; Dunbar et al., 2012; Paulmann & Kotz, 2008a; Provine, 2016; Provine, 2004; Sauter, Eisner, Ekman, & Scott, 2010a; Scherer, 1986, 1995). Crying is already present at birth, while laughter emerges about four months later (Soltis, 2004; Sroufe & Wunsch, 1972; Washburn, 1929). Both vocalizations are quite automatic and stimulus-driven during the first months of life and become more intentional, context-specific during the second half of the first year (Barr, 2006; Barr et al., 2000; Sroufe & Wunsch, 1972; Wolff, 1963). Unlike crying, laughter often appears in the presence of others (Mireault & Reddy, 2016; Provine, 2004, Provine & Fischer, 1989), its occurrence is strengthen by multimodal stimuli (i.e. face and voice) (Vlahovic, Roberts, & Dunbar, 2012), and its causal source varies as the infant gets older, with social stimuli (e.g., playing tug, chasing the baby) being the main elicitor of laughter by the second half of the first year (Sroufe & Wunsch, 1972; Wolff, 1963).

Importantly, the typical production and perception of non-verbal vocalizations is thought to be essential for the emergence of later positive social outcomes such as social bonding, empathy and prosocial behaviors (Decety, 2015; Decety & Howard, 2013; Geangu, 2015; Hoffmann, 2001). Indeed, the presence of an atypical sensitivity to others' emotional non-verbal vocalizations or an atypical production of these signals has been associated with high-risk developmental populations characterized by impaired social functioning, such as autism (Esposito, Nakazawa, Venuti, & Bornstein, 2013; Esposito, Venuti, & Bornstein, 2011; Reddy, Williams, & Vaughan, 2002; Blasi et al., 2015). Furthermore, behavioral evidence suggests that these signals, and in particular laughter, are essential during adult-infant interactions to promote social closeness and interaction, as well as the development of mentalizing skills (Ishijima & Negayama, 2017; Mireault, Sparrow, Poutre, Perdue, & Macke, 2012; Mireault, Poutre, Sargent-Hier, Dias, Perdue & Myrick, 2012). Despite their significance in our early social lives, the processing and use of non-verbal vocalizations of emotions, particularly during early development, remains understudied (Geangu, 2015; Pell et al., 2015; Dunbar et al., 2012; Provine, 1996).

Further neuroimaging studies with infants are needed to clarify the developmental course of both expressions. From this perspective, the investigation of the neurocognitive mechanisms underlying emotional information processing and potential individual variations during infancy is essential for understanding typical and atypical social development, as well as for identifying methods for early detection and intervention (e.g., Bunford, Kujawa, Swain, Fitzgerald, Monk, & Phan, 2017b; Johnson, Gliga, Jones, & Charman, 2015; Morales, Fu, & Pérez-Edgar, 2016). At this respect, infancy offers a unique time window to explore the development of social cognition and their underlying brain networks given that the brain begins to become tunned with social stimuli. Up to date, only two studies have explored the neural correlates underlying the processing of emotional non-verbal vocalizations in infants and both agree to report the recruitment of more neural sources for the processing of crying sounds as compared to laughter sounds at early stages, suggesting the emergence of negativity bias (Blasi et al., 2011; Missana, Altvater-Mackensen, & Grossmann, 2017).

From Affect Sharing to Empathy: In the Search of Prosocial Motivations

Traditionally, it has been hypothesised that the ability to share others' emotions may motivate other-oriented responses, which in turn may support prosocial behaviors (e.g., Decety & Lamm, 2006; Hoffman, 1982; Knafo & Israel, 2012; Singer, 2006). Although affect sharing and empathy have been linked at the conceptual level, there is no empirical evidence supporting this link. Sparse evidence reports that between 6 and 8 months of age infants begin to show other-oriented responses towards others in distress, as indexed by moderate levels of concerned affect (e.g., eyebrows down, brow furrowed, cooing, corners of mouth down) and hypothesis testing behaviors (Hay et al. 1981; Liddle, Bradley & MacGrath, 2015; Roth-Hanania et al., 2011). It is not until the age of 12-14 months when infants exhibit modest attempts to help or comfort others in distress (Howes & Farver, 1987; Liszkowski, Carpenter, Striano, & Tomasello, 2006; Roth-Hanania et al., 2011; Warneken & Tomasello, 2006, 2007; Young, Fox, & Zahn-Waxler, 1999; Zahn-Waxler et al., 1992). These apparently prosocial acts, are believed to arise from early understanding of goal-directed behaviors (Svetlova et al., 2010; Woodward, 1998), and continue to develop gradually into more complex forms during the second year of life (Demetriou & Hay, 2004; Liew et al., 2011; Nichols et al., 2010, 2015; Roth-Hanania et al., 2011; Svetlova et al., 2010; Zahn-Waxler et al., 1992). This development is partially associated with the development of motor and social-cognitive skills necessary to identify the particular needs and adequate interventions as well as perform such complex coordinated behaviors (Paulus, 2014; Roth-Hanania et al., 2011; Svetlova et al., 2010; Walle & Campos, 2012).

Although complex forms of helping, comforting and sharing behaviors may be rare prior to the first year of life, some developmental studies suggest that infants are able to display very simple forms of approach towards others in distress. For example, infants occasionally responded to their distressed peers with approach-oriented behaviors, as exemplified by modest attempts to point, lean, touch or reach towards the victim (Hay et al., 1981; Liddle et al., 2015; Roth-Hanania et al., 2011). Studies using looking time paradigms also show that as early as 6 months of age infants prefer agents who help others to agents who hinder others (Hamlin, Wynn, & Bloom, 2007; Hamlin & Wynn, 2011; Hamlin, 2013, 2015) and agents who comfort rather than harm (Buon et al., 2014; Holvoet, Scola, Arciszewski, & Picard, 2016). As much as these findings have received attention, the motivational mechanisms involved in infants' emerging other-oriented responses are not well understood (Svetlova et al., 2010).

Interestingly, over the last three decades an increasing number of infant EEG research has explored the relation of frontal hemispheric asymmetries in EEG activity and developing motivational tendencies within an approach-withdraw continuum (e.g., Davidson & Fox, 1982, 1989; Dawson, 1994; Diaz & Bell, 2011; Fox & Davidson, 1986, 1987, 1988). In particular, frontal EEG asymmetry measures recorded during emotionally salient situations are considered to be a reliable index of prefrontal associations with individual motivational tendencies to either approach or avoid stimuli perceived as appetitive or aversive (e.g., Coan & Allen, 2004; Davidson & Fox, 1982, 1989; Fox & Davidson, 1986, 1987, 1988). Within this framework, greater relative left frontal activation reflects approach-related tendencies while greater relative right frontal activation reflects withdrawal-related predispositions (Fox, 1991, 1994; Harmon-Jones, Gable, & Peterson, 2010). This notion has been supported by a substantial amount of infant studies examining frontal EEG asymmetry scores during emotional tasks, which have revealed greater left frontal EEG activation in response to typically appetitive stimuli (e.g., mother approach, film of an adult displaying a happy facial expression, positively-valenced infant directed speech) and greater right frontal activation during the presentation of aversive stimuli (e.g., maternal distress simulation, maternal separation, stranger approach, film of an adult displaying a sad facial expression, arm restrain task, negatively-valenced infant directed speech) (e.g., Buss et al., 2003; Davidson & Fox, 1982, 1989; Diaz & Bell, 2011; Fox & Davidson, 1986, 1987, 1988; Killeen & Teti, 2012; LoBue, Coan, Thrasher & DeLoache, 2011; Santesso, Schmidt & Trainor, 2007).

Additionally, frontal asymmetry patterns have also been related to individual differences in social behavior, highlighting the role of this measure as a potential predictor of infants' social competence in peer settings. Multiple longitudinal studies have shown that early patterns of left frontal EEG asymmetry predicted higher levels of sociability during peer interactions across the toddler years. On the contrary, infants' right frontal EEG asymmetry patterns turned out to be good predictors of elevated levels of social reticence during interactions with peers in the toddler years (e.g., Calkins, Fox & Marshall, 1996; Fox, Henderson, Rubin, Calkins, & Schmidt, 2001; Fox et al., 1995; Henderson, Fox & Rubin, 2001). There is also further evidence associating relatively left frontal activation with greater empathic responding (Paulus, Kuhn-Popp, Licata, Sodian, & Meinhardt, 2013). For instance, Paulus et al. (2013) found that found that greater relative left frontal activation at the age of 14 months was associated with infants' better understanding of others' distress at the age of 18 months as well as greater empathic responding during a comforting task at the age of 24 months. Similarly, Licata, Paulus, Kuhn-Popp, Meinhardt, & Sodian (2015) found a link between relative greater left frontal activation at the age of 14 months with higher frequencies of children approaching and initiating contact with their mothers during free play interactions at 50 months.

In light of this information, the use of frontal EEG asymmetry arises as a promising measure to investigate the neurophysiological mechanisms supporting the emergence of other-oriented responses. In other words, this technique offers us with the possibility to explore the neural correlates underlying infants' motivational responses to approach or avoid others experiencing either happiness or distress.

Cognitive Components: Theory of Mind and Emotion Regulation

The capacity for two people to resonate with each other affectively is not sufficient to explain the emergence of more mature empathic responses. The transition from a more basic, self-focused form of empathy to a more complex other-oriented empathic response is possible due to the gradual emergence of cognitive processes that allow the individual to generate second-order representations of the feelings of another person, while regulating the own emotional arousal response to avoid personal distress (e.g., Decety, 2010a; Decety & Meyer, 2008; Decety & Michalska, 2010; Decety & Svetlova, 2012). These cognitive aspects are closely related to the development of theory of mind (ToM) and self-regulation (Decety & Michalska, 2010; Zelazo, Carlson, & Kesek, 2008). Interestingly, the neural correlates involve in both processes undergo a protracted developmental course that would explain the later emergence of the cognitive component of empathy (e.g., Apperly & Butterfill, 2009; Blakemore, 2008, 2012; Kobayashi, Glover, & Temple, 2007). Next, we will discuss each of these processes independently.

Theory of Mind (ToM)

Theory of Mind (ToM) or mentalizing is often defined as the ability to understand other people's mental states, including beliefs, thoughts and feelings (Flavell, 1988; Frith & Frith, 1999; Wellman & Bartsch, 1988). An essential milestone in the development of ToM is the emergence of false belief (FB) understanding, defined as the ability to appreciate that other people's beliefs can differ from reality (Flavell, 1988; Luo, 2011; Rakoczy, 2011; Wellman & Bartsch, 1988). Although for a long period of time it was assumed that children develop this ability around 4 years of age and that younger children do not attribute FBs to a person (e.g., Baron-Cohen et al., 1985; Flavell, 1988; Perner, 1991; Wellman, Cross & Watson, 2001), recent behavioral studies using non-verbal tasks based on looking-time measures suggest that computations about others' beliefs may be already present around the age of 15-18 months (e.g., Onishi & Baillargeon, 2005; Träuble et al., 2010; Scott & Baillargeon, 2009; Song et al., 2008). These new findings are in line with a current model on ToM development proposed by Apperly & Butterfill (2009), in which they suggest that humans possess two distinct mechanisms for reasoning about beliefs: one that emerges early and is efficient but inflexible, and one that emerges later, is dependent on language and executive functions abilities, and is more flexible but also more demanding in terms of processing. Nonetheless, whether these results can be taken as evidence that children in their second year of life are able to attribute beliefs to others is still under debate and several alternative interpretations have been proposed, such the use of behavioral rules previously learned in similar situations (Perner & Ruffman, 2005; Ruffman & Perner, 2005; Song et al., 2008; Trauble et al., 2010). Also, contrary to the usual belief that ToM is fully developed by the age of 5 (Flavell, 1988; Wellman, Cross & Watson, 2001), neuroscientific research has shown that this ability follows a protracted development which extends well beyond the age of 4-years, reaching more mature levels of performance only towards the end of adolescence (e.g., Apperly & Butterfill, 2009; Blakemore, 2012, 2008; Gweon, Dodell-Feder, Bedny & Saxe, 2012; Johnson, 2001; Kobayashi et al., 2007).

To date, several neuroimaging studies have examined the neural correlates associated with the attribution of mental states in adults using a wide variety of stimuli, including stories (Fletcher et al., 1995; Saxe and Kanwisher, 2003), cartoons (Brunet et al., 2000; Gallagher et al., 2000), and animations (Castelli et al., 2000). Together, these studies have documented the existence of a “mentalizing” network, which includes the posterior superior temporal sulcus (pSTS), the temporoparietal junction (TPJ), the temporal lobes, and the medial prefrontal cortex (mPFC) (see Frith & Frith, 2003 for a meta-analysis). Lesion studies have corroborated these findings by showing that damage to the superior temporal lobes (Samson, Apperly, Chiavarino, & Humphreys, 2004) and PFC (Happé, Malhi, & Checkley, 2001; Rowe, Bullock, Polkey, & Morris, 2001) impairs metalizing skills. Nonetheless, there is still some debate regarding whether these regions are specific for metalizing or rather they are part of more domain-general functions.

Recent work in developmental cognitive neuroscience has begun to examine the neural correlates of ToM in children compared to adults (e.g., Gweon et al., 2012; Saxe, Whitifield-Gabrieli, Scholz, & Pelphrey, 2009; Sommer et al., 2010). In particular, these studies suggest that the brain regions normally recruited for ToM in adults are also found in 5- to 12-year-olds children, yet the functional profile of some of these regions undergo age-related changes. For example, the TPJ shows an increasing selective activation with age in response to mental state information (Gweon et al., 2012; Saxe et al., 2009; Sommer et al., 2010). Critically, developmental changes in the TPJ have been correlated with children’s performance on ToM tasks outside the scanner (Gweon et al., 2012). Also, the prefrontal cortex and the posterior cingulate, which are relevant for monitoring and regulating behavior, display a different developmental pattern with children engaging these areas to a larger extent that adults when reasoning about others beliefs (Amodio & Frith, 2006; Sommer et al., 2010). These developmental differences are also corroborated by few developmental EEG studies on FB processing, which reveal that although children’ ERP components are similar to the adult ones, these also show marked differences (Liu, Sabbagh, Gehring, & Wellmann, 2009; Meinhardt, Sodian, Thoermer, Dohnel, & Sommer, 2011). In particular, they tend to be delayed, have greater duration and smaller amplitude, and may even be inverted in polarity and present different scalp distributions.

Although more and more behavioral studies suggest that already in the second year of life infants are sensitive to information about others beliefs, it remains unclear which processes underlie this sensitivity. Certainly, the investigation of the neural underpinnings of belief processing may help us to clarify this gap. We still have only limited understanding of the neural processes underlying infants' performance in ToM tasks and their relation to those reported in older children and in adults. Critically, the understanding of the neural mechanisms underlying ToM in infancy is central to elucidate the developmental course of empathy given that evidence from developmental studies suggest that the progressive emergence of ToM gives way to more sophisticated forms of empathy like concern, hypothesis testing or even attempts to approach/assist the victim. Specifically, these studies suggest that the emergence of behavioral expressions of concern for others during the second year of life appears to be linked with the development of perspective-taking skills (e.g., Knafo, Zahn-Waxler, Van Hulle, Robinson, & Rhee, 2008; Zahn-Waxler et al., 1992). In this respect, a series of longitudinal studies conducted by Zhan-Waxler and colleagues report a significant increase in hypothesis testing behaviors (often considered a cognitive marker of empathy) in conjunction with an increase in empathic concern in response to the observation of others' in distress over the second year of life (Zahn-Waxler, Radke-Yarrow, & King, 1979; Zahn-Waxler et al., 1992; Zahn-Waxler, Robinson, & Emde, 1992). Hypothesis testing and empathy-related responses further develop through childhood (Bengtsson & Arvidsson, 2011) and adolescence (Schwenck et al., 2014), reflecting the protracted development nature of these processes.

Interestingly, the positive link between ToM and empathy development has been partially sustained by few fMRI studies with younger children (Decety, Michalska, & Akitsuki, 2008) and adolescents (Decety, Michalska, Akitsuki, & Lahey, 2009) exposed to painful situations intentionally or accidentally inflicted by another. In particular, these studies show that mentalizing about the pain of others when it has been intentionally caused recruits brain regions linked to the ToM network, namely the medial prefrontal cortex (mPFC), superior temporal sulcus (STS), the temporo-parietal junction (TPJ) and temporal poles (TP). Significant age-related changes in the functional organization of these neural structures was also found (Decety & Michalska, 2010; Killgore, Oki, & Yurgelun-Todd, 2001; Killgore & Yurgelun-Todd, 2007), with older participants showing reduced activity of the amygdala and insula, and increased involvement of the mPFC or TPJ. Although these studies already reflect the existence of developmental changes during childhood, the age-related changes in infancy remain less explored.

Taken together, developmental findings suggest that ToM helps to shape the early experience of affect sharing into a more sophisticated, cognitive form of empathy, which is sustained by neuroscientific advances showing that ToM and cognitive empathy engage common as well as distinct neural networks, with the ventro-medial prefrontal cortex (vmPFC) being a core region for cognitive empathy. Despite these positive findings, there are still some controversy regarding the link between FB understanding (ToM) and empathy since not all developmental studies have succeeded in finding a link between both constructs (Astington & Jenkins, 1995; Hugues, White, Sharpen, & Dunn, 2000) or have failed to report age effects on the development of cognitive empathy (Garaigordobil, 2009). Still more research needs to be done to disentangle what is common to both constructs, ToM and empathy, and how they interact with and modulate each other from infancy to adulthood (Bensalah, Caillies, & Anduze, 2016; Decety & Svetlova, 2012). In this respect, up to know no study has investigated the link between empathy and ToM during the first two years of life or the neural correlates underlying mentalizing skills at this early age.

Emotion Regulation

Emotion regulation is an important cornerstone of children socio-emotional development, as indexed by its protective role in the onset of mood disruptions and behavioral problems during childhood (Calkins & Dedmon, 2000; Calkins & Fox, 2002). Additionally, self-regulation skills are particularly important for the development of appropriate and adaptive social behaviors (Decety & Lamm, 2006; Dennis, 2010; Eisenberg & Fabes, 1992). There is also solid evidence supporting a positive relation between emotional regulation and empathy-related responses in both adults and children. Eisenberg and Fabes (1992) proposed a model suggesting an interaction between the intensity at which emotions are experienced and the extent to which individuals can regulate their emotions. According to this model, individuals with increased emotional intensity and poor regulation skills would be more susceptible to experience personal distress rather than empathy. In contrast, for optimally regulated people, their dispositional emotionality should not be an important contributor to empathy-related responding. These predictions have been corroborated by multiple behavioral studies (e.g., Eisenberg et al., 1996; Eisenberg et al., 1998; Eisenberg & Fabes, 1995; Guthrie et al., 1997; Murphy et al., 1999) and have been documented as early as 4 months of age (Ungerer et al., 1990).

Broadly speaking, emotion regulation refers to a set of processes aimed at evaluating, monitoring, modulating and modifying internal states (i.e. thoughts and emotions) produced by external affective stimuli with the final objective of generating the most adaptive behavioral response to one's goal in a particular situation (Decety & Lamm, 2006; Thompson, 1994). Among the core capacities to support emotion regulation are the ability to control attention, decision-making, and other cognitive processes that take place in emotionally demanding context (Dennis, 2010; Dennis, Malone, & Chen, 2009). Current neuroscientific models of emotional regulation organize these strategies in a continuum that goes from pure attentional (i.e. attention shifting and/or focussing) to more cognitive change strategies (i.e. reappraisal of emotional information) (Gross & Thompson, 2007; Ochsner & Gross, 2005).

Over the course of development, changes in the control of emotions are reflected by the transition from more automatic, reactive forms of self-control, mainly supported by the caregivers and tightly linked to sensory stimuli, to more controlled, self-initiated forms that allow the infant to gain independence for regulation (Bell & Wolfe, 2007; Calkins & Leerkes, 2004; Calkins & Fox, 2002). Early in the first year of life, beginning around 3 months of age, infants already use some rudimentary strategies such as self-soothing (e.g., thumb-sucking), help seeking (e.g., reaching for caregiver), withdrawal behaviors and reflexive crying to alleviate their own distress (Kopp, 1982, 1989; Kopp & Neufeld, 2003; Shapiro, Fagen, Prigot, Carroll, & Shalan, 1998; Stifter & Braungart, 1995; Rothbart, Ziaje, & O'boyle, 1992). Nonetheless, it is by the end of the first year when infants implement more active methods of self-regulation as indexed by the use of specific attention-based strategies (e.g. object distraction, shift attention) to attempt to manage their own emotions (Bell & Wolfe, 2007; Braungart-Rieker & Stifter, 1996; Calkins & Dedmon, 2000; Calkins, Gill, Johnson, & Smith, 1999; Shapiro et al., 1998). This transition is partly explained by the greater involvement of attentional control mechanisms implemented by the executive attention system (Bell & Wolfe, 2007; Calkins & Leerkes, 2004; Fox & Calkins, 2003; Rothbart, Ahadi, &Hershey, 1994), which allow the infant engage and disengage more freely with emotional stimuli. Although the capacity for control of attention begins to emerge toward the end of the first year, its development continues throughout the preschool and school years, gradually leading to the emergence of an effortful control of behavior (Fox & Calkins, 2003; Rothbart el al., 1994; Rothbart & Bates, 2006; Rothbart, Ellis, Rueda, & Posner, 2003).

The development of emotion regulation is functionally linked to the protracted development of the executive functions, and in particular, the executive attention network, both implemented by dorsal and ventral regions of the prefrontal cortex (PFC) (Ochsner, Bunge, Gross, & Gabrieli, 2002; Ochsner & Gross, 2005; Posner & Peterson, 1990; Posner & Rothbart, 2009; Posner, Rueda, & Kanske, 2007). While ventral portions of the PFC appear to underlie rapid and automatic emotional arousal and motivational processes, dorsal portions support more deliberate executive functions such as attention regulation and cognitive control of reactivity and arousal (Dennis, 2010; Luu, Tucker, & Derryberry, 1998; Ochsner et al., 2004). The anterior cingulate cortex (ACC) is also an important structure in emotion regulation as an intermediary between higher order cognition and emotional arousal (Bush, Luu, & Posner, 2000; Luu & Tucker, 2004). Particularly, the ACC is active during conflict monitoring tasks that require control of attention due to the presence of conflicting information, inhibitory control and detection of errors (see Botvinick, 2007 for a review). The protracted developmental course of these networks is evident behaviorally in tasks related to emotional regulation or executive functions, with children's ability to regulate their internal states increasing as they get older (Casey, Giedd, & Thomas, 2000; Decety & Svetolova, 2012; Diamond, 2002; Killgore & Yurgelun-Todd, 2007; Philips, Ladouceur, & Drevets, 2008; Power, Fair, Schlaggar, & Petersen, 2010).

EEG methods have proven to be particularly prolific to investigate how attention is modulated under emotional demands. For instance, some studies show that the induction of negative emotions in children is associated with the recruitment of more cognitive control processes (larger N200 amplitudes) in the service of emotional regulation (Lewis, Granic, & Lamm, 2006; Lewis, Lamm, Segalowitz, Stieben, & Zelazo, 2006; Nelson & Nugent, 1990; Stieben et al., 2007). Similar to EEG research, work focusing on measures of heart rate variability (HRV) has also proven to be relevant in the investigation of emotional regulation (Porges, 1991, 1996). The existing evidence suggests that the suppression of respiratory sinus arrhythmia (RSA) during challenging situations is related to better state regulation, greater self-soothing, and more attentional control in infancy (DeGangi, DiPietro, Greenspan, & Porges, 1991; Huffman et al., 1998).

In sum, the ability to regulate the own emotions is crucial for the development of complex social abilities such as empathy, by enhancing the production of adaptive and appropriate responses to other's emotions. There is evidence suggesting that emotion regulation develops throughout infancy to adolescence and parallels the maturation of executive functions. In this line, recent studies from social neuroscience have stressed the important role of cognitive control processes for child emotional regulation.

Modulation of Empathy Development

Although the generation of empathy partly relies on bottom-up processes, which are automatic and unconscious, from our own experience it is evident that we do not always empathise with others in the same degree (intra-personal differences) and that our ability to experience empathy differs from that of others (inter-personal differences). Then, the question is: where does this variability in the tendency to empathize come from? It is increasingly clear that certain factors either enhance or decrease the occurrence and degree of empathic responses while modulate the neural activity of brain structures linked to the experience of empathy – e.g. anterior insula (AI) and anterior cingulate cortex (ACC) (e.g., Decety & Lamm, 2006; de Vignemont & Singer, 2006; Hein & Singer, 2008). Research on empathy development has stressed the importance of multiple intrapersonal and environmental factors associated with individual differences in the development of empathy (e.g., Eisenberg, Fabes, Schaller, Carlo, & Miller, 1991; Knafo & Uzefovsky, 2013; McDonald & Messinger, 2011; Zahn-Waxler, Robinson, et al., 1992). Next, we will discuss some of these modulating factors, including genetics and temperament as intrapersonal influences, as well as parenting styles as part of environmental (social) influences.

Genetic Factors

Early in life children differ in their expressions of empathy. Nowadays, there is substantial evidence that these individual variations are in part heritable as shown by several genetic studies using twin designs (Davis, Luce, & Kraus, 1994; Knafo, Israel, & Ebstein, 2011; Knafo et al., 2008; Rushton, Fulker, Neale, Nias, & Eysenck, 1986; Volbrecht et al., 2007). Typically, twin designs compare identical twins (monozygotic [MZ]) with fraternal twins (dizygotic [DZ]) reared in their biological families. Since MZ twins share all their genes and DZ twins share on average 50% of their genes, this design assumes that MZ and DZ twins are equal in terms of how similar their environment are, in which case greater similarity of MZ twins for a particular trait reflects genetic influences (*heritability*). Similarities beyond this genetic effect are attributed to the environment the twins share (*shared-environment*) while differences between twins are attributed to an effect of the *non-shared environment*.

Overall, the majority of studies conducted with children that have addressed the genetic and environmental influences on empathy report both genetic and shared environment effects. Notably, the existing evidence suggests that genes account for approximately 30-40% of the variability for empathy (Knafo et al., 2011; Volbrecht et al., 2007; Zahn-Waxler, Robinson, et al., 1992; see Knafo & Uzefovsky, 2013 for meta-analysis). Additionally, when analysing the genetic and environmental influences on the emotional and cognitive aspects of empathy separately, the genetic effects are comparable (i.e. they overlap). Nonetheless, the shared environment seems to account for more variability in cognitive empathy than emotional empathy (Knafo et al., 2008; Volbrecht et al., 2007; Zahn-Waxler, Robinson, et al., 1992). Furthermore, longitudinal studies suggest that the heritability of empathy and prosocial behavior increases with age while the effects of shared environment decrease as children grow up (Knafo & Plomin, 2006; Knafo et al., 2008; Scourfield, John, Martin, & McGuffin, 2004). This meaningful developmental pattern is thought to reflect the strengthening of gene - environment interactions over time, as children have more opportunities to actively select environments that match their genetic predisposition (Fortuna & Knafo, 2014).

Temperament

An increasing body of evidence suggests that certain temperamental factors account for individual differences in toddlers' empathy-related reactions. Because emotionality and self-regulation processes are closely related to the experience of empathy, both aspects of temperament have been extensively studied (Eisenberg, 2000; Eisenberg & Fabes, 1992, 1995; Eisenberg, Spinrad, & Sadovsky, 2006). Regarding the temperamental factor of emotionality, it is possible to identify the factors of negative emotionality and positive emotionality, both previously linked with empathy. Notably, low negative emotionality and positive affect have been often associated with greater empathy-related responses in young children (Eisenberg & Fabes, 1995; Eisenberg et al., 1996; Robinson, Zahn-Waxler, & Emde, 1994; Volbrecht et al., 2007;

Zahn-Waxler, Cole, Welsh, & Fox, 1995). Additionally, fear reactivity, a component of negative emotionality, has been related to low empathic responding in infants and young children (Liew et al., 2011; Spinrad & Sitfter, 2006; van der Mark, Van Ijzendoorn, & Bakermans-Kranenburg, 2002; Young et al., 1999).

Individual differences in the temperamental factor regulation have also been linked to children's empathy-related responses. Notably, effortful control has proven to be a good predictor of empathy-related responses. Although definitions vary, effortful control can be defined as "the ability to voluntary suppress a dominant response in order to perform a non-dominant response (response inhibition)" (Rothbart & Bates, 2006; Rothbart et al., 2003). This construct has been involved in a wide range of self-regulatory outcomes from pre-school to school-aged children (Kochanska, Coy, & Murray, 2001). Empirical evidence has consistently shown that children high in effortful control display higher levels of empathy and prosocial behavior (Guthrie et al., 1997; Kochanska, Gross, Lin, & Nichols, 2002; Kochanska, 1995; Rothbart et al., 1994; Valiente et al., 2004). These findings are consistent with evidence that toddlers' inhibitory control is positively related to their conscience and empathy (Kochanska et al., 1997, 1998, 1999, 2001). Similar pattern of findings have been found for the temperamental regulatory dimensions of falling reactivity in infants exposed to the cry of a peer, suggesting that those infants who recovered faster from peak distress in their everyday life showed reduced self-distress responses (Geangu et al., 2011). Attentional control and attentional orientation, both important regulatory processes, have also been linked to reduced personal distress in infants and school aged children (Geangu et al., 2011; Guthrie et al., 1997).

Parenting Styles

Several social and developmental psychologists have stressed the importance of parenting and parent-child relationships in the development of empathy (Bandura, 1986; Chase-Lansdale, Wakschlag, & Brooks-Gunn, 1995; Hoffman, 2001; Zahn-Waxler & Radke-Yarrow, 1990). Parents who are sensitive to their children's needs and effectively help them to reduce distress, often express and model moral emotions (e.g., guilt, shame, empathy), and develop warm, supportive interactions with their children, are likely to promote and foster the capacity to respond empathically in their offspring (Bandura, 1986; Chase-Lansdale et al., 1995; Eisenberg, 2000; Hoffman, 2001). Traditionally, parental warmth and parental control, two major dimensions of parenting styles have been linked to empathy and prosocial development (Barnett, 1987; Chase-Lansdale et al., 1995; De Wolff & van Ijzendoorn, 1997; Krevans & Gibbs, 1996; Soenens, Duriez, Vansteenkiste, & Goossens, 2007; Zhou et al., 2002).

Empirical research on this topic has shown that children who show more empathy-related behaviors have parents who offer supportive, responsive and warm interactions (parental warmth) (Barnett, 1987; Carlo, Mestre, Samper, Tur, & Armenta, 2010; Chase-Lansdale et al., 1995; Clark & Ladd, 2000; Wolff & van Ijzendoorn, 1997; Krevans & Gibbs, 1996; Robinson et al., 1994; Zhou et al., 2002). Similarly, parental support (Laible & Carlo, 2004; Soenens, Duriez, Vansteenkiste, & Goossens, 2007) and stable secure child-parent relationships (Kestenbaum, Farber, & Sroufe, 1989; Teti & Ablard, 1989) are good predictors of high levels of empathy in children. In contrast, there is substantial support for a positive relationship between excessive parental control and antisocial behaviors. Notably, high parental control mixed with harsh verbal and physical disciplining practices (Eisenberg & Valiente, 2002; Hoffman, 2001; Maccoby & Martin, 1983), low parental warmth combined with inconsistency

(Barnow, Lucht, & Freyberger, 2005), authoritarian or punitive parenting (Grogan-Kaylor, 2005), and permissive or disengaged parenting (Beck & Shaw, 2005; Hawkins et al., 2000) have been all linked to aggressive and antisocial behaviors. Therefore, while supportive parenting styles and practices have been linked to empathy in children, authoritarian and permissive parenting have been linked to antisocial behavior in children.

Introduction to EEG-ERP Methodology

The electroencephalogram (EEG) has been widely used in infancy research to examine different aspects of infant cognitive development ranging from visual perception (Bach, Wolfe, & Maurer, 2005; Pieh, McCulloch, Shahani, & Bach, 2005), auditory perception (Kushnerenko et al., 2002; Kurtzberg et a., 1984), attention (de Haan, & Nelson, 1997, 1998, 1999), memory (Bauer, Wiebe, Carver, Waters, & Nelson, 2003; Carver, Bauer, & Nelson, 2000) or emotion processing from faces and voice (Grossmann, Striano, & Friederici, 2005; Nelson & de Haan, 1996). Importantly, EEG is a relatively inexpensive, non-invasive and easy to use technique, which makes it well-suitable to study developmental populations (Bell & Cuevas, 2012; Thierry, 2005). Furthermore, this method allows to measure infants perception and cognition in the absence of overt behaviors while offers a high temporal resolution, making possible to keep track of the timing and sequence of cognitive processes (Hoehl & Wahl, 2012; Thierry, 2005).

The EEG measures ongoing brain electrical activity at the scalp, reflecting the sum of postsynaptic potentials produced by pyramidal neurons in the cortex (Davidson, Jackson, & Larson, 2000; Hoehl & Wahl, 2012). Multiple neural measures can be derived from the overall EEG signal associated with specific sensory, cognitive and motor events, such as event-related potentials (ERPs), EEG coherence (Bell & Fox, 1996; Mundy, Fox, & Card, 2003), or EEG power (Morasch & Bell, 2011; Stroganova, Orekhova, & Posikera, 1999). In this section, I first review the ERP technique, and then briefly describe each of the main ERP components targeted in the thesis.

ERPs refer to averaged brain electrical activity time-locked to a particular event. By averaging brain electrical responses associated with specific events, it is possible to reduce the noise-to-signal ratio and increase the ability to differentiate specific neural processes from other unwanted noise produced by eye movements or strong motor movements (Luck, 2005; Hoehl & Wahl, 2012). The ERP waveforms are characterized by the presence of peaks and troughs which vary as a function of the physical characteristics of the stimuli and the cognitive demands of the task (Luck, 2005; Thierry, 2005). Early components are thought to index automatic, sensory processes – often modulated by attention – while later ERP components tend to index more effortful, high cognitive processes (Luck, 2005; Thierry, 2005). Up to date, many ERP components have been defined according to its latency, polarity, brain location and stimulus modality. For the purpose of this thesis I will only discuss the components related to infant auditory processing of emotional vocalizations and semantic information processing.

Auditory Processing of Emotions: N100, P200 and LPC

In relation to infants' neural responses to their peer's emotional non-verbal vocalizations (see *Paper 1*), special attention has been placed on the early components N100 and P200 as well as the late positive component (LPC). Importantly, all these components have been related to auditory emotion processing during infancy (Cheng, Lee, Chen, Wang & Decety, 2012; Grossmann, Striano & Friederici, 2005; Missana, Altvater-Mackensen, & Grossmann, 2017) but mostly adulthood (Jessen & Kotz, 2011; Pell et al., 2015; Sauter & Eimer, 2009). Notably, there is a gap in the ERP literature on auditory emotional processing during childhood. The N100 and P200 waveforms are thought to underlie the automatic processing of auditory information across the lifespan. These auditory components can be discerned in infants at fronto-central locations at about the age of 6 months with the N100 peaking around 250 ms after the onset of a sound and the P200 peaking around 350 ms after stimulus presentation (Ceponiene, Cheour, & Naatanen, 1992; Choudhury & Benasich, 2011; Kushnerenko et al., 2002). An increasing number of studies on infants' cortical auditory evoked potentials (CAEPs) suggests that with age the peak latencies of these components decrease while their peak amplitudes increase, specially the amplitude of the negative-going peaks (Choudhury & Benasich, 2011; Novak, Kurtzberg, Kreuzer & Vaughan, 1989; Ohlrich & Barnet, 1972; Ohlrich, Barnet, & Weiss, 1978). Although it is not clear whether the peaks observed during infancy are functionally similar to those found in adults (Ponton, Eggermont, Kwong, Don, 2000; Ponton, Eggermont, Khosla, Kwong, & Don, 2002), it is thought that the observed peaks at the age of 12 months may be functionally similar to those found in 3-9 year old children, which in turn may be the precursors of the adult components (Ceponiene, Cheour & Naatanen, 1998; Neville, Coffey, Holcomb, & Tallal, 1993; Paetau, Ahonen & Salonen, 1995). Undoubtedly, further longitudinal studies in the context of auditory processing are needed to elucidate the developmental course of the auditory evoked potentials and its functional significance across time (see Wunderlich & Cone-Wesson, 2006 for a review).

Traditionally, the N100 component has been suggested to index the processing of acoustic features of sounds (e.g., amplitude, pitch, duration; Näätänen & Picton, 1987) and the allocation of processing resources to form and maintain a sensory memory trace (Obleser & Kotz, 2011). Notably, evidence suggests that the amplitude of the N100 can be modulated by attention, with higher negative amplitudes reflecting the recruitment of more attentional resources (Woldorff et al., 1993; Woods, 1995). The age at which N1 becomes a reliable feature of the auditory evoked potentials is not clear. Although some studies already report an N1 in newborns (Barnet, Ohlrich, Weiss, & Shanks, 1975; Kushnrenko et al., 2002; Little, Thomas, & Letterman, 1999; Molfese, 2000; Ohlrich et al., 1978; Rapin & Graziani, 1967), this component is often absent in young children (Wunderlich & Cone-Wesson, 2006). It is not until later in childhood, around the age of 9, when the N100 is systemically reported (Ceponiene et al., 1998; Pang & Taylor, 2000; Sussman, Steinschneider, Gumenyuk, Grushko & Lawson, 2008; Wunderlich, Cone-Wesson & Shepherd, 2006).

Often following this component, there is the P200, a positive deflection thought to reflect the processing of semantically-relevant acoustic parameters involved in the early meaning detection or general stimulus categorization (Garcia-Larrea, Lukaszewicz, & Mauguiére, 1992; Pell et al., 2015; Schirmer & Kotz, 2006). Further evidence suggests that the P200 can be modulated by stimuli arousal (Jessen & Kotz, 2011; Paulmann, Bleichner, & Kotz, 2013; Pell et al., 2015). Views on the development of the P200 are inconsistent. Some researchers posit that the auditory P2 emerges early in infancy (Barnet et al., 1975; Kurtzberg et al., 1984; Novak et al., 1989), while others state that it does not appear until 5-6 years of age (Ponton et al., 2002; Ceponiene et al., 2002). Interestingly, the scalp distribution of this response is similar between infants and adults, mostly broad across frontal areas (Barnet, 1971; Wunderlich & Cone-Wesso, 2006), while it is generally more posterior in children than in adults (Ponton et al., 2000; Tonquist-Uhlen, 1996). These differences may be reflecting developmental changes in the underlying generating neural networks responsible for these neurophysiological markers.

Later stages of acoustical processing are also affected by the emotional significance of the stimulus, as shown by changes in neural components with longer latencies such as the late positive component (LPC) (Jessen & Kotz, 2011; Kotz & Paulmann, 2011; Paulmann & Pell, 2010; Schirmer & Kotz, 2003, 2006; Schirmer, Chen, Ching, Tan, & Hong, 2013). Traditionally, the LPC has been linked to evaluative processes and sustained attention rather than to mere sensory processing (Cuthbert et al., 2000; Foti et al., 2010; Kanske and Kotz, 2007). In infant research, a series of ERP studies on memory recognition have consistently reported the emergence of enhanced long-latency positive waveforms to infrequently familiar stimuli as compared to novel stimuli by the age of 6 months (Nelson & Collins, 1991; 1992; Nelson & deRegnier, 1992). These results were thought to reflect the updating of memory representations of partially encoded stimuli (Nelson & Collins, 1991; 1992; Nelson & deRegnier, 1992). Similar slow positive waveforms have been reported in infant studies on emotion processing from faces (Nelson & de Haan, 1996) and speech (Grossmann et al., 2005). Although it is unclear whether the slow positive waveforms reported in the aforementioned studies reflect the same cognitive process (i.e. memory updating) given their differences in topography and morphology, all these late latency components have been interpreted as indexing more sustained and effortful operations. To the author knowledge, up to date there is no a single EEG study that has reported frontal late latency components in response to vocal emotional stimuli during childhood. While there has been much progress in the understanding of auditory evoked potentials in infancy and childhood, the emergence and characteristics of late latency positive components linked to emotional auditory processing remains to be further investigated.

Hemispheric differences. Compelling behavioural and neuroimaging evidence supports the emergence of hemispheric specialization for different types of sounds as early as few days after birth (see Paelle, 2012; Schirmer & Kotz, 2006 for a review). In general, empirical evidence emphasizes the dominant role of the left hemisphere in the processing of speech (Liegeois-Chauvel et al., 2004; Scott, Blank, Rosen, & Wise, 2000; Zatorre & Belin, 2001), while greater selective responsiveness in the right hemisphere has been reported in response to human non-speech vocalizations sounds (e.g. crying, laughing) in infants (Blasi et al., 2011, Molfese, Freeman, & Palermo, 1975) and adults (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000). Yet, no differences across hemispheres have been reported in front of most non-human auditory stimuli, whether these are pure tones (Belin, Zatorre, Hoge, Evans, & Pike, 1999) or noise (Hart, Palmer, & Hall, 2003; Overath, Zhang, Sanes, & Poeppel, 2012). Altogether, this evidence suggests that both hemispheres are recruited unevenly by different types of sound, with the left hemisphere being dominant during the processing of fined grained sounds such as speech, and the right hemisphere being dominant during the processing of pitch (Homae, Watanabe, Nakano, Asakawa, & Taga, 2006; Meyer, Liem, Hirsiger, Jancke, & Hanggi, 2013; Schirmer & Kotz, 2006). Given these findings, I decided to explore further the contribution of each hemisphere in the processing of non-verbal emotional vocalizations in the first experimental chapter by including hemisphere (left/right) as a factor in the statistical analysis (see *Paper 1*).

Semantic Processing: N400

As a part of the fourth experimental chapter, the N400 component has also been examined. The N400 is a large negative going component peaking at about 400 ms that has been observed in adults (Ferguson, Cane, Douchkov, & Wright, 2015; Sabbagh & Taylor, 2000), children (Pace, Carver, & Friend, 2013; Sheehan, Namy, & Mills, 2007) and infants as young as 13 months of age (Friedrich & Friederici, 2005; Mills, Conboy, & Paton, 2005). N400 responses peaking at a later latency (600 – 800 ms) have also been observed in 9-month-old infants (Reid et al., 2009). Typically, this component has been related to the processing of semantic information (see Kutas & Federmeier, 2000, 2011 for review) and it has been proved to be sensitive not only to the meaning processing of words (e.g., Camblin, Gordon, & Swaab, 2007; Holcomb, 1993; Kutas & Hillyard, 1980, 1984; van Berkum, Hagoort, & Brown, 1999) but also to the semantic processing of actions (e.g., Bach, Gunter, Knoblich, Prinz, &, Friederici, 2009; Gunter & Bach, 2004; Proverbio & Riva, 2009; Shibata, Gyoba, &, Suzuki, 2009), with higher amplitudes to stimuli that are incongruent with the preceding context. Interestingly, this component has been reported over anterior areas in EEG studies using non-verbal visual stimuli (similar to the one I have used in the forth experimental chapter) designed to explore goal and intention driven action processing (infant studies: Pace, Carver, & Friend, 2013; Reid et al., 2009; Reid & Striano, 2008; adult studies: Ganis, Kutas, & Sereno, 1996; McPherson & Holcomb, 1999; Proverbio et al., 2012; Proverbio & Riva, 2009; Sitnikova, Holcomb, Kiyonaga, & Kuperberg, 2008; Sitnikova, West, Kuperberg, & Holcomb, 2006; West & Holcomb, 2002).

Thesis Aims

Undoubtedly, empathy is a complex phenomenon whose examination is not without difficulties, mostly when involving developing populations. Although it is widely assumed that affect sharing is a likely precursor of empathy, this notion has not been directly tested in infants. We still do not have a clear understanding of the different mechanisms underlying infants' ability to share others' emotions and how they relate to the production of later other-oriented and prosocial responses. There is also some controversy regarding when and how theory of mind processes start modulating infants' ability to resonate with others' emotional states. Therefore, important questions on early empathy development still remain unanswered. The present thesis aims at addressing some of these questions.

Through a series of experimental studies, this thesis aims to provide further evidence regarding the affective and cognitive processes involved in the generation of empathy during infancy, ranging from infants' ability to process emotional cues to infants' ability to process others' mental states. Paper 1 reports a study that examined the neural correlates underlying infants' ability to process emotional cues from non-verbal vocalizations produced by peers (i.e. crying, laughing and coughing), which are thought to be crucial in the elicitation of prosocial behaviors and early precursors in empathy development (Decety, 2015; Decety & Howard, 2013; Geangu, 2015; Hoffmann, 2001). The novelty of this study is that it probes individual differences in infants' neural correlates underlying emotional processing, which is essential for a better understanding of those personal traits that may predispose infants to experience greater empathy. Investigating emerging individual differences is also crucial for the prediction of later behavioural outcomes. In this study, 8-month-old infants' neural responses were measured by using an event-related potential (ERP) paradigm. On the basis of previous studies on emotion perception from speech in infants (Cheng et al., 2012; Grossmann et al., 2005; Missana et al., 2017) and adults (Jessen & Kotz, 2011; Liu et al., 2012; Pell et al., 2015), we hypothesized that infants' ERP responses to emotional non-verbal vocalizations would differentiate from neutral non-verbal vocalizations. Additionally, following previous infant research on temperament (Martinos, Matheson, & de Haan, 2012; Missana, Grigutsch, & Grossmann, 2014; Rajhans, Missana, Krol, & Grossmann, 2015; Ravicz, Perdue, Westerlund, Vanderwert, & Nelson, 2015), we predicted a significant relation between aspects of infants' negative emotionality and their ERP responses to their peers' emotional non-verbal vocalizations.

Paper 2 expands on Paper 1 by investigating the link between infants' early responsiveness to their peers' crying and laughing and the neural correlates underlying these behaviours in 8-month-olds. The main objective was to clarify the neural indices of motivational tendencies underpinning infants' emerging other-oriented responses to their peers' negative and positive emotions. This is important since early afftect sharing may motivate later other-oriented responses. Identifying the neurophysiological mechanisms underlying approach/withdrawal motivations in infancy will help us better understand how such other-oriented responses develop. In our second study, we used frontal EEG asymmetry analysis as our method. This measure has been previously used to investigate infants' motivational tendencies to approach or avoid emotional situations (e.g., Davidson & Fox, 1982, 1989; Fox & Davidson, 1986, 1987, 1988). Following previous infant EEG studies on emotion reactivity (e.g., Buss et al., 2003; Davidson & Fox, 1982, 1898; Fox & Davidson, 1988; Jones et al., 2000), we hypothesized that those infants who show more right frontal activation when observing a peer crying would respond with more withdrawal-related behaviors (e.g., negative vocalizations, facial expressions of anger, attempts to escape from chair) towards a peer crying. Additionally, we hypothesised that infants who show more left frontal activation when observing a peer laughing would respond with more approach-related behaviors (e.g., positive vocalizations, facial expressions of joy, attempts to reach towards the stimuli) in response to a peer laughing. Together, the first two studies provide substantial data regarding infants' responsiveness to their peers' positive and negative emotions, adding new insights into the field of social cognition development.

Following on, Papers 3 and 4 address higher order cognitive processes by investigating the potential neurocognitive mechanisms underlying affective and cognitive aspects of empathy. The study presented in Paper 3 used electromyopraphy (EMG) to examine the role of motor mimicry and emotion evaluation processes as potential neurocgontive mechanisms involved in the generation of in infants' spontaneous facial reactions (SFRs) to others' emotional facial expressions. Infants were presented three dynamic facial expressions (i.e., happiness, anger, and fear). We measured three facial muscle groups that are selectively activated in response to these facial displays (i.e., zygomaticus major for smiling during happiness, corrugator supercilli for frowning in anger, and frontalis for forehead raising in anger displays). The main goal of this study was to test the automatic transmission of emotions account in infancy, where the influence of language, cultural norms and values in the processing of emotional information is minimal. If SFRs rely solely on motor mimicry processes then we would expect infants' SFRs towards others' facial emotional expressions to closely resemble the observed motor model (e.g., the activation of the zygomaticus major – the muscle which raise the corner of the mouth during smiling - when observing someone smiling but not when observing a fearful face). Conversely, if SFRs rely on additional neurocognitive mechanisms, different to motor mimicry, we would expect infants' SFRs to converge with their own, i.e., the observer's, affective state, which might differ from the emotion perceived (e.g., fear in response to anger).

Paper 4 goes on to explore the ontogenesis of cognitive aspects of empathy by examining the neural correlates underlying 15-month-olds' ability to process others' beliefs, thought to be crucial for the development of more mature forms of empathy during the second year of life. This fourth study used a non-verbal false belief (FB) task consisting of visual narratives depicting a female agent acting congruently or incongruently with her FB about the location of an object. EEG activity was recorded during the entire duration of the task. The main objective was to test the extent to which infants' brain responses are sensitive to the incongruences between the agent's actions and the visual narrative suggestive of her FBs by analysing the effects on the N400 component. We anticipated that if 15-month-old infants in our study process the character's actions as being related to the narrative context suggestive of her knowledge about the object's location rather the infants' own knowledge about reality, then an increased N400 will be observed during the last scene of the FBi (false-belief incongruent) trials compared to the FBc (false-belief congruent) trials. Alternatively, if infants are more likely to process the character's actions in relation to the real location of the object, we expect a more negative anterior N400 to be elicited by the FBc than FBi trials.

As a whole, this thesis extends our knowledge of early empathy development by investigating several key processes and mechanisms underpinning the generation of empathic responses during infancy. Identifying the neurophysiological mechanisms involved in early forms of empathy should help us to better understand the ontogeny of some developmental disorders such as autism or psychopathy, in which empathic deficits are common. In this way, the findings here may help improve early diagnosis of children with atypical social development and contribute to more efficient prevention and intervention programmes for these populations.

References

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

Adolphs, R., Sears, L., & Piven, J. (2001). Abnormal processing of social information from faces in autism. *Journal of cognitive neuroscience*, *13*(2), 232-240.

Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: the medial frontal cortex and social cognition. *Nature Reviews Neuroscience, 7*(4), 268-277.

Apperly, I. A., & Butterfill, S. A. (2009). Do humans have two systems to track beliefs and belief-like states?. *Psychological review*, *116*(4), 953.

Astington, J. W., & Jenkins, J. M. (1995). Theory of mind development and social understanding. *Cognition & Emotion*, *9*(2-3), 151-165.

Balconi, M., & Bortolotti, A. (2013). The "simulation" of the facial expression of emotions in case of short and long stimulus duration. The effect of pre-motor cortex inhibition by rTMS. *Brain and cognition*, *83*(1), 114-120.

Bandura, A. (1986). *Social foundations of thought and action: A social-cognitive theory*. Englewood Cliffs, NJ: Prentice-Hall.

Barnet, A.B. (1971). EEG audiometry in children under 3 years of age. *Acta Otolaryngologica, 72*, 1–13.

Barnet, A.B., Ohlrich, E.S., Weiss, I.P., & Shanks, B.L. (1975). Auditory evoked potentials during sleep in normal children from 10 days to 3 years of age. *Electroen Clin Neuro*, *39*, 29–41.

Barnow, S., Lucht, M., & Freyberger, H. J. (2005). Correlates of aggressive and delinquent conduct problems in adolescence. *Aggressive behavior*, *31*(1), 24-39.

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

Barr, R. G. (2006). Crying behavior and its importance for psychosocial development in children. *Encyclopedia on early childhood development. Montreal (QC): Centre of Excellence for Early Childhood Development*, 1-10.

Barr, R. G., Hopkins, B., & Green, J. A. (2000). *Crying as a sign, a symptom and a signal. Clinical, emotional and developmental aspects of infant and toddler crying*. Cambridge University Press.

Barrett, L. F., & Kensinger, E. A. (2010). Context is routinely encoded during emotion perception. *Psychological Science*, *21*(4), 595-599.

Barrett, L. F., Mesquita, B., & Gendron, M. (2011). Context in emotion perception. *Current Directions in Psychological Science*, *20*(5), 286-290.

Batson, C.D. (1991). *The altruism question: Toward a social psychological answer*. Hillsdale, NJ: Erlbaum

Batson, C. D. (2009). These things called empathy. In J. Decety & W. Ickes (Eds.), *The Social Neuroscience of Empathy* (pp. 3-15). Cambridge, MA: MIT Press.

Batson, C. D. (2011). *Altruism in humans*. New York: Oxford University Press.

Bauer, P. J., Wiebe, S. A., Carver, L. J., Waters, J. M., & Nelson, C. A. (2003). Developments in long-term explicit memory late in the first year of life: Behavioral and electrophysiological indices. *Psychological Science*, *14*(6), 629-635.

Baumgartner, T., Willi, M., & Jäncke, L. (2007). Modulation of corticospinal activity by strong emotions evoked by pictures and classical music: a transcranial magnetic stimulation study. *Neuroreport*, *18*(3), 261-265.

Beall, P. M., Moody, E. J., McIntosh, D. N., Hepburn, S. L., & Reed, C. L. (2008). Rapid facial reactions to emotional facial expressions in typically developing children and children with autism spectrum disorder. *Journal of experimental* *child psychology*, *101*(3), 206-223.

Beck, J. E., & Shaw, D. S. (2005). The influence of perinatal complications and environmental adversity on boys' antisocial behavior. *Journal of Child Psychology and Psychiatry*, *46*(1), 35-46.

Belin, P., Zatorre, R. J., Hoge, R., Evans, A. C., & Pike, B. (1999). Event-related fMRI of the auditory cortex. *Neuroimage*, *10*(4), 417-429.

Belin, P., Zatorre, R. J., Lafaille, P., Ahad, P., & Pike, B. (2000). Voice-selective areas in human auditory cortex. *Nature*, *403*(6767), 309.

Bell, M. A., & Cuevas, K. (2012). Using EEG to study cognitive development: Issues and practices. *Journal of Cognition and Development*, *13*(3), 281-294.

Bell, M. A., & Fox, N. A. (1996). Crawling experience is related to changes in cortical organization during infancy: Evidence from EEG coherence. *Developmental psychobiology*, *29*(7), 551-561.

Bell, M. A., & Wolfe, C. D. (2007). The cognitive neuroscience of early socioemotional development. In C. A. Brownell & C. B. Kopp (Eds.), *Socioemotional development in the toddler years: Transitions and transformations* (pp. 345-369). New York: Guilford Press

Bengtsson, H., & Arvidsson, Å. (2011). The impact of developing social perspective-taking skills on emotionality in middle and late childhood. *Social Development*, *20*(2), 353-375.

Bensalah, L., Caillies, S., & Anduze, M. (2016). Links among cognitive empathy, theory of mind, and affective perspective taking by young children. *The Journal of genetic psychology*, *177*(1), 17-31.

Blair, R. J. R. (2001). Neuro-cognitive models of aggression, the antisocial personality disorders and psychopathy. *Journal of Neurology, Neurosurgery & Psychiatry*, 71, 727–731.

Blair, R. J. R. (2005). Responding to the emotions of others: Dissociating forms of empathy through the study of typical and psychiatric populations. *Consciousness and Cognition, 14*(4), 698-718.

Blair, R. J. R. (2008). Fine cuts of empathy and the amygdala: dissociable deficits in psychopathy and autism. *The Quarterly Journal of Experimental Psychology*, *61*(1), 157-170.

Blair, R. J., Colledge, E., Murray, L., & Mitchell, D. G. (2001). A selective impairment in the processing of sad and fearful expressions in children with psychopathic tendencies. *J Abnorm Child Psychol, 29*(6), 491-498.

Blair, R. J. R., Mitchell, D. G. V., Peschardt, K. S., Colledge, E., Leonard, R. A., Shine, J. H., Murray, L.K., & Perrett, D. I. (2004). Reduced sensitivity to others' fearful expressions in psychopathic individuals. *Personality and Individual Differences*, *37*(6), 1111-1122.

Blair, J., Sellars, C., Strickland, I., Clark, F., Williams, A., Smith, M., & Jones, L. (1996). Theory of mind in the psychopath. *Journal of Forensic Psychiatry*, *7*(1), 15-25.

Blairy, S., Herrera, P., & Hess, U. (1999). Mimicry and the judgment of emotional facial expressions. *Journal of Nonverbal behavior*, *23*(1), 5-41.

Blakemore, S. J. (2008). Development of the social brain during adolescence. *Quarterly Journal of Experimental Psychology, 61*(1), 40-49.

Blakemore, S. J. (2012). Imaging brain development: The adolescent brain. *Neuroimage, 61*(2), 397-406.

Blakemore, S. J., & Decety, J. (2001). From the perception of action to the understanding of intention. *Nature reviews. Neuroscience*, *2*(8), 561.

Blasi, A., Lloyd-Fox, S., Sethna, V., Brammer, M. J., Mercure, E., Murray, L., ... & Johnson, M. H. (2015). Atypical processing of voice sounds in infants at risk for autism spectrum disorder. *cortex*, *71*, 122-133.

Blasi, A., Mercure, E., Lloyd-Fox, S., Thomson, A., Brammer, M., Sauter, D., ... & Gasston, D. (2011). Early specialization for voice and emotion processing in the infant brain. *Current Biology*, *21*(14), 1220-1224.

Botvinick, M. M. (2007). Conflict monitoring and decision making: reconciling two perspectives on anterior cingulate function. *Cognitive, Affective, & Behavioral Neuroscience*, *7*(4), 356-366.

Braungart-Rieker, J. M., & Stifter, C. A. (1996). Infants' responses to frustrating situations: Continuity and change in reactivity and regulation. *Child development*, *67*(4), 1767-1779.

Brunet, E., Sarfati, Y., Hardy-Bayle, M. C., & Decety, J. (2000). A PET investigation of the attribution of intentions with a nonverbal task. *Neuroimage, 11*(2), 157-166.

Bugental, D. E., Kaswan, J. W., Love, L. R., & Fox, M. N. (1970). Child versus adult perception of evaluative messages in verbal, vocal, and visual channels. *Developmental Psychology*, *2*(3), 367.

Bunford, N., Kujawa, A., Swain, J. E., Fitzgerald, K. D., Monk, C. S., & Phan, K. L. (2017). Attenuated neural reactivity to happy faces is associated with rule breaking and social problems in anxious youth. *European child & adolescent psychiatry*, *26*(2), 215-230.

Buon, M., Jacob, P., Margules, S., Brunet, I., Dutat, M., Cabrol, D., & Dupoux, E. (2014). Friend or foe? Early social evaluation of human interactions. *PloS one*, *9*(2), e88612.

Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in cognitive sciences*, *4*(6), 215-222.

Buss, K. A., Schumacher, J. R., 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. *Behav Neurosci, 117*(1), 11-20.

Cacioppo, J. T., Petty, R. E., Losch, M. E., & Kim, H. S. (1986). Electromyographic activity over facial muscle regions can differentiate the valence and intensity of affective reactions. *Journal of personality and social psychology*, *50*(2), 260.

Calkins, S. D., & Dedmon, S. E. (2000). Physiological and behavioral regulation in two-year-old children with aggressive/destructive behavior problems. *Journal of abnormal child psychology*, *28*(2), 103-118.

Calkins, S. D., Fox, N. A., & Marshall, T. R. (1996). Behavioral and physiological antecedents of inhibited and uninhibited behavior. *Child Development, 67*(2), 523-540.

Calkins, S. D., & Fox, N. A. (2002). Self-regulatory processes in early personality development: A multilevel approach to the study of childhood social withdrawal and aggression. *Development and psychopathology*, *14*(3), 477-498.

Calkins, S. D., Gill, K. L., Johnson, M. C., & Smith, C. L. (1999). Emotional reactivity and emotional regulation strategies as predictors of social behavior with peers during toddlerhood. *Social development*, *8*(3), 310-334.

Calkins, S. D., & Leerkes, E. M. (2004). Early attachment processes and the development of emotional self-regulation. *Handbook of self-regulation: Research, theory, and applications*, 324-339.

Carlo, G., Mestre, M. V., Samper, P., Tur, A., & Armenta, B. E. (2010). Feelings or cognitions? Moral cognitions and emotions as longitudinal predictors of prosocial and aggressive behaviors. *Personality and Individual Differences*, *48*(8), 872-877.

Caron, A. J., Caron, R. F., & MacLean, D. J. (1988). Infant discrimination of naturalistic emotional expressions: The role of face and voice. *Child development*, 604-616.

Carr, L., Iacoboni, M., Dubeau, M. C., Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proceedings of the national Academy of Sciences*, *100*(9), 5497-5502.

Carver, L. J., Bauer, P. J., & Nelson, C. A. (2000). Associations between infant brain activity and recall memory. *Developmental Science*, *3*(2), 234-246.

Casey, B. J., Giedd, J. N., & Thomas, K. M. (2000). Structural and functional brain development and its relation to cognitive development. *Biological psychology*, *54*(1), 241-257.

Casey, B. J., Jones, R. M., & Hare, T. A. (2008). The adolescent brain. *Annals of the New York Academy of Sciences*, *1124*(1), 111-126.

Casey, B. J., Jones, R. M., & Somerville, L. H. (2011). Braking and accelerating of the adolescent brain. *Journal of Research on Adolescence*, *21*(1), 21-33.

Castelli, F., Frith, C., Happé, F., & Frith, U. (2002). Autism, Asperger syndrome and brain mechanisms for the attribution of mental states to animated shapes. *Brain*, *125*(8), 1839-1849.

Castelli, F., Happe, F., Frith, U., & Frith, C. (2000). Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. *Neuroimage, 12*(3), 314-325.

Čeponienė, R., Cheour, M., & Näätänen, R. (1998). Interstimulus interval and auditory event-related potentials in children: Evidence for multiple generators. *Electroencephalography and Clinical Neurophysiology, 108*(4), 345-354

Chase-Lansdale, P. L., Wakschlag, L. S., & Brooks-Gunn, J. (1995). A psychological perspective on the development of caring in children and youth: The role of the family. *Journal of Adolescence*, *18*(5), 515-556.

Cheng, Y., Lee, S. Y., Chen, H. Y., Wang, P. Y., & Decety, J. (2012). Voice and emotion processing in the human neonatal brain. *Journal of cognitive neuroscience*, *24*(6), 1411-1419.

Choudhury, N., & Benasich, A. A. (2011). Maturation of auditory evoked potentials from 6 to 48 months: prediction to 3 and 4 year language and cognitive abilities. *Clinical Neurophysiology*, *122*(2), 320-338.

Chronaki, G., Benikos, N., Fairchild, G., & Sonuga-Barke, E. J. (2015). Atypical neural responses to vocal anger in attention-deficit/hyperactivity disorder. *Journal of Child Psychology and Psychiatry*, *56*(4), 477-487.

Chronaki, G., Broyd, S., Garner, M., Hadwin, J. A., Thompson, M. J., & Sonuga-Barke, E. J. (2012). Isolating N400 as neural marker of vocal anger processing in 6–11-year old children. *Developmental Cognitive Neuroscience*, *2*(2), 268-276.

Clark, K. E., & Ladd, G. W. (2000). Connectedness and autonomy support in parent–child relationships: Links to children's socioemotional orientation and peer relationships. *Developmental psychology*, *36*(4), 485.

Coan, J. A., & Allen, J. J. (2004). Frontal EEG asymmetry as a moderator and mediator of emotion. *Biol Psychol, 67*(1-2), 7-49.

Coelho, C. M., Lipp, O. V., Marinovic, W., Wallis, G., & Riek, S. (2010). Increased corticospinal excitability induced by unpleasant visual stimuli. *Neuroscience letters*, *481*(3), 135-138.

Conty, L., Dezecache, G., Hugueville, L., & Grèzes, J. (2012). Early binding of gaze, gesture, and emotion: neural time course and correlates. *Journal of Neuroscience*, *32*(13), 4531-4539.

Coombes, S. A., Tandonnet, C., Fujiyama, H., Janelle, C. M., Cauraugh, J. H., & Summers, J. J. (2009). Emotion and motor preparation: a transcranial magnetic stimulation study of corticospinal motor tract excitability. *Cognitive, Affective, & Behavioral Neuroscience*, *9*(4), 380-388.

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

Crone, E. A., & Ridderinkhof, K. R. (2011). The developing brain: from theory to neuroimaging and back. *Developmental Cognitive Neuroscience*, *1*(2), 101-109.

Cuthbert, B. N., Schupp, H. T., Bradley, M. M., Birbaumer, N., & Lang, P. J. (2000). Brain potentials in affective picture processing: covariation with autonomic arousal and affective report. *Biological psychology*, *52*(2), 95-111.

Dapretto, M., Davies, M. S., Pfeifer, J. H., Scott, A. A., Sigman, M., Bookheimer, S. Y., & Iacoboni, M. (2006). Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders. *Nature neuroscience*, *9*(1), 28.

Davidson, R. J., & Fox, N. A. (1982). Asymmetrical Brain Activity Discriminates between Positive and Negative Affective Stimuli in Human Infants. *Science, 218*(4578), 1235-1237.

Davidson, R. J., & Fox, N. A. (1989). Frontal Brain Asymmetry Predicts Infants Response to Maternal Separation. *Journal of Abnormal Psychology, 98*(2), 127-131.

Davidson, R. J., Jackson, D. C., & Larson, C. L. (2000). Human electroencephalography. *Handbook of psychophysiology*, *2*, 27-52.

Davis, M. H., Luce, C., & Kraus, S. J. (1994). The heritability of characteristics associated with dispositional empathy. *Journal of personality*, *62*(3), 369-391.

Dawson, G. (1994). Frontal electroencephalographic correlates of individual differences in emotion expression in infants: a brain systems perspective on emotion. *Monogr Soc Res Child Dev, 59*(2-3), 135-151.

De Haan, M., Belsky, J., Reid, V., Volein, A., & Johnson, M. H. (2004). Maternal personality and infants' neural and visual responsivity to facial expressions of emotion. *Journal of Child Psychology and Psychiatry*, *45*(7), 1209-1218.

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., & Nelson, C. A. (1999). Brain activity differentiates face and object processing in 6-month-old infants. *Developmental psychology*, *35*(4), 1113.

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 Vignemont, F., & Singer, T. (2006). The empathic brain: how, when and why?. *Trends in cognitive sciences*, *10*(10), 435-441.

De Waal, F. (2009). *Primates and philosophers: How morality evolved*. Princeton University Press.

Decety, J. (2005). Perspective taking as the royal avenue to empathy. In B.F. Malle & S.D. Hodges (Eds.), *Other minds: How humans bridge the divide between self and others* (pp. 143-157). New York: Guildford Press.

Decety, J. (2007). A social cognitive neuroscience model of human empathy. In E. Harmon-Jones & P. Winkielman (Eds.), *Social neuroscience: Integrating biological and psychological explanations of social behavior* (pp. *246*, 270). New York: Guilford Press

Decety, J. (2010a). The neurodevelopment of empathy in humans. *Dev Neurosci, 32*(4), 257-267.

Decety, J. (2010b). To what extent is the experience of empathy mediated by shared neural circuits?. *Emotion Review*, *2*(3), 204-207.

Decety, J. (2015). The neural pathways, development and functions of empathy. *Current Opinion in Behavioral Sciences*, *3*, 1-6.

Decety, J., & Grèzes, J. (2006). The power of simulation: imagining one's own and other's behavior. *Brain research*, *1079*(1), 4-14.

Decety, J., & Howard, L. H. (2013). The role of affect in the neurodevelopment of morality. *Child Development Perspectives*, *7*(1), 49-54.

Decety, J., & Jackson, P. L. (2004). The functional architecture of human empathy. *Behav Cogn Neurosci Rev, 3*(2), 71-100.

Decety, J., & Lamm, C. (2006). Human empathy through the lens of social neuroscience. *ScientificWorldJournal, 6*, 1146-1163.

Decety, J., & Meyer, M. (2008). From emotion resonance to empathic understanding: A social developmental neuroscience account. *Development and Psychopathology, 20*(4), 1053-1080.

Decety, J., & Michalska, K. J. (2010). Neurodevelopmental changes in the circuits underlying empathy and sympathy from childhood to adulthood. *Developmental Science, 13*(6), 886-899.

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., Michalska, K. J., Akitsuki, Y., & Lahey, B. B. (2009). Atypical empathic responses in adolescents with aggressive conduct disorder: a functional MRI investigation. *Biological psychology*, *80*(2), 203-211.

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

Degangi, G. A., Dipietro, J. A., Greenspan, S. I., & Porges, S. W. (1991). Psychophysiological characteristics of the regulatory disordered infant. *Infant Behavior and Development*, *14*(1), 37-50.

Dennis, T. A. (2010). Neurophysiological markers for child emotion regulation from the perspective of emotion–cognition integration: Current directions and future challenges. *Developmental neuropsychology*, *35*(2), 212-230.

Dennis, T. A., Malone, M. M., & Chen, C. C. (2009). Emotional face processing and emotion regulation in children: An ERP study. *Developmental neuropsychology*, *34*(1), 85-102.

Dezecache, G., Eskenazi, T., & Grèzes, J. (2016). Emotional Convergence: A Case of Contagion? In S.S. Obhi & E.S. Cross (Eds.), *Shared Representations: Sensorimotor Foundations of Social Life.* Cambridge University Press.

Diamond, A. (2002). Normal development of prefrontal cortex from birth to young adulthood: Cognitive functions, anatomy, and biochemistry. *Principles of frontal lobe function*, 466-503.

Diaz, A., & Bell, M. A. (2012). Frontal EEG asymmetry and fear reactivity in different contexts at 10 months. *Developmental Psychobiology, 54*(5), 536-545.

Dimberg, U. (1982). Facial reactions to facial expressions. *Psychophysiology*, *19*(6), 643-647.

Dimberg, U., Thunberg, M., & Elmehed, K. (2000). Unconscious facial reactions to emotional facial expressions. *Psychological science*, *11*(1), 86-89.

Dolan, M., & Fullam, R. (2004). Theory of mind and mentalizing ability in antisocial personality disorders with and without psychopathy. *Psychol Med, 34*(6), 1093-1102.

Dondi, M., Simion, F., & Caltran, G. (1999). Can newborns discriminate between their own cry and the cry of another newborn infant?. *Developmental psychology*, *35*(2), 418.

Dunbar, R.I., Baron, R., Frangou, A., Pearce, E., van Leeuwin, E. J. C., Stow, J., … van Vugt, M. (2012). Social laughter is correlated with an elevated pain threshold. *Proceedings of the Royal Society B: Biological Sciences, 22*(279), 1161-1167.

Dziobek, I., Rogers, K., Fleck, S., Bahnemann, M., Heekeren, H. R., Wolf, O. T., & Convit, A. (2008). Dissociation of cognitive and emotional empathy in adults with Asperger syndrome using the Multifaceted Empathy Test (MET). *Journal of autism and developmental disorders*, *38*(3), 464-473.

Eisenberg, N. (2000). Emotion, regulation, and moral development. *Annual review of psychology*, *51*(1), 665-697.

Eisenberg, N., & Eggum, N. D. (2009). Empathic responding: Sympathy and personal distress. *The social neuroscience of empathy*, *6*, 71-83.

Eisenberg, N., & Fabes, R. A. (1992). Emotion, regulation, and the development of social competence. In M. S. Clark (Ed.), *Review of Personality and Social Psychology: Emotion and Social Behavior* (pp.119-150). Newbury Park, CA: Sage.

Eisenberg, N., & Fabes, R. A. (1995). The relation of young children's vicarious emotional responding to social competence, regulation, and emotionality. *Cognition & Emotion*, *9*, 203-229.

Eisenberg, N., Fabes, R. A., Murphy, B., Karbon, M., Smith, M., & Maszk, P. (1996). The relations of children's dispositional empathy-related responding to their emotionality, regulation, and social functioning. *Developmental psychology*, *32*(2), 195.

Eisenberg, N., Fabes, R. A., Schaller, M., Carlo, G., & Miller, P. A. (1991). The relations of parental characteristics and practices to children's vicarious emotional responding. *Child development*, *62*(6), 1393-1408.

Eisenberg, N., Fabes, R. A., Shepard, S. A., Murphy, B. C., Jones, S., & Guthrie, I. K. (1998). Contemporaneous and longitudinal prediction of children's sympathy from dispositional regulation and emotionality. *Developmental Psychology*, *34*, 910.

Eisenberg, N., Spinrad, T. L., & Sadovsky, A. (2006). Empathy-related responding in children. *Handbook of moral development*, *517*, 549.

Eisenberg, N., & Valiente, C. (2002). Parenting and children’s prosocial and moral development. *Handbook of parenting*, *5*, 111-142.

Engen, H. G., & Singer, T. (2013). Empathy circuits. *Curr Opin Neurobiol, 23*(2), 275-

282.

Ernst, M. (2014). The triadic model perspective for the study of adolescent motivated behavior. *Brain Cognition, 89*, 104–111.

Ernst, M., Pine, D., Hardin, M., (2006). Triadic model of the neurobiology of motivated behavior in adolescence. *Psychological Medicine, 36*, 299–31.

Esposito, G., Nakazawa, J., Venuti, P., & Bornstein, M. H. (2013). Componential deconstruction of infant distress vocalizations via tree-based models: A study of cry in autism spectrum disorder and typical development. *Research in Developmental Disabilities*, *34*(9), 2717-2724.

Esposito, G., Venuti, P., & Bornstein, M. H. (2011). Assessment of distress in young children: A comparison of autistic disorder, developmental delay, and typical development. *Research in Autism Spectrum Disorders*, *5*(4), 1510-1516.

Fan, Y., Duncan, N. W., de Greck, M., & Northoff, G. (2011). Is there a core neural network in empathy? An fMRI based quantitative meta-analysis. *Neurosci Biobehav Rev, 35*(3), 903-911.

Fernald, A. (1993). Approval and disapproval: Infant responsiveness to vocal affect in familiar and unfamiliar languages. *Child development*, *64*(3), 657-674.

Fernald, A., Taeschner, T., Dunn, J., Papousek, M., Deboyssonbardies, B., & Fukui, I. (1989). A Cross-Language Study of Prosodic Modifications in Mothers and Fathers Speech to Preverbal Infants. *Journal of Child Language, 16*(3), 477-501.

Field, T., Diego, M., Hernandez-Reif, M., & Fernandez, M. (2007). Depressed mothers' newborns show less discrimination of other newborns' cry sounds. *Infant Behavior and Development*, *30*(3), 431-435.

Field, T., Pickens, J., Fox, N. A., Gonzalez, J., & Nawrocki, T. (1998). Facial expression and EEG responses to happy and sad faces/voices by 3-month-old infants of depressed mothers. *British Journal of Developmental Psychology*, *16*(4), 485-494.

Flavell, J. H. (1988). The development of children’s knowledge about the mind: From cognitive connections to mental representations. In J. W. Astington, P.L. Harris, & D.R. Olson (Eds.), *Developing theories of mind* (pp. 244-267). New York: Cambridge University Press.

Fletcher, P. C., Happe, F., Frith, U., Baker, S. C., Dolan, R. J., Frackowiak, R. S., & Frith, C. D. (1995). Other minds in the brain: a functional imaging study of “theory of mind” in story comprehension. *Cognition*, *57*(2), 109-128.

Flom, R., & Bahrick, L. E. (2007). The development of infant discrimination of affect in multimodal and unimodal stimulation: The role of intersensory redundancy. *Developmental psychology*, *43*(1), 238.

Fortuna, K., & Knafo, A. (2014). Parental and genetic contributions to prosocial behavior during childhood. *Prosocial development: A multidimensional approach*, 70-89.

Foti, D., Olvet, D. M., Klein, D. N., & Hajcak, G. (2010). Reduced electrocortical response to threatening faces in major depressive disorder. *Depression and anxiety*, *27*(9), 813-820.

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

Fox, N. A. (1994). Dynamic cerebral processes underlying emotion regulation. *Monographs of the society for research in child development*, *59*(2-3), 152-166.

Fox, N. A., & Calkins, S. D. (2003). The development of self-control of emotion: Intrinsic and extrinsic influences. *Motivation and emotion*, *27*(1), 7-26.

Fox, N. A., & Davidson, R. J. (1986). Taste-Elicited Changes in Facial Signs of Emotion and the Asymmetry of Brain Electrical-Activity in Human Newborns. *Neuropsychologia, 24*(3), 417-422.

Fox, N. A., & Davidson, R. J. (1987). Patterns of Eeg Asymmetry Reflect the Presence of Discrete Emotions in 10-Month-Old Infants. *Journal of Clinical and Experimental Neuropsychology, 9*(1), 71-71.

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.

Fox, N. A., Henderson, H. A., Rubin, K. H., Calkins, S. D., & Schmidt, L. A. (2001). Continuity and discontinuity of behavioral inhibition and exuberance: Psychophysiological and behavioral influences across the first four years of life. *Child Development, 72*(1), 1-21.

Fox, N. A., Rubin, K. H., Calkins, S. D., Marshall, T. R., Coplan, R. J., Porges, S. W., Long, J.M., & Stewart, S. (1995). Frontal activation asymmetry and social competence at four years of age. *Child Development, 66*(6), 1770-1784.

Fox, S. E., Wagner, J. B., Shrock, C. L., Tager-Flusberg, H., & Nelson, C. A. (2013). Neural processing of facial identity and emotion in infants at high-risk for autism spectrum disorders. *Frontiers in human neuroscience*, *7*.

Frith, C. D. (2007). The social brain?. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *362*(1480), 671-678.

Frith, C. D., & Frith, U. (1999). Interacting minds--a biological basis. *Science*, *286*(5445), 1692-1695.

Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *358*(1431), 459-473.

Gallagher, H. L., Happé, F., Brunswick, N., Fletcher, P. C., Frith, U., & Frith, C. D. (2000). Reading the mind in cartoons and stories: an fMRI study of 'theory of mind'in verbal and nonverbal tasks. *Neuropsychologia*, *38*(1), 11-21.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*(2), 593-609.

Garaigordobil, M. (2009). A comparative analysis of empathy in childhood and adolescence: Gender differences and associated socio-emotional variables. *International Journal of Psychology and psychological therapy*, *9*(2).

García-Larrea, L., Lukaszewicz, A. C., & Mauguiére, F. (1992). Revisiting the oddball paradigm. Non-target vs. neutral stimuli and the evaluation of ERP attentional effects. *Neuropsychologia*, *30*(8), 723-741

Geangu, E. (2015). Development of empathy furing early childhood across cultures. In J. D. Wright (Ed.), *International Encyclopedia of the Social and Behavioral Sciences* (pp. 549–553). Elsevier.

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

Geangu, E., Hauf, P., Bhardwaj, R., & Bentz, W. (2011). Infant pupil diameter changes in response to others' positive and negative emotions. *PloS one*, *6*(11), e27132.

Giedd, J. N., Blumenthal, J., Jeffries, N. O., Castellanos, F. X., Liu, H., Zijdenbos, A., ... & Rapoport, J. L. (1999). Brain development during childhood and adolescence: a longitudinal MRI study. *Nature neuroscience*, *2*(10), 861-863.

Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., ... & Rapoport, J. L. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National academy of Sciences of the United States of America*, *101*(21), 8174-8179.

Gottlieb G. (1971). Ontogenesis of sensory function in birds and mammals. In E. Tobach, L.R. Aronson, & E. Shaw (Eds.), The biopsychology of development (pp. 67–128). New York: Academic Press

Grèzes, J. & Dezecache, G. (2014). How do shared-representations and emotional processes cooperate in response to social threat signals ? *Neuropsychologia,* 1–10.

Grogan-Kaylor, A. (2005). Corporal punishment and the growth trajectory of children's antisocial behavior. *Child Maltreatment*, *10*(3), 283-292.

Gross, J. J., & Thompson, R. A. (2007). Emotion regulation: Conceptual foundations. In J. Gross (Ed.), *Handbook of Emotion Regulation* (pp. 3-24). New York: Guilford Press.

Grossmann, T. (2010). The development of emotion perception in face and voice during infancy. *Restorative neurology and neuroscience*, *28*(2), 219-236.

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

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.

Gurthrie, I. K., Eisenberg, N., Fabes, R. A., Murphy, B. C., Holmgren, R., Mazsk, P., & Suh, K. (1997). The relations of regulation and emotionality to children's situational empathy-related responding. *Motivation and Emotion*, *21*(1), 87-108.

Gweon, H., Dodell-Feder, D., Bedny, M., & Saxe, R. (2012). Theory of mind performance in children correlates with functional specialization of a brain region for thinking about thoughts. *Child development*, *83*(6), 1853-1868.

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.

Hamilton, A. (2015). The social function of the human mirror system: a motor chauvinist view. In S.S. Obhi & E.S. Cross (Eds.), *Shared Representations: Sensoriomotor foundations of social life*. Cambridge University Press.

Hamlin, J. K. (2013). Moral judgment and action in preverbal infants and toddlers: Evidence for an innate moral core. *Current Directions in Psychological Science*, *22*(3), 186-193.

Hamlin, J. K. (2015). Does the Infant Possess a Moral Concept?. In E. Margolis & S. Laurence (Eds.), *The conceptual mind: New directions in the study of concepts* (pp. 477-518). Cambridge, MA: The MIT Press.

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

Hamlin, J. K., & Wynn, K. (2011). Young infants prefer prosocial to antisocial others. *Cognitive development*, *26*(1), 30-39.

Happé, F., Ehlers, S., Fletcher, P., Frith, U., Johansson, M., Gillberg, C., Dolan, R., Frackowiak, R., & Frith, C. (1996). 'Theory of mind'in the brain. Evidence from a PET scan study of Asperger syndrome. *Neuroreport*, *8*(1), 197-201.

Happé, F., Malhi, G. S., & Checkley, S. (2001). Acquired mind-blindness following frontal lobe surgery? A single case study of impaired 'theory of mind'in a patient treated with stereotactic anterior capsulotomy. *Neuropsychologia*, *39*(1), 83-90.

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. *Biol Psychol, 84*(3), 451-462.

Harris, P. L. (1994). The child's understanding of emotion: Developmental change and the family environment. *Journal of Child Psychology and Psychiatry*, *35*(1), 3-28.

Hart, H. C., Palmer, A. R., & Hall, D. A. (2003). Amplitude and frequency-modulated stimuli activate common regions of human auditory cortex. *Cerebral Cortex*, *13*(7), 773-781.

Hastings, M. E., Tangney, J. P., & Stuewig, J. (2008). Psychopathy and identification of facial expressions of emotion. *Personality and individual differences*, *44*(7), 1474-1483.

Hatfield, E., Cacioppo, J. T. & Rapson, R. L. (1993).Emotional contagion. *Current Directions Psychological Science, 2*, 96–100.

Hatfield, E., Cacioppo, J. T., & Rapson, R. L. (1994). *Emotional contagion*: Cambridge studies in emotion and social interaction. Cambridge, UK: Cambridge University Press.

Hatfield, E., Rapson, R. L., & Le, Y. C. (2009). *Emotional contagion and empathy*. MIT. Cambridge, MA.

Haviland, J. M., & Lelwica, M. (1987). The Induced Affect Response - 10-Week-Old Infants Responses to 3 Emotion Expressions. *Developmental Psychology, 23*(1), 97-104.

Hawkins, J. D., Herrenkohl, T. I., Farrington, D. P., Brewer, D., Catalano, R. F., Harachi, T. W., & Cothern, L. (2000). Predictors of Youth Violence. *Juvenile Justice Bulletin*.

Hay, D. F., Nash, A., & Pedersen, J. (1981). Responses of 6-Month-Olds to the Distress of Their Peers. *Child Development, 52*(3), 1071-1075.

Hein, G., & Singer, T. (2008). I feel how you feel but not always: the empathic brain and its modulation. *Current Opinion in Neurobiology, 18*(2), 153-158.

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 and Adolescent Psychiatry, 40*(1), 68-74.

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.

Hess, U., Adams Jr, R., & Kleck, R. (2005). Who may frown and who should smile? Dominance, affiliation, and the display of happiness and anger. *Cognition & Emotion*, *19*(4), 515-536.

Hess, U., & Fischer, A. (2013). Emotional mimicry as social regulation. *Personality and Social Psychology Review*, *17*(2), 142-157.

Hill, E. L., & Frith, U. (2003). Understanding autism: insights from mind and brain. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *358*(1430), 281-289.

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

Hoffman, M. (1975). Development synthesis of affect and cognition and its implications of altruistic motivation. *Developmental Psychology, 23*, 97-104.

Hoffman, M. (1982). Development of prosocial motivation: Empathy and guilt. In N. Eisenberg (Ed.), *The development of prosocial behavior* (pp. 281-313). New York: Academic Press.

Hoffman, M. L. (2001). *Empathy and moral development: Implications for caring and justice*. Cambridge University Press.

Holvoet, C., Scola, C., Arciszewski, T., & Picard, D. (2016). Infants' preference for prosocial behaviors: A literature review. *Infant Behavior and Development*, *45*, 125-139.

Homae, F., Watanabe, H., Nakano, T., Asakawa, K., & Taga, G. (2006). The right hemisphere of sleeping infant perceives sentential prosody. *Neuroscience research*, *54*(4), 276-280.

Hornik, R., Risenhoover, N., & Gunnar, M. (1987). The effects of maternal positive, neutral, and negative affective communications on infant responses to new toys. *Child development*, 937-944.

Howes, C., & Farver, J. (1987). Toddler's response to the distress of their peers. *Journal of Applied Developmental Psychology*, 8, 441-45.

Huffman, L. C., Bryan, Y. E., & del Carmen, R. del, CR, Pedersen, FA, Doussard-Roosevelt, JA, & Porges, SW (1998). Infant temperament and cardiac vagal tone: assessments at twelve weeks of age. *Child Development*, *69*, 624-635.

Hughes, C., White, A., Sharpen, J., & Dunn, J. (2000). Antisocial, angry, and unsympathetic:"Hard-to-manage" preschoolers' peer problems and possible cognitive influences. *The Journal of Child Psychology and Psychiatry and Allied Disciplines*, *41*(2), 169-179.

Huttenlocher, P. R., & Dabholkar, A. S. (1997). Regional differences in synaptogenesis in human cerebral cortex. *Journal of comparative Neurology*, *387*(2), 167-178.

Ishijima, K., & Negayama, K. (2017). Development of mother–infant interaction in tickling play: The relationship between infants' ticklishness and social behaviors. *Infant Behavior and Development*, *49*, 161-167.

Isomura, T., & Nakano, T. (2016). Automatic facial mimicry in response to dynamic emotional stimuli in five-month-old infants. *Proceedings of the Royal Society B-Biological Sciences, 283*(1844).

Jessen, S., & Kotz, S. A. (2011). The temporal dynamics of processing emotions from vocal, facial, and bodily expressions. *Neuroimage*, *58*(2), 665-674.

Johnson, M. H. (2001). Functional brain development in humans. *Nature reviews. Neuroscience*, *2*(7), 475.

Johnson, M. H., Gliga, T., Jones, E., & Charman, T. (2015). Annual Research Review: Infant development, autism, and ADHD–early pathways to emerging disorders. *Journal of Child Psychology and Psychiatry*, *56*(3), 228-247.

Kahana-Kalman, R., & Walker-Andrews, A. S. (2001). The role of person familiarity in young infants' perception of emotional expressions. *Child Development, 72*(2), 352-369.

Kanske, P., & Kotz, S. A. (2007). Concreteness in emotional words: ERP evidence from a hemifield study. *Brain research*, *1148*, 138-148.

Kestenbaum, R., Farber, E. A., & Sroufe, L. A. (1989). Individual differences in empathy among preschoolers: Relation to attachment history. *New Directions for Child and Adolescent Development*, *1989*(44), 51-64.

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.

Kilford, E. J., Garrett, E., & Blakemore, S. J. (2016). The development of social cognition in adolescence: An integrated perspective. *Neuroscience & Biobehavioral Reviews*, *70*, 106-120.

Killeen, L. A., & Teti, D. M. (2012). Mothers' frontal EEG asymmetry in response to infant emotion states and mother-infant emotional availability, emotional experience, and internalizing symptoms. *Development and Psychopathology, 24*(1), 9-21.

Killgore, W. D., Oki, M., & Yurgelun-Todd, D. A. (2001). Sex-specific developmental changes in amygdala responses to affective faces. *Neuroreport*, *12*(2), 427-433.

Killgore, W. D., & Yurgelun-Todd, D. A. (2007). Unconscious processing of facial affect in children and adolescents. *Social Neuroscience*, *2*(1), 28-47.

Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: an account of the mirror neuron system. *Cognitive processing*, *8*(3), 159-166.

Knafo, A., & Israel, S. (2012). Empathy, prosocial behavior, and other aspects of kindness. In M. Zentner & R. L. Shiner (Eds.), The *Handbook of temperament* (pp. 168-182). New York: Guilford Press.

Knafo, A., Israel, S., & Ebstein, R. P. (2011). Heritability of children's prosocial behavior and differential susceptibility to parenting by variation in the dopamine receptor D4 gene. *Development and psychopathology*, *23*(1), 53-67.

Knafo, A., & Plomin, R. (2006). Prosocial behavior from early to middle childhood: genetic and environmental influences on stability and change. *Developmental psychology*, *42*(5), 771.

Knafo, A., & Uzefovsky, F. (2013). Variation in empathy: The interplay of genetic and environmental factors. In M. H. Bornstein, D. W. Haley, & M. T. Legerstee (Eds.), *The infant mind: Origins of the social brain*, (pp. 97-122). New York: Guilford Press.

Knafo, A., Zahn-Waxler, C., Van Hulle, C., Robinson, J. L., & Rhee, S. H. (2008). The developmental origins of a disposition toward empathy: Genetic and environmental contributions. *Emotion*, *8*(6), 737.

Kobayashi, C., Glover, G. H., & Temple, E. (2007). Children's and adults' neural bases of verbal and nonverbal 'theory of mind'. *Neuropsychologia*, *45*(7), 1522-1532.

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.

Kochanska, G. (1995). Children's temperament, mothers' discipline, and security of attachment: Multiple pathways to emerging internalization. *Child development*, *66*(3), 597-615.

Kochanska, G., Coy, K. C., & Murray, K. T. (2001). The development of self-regulation in the first four years of life. *Child development*, *72*(4), 1091-1111.

Kochanska, G., Forman, D. R., & Coy, K. C. (1999). Implications of the mother-child relationship in infancy for socialization in the second year of life. *Infant Behavior and Development*, *22*(2), 249-265.

Kochanska, G., Gross, J. N., Lin, M. H., & Nichols, K. E. (2002). Guilt in young children: Development, determinants, and relations with a broader system of standards. *Child development*, *73*(2), 461-482.

Kochanska, G., Murray, K., & Coy, K. C. (1997). Inhibitory control as a contributor to conscience in childhood: From toddler to early school age. *Child development*, *68*(2), 263-277.

Kochanska, G., Tjebkes, J. L., & Fortnan, D. R. (1998). Children's emerging regulation of conduct: Restraint, compliance, and internalization from infancy to the second year. *Child development*, *69*(5), 1378-1389.

Kopp, C. B. (1982). Antecedents of self-regulation: A developmental perspective. *Developmental psychology*, *18*(2), 199.

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

Kopp, C. B., & Neufeld, S. J. (2003). Emotional development during infancy. In R.J. Davidson, K.R. Scherer, & H.H. Goldsmith (Eds.), *Handbook of affective sciences* (pp. 347-374). New York: Oxford University Press.

Krevans, J., & Gibbs, J. C. (1996). Parents' use of inductive discipline: Relations to children's empathy and prosocial behavior. *Child development*, *67*(6), 3263-3277.

Kurtzberg, D., Hilpert P. .L, Kreuzer J. A., & Vaughan H. G. J. (1984). Differential maturation of cortical auditory evoked potentials to speech sounds in normal full term and very low-birthweight infants. *Dev Med Child Neurol, 26*, 466–475.

Kushnerenko, E., Ceponiene, R., Balan, P., Fellman, V., Huotilainen, M., & Näätänen, R. (2002). Maturation of the auditory event-related potentials during the first year of life. *Neuroreport*, *13*(1), 47-51.

Laible, D. J., & Carlo, G. (2004). The differential relations of maternal and paternal support and control to adolescent social competence, self-worth, and sympathy. *Journal of Adolescent Research*, *19*(6), 759-782.

Lanzetta, J. T., & Englis, B. G. (1989). Expectations of cooperation and competition and their effects on observers' vicarious emotional responses. *Journal of personality and social psychology*, *56*(4), 543.

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.

Leocani, L., Toro, C., Manganotti, P., Zhuang, P., & Hallett, M. (1997). Event-related coherence and event-related desynchronization/synchronization in the 10 Hz and 20 Hz EEG during self-paced movements. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *104*(3), 199-206.

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. (2008). Tuning the developing brain to social signals of emotions. *Nature Reviews Neuroscience*, *10*(1), nrn2554.

Lerner, M. D., McPartland, J. C., & Morris, J. P. (2013). Multimodal emotion processing in autism spectrum disorders: an event-related potential study. *Developmental cognitive neuroscience*, *3*, 11-21.

Lewis, M. D., Granic, I., & Lamm, C. (2006). Neurocognitive mechanisms of emotion regulation and behavioral flexibility in aggressive children. *Proceedings of the New York Academy of Sciences, USA*, *1094*, 164-177.

Lewis, M. D., Lamm, C., Segalowitz, S. J., Stieben, J., & Zelazo, P. D. (2006). Neurophysiological correlates of emotion regulation in children and adolescents. *Journal of cognitive neuroscience*, *18*(3), 430-443.

Lewkowicz, D. J. (1988a). Sensory dominance in infants: I. Six-month-old infants' response to auditory-visual compounds. *Developmental Psychology*, *24*(2), 155.

Lewkowicz, D. J. (1988b). Sensory dominance in infants: II. Ten-month-old infants' response to auditory-visual compounds. *Developmental Psychology*, *24*(2), 172.

Licata, M., Paulus, M., Kuhn-Popp, N., Meinhardt, J., & Sodian, B. (2015). Infant frontal asymmetry predicts child emotional availability. *International Journal of Behavioral Development, 39*(6), 492-496.

Liddle, M. J. E., Bradley, B. S., & Mcgrath, A. (2015). Baby empathy: Infant distress and peer prosocial responses. *Infant Mental Health Journal*, *36*, 446–458.

Liegeois-Chauvel, C., Musolino, A., Badier, J. M., Marquis, P., & Chauvel, P. (1994). Evoked potentials recorded from the auditory cortex in man: evaluation and topography of the middle latency components. *Electroenceph clin Neurophysiol, 92*, 204-214.

Liew, J., Eisenberg, N., Spinrad, T. L., Eggum, N. D., Haugen, R. G., Kupfer, A., Reiser, M.R., Smith, C.L., Lemery-Chalfant, K., & Baham, M. E. (2011). Physiological Regulation and Fearfulness as Predictors of Young Children's Empathy-related Reactions. *Social Development, 20*(1), 111-113.

Likowski, K. U., Mühlberger, A., Seibt, B., Pauli, P., & Weyers, P. (2011). Processes underlying congruent and incongruent facial reactions to emotional facial expressions. *Emotion*, *11*(3), 457.

Lipps, T. (1907). Das wissen von fremden Ichen. *Psychologische untersuchungen*, *1*(4), 694-722.

Liszkowski, U., Carpenter, M., Striano, T., & Tomasello, M. (2006). 12-and 18-month-olds point to provide information for others. *Journal of Cognition and Development*, *7*(2), 173-187.

Little, V. M., Thomas, D. G., & Letterman, M. R. (1999). Single-trial analyses of developmental trends in infant auditory event-related potentials. *Developmental Neuropsychology*, *16*(3), 455-478.

Liu, T., Pinheiro, A. P., Deng, G., Nestor, P. G., McCarley, R. W., & Niznikiewicz, M. A. (2012). Electrophysiological insights into processing nonverbal emotional vocalizations. *NeuroReport*, *23*(2), 108-112.

Liu, D., Sabbagh, M. A., Gehring, W. J., & Wellman, H. M. (2009). Neural correlates of children's theory of mind development. *Child Development, 80*(2), 318-326.

LoBue, V., Coan, J. A., Thrasher, C., & DeLoache, J. S. (2011). Prefrontal Asymmetry and Parent-Rated Temperament in Infants. *PLoS One, 6*(7).

Ludemann, P. M., & Nelson, C. A. (1988). Categorical representation of facial expressions by 7-month-old infants. *Developmental Psychology*, *24*(4), 492.

Luo, Y. (2011). Do 10-month-old infants understand others' false beliefs? *Cognition, 121*(3), 289-298.

Luu, P., & Tucker, D. M. (2004). Self-regulation by the medial frontal cortex. *Consciousness, emotional self-regulation and the brain*, 123-129.

Luu, P., Tucker, D. M., & Derryberry, D. (1998). Anxiety and the motivational basis of working memory. *Cognitive Therapy and Research*, *22*(6), 577-594.

McCall, C., & Singer, T. (2013). Empathy and the brain. In S. Baron-Cohen, D. J. Cohen, & H. Tager-Flusberg (Eds.), *Understanding other minds: Perspectives from developmental social neuroscience*, 194-209. Oxford, UK: Oxford University Press.

Maccoby, E. E., & Martin, J. A. (1983). Socialization in the context of the family: Parent-child interaction. In P. H. Mussen (Ed.), *Handbook of child psychology Vol 4* (pp. 1-101). Chichester, New York: Wiley.

Magnée, M. J., Stekelenburg, J. J., Kemner, C., & de Gelder, B. (2007). Similar facial electromyographic responses to faces, voices, and body expressions. *Neuroreport*, *18*(4), 369-372.

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

Marshall, P. J., & Meltzoff, A. N. (2011). Neural mirroring systems: Exploring the EEG mu rhythm in human infancy. *Developmental Cognitive Neuroscience*, *1*(2), 110-123.

Martin, G. B., & Clark, R. D. (1982). Distress crying in neonates: Species and peer specificity. *Developmental psychology*, *18*(1), 3.

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.

Meinhardt, J., Sodian, B., Thoermer, C., Dohnel, K., & Sommer, M. (2011). True- and false-belief reasoning in children and adults: an event-related potential study of theory of mind. *Developmental Cognitive Neuroscience, 1*(1), 67-76.

Meyer, M., Liem, F., Hirsiger, S., Jäncke, L., & Hänggi, J. (2013). Cortical surface area and cortical thickness demonstrate differential structural asymmetry in auditory-related areas of the human cortex. *Cerebral Cortex*, *24*(10), 2541-2552.

Michael, J., Sandberg, K., Skewes, J., Wolf, T., Blicher, J., Overgaard, M., & Frith, C. D. (2014). Continuous theta-burst stimulation demonstrates a causal role of premotor homunculus in action understanding. *Psychological Science*, *25*(4), 963-972.

Mills, K.L., Goddings, A.-L., Herting, M.M., Meuwese, R., Blakemore, S.-J., Crone, E.A., Dahl, R.E., Gürogˇlu, B., Raznahan, A., Sowell, E.R., Tamnes, C.K. (2016).

Structural brain development between childhood and adulthood: convergence across four longitudinal samples. *Neuroimage, 141*, 273–281.

Minagawa-Kawai, Y., Matsuoka, S., Dan, I., Naoi, N., Nakamura, K., & Kojima, S. (2008). Prefrontal activation associated with social attachment: facial-emotion recognition in mothers and infants. *Cerebral Cortex*, *19*(2), 284-292.

Mireault, G., Poutre, M., Sargent-Hier, M., Dias, C., Perdue, B., & Myrick, A. (2012). Humour perception and creation between parents and 3-to 6-month-old infants. *Infant and Child Development*, *21*(4), 338-347.

Mireault, G. C., & Reddy, V. (2016). *Humor in infants: developmental and psychological perspectives*. Springer International Publishing.

Mireault, G., Sparrow, J., Poutre, M., Perdue, B., & Macke, L. (2012). Infant humor perception from 3-to 6-months and attachment at one year. *Infant Behavior and Development*, *35*(4), 797-802.

Missana, M., Altvater-Mackensen, N., & Grossmann, T. (2017). Neural correlates of infants' sensitivity to vocal expressions of peers. *Developmental Cognitive Neuroscience*, *26*, 39-44.

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*(4), e93728.

Molfese, D. L. (2000). Predicting dyslexia at 8 years of age using neonatal brain responses. *Brain and language*, *72*(3), 238-245.

Molfese, D. L., Freeman Jr, R. B., & Palermo, D. S. (1975). The ontogeny of brain lateralization for speech and nonspeech stimuli. *Brain and language*, *2*, 356-368.

Montague, D. P., & Walker-Andrews, A. S. (2001). Peekaboo: a new look at infants' perception of emotion expressions. *Developmental psychology*, *37*(6), 826.

Moody, E. J., McIntosh, D. N., Mann, L. J., & Weisser, K. R. (2007). More than mere mimicry? The influence of emotion on rapid facial reactions to faces. *Emotion*, *7*(2), 447-457.

Morales, S., Fu, X., & Pérez-Edgar, K. E. (2016). A developmental neuroscience perspective on affect-biased attention. *Developmental cognitive neuroscience*, *21*, 26-41.

Morasch, K. C., & Bell, M. A. (2011). The role of inhibitory control in behavioral and physiological expressions of toddler executive function. *Journal of Experimental Child Psychology*, *108*(3), 593-606.

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.

Mundy, P., Fox, N., & Card, J. (2003). EEG coherence, joint attention and language development in the second year. *Developmental Science*, *6*(1), 48-54.

Murphy, B. C., Shepard, S. A., Eisenberg, N., Fabes, R. A., & Guthrie, I. K. (1999). Contemporaneous and longitudinal relations of dispositional sympathy to emotionality, regulation, and social functioning. *The Journal of Early Adolescence*, *19*(1), 66-97.

Näätänen, R., Paavilainen, P., Rinne, T., & Alho, K. (2007). The mismatch negativity (MMN) in basic research of central auditory processing: a review. *Clinical neurophysiology*, *118*(12), 2544-2590.

Näätänen, R., & Picton, T. (1987). The N1 wave of the human electric and magnetic response to sound: a review and an analysis of the component structure. *Psychophysiology*, *24*(4), 375-425.

Nakato, E., Otsuka, Y., Kanazawa, S., Yamaguchi, M. K., & Kakigi, R. (2011). Distinct differences in the pattern of hemodynamic response to happy and angry facial expressions in infants—A near-infrared spectroscopic study. *NeuroImage*, *54*(2), 1600-1606.

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

Nelson, C. A., & Collins, P. F. (1991). Event-related potential and looking-time analysis of infants' responses to familiar and novel events: Implications for visual recognition memory. *Developmental Psychology*, *27*(1), 50.

Nelson, C. A., & Collins, P. F. (1992). Neural and behavioral correlates of visual recognition memory in 4-and 8-month-old infants. *Brain and Cognition*, *19*(1), 105-121.

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., & deRegnier, R. A. (1992). Neural correlates of attention and memory in the first year of life. *Developmental Neuropsychology*, *8*(2-3), 119-134

Nelson, E. E., Jarcho, J. M., & Guyer, A. E. (2016). Social re-orientation and brain development: An expanded and updated view. *Developmental cognitive neuroscience*, *17*, 118-127

Nelson, E. E., Leibenluft, E., McClure, E. B., & Pine, D. S. (2005). The social re-orientation of adolescence: a neuroscience perspective on the process and its relation to psychopathology. *Psychological medicine*, *35*(2), 163-174.

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

Nelson, C. A., & Nugent, K. M. (1990). Recognition memory and resource allocation as revealed by children's event-related potential responses to happy and angry faces. *Developmental Psychology*, *26*(2), 171.

Neville, H. J., Coffey, S. A., Holcomb, P. J., & Tallal, P. (1993). The neurobiology of sensory and language processing in language-impaired children. *Journal of Cognitive Neuroscience*, *5*(2), 235-253.

Nichols, S. R., Svetlova, M., & Brownell, C. A. (2009). The role of social understanding and empathic disposition in young children’s responsiveness to distress in parents and peers. *Cognition, brain, behavior: an interdisciplinary journal*, *13*(4), 449.

Nichols, S. R., Svetlova, M., & Brownell, C. A. (2010). Toddlers' Understanding of Peers' Emotions. *Journal of Genetic Psychology, 171*(1), 35-53.

Nichols, S. R., Svetlova, M., & Brownell, C. A. (2015). Toddlers’ responses to infants’ negative emotions. *Infancy*, *20*(1), 70-97.

Novak, G. P., Kurtzberg, D., Kreuzer, J. A., & Vaughan, H. G. (1989). Cortical responses to speech sounds and their formants in normal infants: maturational sequence and spatiotemporal analysis. *Electroencephalography and clinical neurophysiology*, *73*(4), 295-305.

Obleser, J., & Kotz, S. A. (2011). Multiple brain signatures of integration in the comprehension of degraded speech. *Neuroimage*, *55*(2), 713-723.

Ochsner, K. N., Bunge, S. A., Gross, J. J., & Gabrieli, J. D. (2002). Rethinking feelings: an FMRI study of the cognitive regulation of emotion. *Journal of cognitive neuroscience*, *14*(8), 1215-1229.

Ochsner, K. N., & Gross, J. J. (2005). The cognitive control of emotion. *Trends in cognitive sciences*, *9*(5), 242-249.

Ochsner, K. N., Ray, R. D., Cooper, J. C., Robertson, E. R., Chopra, S., Gabrieli, J. D., & Gross, J. J. (2004). For better or for worse: neural systems supporting the cognitive down-and up-regulation of negative emotion. *Neuroimage*, *23*(2), 483-499.

Ohlrich, E. S., & Barnet, A. B. (1972). Auditory evoked responses during the first year of life. *Electroencephalography and Clinical Neurophysiology*, *32*(2), 161-169.

Ohlrich, E. S, Barnet, A. B, Weiss, I. P., & Shanks, B. L. (1978). Auditory evoked potential development in early childhood: a longitudinal study. *Electroencephalogr Clin Neurophysiol, 44*, 411–23.

Oliveri, M., Babiloni, C., Filippi, M. M., Caltagirone, C., Babiloni, F., Cicinelli, P., ... & Rossini, P. M. (2003). Influence of the supplementary motor area on primary motor cortex excitability during movements triggered by neutral or emotionally unpleasant visual cues. *Experimental brain research*, *149*(2), 214-221.

Onishi, K. H., & Baillargeon, R. (2005). Do 15-month-old infants understand false beliefs?. *Science*, *308*(5719), 255-258.

Oostenbroek, J., Suddendorf, T., Nielsen, M., Redshaw, J., Kennedy-Costantini, S., Davis, J., ... & Slaughter, V. (2016). Comprehensive longitudinal study challenges the existence of neonatal imitation in humans. *Current Biology*, *26*(10), 1334-1338.

Otsuka, Y., Nakato, E., Kanazawa, S., Yamaguchi, M. K., Watanabe, S., & Kakigi, R. (2007). Neural activation to upright and inverted faces in infants measured by near infrared spectroscopy. *NeuroImage*, *34*(1), 399-406.

Overath, T., Zhang, Y., Sanes, D. H., & Poeppel, D. (2012). Sensitivity to temporal modulation rate and spectral bandwidth in the human auditory system: fMRI evidence. *Journal of neurophysiology*, *107*(8), 2042-2056.

Ozonoff, S., Pennington, B. F., & Rogers, S. J. (1990). Are there emotion perception deficits in young autistic children?. *Journal of Child Psychology and Psychiatry*, *31*(3), 343-361.

Paetau, R., Ahonen, A., Salonen, O., & Sams, M. (1995). Auditory evoked magnetic fields to tones and pseudowords in healthy children and adults. *Journal of clinical neurophysiology: official publication of the American Electroencephalographic Society*, *12*(2), 177-185.

Pang, E. W., & Taylor, M. J. (2000). Tracking the development of the N1 from age 3 to adulthood: an examination of speech and non-speech stimuli. *Clinical Neurophysiology*, *111*(3), 388-397.

Paulmann, S., Bleichner, M., & Kotz, S. A. (2013). Valence, arousal, and task effects in emotional prosody processing. *Frontiers in Psychology, 4*, 107-116.

Paulmann, S., & Pell, M. D. (2010). Contextual influences of emotional speech prosody on face processing: how much is enough?. *Cognitive, Affective, & Behavioral Neuroscience*, *10*(2), 230-242.

Paulmann, S., Pell, M. D., & Kotz, S. A. (2008). Functional contributions of the basal ganglia to emotional prosody: Evidence from ERPs. *Brain Research*, *1217*, 171-178.

Paulus, M. (2014). The emergence of prosocial behavior: why do infants and toddlers help, comfort, and share?. *Child Development Perspectives*, *8*(2), 77-81.

Paulus, M., Kuhn-Popp, N., Licata, M., Sodian, B., & Meinhardt, J. (2013). Neural correlates of prosocial behavior in infancy: Different neurophysiological mechanisms support the emergence of helping and comforting. *Neuroimage, 66*, 522-530.

Pell, M. D., Rothermich, K., Liu, P., Paulmann, S., Sethi, S., & Rigoulot, S. (2015). Preferential decoding of emotion from human non-linguistic vocalizations versus speech prosody. *Biological psychology*, *111*, 14-25.

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.

Perner, J. (1991). Understanding the representational mind. Cambridge, MA: The MIT Press.

Perner, J., & Ruffman, T. (2005). Infants' insight into the mind: How deep?. *Science, 308*, 214–216.

Pessoa, L. (2017). A Network Model of the Emotional Brain. *Trends in Cognitive Sciences*, *21***,** 357–371.

Pfeifer, J. H., & Allen, N. B. (2012). Arrested development? Reconsidering dual-systems models of brain function in adolescence and disorders. *Trends in cognitive sciences*, *16*(6), 322-329.

Pfeifer, J. H., & Allen, N. B. (2016). The audacity of specificity: Moving adolescent developmental neuroscience towards more powerful scientific paradigms and translatable models. *Developmental cognitive neuroscience*, *17*, 131.

Pfeifer, J. H., Iacoboni, M., Mazziotta, J. C., & Dapretto, M. (2008). Mirroring others' emotions relates to empathy and interpersonal competence in children. *Neuroimage*, *39*(4), 2076-2085.

Phillips, M. L., Ladouceur, C. D., & Drevets, W. C. (2008). A neural model of voluntary and automatic emotion regulation: implications for understanding the pathophysiology and neurodevelopment of bipolar disorder. *Molecular psychiatry*, *13*(9), 829.

Ponton, C. W., Eggermont, J. J., Kwong, B., & Don, M. (2000). Maturation of human central auditory system activity: evidence from multi-channel evoked potentials. *Clin Neurophysiol, 111*, 220–236.

Ponton, C. W, Eggermont, J. J., Khosla, D., Kwong, B., & Don, M. (2002). Maturation of human central auditory system activity: separating auditory evoked potentials by dipole source modeling. *Clin Neurophysiol, 113*, 407–420.

Porges, S. W. (1991). Vagal mediation of respiratory sinus arrhythmia. *Annals of the New York Academy of Sciences*, *618*(1), 57-66.

Porges, S. W. (1996). Physiological regulation in high-risk infants: A model for assessment and potential intervention. *Development and Psychopathology*, *8*(1), 43-58.

Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual review of neuroscience*, *13*(1), 25-42.

Posner, M. I., & Rothbart, M. K. (2009). Toward a physical basis of attention and self-regulation. *Physics of life reviews*, *6*(2), 103-120.

Posner, M. I., Rueda, M. R., & Kanske, P. (2007). Probing the mechanisms of attention. In J. T. Cacioppo, J. G. Tassinary, & G.G. Berntson (Eds.), *Handbook of* *psychophysiology,* 3rd edition, (pp. 410-432). Cambridge, UK: Cambridge University Press.

Power, J. D., Fair, D. A., Schlaggar, B. L., & Petersen, S. E. (2010). The development of human functional brain networks. *Neuron*, *67*(5), 735-748.

Preston, S. D., & De Waal, F. B. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and brain sciences*, *25*(1), 1-20.

Prior, M., Dahlstrom, B., & Squires, T. L. (1990). Autistic children's knowledge of thinking and feeling states in other people. *Journal of Child Psychology and Psychiatry*, *31*(4), 587-601.

Provine, R. R. (1997). Yawns, laughs, smiles, tickles, and talking: Naturalistic and laboratory studies of facial action and social communication. *The psychology of facial expression*, *158*.

Provine R. R. (2000) *Laughter: a scientific investigation*. New York: Viking Penguin.

Provine, R. R. (2004). Laughing, tickling, and the evolution of speech and self. *Current Directions in Psychological Science*, *13*(6), 215-218.

Provine, R. R. (2016). Laughter as a scientific problem: An adventure in sidewalk neuroscience. *Journal of Comparative Neurology*, *524*(8), 1532-1539.

Provine, R. R., & Fischer, K. R. (1989). Laughing, smiling, and talking: Relation to sleeping and social context in humans. *Ethology*, *83*(4), 295-305.

Rajhans, P., Missana, M., Krol, K. M., & Grossmann, T. (2015). The association of temperament and maternal empathy with individual differences in infants' neural responses to emotional body expressions. *Development and psychopathology*, *27*(4pt1), 1205-1216.

Rakoczy, H. (2012). Do infants have a theory of mind? *British Journal of Developmental Psychology, 30*(1), 59-74.

Rapin, I., & Graziani, L. J. (1967). Auditory-evoked responses in normal, brain-damaged, and deaf infants. *Neurology, 17*, 881–894.

Ravicz, M. M., Perdue, K. L., Westerlund, A., Vanderwert, R. E., & Nelson, C. A. (2015). Infants' neural responses to facial emotion in the prefrontal cortex are correlated with temperament: a functional near-infrared spectroscopy study. *Frontiers in psychology*, *6*.

Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A., ... & Acker, J. D. (2005). Regional brain changes in aging healthy adults: general trends, individual differences and modifiers. *Cerebral cortex*, *15*(11), 1676-1689.

Reddy, V., Williams, E., & Vaughan, A. (2002). Sharing humour and laughter in autism and Down's syndrome. *British journal of psychology*, *93*(2), 219-242.

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

Richell, R. A., Mitchell, D. G. V., Newman, C., Leonard, A., Baron-Cohen, S., & Blair, R. J. R. (2003). Theory of mind and psychopathy: can psychopathic individuals read the 'language of the eyes'?. *Neuropsychologia*, *41*(5), 523-526.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Opinion: Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature reviews. Neuroscience*, *2*(9), 661.

Robinson, J. L., Zahn-Waxler, C., & Emde, R. N. (2001). Relationship context as a moderator of sources of individual differences in empathic development. *Infancy to early childhood: Genetic and environmental influences on developmental change*, 257-268.

Rogers, J., Viding, E., Blair, R. J., Frith, U., & Happe, F. (2006). Autism spectrum disorder and psychopathy: shared cognitive underpinnings or double hit?. *Psychological medicine*, *36*(12), 1789-1798.

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

Rothbart, M. K., Ahadi, S. A., & Hershey, K. L. (1994). Temperament and social behavior in childhood. *Merrill-Palmer Quarterly (1982-)*, 21-39.

Rothbart, M. K., & Bates, J. E. (2006). Temperament. In W. Damon, & R. M. Lerner (Eds.), *Handbook of child psychology*, Vol 3.

Rothbart, M. K., Ellis, L. K., Rueda, R.M., & Posner, M. I. (2003). Developing mechanisms of temperamental effortful control. *Journal of personality*, *71*(6), 1113-1144.

Rothbart, M. K., Ziaie, H., & O'boyle, C. G. (1992). Self‐regulation and emotion in infancy. *New directions for child and adolescent development*, *1992*(55), 7-23.

Rowe, A. D., Bullock, P. R., Polkey, C. E., & Morris, R. G. (2001). Theory of mind'impairments and their relationship to executive functioning following frontal lobe excisions. *Brain*, *124*(3), 600-616.

Ruffman, T., & Perner, J. (2005). Do infants really understand false belief?: Response to Leslie. *Trends in cognitive sciences*, *9*(10), 462-463.

Rushton, J. P., Fulker, D. W., Neale, M. C., Nias, D. K., & Eysenck, H. J. (1986). Altruism and aggression: The heritability of individual differences. *Journal of personality and social psychology*, *50*(6), 1192.

Sagi, A., & Hoffman, M. L. (1976). Empathic Distress in Newborn. *Developmental Psychology, 12*(2), 175-176.

Samson, D., Apperly, I. A., Chiavarino, C., & Humphreys, G. W. (2004). Left temporoparietal junction is necessary for representing someone else's belief. *Nature neuroscience*, *7*(5), 499.

Santesso, D. L., Schmidt, L. A., & Trainor, L. J. (2007). Frontal brain electrical activity (EEG) and heart rate in response to affective infant-directed (ID) speech in 9-month-old infants. *Brain and Cognition, 65*(1), 14-21.

Sauter, D. A., Eisner, F., Ekman, P., & Scott, S. K. (2010). Cross-cultural recognition of basic emotions through nonverbal emotional vocalizations. *Proceedings of the National Academy of Sciences*, *107*(6), 2408-2412.

Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people: the role of the temporo-parietal junction in “theory of mind”. *Neuroimage*, *19*(4), 1835-1842.

Saxe, R. R., Whitfield-Gabrieli, S., Scholz, J., & Pelphrey, K. A. (2009). Brain regions for perceiving and reasoning about other people in school-aged children. *Child Development, 80*(4), 1197-1209.

Scherer, K. R. (1986). Vocal affect expression: A review and a model for future research. *Psychological Bulletin, 99*(2), 143-165.

Scherer, K. R. (1995). Expression of emotion in voice and music. *Journal of voice*, *9*(3), 235-248.

Scherf, K. S., Smyth, J. M., & Delgado, M. R. (2013). The amygdala: an agent of change in adolescent neural networks. *Hormones and Behavior*, *64*(2), 298-313.

Schirmer, A., Chen, C. B., Ching, A., Tan, L., & Hong, R. Y. (2013). Vocal emotions influence verbal memory: neural correlates and interindividual differences. *Cognitive, Affective, & Behavioral Neuroscience*, *13*(1), 80-93.

Schirmer, A., & Kotz, S. A. (2006). Beyond the right hemisphere: brain mechanisms mediating vocal emotional processing. *Trends in Cognitive Sciences*, *10*(1), 24-30.

Schutter, D. J., Hofman, D., & Van Honk, J. (2008). Fearful faces selectively increase corticospinal motor tract excitability: a transcranial magnetic stimulation study. *Psychophysiology*, *45*(3), 345-348.

Schwenck, C., Göhle, B., Hauf, J., Warnke, A., Freitag, C. M., & Schneider, W. (2014). Cognitive and emotional empathy in typically developing children: The influence of age, gender, and intelligence. *European Journal of Developmental Psychology*, *11*(1), 63-76.

Scott, R. M., & Baillargeon, R. (2009). Which penguin is this? Attributing false beliefs about object identity at 18 months. *Child development*, *80*(4), 1172-1196.

Scott, S. K., Blank, C. C., Rosen, S., & Wise, R. J. (2000). Identification of a pathway for intelligible speech in the left temporal lobe. *Brain*, *123*(12), 2400-2406.

Scourfield, J., John, B., Martin, N., & McGuffin, P. (2004). The development of prosocial behavior in children and adolescents: a twin study. *Journal of Child Psychology and Psychiatry*, *45*(5), 927-935.

Serrano, J. M., Iglesias, J., & Loeches, A. (1995). Infants' responses to adult static facial expressions. *Infant Behavior & Development, 18*(4), 477-482.

Shapiro, B., Fagen, J., Prigot, J., Carroll, M., & Shalan, J. (1998). Infants' emotional and regulatory behaviors in response to violations of expectancies. *Infant Behavior and Development*, *21*(2), 299-313.

Shaw, P., Kabani, N. J., Lerch, J. P., Eckstrand, K., Lenroot, R., Gogtay, N., ... & Giedd, J. N. (2008). Neurodevelopmental trajectories of the human cerebral cortex. *Journal of Neuroscience*, *28*(14), 3586-3594.

Simner, M. L. (1971). Newborns Response to Cry of Another Infant. *Developmental Psychology, 5*(1), 136-150.

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

Singer, T., & Lamm, C. (2009). The social neuroscience of empathy. *Ann N Y Acad Sci, 1156*, 81-96.

Smith, A. (1976). *The Theory of Moral Sentiments*. Oxford, UK: Oxford University Press.

Soenens, B., Duriez, B., Vansteenkiste, M., & Goossens, L. (2007). The intergenerational transmission of empathy-related responding in adolescence: The role of maternal support. *Personality and Social Psychology Bulletin*, *33*(3), 299-311.

Soltis, J. (2004). The signal functions of early infant crying. *Behavioral and Brain Sciences*, *27*(4), 443-458.

Sommer, M., Meinhardt, J., Eichenmuller, K., Sodian, B., Dohnel, K., & Hajak, G. (2010). Modulation of the cortical false belief network during development. *Brain Research, 1354*, 123-131.

Somerville, L. H., & Casey, B. J. (2010). Developmental neurobiology of cognitive control and motivational systems. *Current opin*

Song, H. J., Onishi, K. H., Baillargeon, R., & Fisher, C. (2008). Can an agent’s false belief be corrected by an appropriate communication? Psychological reasoning in 18-month-old infants. *Cognition*, *109*(3), 295-315.

Sonnby-Borgström, M., Jönsson, P., & Svensson, O. (2003). Emotional empathy as related to mimicry reactions at different levels of information processing. *Journal of Nonverbal behavior*, *27*(1), 3-23.

Soussignan, R., Chadwick, M., Philip, L., Conty, L., Dezecache, G., & Grèzes, J. (2013). Self-relevance appraisal of gaze direction and dynamic facial expressions: effects on facial electromyographic and autonomic reactions. *Emotion*, *13*(2), 330.

Sowell, E. R., Peterson, B. S., Thompson, P. M., Welcome, S. E., Henkenius, A. L., & Toga, A. W. (2003). Mapping cortical change across the human life span. *Nature neuroscience*, *6*(3), 309.

Spencer, H. (1870). *The Principles of Psychology* (Vol. 1, 2nd ed.). London, UK: Williams and Norgate.

Sroufe, L. A., & Wunsch, J. P. (1972). The development of laughter in the first year of life. *Child Development*, 1326-1344.

Stadler, W., Ott, D. V., Springer, A., Schubotz, R. I., Schütz-Bosbach, S., & Prinz, W. (2012). Repetitive TMS suggests a role of the human dorsal premotor cortex in action prediction. *Frontiers in human neuroscience*, *6*.

Steinberg, L. (2008). A social neuroscience perspective on adolescent risk-taking. *Developmental Review. 28* (1), 78–106.

Stern, D.N. (1985). *The Interpersonal World of the Infant*. New York: John Wiley.

Stevenson, R. A., & James, T. W. (2008). Affective auditory stimuli: Characterization of the International Affective Digitized Sounds (IADS) by discrete emotional categories. *Behavior Research Methods*, *40*(1), 315-321.

Stieben, J., Lewis, M. D., Granic, I., Zelazo, P. D., Segalowitz, S., & Pepler, D. (2007). Neurophysiological mechanisms of emotion regulation for subtypes of externalizing children. *Development and Psychopathology*, *19*(2), 455-480.

Stifter, C. A., & Braungart, J. M. (1995). The regulation of negative reactivity in infancy: Function and development. *Developmental Psychology*, *31*(3), 448.

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

Sussman, E., Steinschneider, M., Gumenyuk, V., Grushko, J., & Lawson, K. (2008). The maturation of human evoked brain potentials to sounds presented at different stimulus rates. *Hearing research*, *236*(1-2), 61-79.

Svetlova, M., Nichols, S. R., & Brownell, C. A. (2010). Toddlers' Prosocial Behavior: From Instrumental to Empathic to Altruistic Helping. *Child Development, 81*(6), 1814-1827.

Tassinary, L. G., & Cacioppo, J. T. (1992). Unobservable facial actions and emotion. *Psychology Science, 3*(1), 28-33.

Teti, D. M., & Ablard, K. E. (1989). Security of attachment and infant-sibling relationships: A laboratory study. *Child development*, 1519-1528.

Thompson, R. A. (1994). Emotion regulation: A theme in search of definition. *Monographs of the society for research in child development*, *59*(2-3), 25-52.

Tonnquist-Uhlen, I. (1996). Topography of auditory evoked long-latency potentials in children with severe language impairment: the P2 and N2 components. *Ear and Hearing*, *17*(4), 314-326.

Toro, C., Deuschl, G., Thatcher, R., Sato, S., Kufta, C., & Hallett, M. (1994). Event-related desynchronization and movement-related cortical potentials on the ECoG and EEG. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *93*(5), 380-389.

Träuble, B., Marinović, V., & Pauen, S. (2010). Early theory of mind competencies: do infants understand others' beliefs?. *Infancy*, *15*(4), 434-444.

Trevarthen, C. (1979). Communication and cooperation in early infancy: A description of primary intersubjectivity. In M. Bullowa (Ed.), *Before speech: The beginning of interpersonal communication* (pp. 321-347). London, UK: Cambridge University Press.

Tzourio-Mazoyer, N., De Schonen, S., Crivello, F., Reutter, B., Aujard, Y., & Mazoyer, B. (2002). Neural correlates of woman face processing by 2-month-old infants. *Neuroimage*, *15*(2), 454-461

Ungerer, J. A., Dolby, R., Waters, B., Barnett, B., Kelk, N., & Lewin, V. (1990). The early development of empathy: Self-regulation and individual differences in the first year. *Motivation and emotion*, *14*(2), 93-106.

Upshaw, M. B., Kaiser, C. R., & Sommerville, J. A. (2015). Parents' empathic perspective taking and altruistic behavior predicts infants' arousal to others' emotions. *Frontiers in psychology*, *6*.

Valiente, C., Eisenberg, N., Fabes, R. A., Shepard, S. A., Cumberland, A., & Losoya, S. H. (2004). Prediction of children's empathy-related responding from their effortful control and parents' expressivity. *Developmental psychology*, *40*(6), 911.

Van der Mark, I. L., IJzendoorn, M. H. V., & Bakermans-Kranenburg, M. J. (2002). Development of empathy in girls during the second year of life: Associations with parenting, attachment, and temperament. *Social Development*, *11*(4), 451-468.

Vaish, A., Grossmann, T., & Woodward, A. (2008). Not all emotions are created equal: the negativity bias in social-emotional development. *Psychological bulletin*, *134*(3), 383.

Vlahovic, T. A., Roberts, S., & Dunbar, R. (2012). Effects of duration and laughter on subjective happiness within different modes of communication. *Journal of Computer‐Mediated Communication*, *17*(4), 436-450.

Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happe, F., Falkai, P., Maier, W., Shah, N.J., Fink, G.R., & Zilles, K. (2001). Mind reading: neural mechanisms of theory of mind and self-perspective. *Neuroimage, 14*(1 Pt 1).

Volbrecht, M. M., Lemery-Chalfant, N., Aksan, N., Zahn-Waxler, C. & Goldsmith, H.H. (2007). Examining the familial link between positive affect and empathy development in the second year. *The Journal of genetic psychology,168*(2), 105-130.

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

Vuilleumier, P., Richardson, M. P., Armony, J. L., Driver, J., & Dolan, R. J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature neuroscience*, *7*(11), 1271.

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

Walker-Andrews, A. S., & Grolnick, W. (1983). Discrimination of vocal expressions by young infants. *Infant Behavior and Development*, *6*(4), 491-498.

Walker-Andrews, A. S., & Lennon, E. (1991). Infants' discrimination of vocal expressions: Contributions of auditory and visual information. *Infant Behavior and Development*, *14*(2), 131-142.

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.

Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *science*, *311*(5765), 1301-1303.

Warneken, F., & Tomasello, M. (2007). Helping and cooperation at 14 months of age. *Infancy*, *11*(3), 271-294.

Washburn, R. W. (1929). A study of the smiling and laughing of infants in the first year of life. *Genetic Psychology Monographs*, *6*, 403-537.

Wellman, H. M., & Bartsch, K. (1988). Young children's reasoning about beliefs. *Cognition, 30*(3), 239-277.

Wellman, H. M., Cross, D., & Watson, J. (2001). Meta-analysis of theory-of-mind development: the truth about false belief. *Child Development, 72*(3), 655-684.

Werker, J. F., & Hensch, T. K. (2015). Critical periods in speech perception: new directions. *Annual review of psychology*, *66*.

Woldorff, M. G., Gallen, C. C., Hampson, S. A., Hillyard, S. A., Pantev, C., Sobel, D., & Bloom, F. E. (1993). Modulation of early sensory processing in human auditory cortex during auditory selective attention. *Proceedings of the National Academy of Sciences*, *90*(18), 8722-8726.

Wolff, P.H. (1963). Observations on the early development of smiling. In B.M. Foss (Ed.), *Determinants of Infant Behavior II* (pp. 113-138). London: Methuen.

Wolff, M. S., & Ijzendoorn, M. H. (1997). Sensitivity and attachment: A meta-analysis on parental antecedents of infant attachment. *Child development*, *68*(4), 571-591.

Woods, D. L. (1995). The component structure of the N1 wave of the human auditory evoked potential. *Electroencephalography and Clinical Neurophysiology*, *44,* 102–109.

Woodward, A. L. (1998). Infants selectively encode the goal object of an actor's reach. *Cognition*, *69*(1), 1-34.

Wunderlich, J. L., & Cone-Wesson, B. K. (2006). Maturation of CAEP in infants and children: A review. *Hearing Research*, *212*(1), 212-223.

Wunderlich, J. L., Cone-Wesson, B. K., & Shepherd, R. (2006). Maturation of the cortical auditory evoked potential in infants and young children. *Hearing research*, *212*(1-2), 185-202.

Yakovlev, P.A., Lecours, I.R. (1967). The myelogenetic cycles of regional maturation of the brain. In: Minkowski, A. (Ed.), *Regional Development of the Brain in Early Life*. Oxford: Blackwell, pp. 3–70.

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.

Zahn-Waxler, C., Cole, P. M., Welsh, J. D., & Fox, N. A. (1995). Psychophysiological correlates of empathy and prosocial behaviors in preschool children with behavior problems. *Development and Psychopathology*, *7*(1), 27-48.

Zahn-Waxler, C., & Radke-Yarrow, M. (1990). The origins of empathic concern. *Motivation and emotion*, *14*(2), 107-130.

Zahn-Waxler, C., Radke-Yarrow, M., & King, R. A. (1979). Child rearing and children's prosocial initiations toward victims of distress. *Child development*, 319-330.

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

Zahn-Waxler, C., Robinson, J. L., & Emde, R. N. (1992). The development of empathy in twins. *Developmental psychology*, *28*(6), 1038.

Zatorre, R. J., Belin, P., & Penhune, V. B. (2002). Structure and function of auditory cortex: music and speech. *Trends in cognitive sciences*, *6*(1), 37-46.

Zaki, J., & Ochsner, K. (2013). Neural sources of empathy: An evolving story. In S. Baron-Cohen, D. J. Cohen, & H. Tager-Flusberg (Eds.), *Understanding other minds: Perspectives from developmental social neuroscience* (pp. 214-32). Oxford, UK: Oxford University Press.

Zelazo, P. D., Carlson, S. M., & Kesek, A. (2008). The development of executive function in childhood.

Zhang, D., Liu, Y., Hou, X., Sun, G., Cheng, Y., & Luo, Y. (2014). Discrimination of fearful and angry emotional voices in sleeping human neonates: a study of the mismatch brain responses. *Frontiers in behavioral neuroscience*, *8*.

Zhou, Q., Eisenberg, N., Losoya, S. H., Fabes, R. A., Reiser, M., Guthrie, I. K., ... & Shepard, S. A. (2002). The relations of parental warmth and positive expressiveness to children's empathy-related responding and social functioning: A longitudinal study. *Child development*, *73*(3), 893-915.

Individual Differences in Infants' Neural Responses to their Peers' Cry and Laughter

Maria M. Crespo-Llado[1], Ross E. Vanderwert[2], and Elena Geangu[1]

[1]Lancaster University, [2]Cardiff University

Author Note

A version of this paper is under review:
Crespo-Llado, M.M., Vanderwert, R.E., & Geangu, E. (under review). Individual Differences in Infants' Neural Responses to their Peers' Cry and Laughter. *Biological Psychology.*

Abstract

Infants' ability to process others' emotional expressions is fundamental for the later development of children's interpersonal and social skills. Much research has been done on how infants process emotions from faces and speech, while less is known about how infants process emotions embedded in non-verbal vocalizations and how individual differences may affect this ability. Here, we recorded event-related potentials (ERPs) from 8-month-old infants while they were listening sounds of another infant crying, laughing and coughing. Infants' temperament was measured via parent report using the Infant Behavior Questionnaire -Revised (IBQ-R). Our ERP results revealed that hearing another infant laugh and cry elicited differential ERP activity at frontal locations, as indexed by differences in the N100, P200 and LPC components. Hearing another infant crying elicited an early enhanced negativity (N100) and a later enhanced positivity (LPC) compared to positive and neutral peers' non-verbal vocalizations of emotions, whereas P200 amplitudes did not show any differentiation among conditions. Temperamental differences in negative emotionality showed significant relations with the amplitude of P200 and LPC responses to non-verbal emotional vocalizations. These results shed new light into the links between infant temperament and emotion information processing development, with potential implications for understanding the ontogeny of complex social skills.

Introduction

Non-verbal vocalizations of emotions such as laughter and crying are human universals, providing unambiguous and genuine information about our emotions (Barr, Hopkins & Green, 2000; Dunbar, Baron, & Frangou, 2012; Paulmann & Kotz, 2008a; Provine, 2016; Provine, 2004; Sauter, Eisner, Ekman, & Scott, 2010a; Scherer, 1986, 1995). Both the production and the accurate interpretation of these social signals are thought to play crucial roles in communication, social bonding, and elicitation of prosocial behaviors and may be the early precursors to empathy development (Decety, 2015; Decety & Howard, 2013; Geangu, 2015; Hoffmann, 2001). Evidence sugests that the atypical production and perception of non-verbal vocalizations during the first year of life may be a good predictor of the later emergence of developmental disorders characterized by deficts in social communication skills such as autism (Esposito, Nakazawa, Venuti, & Bornstein, 2013; Esposito, Venuti, & Bornstein, 2011; Reddy, Williams, & Vaughan, 2002; Blasi et al., 2015). Despite their significance, our ability to process, respond, and use non-verbal vocalizations of emotions, particularly in early development, remains understudied (Geangu, 2015; Pell et al., 2015; Dunbar et al., 2012, Provine, 1996).

Infancy is a crucial time period for tuning and optimising the brain circuitry for processing stimuli with socio-emotional relevance and emotional responsivity, setting the stage for both the refinement of the early acquired social skills and the emergence of new and more complex ones later in life (Johnson, 2011; Karmiloff-Smith, 1998). From this perspective, the investigation of the neurocognitive mechanisms underlying emotional information processing and potential individual variations during infancy is essential for understanding typical and atypical social development, as well as for identifying methods for early detection and intervention (e.g., Bunford, Kujawa, Swain, Fitzgerald, Monk, & Phan, 2017; Johnson, Gliga, Jones, & Charman, 2015; Morales, Fu, & Pérez-Edgar, 2016). Towards this aim, the current study investigates infants' neural responses to their peers' non-verbal vocalizations of emotions and temperamental variations in such responses by using event-related potentials (ERPs).

Within a few hours after birth infants already manifest distress vocalizations when they hear the sound of another infant crying (Dondi, Simion & Caltran, 1999; Field, Diego, Hernandez-Reif & Fernandez, 2007; Geangu, Benga, Stahl & Striano, 2010; Martin & Clark, 1982; Sagi & Hoffman, 1976; Simner, 1971). Such distress responses are more intense when neonates hear a human infant cry rather than an infant chimpanzee cry (Martin & Clark, 1982), while artificial noise does not elicit such responses (Sagi & Hoffman, 1976; Simner, 1971). Neonates also have the capacity to perceptually discriminate between their own cry and the cry of another same age infant (Dondi et al., 1999; Martin & Clark, 1982). Throughout the first year of life, infants continue to respond with facial and vocal distress to the crying sounds of their peers (Geangu et al., 2010), and this increase in arousal persists throughout toddlerhood, although with lesser intensity (Nichols, Svetlova, & Brownell, 2009, 2015). When jointly presented with the corresponding facial expressions, these overt responses elicited by peer emotional vocalizations are accompanied by autonomic arousal changes. In 6-, 12-, and 15-months-old infants (Geangu, Hauf, Bhardwaj, & Bentz, 2011; Upshaw, Kaiser, & Sommerville, 2015), observation of audio-video recordings of a peer crying or laughing elicited an increase in pupil diameter reflecting autonomic sympathetic activation (Bradley, Miccoli, Escrig, & Lang, 2008). The valence of the stimuli, however, moderated the latency of pupil response with crying eliciting an early response already present at 6 months while laughter showed a delayed pupil response at 6 months but had a similar latency as crying by 12 months (Geangu et al., 2011). Overall, observing a peer crying elicited greater arousal compared to observing a peer laughing (Geangu et al., 2011; Upshaw et al., 2015). Taken together, these early signs of affect sharing suggest that infants' ability to detect and process non-verbal vocalizations of emotions is present from birth and continues to develop throughout infancy.

Schirmer and Kotz (2006) proposed a three-stage model for processing emotional vocalizations based on electrophysiology evidence from adults. At the first stage of processing, the brain shows sensitivity to the embedded emotional information as early as 100-200 ms after stimulus onset, as indexed by the emergence of an N100 and P200 (Jessen & Kotz, 2011; Liu et al., 2012; Pell et al., 2015; Paulmann, Bleichner, & Kotz, 2013; Schirmer, Kotz, & Friederici, 2005). The N100, a negative deflection in the ERP waveform occurring around 100 ms, is considered to be an index of early sensory encoding of the physical properties of the sound (Näätänen & Picton, 1987) and the effort associated with the allocation of processing resources to form and maintain a sensory memory trace (Obleser & Kotz, 2011). Recently, evidence found that the amplitude of the N100 is modulated by the emotional valence of auditory stimuli (Jessen & Kotz, 2011; Liu et al, 2012). The positive component observed around 200 ms (P200) is proposed to reflect the processing of the semantically-relevant acoustic parameters involved in the early meaning detection or general stimulus categorization at the second stage of the model (Garcia-Larrea, Lukaszewicz, & Mauguiére, 1992; Pell et al., 2015). The P200 is modulated by the motivational saliency of the acoustic signal as indicated by both the discrete emotional qualities of the stimulus and the associated arousal (Paulmann et al., 2013). The latency of both the N100 and the P200 shows that non-verbal vocalizations of emotions are processed much faster than emotional speech prosody, emphasizing the heightened relevance afforded by these crude means of expressing genuine emotions (Pell et al., 2015). More advanced analysis of the emotional meaning expressed by human vocalizations, including their social relevance and memory representations (Jessen & Kotz, 2011; Kotz & Paulmann, 2011; Paulmann & Pell, 2010; Schirmer & Kotz, 2003, 2006; Schirmer, Chen, Ching, Tan, & Hong, 2013) are usually reported at the third stage of processing, as indicated by the late positive component (LPC). For example, the amplitude of the LPC has been found to vary as a function of stimulus level of arousal and emotional expression, with increased amplitude for cues of threat (e.g., anger) compared to non-threat (e.g., sadness, happiness) or for expressions with higher versus lower levels of arousal (Paulmann et al., 2013; Pell et al., 2015). Such differences may reflect the evaluation of the stimulus meaning as related to the representations stored in an individual's memory; with preferential allocation of processing resources to the stimuli highly relevant for the individual (Hinojosa et al., 2009; Paulmann et al., 2013; Pell et al., 2015; Kanske & Kotz, 2007). The emotional modulations of the LPC are also more pronounced and faster for non-verbal vocalizations of emotions compared to emotional prosody embedded in speech (Pell et al., 2015), suggesting that the emotional meaning of non-verbal vocalizations maintain prioritised processing continuing into adulthood.

Emotionally loaded human vocalizations have been reported to modulate infant ERP responses as well (Cheng, Lee, Chen, Wang & Decety, 2012; Grossmann, Striano, & Friederici, 2005; Missana, Alvater-Mackensen, & Grossman, 2017; Zhang et al., 2014). The infant brain seems to differentiate between emotional prosody embedded in speech soon after birth (Cheng et al., 2012; Zhang et al., 2014) and suggests that at this age the discrimination is automatic, and possibly related to the activity of primary and non-primary auditory areas in the temporal cortex (Näätänen, Paavilainen, Rinne, & Alho, 2007). While there is limited evidence to make such claims, auditory processing of emotion prosody in infancy and childhood resembles adult-like processing demonstrating sensitivity to emotional content both at early processing stages (Chronaki et al., 2012; Grossmann et al., 2013) and at later ones, including the LPC (Grossmann et al., 2005). Recent evidence from an EEG study suggests that 8-month-old infants' ERP responses may also be sensitive to peers' non-verbal vocalizations of emotions (Missana, Alvater-Mackensen, & Grossmann, 2007). In this study infants were presented with the sounds of their peers' cry and laughter, as well as the neutral humming of an adult. While early positive and negative components were selectively modulated to either peer crying or laughter sounds as compared to neutral vocalizations, no differentiation between emotions was reported at late stages of processing. The aforementioned findings have been partially corroborated by an fMRI study that examined the infants' brain responses to crying, laughter and coughing sounds produced by adults (Blasi et al., 2011). In this case, crying but not laughter vocalizations evoked a stronger activation in infants' insula and orbitofrontal cortex compared to neutral vocalizations. Unlike Missana et al. (2017), this study did not find any differences between laughing and neutral vocalizations.

The disparate results reported by these studies may be explained by the differences in the temporal resolution of the methods used (EEG/ERP vs. fMRI) and the fact that they may reflect different stages of processing, or they may be due to differences in the stimuli. While Blasi et al. (2011) compared hemodynamic responses to non-verbal vocalizations produced by adults, Missana et al. (2017) contrasted ERPs to peer emotional non-verbal vocalizations with adult neutral vocalizations. As reported above, behavioural studies have demonstrated infants' sensitivity to the age of the voice expressing non-verbal vocalizations of emotions (Martin & Clark, 1982). Further, the effect of familiarity, a well-known effect in the processing of visual information (e.g., faces – Kahana-Kalman & Walker-Andrews, 2003; de Haan, Johnson, & Halit, 2003), may have driven the reported ERP findings, not by the emotional content, but by the degree of familiarity of adult versus peer voices (Kooijmann, Hagoort, & Cutler, 2005; Thierry, Vihman, & Roberts, 2003). Thus, contrasting infants' ERP responses to emotional and neutral non-verbal vocalizations which both belong to their peers is essential for providing a clear picture of the neurocognitive mechanisms involved in processing this type of emotional expressions.

Additionally, despite the well-known fact that humans vary greatly in how they respond to emotional cues, none of the above studies has examined the role of individual differences in the processing of vocal emotional cues. Importantly, individuals vary greatly in terms of how intensely they react to emotional information (Hamann & Canli, 2004). These differences are present starting with early infancy (Fox et al., 2005) and have been associated with individual temperamental characteristics (e.g., Jarcho et al., 2014). Variations in temperamental reactivity and self-regulation are thought to stem from a person's enduring biological make-up, shaped by the interplay between heredity, maturation and experience (Rothbart & Derryberry, 1981). Infants' and young children's temperamental characteristics manifest stable influences on an individual's emotional life (Jarcho et al., 2014) and are significantly linked to adult personality traits (Kagan et al., 1984; Fox et al., 2005). Importantly, these early individual differences in emotional reactivity and regulation are important predictors for several socio-emotional development outcomes. Understanding how temperamental differences in emotional reactivity and regulation relate to the processing of emotional cues beginning with infancy is thus crucial for the early detection and intervention of those individuals more likely to manifest atypical patterns of development (e.g., the development of anxiety disorders, depression, aggression and conduct disorders – Frick & Morris, 2004; Olson, Sameroff, Kerr, Lopez, & Wellman, 2005; Pérez-Edgar & Fox, 2005). Recent studies have shown that infants' neural responses to visual cues of others' emotions are significantly related to their temperamental characteristics (Martinos, Matheson, & de Haan, 2012; Missana, Grigutsch, & Grossmann, 2014; Rajhans, Missana, Krol, & Grossmann, 2015; Ravicz, Perdue, Westerlund, Vanderwert, & Nelson, 2015). In particular, infants with a disposition to express negative emotions during everyday life were more likely to manifest increased attention allocation to positive facial expressions (Martinos et al., 2012). In contrast, infants lower on negative emotionality were more likely to allocate their attention to processing negative emotional expressions (Rajhans et al., 2015). Infants' with better emotion regulation abilities also seem to allocate more attention in processing fearful emotional facial expressions (Martinos et al., 2012). The specific ability to recover from peak arousal was related to the degree of attentional engagement in processing angry facial expressions, suggesting that those infants who are better able to control their own state, are more likely to focus on processing facial cues of threat (Missana et al., 2014). Further, both infants' regulatory abilities and aspects of their negative emotionality have been significantly associated with their behavioral emotional responses to peer cry sounds (Geangu et al., 2011). Taken together, this suggests that temperament may play in important role in individual differences in the processing of emotional vocalizations. This is the first study to systematically investigate temperamental variance in infants' neural responses to their peers' non-verbal vocalizations of emotions.

The aim of our study is two-fold: to test whether infants' neural processing of peers' non-verbal emotional vocalizations is sensitive to the valence of the conveyed emotion; and whether these neural responses can be modulated by the infants' temperamental characteristics. Towards these aims, we measured 8-month-old infants' ERPs in response to audio recordings of emotional (negative/crying and positive/laughing) and non-emotional (i.e., coughing) non-verbal vocalizations. Crucially, unlike Missana et al. (2017), all the non-verbal vocalizations in this study were produced by infants. On the basis of previous studies on emotion perception from voice in both infants (Cheng et al., 2012; Grossmann et al., 2005; Missana et al., 2017; Zhang et al., 2014) and adults (Jessen & Kotz, 2011; Liu et al., 2012; Paulmann et al., 2013; Pell et al., 2015; Schirmer et al., 2005), we examined differences between affective and neutral auditory stimuli at the level of the early ERP components, in particular those corresponding to the N100 and the P200. Given the sensitivity of the N100 and P200 amplitude to emotional information, we hypothesized that emotional non-verbal vocalizations would evoke larger N100 and P200 amplitudes relative to neutral vocalizations. In addition, we hypothesized that the emotional sounds would evoke sustained cognitive processing in comparison to the neutral condition, as reflected by a LPC. In terms of the temperamental characteristics, we predicted a significant relation between aspects of infants' negative emotionality and their ERP responses to their peers' non-verbal vocalizations of emotions since this relation has been more systematically reported in previous studies.

Methods

Participants

Thirty 8-month old infants (13 females, M_{age} = 291.90 days, SD_{age} = 110.49 days) were included in the final EEG data analysis. An additional 14 infants were tested but not included in the final sample due to excessive artifacts and insufficient number of trials (*N* = 10) or missing IBQ-R data (*N* = 4). All participants were recruited from a small urban area in North West England, did not suffer from any neurological or other medical condition, and were observed to have a normal audition for their age.

Prior to the experiment, all parents were informed that at the end of the experiment they would receive £10 in order to cover traveling expenses and that the infant will be rewarded with a book for their participation. Informed consent was obtained from all parents. All data were collected in accordance with the ethical principles of the Declaration of Helsinki (BMJ 1991; 302: 1194) and the study was approved by the Faculty Ethics Committee.

Stimuli

A sample of 12 non-verbal emotional vocalizations produced by pre-verbal infants was gathered from sound library sources. The stimuli consisted of 4 positive (i.e., laughter), 4 negative (i.e., crying), and 4 neutral (i.e., coughing) non-speech sounds. Each vocalization was produced by a different individual. The use of coughing sounds as emotionally neutral contrasts is in line with previous investigations of auditory emotion processing (Armony, Chochol, Fecteau, & Belin, 2007; Blasi et al., 2011; Fecteau, Belin, Joanette, & Armony, 2007). The sound recordings were edited to a 1.4 sec length and rated by a group of 20 university students (10 females; M_{age} = 26 years; *SD* = 2.82 years) with respect to perceived arousal and authenticity of the emotion by using a 7-point Likert scale (Table 1).

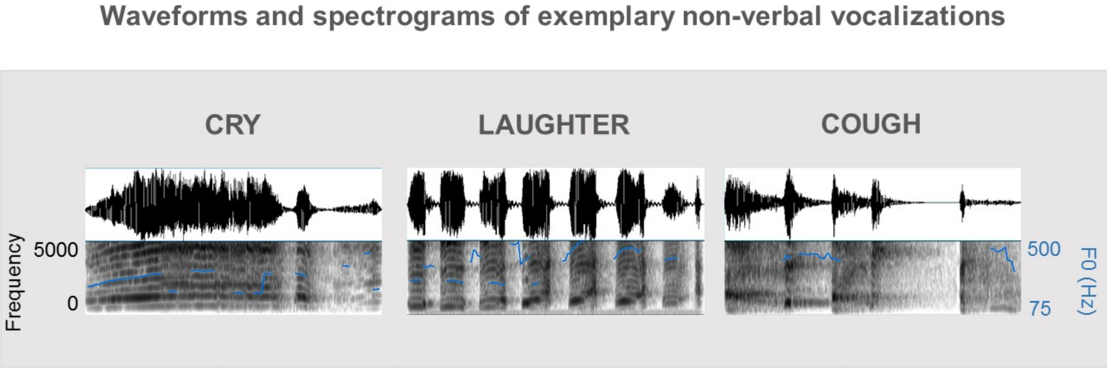
Table 1.
Mean (and SD) authenticity and arousal ratings for the non-verbal emotion stimuli.

	Arousal			Authenticity		
	1 extremely weak	*to*	*7 extremely strong*	*1 extremely false*	*to*	*7 extremely authentic*
Crying		6.19 (0.43)			5.83 (0.16)	
Laughter		6.25 (0.40)			5.49 (0.28)	
Coughing		3.74 (1.09)			5.21 (0.31)	

Note. Ratings from $n = 20$ adults

Separate one-way ANOVA with emotion (laugh/positive, cry/negative, cough/neutral) as a factor was performed on the arousal and authenticity ratings for the non-verbal stimuli. No significant differences between affective stimuli were found on authenticity (*F(2, 59)* = 1.693; *p* = .193), while a main effect of emotion was obtained for the arousal ratings (*F(2, 59)* = 80.244; *p* < .001). Post-hoc comparisons revealed that coughing sounds were rated as less arousing than both crying (*p* < .001) and laughing vocalizations (*p* < .001).

In addition, participants were asked to indicate the valence of the stimuli (positive, negative or neutral). On average, crying sounds were judged as "negative" by 97% of participants, laughing sounds were rated as "positive" by 99% of participants, and neutral sounds were rated as "neutral" by 75% of participants. These ratings are similar to those reported in previous studies using vocal emotional expressions (e.g., Belin et al., 2008; Pell et al., 2015). Basic acoustic properties of the stimuli are presented in Figure 1. The non-verbal vocalizations were edited so that all audio stimuli had an average root mean square intensity of 40 dB, after edge smoothing (linear rise/fall times of 20 ms) by applying cosine-squared ramps to the onset and offset. All sounds were bandpass filtered from 1 to 10,000 Hz with a digital finite impulse response filter in order to remove any potential background noise.



Condition	Mean f_0 (Hz)	Range f_0 (Hz)	Mean Intensity (dB)	Range Intensity (dB)
Negative – Cry	318.776	288.288	71.467	24.510
Positive – Laughter	412.909	235.136	71.306	27.140
Neutral - Cough	354.722	140.942	64.167	26.567

*Figure 1***.** Waveforms and spectrograms of exemplary non-verbal vocalizations included in the study and the average acoustic features for each affective category. The fundamental frequency (f_0) or pitch is measured in Hertz (Hz), while the intensity in decibels (dB). The values represent the averages across all exemplars within a category, calculated for the entire stimulus duration. The range for f_0 and intensity is calculated by subtracting the minimum from the maximum value recorded for each stimulus and then averaged across all exemplars.

Temperament Measure: Infant Behavior Questionnaire - Revised (IBQ-R)

Parental reports of infant temperament were obtained using the Infant Behavior Questionnaire – Revised (IBQ-R) that characterises temperament along 3 scales and 14 subscales from a total of 191 items. This instrument is widely used and is typically reported to have satisfactory reliability and validity (Rothbart & Gartstein, 2003). For the current study, we focused on the temperamental dimension *Negative Emotionality* and its subscales since this dimension had been previously related to differences in infant ERP responses to emotional information conveyed by facial and body expressions (Martinos et al., 2012; Missana et al., 2014; Rajhans et al., 2015). *Negative Emotionality* ($\alpha = .757$) refers to the tendency to show various forms of negative affect such as generalised distress, fear, and anger, and it is defined by four scales: *Sadness* (lowered mood and activity related to personal suffering, physical state, object loss, or inability to perform a desired action; general low mood, α = .763), *Distress to Limitations* (fussing, crying or showing distress while in a confining place or position; in caretaking activities; or when unable to perform a desired action, α = .810), *Fear* (startle or distress to sudden changes in stimulation, novel physical objects or social stimuli; inhibited approach to novelty, α = .902) and *Falling Reactivity* (rate of recovery from peak distress, excitement, or general arousal; ease of falling asleep – typically regarded to reflect infants' ability to regulate their own state, α = .883). Table 2 illustrates a description of the full distribution of the IBQ-R scores for the main temperamental dimensions (and its subscales) for the whole sample.

Table 2.
Descriptive statistics for infants' IBQ-R scores on the temperamental dimensions and its subscales (N = 30).

	Mean	*SD*	*Skewness*	*Kurtosis*
Negative Emotionality	3.195	.641	-.153	-.972
Distress	3.93	.866	-.077	-.242
Fear	2.417	.889	.640	-.275
Falling Reactivity	5.059	.966	-.585	.640
Sadness	3.494	.877	-.095	-.979
Surgency	5.154	.568	.281	-1.111
Approach	5.545	.604	-.093	-.307
Vocal Reactivity	5.298	.746	-.097	-.873
High Intensity Pleasure	6.154	.492	-.241	-.204
Smiling	4.848	.876	.136	-1.221
Activity Level	4.781	.889	.220	-1.280
Perceptual Sensitivity	4.297	1.099	.178	-.704
Regulation	4.756	.484	-.330	1.026
Low Intensity Pleasure	4.822	.815	.805	-.306
Cuddliness	5.434	.749	-.610	.014
Orienting	3.928	1.013	-.144	-.392
Soothability	4.839	.644	-1.229	2.144

Procedure

ERPs were recorded while infants sat on their parent's lap at a distance of approximately 70 cm from a 17-inch monitor in a dimly lit room. The auditory stimuli were randomly presented using MATLAB software (MathWorks, Natick, MA), over two hidden speakers placed to the left and right of the monitor. No more than two sounds of the same emotional category were presented consecutively. A trial consisted of 1400 ms sound stimulus followed by a silent inter-stimulus interval, which varied randomly in duration between 1200 ms and 2000 ms. A black fixation cross on a grey background was displayed on the monitor during the entire procedure. The procedure continued until a maximum of 138 trials were presented (46 per category) or until the infant showed signs of boredom and unrest. In order to minimize infants' movements and maintain their interest, an experimenter was present to quietly blow soap bubbles throughout the whole procedure. Both the parent and the experimenter avoided visual contact and any attempt for social interaction with the infant. The procedure lasted approximately 8 min. After stimulus presentation, parents filled in the IBQ-R questionnaire.

Electroencephalogram Recording and Data Analysis

The EEG was recorded continuously using a 128-electrode HydroCel Geodesic Sensor Net (Electrical Geodesic Inc., Eugene, OR) and amplified using an EGI NetAmps 300 amplifier. The signal was referenced online to the vertex electrode (Cz), a bandpass filter of .1-100 Hz was applied, and the data were sampled at 500 Hz. Impedances were checked prior to the beginning of the recording and considered acceptable if lower than 50 KΩ. EEG data were further processed offline using NetStation v4.6.4 (Eugene, OR). The signal was band-pass filtered (0.3-30 Hz), and the ERP trials were segmented with a 200 ms baseline and 1400 ms following stimulus onset. Data were corrected to the average voltage during baseline and re-referenced to the algebraic mean of channels. To eliminate artifacts, trials were automatically rejected whenever the signal exceeded ± 200 μV at any electrode for more than eighteen channels. Of the remaining trials, individual bad channels were replaced using spherical spline interpolation. Data were further checked through visual inspection for eye-movements, eye-blinks and other body movement artifacts not detected by the automated algorithm. Individual subject averages were computed separately for each channel across all trials within each condition and then data re-referenced to the average reference. Across participants, the mean number of trials contributing to the average ERP was 18 per each condition (Coughing: *M* = 18.41, *SD* = 6.49; Crying: *M* = 17.19, *SD* = 5.67; Laughing: *M* = 18.53, *SD* = 5.88).

On the basis of visual inspection of ERP waveforms and previous adult and infant auditory ERP studies (Kushnerenko, Ceponiene, Balan, Fellman, & Näätänen, 2002; Kushnerenko et al, 2007; Little, Thomas, & Letterman, 1999; Ohlrich & Barnet, 1972; Shucard, Shucard, Cummins, & Campos, 1981; Shucard, Shucard, & Thomas, 1987; Wunderlich & Cone-Wesson, 2006), mean amplitudes were analysed at three time-windows at frontal locations: 50-150ms (N100), 150-200ms (P200), and 550-950ms (LPC). At central locations, mean amplitude effects were assessed for the time window of 150-200ms (P200). The regions of interest (ROIs) were: frontal (left - 23, 24, 27, 28; right - 3, 117, 123, 124), and central (left - 36, 41, 42, 47; right - 93, 96, 103, 104). Separate 3 (emotion: positive, negative, neutral) x 2 (hemisphere: left, right) repeated-measures ANOVAs were conducted for each of these time windows at their respective regions of interest. We did not correct the results for multiple comparisons to avoid inflating Type II error and thereby obscuring expected results (O'Reilly et al., 2017; Rothman 1990, 2014). Multiple comparisons were kept to the minimum by using hypothesis-led predictions informed by previous research (e.g. Grossmann et al., 2005; Liu et al. 2012, Missana et al., 2017; Pell et al., 2015). All ERP statistical tests were conducted at .05 level of significance (two-tailed). Note that we labelled the ERP components included in the statistical analysis according their polarity and peak latency.

Results

The grand averages for all conditions at different scalp locations are presented in Figure 2. A more detailed illustration of the scalp topographies for the frontal components is included in Figure 3. No gender effects were found for any of the ERP components. For further information see Appendix A.

ERP analysis

Frontal

N100 (50-150 ms)

A main effect of emotion was found for the N100 mean amplitude at frontal leads, *F(2,58)* = 5.847; *p* = 0.005; η^2 = 0.168. Pairwise comparisons revealed that the N100 was significantly more negative for crying (*M* = -.547 µV; *SE* = .527) than for laughter sounds (*M* = 1.931 µV; *SE* = .571; *p* = .007). This effect remained when correcting for multiple comparisons (*p* = .020). No significant differences were observed between the neutral and emotional sounds (*p* > .069). No other main effects or interaction was found (*p* > .262).

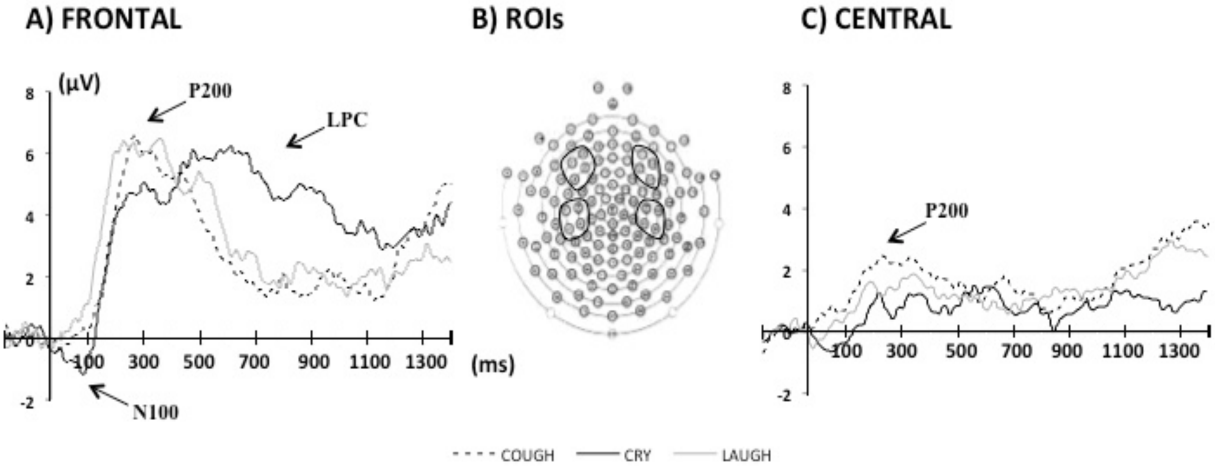


*Figure 2***.** Grand average ERPs for the crying (dark solid line), laughter (light gray solid line) and coughing (dotted line) sounds over frontal (A), and central (C) locations. The location of the analyzed ROIs is indicated in B).

P200 (150-200 ms)

At frontal locations, the analysis of P200 mean amplitude revealed a significant main effect of emotion, *F(2,58)* = 4.481; *p* = 0.016; η^2 = 0.134. Pairwise comparisons revealed that laughter sounds elicited more positive P200 amplitudes (*M* = 6.241 µV; *SE* = .848) than crying vocalizations (*M* = 3.510 µV; *SE* = .745; *p* = .012), and marginally more positive amplitudes than coughing sounds (*M* = 4.645 µV; *SE* = .713; *p* = .057). The difference between crying and laughter sounds on P200 amplitudes survived after applying Bonferroni correction (*p* = .036). No differences were observed between crying and coughing vocalizations (*p* > .223). Similar mean amplitudes were recorded for both hemispheres, *F(1,29)* = .476; *p* = .496; η^2 = .016 . No significant emotion x hemisphere interaction was found, *F(2,58)* = .449; *p* = .640; η^2 = .015.

Given the temporal proximity between this component and the N100 at frontal locations, it is possible that variations in the N100 parameters may have affected the P200 component differently across conditions. Thus, complementary peak-to-peak measurement and analysis were performed to control for N100 variations. With this purpose, same statistical analyses were performed on the measure of the mean amplitude difference between the peak of the P200 and the N100 (i.e. P200-N100). These analyses revealed no significant main effects or interactions (*p* > .606). Therefore, when accounting for peak-to-peak amplitude differences, the main effect of emotion disappears.

LPC (550-950 ms)

For this late time window at frontal locations, a main effect of emotion was found for the mean amplitude, *F(2,58)* = 4.161; *p* = 0.020; η^2 = 0.125. Follow up planned comparisons revealed that LPC amplitudes were more positive for crying (*M* = 4.754 µV; *SE* = .812) than laughter (*M* = 2.480 µV; *SE* = .603; *p* = .028) and coughing sounds (*M* = 2.163 µV; *SE* = .726; *p* = .030). These differences did not hold after Bonferroni corrections (*p* = .085 and *p* = .089 respectively). No difference was observed between laughter and coughing sounds (*p* = .691).

No other main effects or interaction were found ($p > .341$).

Central

P200 (150 -250 ms)

A similar mean amplitude was elicited by all conditions, $F(2,58) = 2.114$; $p = .130$; $\eta^2 = .068$. No main effect of hemisphere, $F(1,29) = .150$; $p = .702$; $\eta^2 = .005$, or interaction between condition and hemisphere was identified, $F(2,58) = 2.768$; $p = .071$; $\eta^2 = .087$.

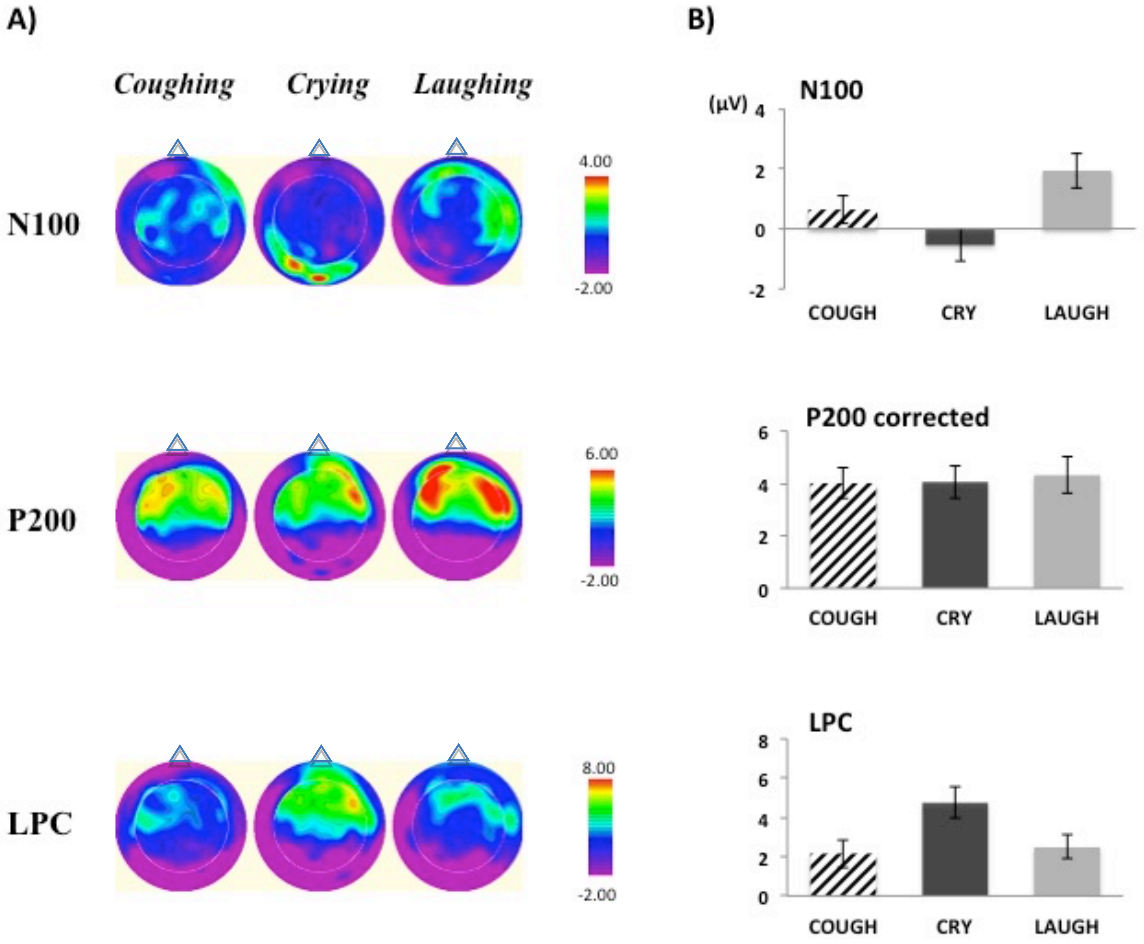


Figure 3. Scalp topographies for the frontal ERP components. (A) Voltage topographies of the frontal ERP components over the scalp for coughing (first column), crying (middle column) and laughing (last column) sounds. (B) Bar graphs showing the mean amplitude values (plus standard errors of the mean) per experimental condition for the frontal ERP components. The mean amplitude values for P200 are controlled for N100 variations.

Correlational Analysis

Pearson correlations (two tailed, $p < .05$) were computed to examine the relations between infants' general score on the *Negative Emotionality scale*, as well as the scores for its subscales (i.e., Sadness, Distress to Limitations, Fear, and Falling Reactivity), and the mean amplitude difference scores of the N100, P200 corrected and LPC between affective conditions (i.e., laughter *vs*. cry, cry *vs.* coughing, laughter *vs.* coughing). For each time window the mean amplitude obtained in response to coughing sounds was subtracted from the mean amplitude recorded in response to laughter sounds (i.e. Laughter [Lg] – Coughing [Cg]: $N100_{Lg-Cg}$, $P200_{Lg-Cg}$, LPC_{Lg-Cg}) and crying sounds (i.e. Crying [Cr] – Coughing [Cg]: $N100_{Cr-Cg}$, $P200_{Cr-Cg}$, LPC_{Cr-Cg}). In addition, for each component the mean amplitude elicited by crying sounds was subtracted from the mean amplitude elicited by laughter sounds (i.e. Laughter [Lg] – Crying [Cr]: $N100_{Lg-Cr}$, $P200_{Lg-Cr}$, LPC_{Lg-Cr}).

For the N100, there was no apparent relation between negative emotionality scores and the amplitude difference scores ($p > .647$).

For the P200 corrected, the factor negative emotionality was negatively associated with the $P200_{Lg-Cg}$ amplitude difference score, $r(30) = -.400$, $p = .028$. Additionally, our analysis revealed a significant positive correlation between infant's ability to recover from distress (IBQ-R Falling Reactivity scale) and the mean amplitude scores for $P200_{Lg-Cg}$ ($r(30) = .513$, $p = .004$) and $P200_{Cr-Cg}$ scores ($r(30) = .481$, $p = .007$) (Figure 4). These correlations did not hold after correcting for multiple comparisons with an adjusted alpha of .05/15 = .003.

For the LPC component, no association was observed with the main factor negative emotionality ($p >.129$). Nonetheless, a closer inspection of the subscales revealed a significant negative correlation between infants' ability to recover from distress (IBQ-R Falling Reactivity scale) and the LPC_{Lg-Cr} score, $r(30) = -.527$, $p = .003$ (Figure 4). Our analyses also showed a significant positive correlation between the scale falling reactivity and the LPC_{Cr-Cg} amplitude difference score, *r(30)* = .558, *p* = .001 (Figure 4). These correlations survived the Bonferroni correction for multiple comparisons.

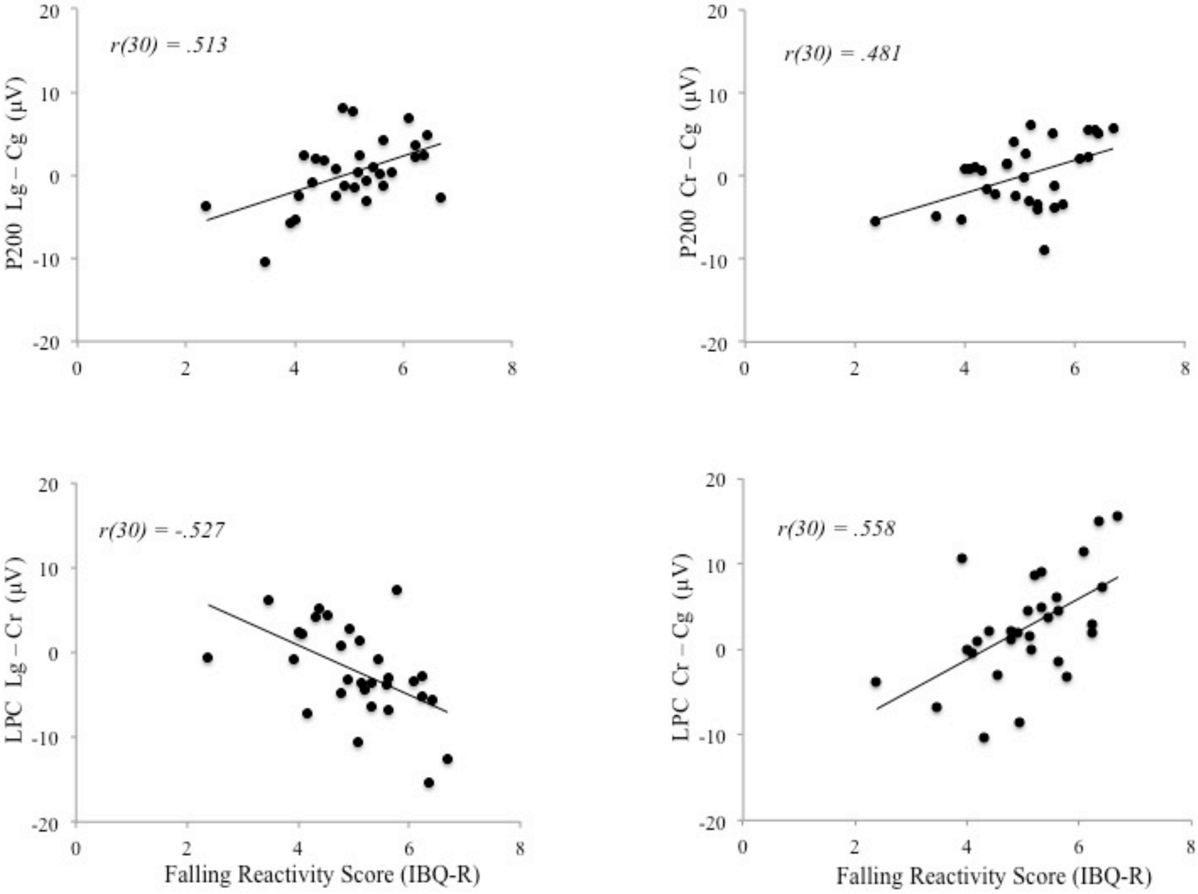


Figure 4. Correlations between infant ERP data and Falling Reactivity scores (IBQ-R). This figure shows the correlation between the mean amplitude difference scores of the frontal P200 corrected and frontal LPC and infants' scores on IBQ-R falling reactivity (the correlations are significant on the *p* < .01 level).

Discussion

Non-verbal vocalizations such as cry and laughter are powerful cues for communicating emotions (Barr et al., 2000; Davila Ross et al., 2009; Dunbar et al., 2012; Pell et al., 2015; Provine 2015; Sauter, Eisner, Ekman, & Scott, 2010; Scherer, 1986, 1995; Scott, Lavan, Chen, & McGettigan, 2014). Particularly the cry and laughter of pre-verbal infants, the primary means of vocal communication at this age, are highly efficient in eliciting a response from others (e.g., Sagi & Hoffman, 1976; Sander, Frome, & Scheich, 2007; Simner, 1971). In this study, we aimed to investigate 8-months-old infants' ERP responses to their peers' non-verbal vocalizations of emotions and whether these were modulated by temperamental characteristics. Sounds of infants crying and laughing were presented alongside neutral non-verbal productions (i.e., coughing) and parents reported on their infants' temperamental characteristics. Results showed that the processing of emotional information from non-verbal vocalizations at the age of 8 months was associated with differential ERP activity at frontal locations, indexed by the N100, P200 and LPC components. Importantly, the differentiation in response between emotional and non-emotional stimuli was significantly related to temperamental differences in negative emotionality.

ERP Results

In line with several previous studies reporting a sensitivity to emotional vocalizations within the early stages of auditory processing (Missana et al., 2017; Pell et al., 2015; Schirmer & Kotz, 2006), our results show that 8-months-old infants responded with a more negative N100 amplitude to their peers' crying sounds than to their peers' laughter sounds. Infants' N100 amplitudes were also more negative when hearing another infant crying than when hearing another infant coughing, yet the difference did not reach significance. The N100 is considered to be at least partially generated by the processing of the acoustic input in the auditory cortex (Eggermont & Ponton, 2003; Näätänen & Picton, 1987). Empirical evidence from infants suggests that the N100 is not likely to be influenced by the novelty of the sound, but more likely to be modulated by other auditory properties such as spectral richness (Csibra, Kushnerenko, & Grossmann, 2008; Kushnerenko et al., 2007), the sound intensity at the edges (e.g. slope, amplitude of sounds rise/fall) (Čeponiene, Aku, Westerfield, Torki, & Townsend, 2005; Čeponiene, Torki, Alku, Koyama, & Townsend, 2008), and fundamental frequency (Annett & Kotz, 2006; Kotz & Paulmann, 2011). The early processing of auditory cues contributes to the extraction of the emotional salience (Jessen & Kotz, 2008; Schirmer & Kotz,

2006) and may explain the differences observed in our study, with crying and laughing sounds being the most distinct in relation to each other.

Because of the sensitivity of N100 amplitude to sound audibility and acoustic energy levels, these results suggest that infant crying is perceptually more salient than laughter sounds (regardless of their equal intensity and duration) leading to an early detection and orienting response. Yet, these results do not provide information about the specific acoustic features that may have contributed to the effect of emotion on the N100. Although the auditory stimuli used in this study was designed to control for a wide range of acoustic parameters, some of the fundamental acoustic characteristics (e.g., mean fundamental frequency, harmonics, spectral structure variation) were preserved in order to maintain the ecological validity and generalizability of results. Undoubtly, it will be particularly interesting for future research to show which, if any, of these properties may be driving the effect of emotion. Interestingly, the differences found on the N100 mean amplitude among emotional vocalisations fit with the fundamental frequency (f0) indexes reported for these sounds, with the highest f0 mean corresponding to crying sounds and the lowest to laughing sounds, with coughing sounds being in the middle. However, without directly testing these hypothesis, it is not possible to provide a conclusive answer in this respect.

Contrary to our expectations, emotional non-verbal vocalizations did not elicit a larger P200 at frontal and central areas as opposed to neutral vocalization. Although laughter appeared to elicit larger amplitudes compared to the sound of peers crying and coughing, this effect did not hold when correcting for the N100 amplitude differences. Therefore, all non-verbal vocalizations, independently of emotion, evoked a P200 of similar amplitude at frontal and central locations. The P200 has been traditionally associated with attentional shifts that facilitate preferential processing of emotionally or motivationally relevant stimuli (Paulmann et al., 2013; Paulmann et al., 2010; Schutter et al., 2004). In consonance with these interpretations, our results may suggest that 8-monht-old infants in this study perceived all non-verbal vocalizations as socially relevant information. However, our P200 results do not fit with the existing limited evidence on emotional processing using non-verbal vocalizations. For instance, in infants, Missana et al. (2017) reported a main effect of emotion at central locations at a later time window (P300: 200 - 350 ms), with peer laughter vocalizations eliciting higher positive amplitudes compared to infant crying and adult neutral sounds. This positive enhancement to laughing vocalizations was thought to reflect processes detecting the familiarity of positive affect expressed in voices. Conversely, ERP research in adults tends to report larger P200 amplitudes for emotionally than for neutrally non-verbal vocalizations (e.g., Jessen & Kotz, 2011; Liu et al., 2012; Sauter & Eimer, 2009). The lack of consistency across studies regarding the P200 response may be reflecting developmental differences in the ability to process emotional cues from non-verbal vocalizations, with emotionally non-verbal vocalizations (positive and negative) being only preferentially processed later in time. Further research is needed to compare ERP signature in infants and adults exposed to same non-verbal stimuli. Additionally, little it is known about how preschool- and school-aged children process emotion form this type of vocalizations.

Our study also revealed late effects of emotion, with the sounds of crying peers eliciting higher amplitude of the frontal LPC compared to both laughter and coughing. Modulations of the LPC by the valence of verbal and non-verbal emotion vocalizations was systematically reported in adults and it is proposed to reflect the sustained cognitive processing of these social cues (e.g., Jessen & Kotz, 2011; Kotz & Paulmann, 2011; Paulmann et al., 2013; Schirmer et al., 2013; Schirmer & Kotz, 2006; Wildgruber, Ethofer, Grandjean, & Kreifelts, 2009). In infants, differentiation at the level of similar positive slow waves has been suggested to reflect the updating of existing memory representations (Nelson, Thomas, de Haan, & Wewerka, 1998). Our results showed that after 8-month-olds perceive both cry and laughter as similarly salient social cues, they engage in the sustained processing of only the cry sounds. These findings are in line with previous reports that listening to adult crying compared to laughter and neutral non-verbal vocalizations leads 3- to 7-month-old infants to increased activation of the orbitofrontal cortex and the insula (Blasi et al., 2011), areas known to be involved in the automatic appraisal of the emotional stimuli outside awareness and the generation of emotional experiences (see Koelsch et al., 2015 for a review). Our findings are in contrast to those recently reported by Missana et al. (2017), who found no difference in LPC amplitude between crying and laughing that may come down to some differences in methods. In our study we used positive, negative, and neutral vocalizations from other infants, which have greater salience in meaning to infants (Dondi et al., 1999; Martin & Clark, 1982) whereas Missana et al. (2017) included adults humming as a neutral stimulus. It is thus possible that the lack of LPC differentiation between the emotional conditions reported by Missana et al. (2017) was driven by the contrast between infant and adult voices.

The selective enhancement of the N100 and LPC components for the processing of peer crying vocalizations in the current ERP study is in line with a substantial body of evidence suggesting the emergence of a negativity bias in the processing of emotional information at the age of 7 months, with enhanced allocation of attention and sensorial processing for negative emotions rather than positive (see Vaish, Grossman, & Woodward for a review). ERP studies on infants' perception of emotional faces and voices have provided some indirect evidence in this respect. For instance, the perception of angry and fearful voices has been associated with larger ERP amplitudes than happy or neutral prosodies, suggesting increased attention for negative emotional expressions (Cheng et al., 2014; Grossman et al., 2005). Accordingly, infants use more successfully negative cues than positive cues to efficiently guide their own behavior in new or ambiguous situations (e.g., Hertenstein & Campos, 2001; Hornik, Risenhoover, & Gunnar, 1987; Mumme & Fernald, 2003; Mumme, Fernald, & Herrera, 1996).

One possible explanation is that negative emotional expressions are more salient than the positive ones given that they convey information regarding possible threats in the environment relevant to the self (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001). Indeed, threat-related emotions are hypothesized to carry greater informational value than positive ones, and to thus require greater attention and cognitive processing (e.g., Cacioppo & Berntson, 1999; Peeters & Czapinski, 1990; Vuilleumier, 2005; Williams, 2006). Therefore, our study extends previous research by showing that 8-month-old infants also manifest a negativity bias in their processing of peers' non-verbal vocalizations of emotions.

Effects of Negative Emotionality on Vocal Emotion Processing

Variations in infants' tendencies to respond with negative emotionality during everyday life events were not related to differences in N100 amplitude between conditions. One possible explanation is that at such an early stage of processing, infants are primarily extracting the sensory properties of the stimuli, operations that are not related to individual differences in emotional responsiveness. It is also possible that these relations become more obvious once these individual differences manifest with higher intensity and in a more stable manner later in ontogeny since adults who tend to be highly anxious show increased N100 amplitude for emotional non-verbal vocalizations (Pell et al., 2015).

Although we did not find a link between individual differences and the N100 component, we found that variations in infants' ability to recover from distress (IBQ-R Fall Reactivity) were related to differences in the amplitude of the P200 and LPC components. Specifically, the temperamental scale fall reactivity helped to clarify differences for the P200 amplitude between emotional and neutral non-verbal vocalizations. The higher parents rated their infants' ability to recover from distress, the more positive the amplitude of the P200 for emotional (crying and laughter) as compared to neutral non-verbal vocalizations (coughing). This suggests that infants better at self-regulation were better at extracting emotionally relevant information. Likewise, fall reactivity helped to clarify differences for the LPC amplitude between threatening (crying) and non-threatening stimuli (laughter and coughing), with infants rated higher in their ability to recover from distress being more likely to exhibit larger LPC amplitudes for crying as opposed to laughter and coughing. Hence, this suggests that infants better at self-regulation were also more efficient recruiting further cognitive resources for threat-related stimuli. These results go in line with recent findings suggesting a relation between infants' temperamental variations in fall reactivity and their ERP responses to emotional facial expressions (Martinos et al., 2010; Missana et al., 2014). Overall, these studies showed that infants who were better at recovering from distress displayed larger Nc responses (marker of attention) to fearful faces (Martinos et al., 2012) and anger faces (Missana et al., 2014), suggesting that infants higher on regulatory skills deployed greater effort to take control of attention and regulate their emotions when viewing negative emotions.

Additionally, the temperamental factor negative emotionality was related to variations in the amplitude of the P200. In this case, low levels of negative emotionality enlarged the differentiation of infants' ERP responses between positive and neutral sounds such that infants lower in negative emotionality exhibited larger P200 amplitudes for peer laughter as compared to peer coughing sounds. Notably, infants with low negative emotionality have been reported to be less prone to intense and frequent negative emotions in their everyday life, and more likely to experience positive affect (Rothbart & Ahadi, 1994; Rothbart, Ahadi, Hershey, & Fisher, 2001). Thus, it is possible that infants with lower levels of negative emotionality were better at distinguishing positive emotionally loaded vocalizations from neutrally loaded vocalizations at the level of the P200 due to they are more familiar with the expression of positive emotions. In support of this view, Missana et al. (2017) suggested that larger early positivities for peer laughter vocalizations (as opposed to coughing and crying sounds) reflected infants' detection of familiarity. However, this interpretation must be taken with caution given the limited evidence available and the mixed results. In contraposition to our results, Martinos et al. (2012) reported a link between high negative emotionality and increased ERP responses to positive facial expressions (Martinos et al., 2012). Nonetheless, these dissimilarities may also be accounted by differences in stimuli. Further studies are needed to elucidate the relationship between the temperamental factor negative emotionality and infants' processing of emotional information.

Limitations and Conclusions

This study is not without limitations. Although the sample size included in this study could be regarded as relatively small in comparison to other investigations of temperamental variations in infants, a post hoc power analysis using the programme GPower (Erdfelder, Faul & Buchaner, 1996) revealed that our study had ample power (over 95%) to detect an effect of emotion for the N100 and LPC components. To check whether the absence of a significant main effect of emotion for the P200 were due to a lack of statistical power, we conducted a post hoc analysis with power ($1 - \beta$) set at 0.90 and $\alpha = .05$ (two-tailed). The projected sample size would have to increase to 174 for this within-group comparison of $\eta^2_p = .003$ to reach statistical significance. A second limitation is linked to our stimuli. In particular, 25% of the adult raters judged the neutral sounds as something other than neutral. This may mean that any contrast involving neutral stimuli was not nearly as robust as one would hope. Interferingly similar data has been obtained with visual stimuli, indicating that neutral faces in particular may be interpreted as potentially negative or threatening given their ambiguity and lack of clear approach signals (Lee, Kang, Park, Kim, & An, 2008; Wieser & Brosch, 2012).

To summarize, our ERP data suggests that 8-month-old infants discriminated between emotionally valenced and neutral non-verbal vocalizations even when they were presented with the more difficult task of processing infant only voices. Although 8-month-old infants appeared to perceive all non-verbal vocalizations as salient, only the sounds of another infant crying elicited enhanced auditory processing during early stages and engaged in further sustained processing at later stages of sensory processing. Importantly, infants' ability to regulate high states of arousal was significantly related to their ability to discriminate between emotional and neutral stimul and their preferential processing of crying vocalizations at later stages. This is particularly important given the high relevance of the individual variability in reactivity and regulation for different typical and atypical social development outcomes (e.g., Frick & Morris, 2004; Pérez-Edgar & Fox, 2005; Olson et al., 2005). Our findings add novel information to an increasing body of knowledge suggesting important links between infant temperament and emotion information processing development, with potential implications for understanding the ontogeny of complex social skills, such as empathy.

References

Armony, J. L., Chochol, C., Fecteau, S., & Belin, P. (2007). Laugh (or cry) and you will be remembered: influence of emotional expression on memory for vocalizations. *Psychological Science*, *18*(12), 1027-1029.

Barr, R. G., Hopkins, B., & Green, J. A. (2000). *Crying as a sign, a symptom, and a signal: Clinical, emotional and developmental aspects of infant and toddler crying* (No. 152). Cambridge University Press.

Belin, P., Fecteau, S., Charest, I., Nicastro, N., Hauser, M. D., & Armony, J. L. (2008). Human cerebral response to animal affective vocalizations. *Proceedings of the Royal Society of London B: Biological Sciences*, *275*(1634), 473-481

Blasi, A., Mercure, E., Lloyd-Fox, S., Thomson, A., Brammer, M., Sauter, D., Deeley, Q., Barker, G.J., Renvall, V., Deoni, S. & Gasston, D. (2011). Early specialization for voice and emotion processing in the infant brain. *Current Biology*, *21*(14), 1220-1224

Bradley, M. M., Miccoli, L., Escrig, M. A., & Lang, P. J. (2008). The pupil as a measure of emotional arousal and autonomic activation. *Psychophysiology*, *45*(4), 602-607.

Bunford, N., Kujawa, A., Swain, J. E., Fitzgerald, K. D., Monk, C. S., & Phan, K. L. (2017). Attenuated neural reactivity to happy faces is associated with rule breaking and social problems in anxious youth. *European child & adolescent psychiatry*, *26*(2), 215-230.

Cacioppo, J. T., & Berntson, G. G. (1999). The affect system architecture and operating characteristics. *Current directions in psychological science*, *8*(5), 133-137.

Čeponienė, R., Alku, P., Westerfield, M., Torki, M., & Townsend, J. (2005). ERPs differentiate syllable and nonphonetic sound processing in children and adults. *Psychophysiology*, *42*(4), 391-406.

Čeponienė, R., Cheour, M., & Näätänen, R. (1998). Interstimulus interval and auditory event-related potentials in children: Evidence for multiple generators. *Electroencephalography and Clinical Neurophysiology, 108*(4), 345–354.

Čeponienė, R., Rinne, T., & Näätänen, R. (2002). Maturation of cortical sound processing as indexed by event-related potentials. *Clinical Neurophysiology, 113*(6), 870–82.

Čeponienė, R., Torki, M., Alku, P., Koyama, A., & Townsend, J. (2008). Event-related potentials reflect spectral differences in speech and non-speech stimuli in children and adults. *Clinical Neurophysiology*, *119*(7), 1560-1577.

Cheng, Y., Lee, S. Y., Chen, H. Y., Wang, P. Y., & Decety, J. (2012). Voice and emotion processing in the human neonatal brain. *Journal of cognitive neuroscience*, *24*(6), 1411-1419.

Chronaki, G., Broyd, S., Garner, M., Hadwin, J. A., Thompson, M. J., & Sonuga-Barke, E. J. (2012). Isolating N400 as neural marker of vocal anger processing in 6–11-year old children. *Developmental Cognitive Neuroscience*, *2*(2), 268-276.

Csibra, G., Kushnerenko, E. & Grossmann, T. (2008). Electrophysiological Methods in Studying Infant Cognitive Development. In C.A. Nelson and M. Luciana (Eds.). *Handbook of developmental cognitive neuroscience*. MIT Press.

Decety, J. (2015). The neural pathways, development and functions of empathy. *Current Opinion in Behavioral Sciences*, *3*, 1-6.

Decety, J., & Howard, L. H. (2013). The Role of Affect in the Neurodevelopment of Morality. *Child Development Perspectives, 7*, 49–54.

Dondi, M., Simion, F., & Caltran, F. Can newborns discriminate between their own cry and the cry of another newborn infant? *Developmental Psychology, 35*(2), 418-426.

Dunbar, R.I., Baron, R., Frangou, A. et al. (2012). Social laughter is correlated with an elevated pain threshold. *Proceedings of the Royal Society B: Biological Sciences, 22*(279), 1161–1167.

Eisenberg, N., & Fabes, R. A. (1995). The relation of young children's vicarious emotional responding to social competence, regulation, and emotionality. *Cognition & Emotion*, *9*(2-3), 203-228.

Eisenberg, N., Fabes, R. A., Murphy, B., Karbon, M., Smith, M., & Maszk, P. (1996). The relations of children's dispositional empathy-related responding to their emotionality, regulation, and social functioning. *Developmental psychology*, *32*(2), 195.

Eggermont, J. J., & Ponton, C. W. (2003). Auditory-evoked potential studies of cortical maturation in normal hearing and implanted children: correlations with changes in structure and speech perception. *Acta oto-laryngologica*, *123*(2), 249-252.

Esposito, G., Nakazawa, J., Venuti, P., & Bornstein, M. H. (2013). Componential deconstruction of infant distress vocalizations via tree-based models: A study of cry in autism spectrum disorder and typical development. *Research in Developmental Disabilities*, *34*(9), 2717-2724.

Esposito, G., Venuti, P., & Bornstein, M. H. (2011). Assessment of distress in young children: A comparison of autistic disorder, developmental delay, and typical development. *Research in Autism Spectrum Disorders*, *5*(4), 1510-1516.

Fecteau, S., Belin, P., Joanette, Y., & Armony, J. L. (2007). Amygdala responses to nonlinguistic emotional vocalizations. *Neuroimage*, *36*(2), 480-487.

Field, T., Diego, M., & Hernandez-Reif, M. (2009). Infants of Depressed Mothers Are Less Responsive To Faces and Voices: A Review. *Infant Behavior & Development*, *32*(3), 239–244.

Fox, N.A., Nichols, K.E., Henderson, H.A., Rubin, K., Schmidt, L., Hamer, D., Ernst, M. & Pine, D.S., 2005. Evidence for a gene-environment interaction in predicting behavioral inhibition in middle childhood. *Psychological Science*, *16*(12), 921-926.

Frick, P., & Morris, A. (2004). Temperament and developmental pathways to conduct problems. *Journal of Clinical Child & Adolescent Psychology, 33*(1), 54-68.

García-Larrea, L., Lukaszewicz, A. C., & Mauguiére, F. (1992). Revisiting the oddball paradigm. Non-target vs neutral stimuli and the evaluation of ERP attentional effects. *Neuropsychologia*, *30*(8), 723-741

Geangu, E. (2015). Development of empathy during early childhood across cultures. In Wright, J. D. (Eds.), *International encyclopedia of the social and behavioral sciences* (pp. 549-553). Elsevier.

Geangu, E., Benga, O., Stahl, D. & Striano, T. (2010). Individual Differences in Infants' Emotional Resonance to a Peer in Distress: Self–Other Awareness and Emotion Regulation. *Social Development, 20*: 450–470.

Geangu, E., Hauf, P., Bhardwaj, R., & Bentz, W. (2011). Infant Pupil Diameter Changes in Response to Others' Positive and Negative Emotions. *PLoS ONE, 6*(11), e27132.

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*(6), 1825–1828.

Grossmann, T., Vaish, A., Franz, J., Schroeder, R., Stoneking, M., & Friederici, A. D. (2013). Emotional voice processing: investigating the role of genetic variation in the serotonin transporter across development. *PloS ONE*, *8*(7), e68377.

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

Hoffman, M. L. (2001). *Empathy and moral development: Implications for caring and justice*. Cambridge University Press.

Jarcho, J.M., Fox, N.A., Pine, D.S., Leibenluft, E., Shechner, T., Degnan, K.A., Perez-Edgar, K., & Ernst, M., 2014. Enduring influence of early temperament on neural mechanisms mediating attention–emotion conflict in adults. *Depression and anxiety*, *31*(1), 53-62.

Jessen, S., & Kotz, S. A. (2011). The temporal dynamics of processing emotions from vocal, facial, and bodily expressions, *NeuroImage, 58*(2), 665-674.

Johnson, H. (2011). Interactive specialization: a domain-general framework for human functional brain development?. *Developmental Cognitive Neuroscience, 1*(1), 7-21.

Johnson, M. H., Gliga, T., Jones, E., & Charman, T. (2015). Annual Research Review: Infant development, autism, and ADHD–early pathways to emerging disorders. *Journal of Child Psychology and Psychiatry*, *56*(3), 228-247.

Karmiloff-Smith, A. (1998). Development itself is the key to understanding developmental disorders. *Trends in cognitive sciences*, *2*(10), 389-398.

Koelsch, S., Jacobs, A. M., Menninghaus, W., Liebal, K., Klann-Delius, G., von Scheve, C., & Gebauer, G. (2015). The quartet theory of human emotions: an integrative and neurofunctional model. *Physics of life reviews*, *13*, 1-27.

Kooijman, V., Hagoort, P., & Cutler, A. (2005). Electrophysiological evidence for prelinguistic infants' word recognition in continuous speech. *Cognitive Brain Research*, *24*(1), 109-116.

Kotz, S. A., & Paulmann, S. (2011). Emotion, language, and the brain. *Language and Linguistics Compass*, *5*(3), 108-125.

Kushnerenko, E., Ceponiene, R., Balan, P., Fellman, V., & Näätänen, R. (2002a). Maturation of the auditory change detection response in infants: a longitudinal ERP study. *Neuroreport*, *13*(15), 1843-1848.

Kushnerenko, E., Ceponiene, R., Balan, P., Fellman, V., Huotilainen, M., & Näätänen, R. (2002b). Maturation of the auditory event-related potentials during the first year of life. *Neuroreport*, *13*(1), 47-51.

Kushnerenko, E., Winkler, I., Horváth, J., Näätänen, R., Pavlov, I., Fellman, V., & Huotilainen, M. (2007). Processing acoustic change and novelty in newborn infants. *European Journal of Neuroscience*, *26*(1), 265-274.

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

Little, V. M., Thomas, D. G., & Letterman, M. R. (1999). Single-trial analyses of developmental trends in infant auditory event-related potentials. *Developmental Neuropsychology*, *16*(3), 455-478.

Liu, T., Pinheiro, A. P., Deng, G., Nestor, P. G., McCarley, R. W., & Niznikiewicz, M. A. (2012). Electrophysiological insights into processing non-verbal emotional vocalizations. *Neuroreport, 23*(2), 108–112.

Lloyd-Fox, S., Blasi, A., Mercure, E., Elwell, C. E., & Johnson, M. H. (2012). The emergence of cerebral specialization for the human voice over the first months of life. *Social Neuroscience*, *7*(3), 317-330.

Martin, G. B., & Clark, R. D. (1982). Distress crying in neonates: Species and peer specificity. *Developmental Psychology, 18*, 3–9.

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.

Mireault, G. C., Crockenberg, S. C., Sparrow, J. E., Pettinato, C. A., Woodard, K. C., & Malzac, K. (2014). Social looking, social referencing and humor perception in 6-and-12-month-old infants. *Infant Behavior and Development*, *37*(4), 536-545.

Missana, M., Altvater-Mackensen, N., & Grossmann, T. (2017). Neural correlates of infants' sensitivity to vocal expressions of peers, *Developmental Cognitive Neuroscience, 26*, 39-44.

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*(4), e93728.

Morales, S., Fu, X., & Pérez-Edgar, K. E. (2016). A developmental neuroscience perspective on affect-biased attention. *Developmental cognitive neuroscience*, *21*, 26-41.

Näätänen, R., Paavilainen, P., Rinne, T., & Alho, K. (2007). The mismatch negativity (MMN) in basic research of central auditory processing: a review. *Clinical Neurophysiology*, *118*(12), 2544-2590.

Näätänen, R., & Picton, T. (1987). The N1 wave of the human electric and magnetic response to sound: a review and an analysis of the component structure. *Psychophysiology*, *24*(4), 375-425.

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.

Nichols, S. R., Svetlova, M., & Brownell, C. A. (2009). The role of social understanding and empathic disposition in young children's responsiveness to distress in parents and peers. *Cognition, Brain, Behavior : An Interdisciplinary Journal*, *13*(4), 449–478.

Nichols, S. R., Svetlova, M., & Brownell, C. A. (2015), Toddlers' Responses to Infants' Negative Emotions. *Infancy, 20*, 70–97.

Nwokah, E. E., Hsu, H. C., Dobrowolska, O., & Fogel, A. (1994). The development of laughter in mother-infant communication: Timing parameters and temporal sequences. *Infant Behavior and Development*, *17*(1), 23-35.

Obleser, J., & Kotz, S. A. (2011). Multiple brain signatures of integration in the comprehension of degraded speech. *Neuroimage*, *55*(2), 713-723.

Ohlrich, E. S., & Barnet, A. B. (1972). Auditory evoked responses during the first year of life. *Electroencephalography and clinical neurophysiology*, *32*(2), 161-169.

Olson, S. L., Sameroff, A. J., Kerr, D. C. R., Lopez, N. L., & Wellman, H. M. (2005). Developmental foundations of externalizing problems in young children: the role of effortful control. *Developmental Psychopathology, 17*, 25–45.

Ostwald, P. F., & Murry, T. (1985). The communicative and diagnostic significance of infant sounds. In B.M. Lester and C. F. Zachariah Boukydis (Eds.) *Infant crying. Theoretical and research perspectives* (pp. 139-158). Plenum Press, London – New-York.

Parise, E., Friederici, A. D., & Striano, T. (2010). "Did you call me?" 5-month-old infants own name guides their attention. *PloS one*, *5*(12), e14208.

Paulmann, S., Bleichner, M., & Kotz, S. A. (2013). Valence, arousal, and task effects in emotional prosody processing. *Frontiers in psychology, 4*, 107 – 116.

Paulmann, S., & Kotz, S.A. (2008). An ERP investigation on the temporal dynamics of emotional prosody and emotional semantics in pseudo- and lexical-sentence context. *Brain and Language*, *105*(1), 59-69.

Paulmann, S., & Pell, M. D. (2010). Contextual influences of emotional speech prosody on face processing: how much is enough?. *Cognitive, Affective, & Behavioral Neuroscience*, *10*(2), 230-242.

Peeters, G., & Czapinski, J. (1990). Positive-negative asymmetry in evaluations: The distinction between affective and informational negativity effects. *European review of social psychology*, *1*(1), 33-60.

Pell M. D., Rothermich K., Liu P., Paulmann S., Sethi S., Rigoulot S. (2015). Preferential decoding of emotion from human non-linguistic vocalizations versus speech prosody. *Biological Psychology, 111*, 14–25.

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*, nsn046.

Pérez-Edgar, K., & Fox, N. A. (2005). Temperament and anxiety disorders. *Child and Adolescent Psychiatric Clinics of North America, 14*, 681-706.

Provine, R. R. (1996). Laughter. *American scientist*, *84*(1), 38-45.

Provine, R. R. (2004). Laughing, tickling, and the evolution of speech and self. *Current Directions in Psychological Science*, *13*(6), 215-218.

Provine, R. R. (2016). Laughter as a scientific problem: An adventure in sidewalk neuroscience. *The Journal of Comparative Neurology, 524*, 1532–1539.

Purhonen, M., Kilpeläinen-Lees, R., Pääkkönen, A., Yppärilä, H., Lehtonen, J., & Karhu, J. (2001). Effects of maternity on auditory event-related potentials to human sound. *Neuroreport*, *12*(13), 2975-2979.

Purhonen, M., Kilpeläinen-Lees, R., Valkonen-Korhonen, M., Karhu, J., & Lehtonen, J. (2004). Cerebral processing of mother's voice compared to unfamiliar voice in 4-month-old infants. *International Journal of Psychophysiology*, *52*(3), 257-266.

Purhonen, M., Kilpeläinen-Lees, R., Valkonen-Korhonen, M., Karhu, J., & Lehtonen, J. (2005). Four-month-old infants process own mother's voice faster than unfamiliar voices—electrical signs of sensitization in infant brain. *Cognitive Brain Research*, *24*(3), 627-633.

Rajhans, P., Missana, M., Krol, K. M., & Grossmann, T. (2015). The association of temperament and maternal empathy with individual differences in infants' neural responses to emotional body expressions. *Developmental Psychopathology,* 27, 1205-1216.

Ravicz, M. M., Perdue, K. L., Westerlund, A., Vanderwert, R. E., & Nelson, C. A. (2015). Infants' neural responses to facial emotion in the prefrontal cortex are correlated with temperament: a functional near-infrared spectroscopy study. *Frontiers in psychology*, *6*.

Reddy, V. (2001). Infant clowns: The interpersonal creation of humour in infancy. *Enfance*, *53*(3), 247-256.

Reddy, V. (2008). *How Infants Know Minds*. Cambridge, MA: Harvard University Press.

Reddy, V., Williams, E., & Vaughan, A. (2002). Sharing humour and laughter in autism and Down's syndrome. *British journal of psychology*, *93*(2), 219-242.

Ross, M. D., Owren, M. J., & Zimmermann, E. (2009). Reconstructing the evolution of laughter in great apes and humans. *Current Biology*, *19*(13), 1106-1111.

Rothbart, M. K., & Ahadi, S. A. (1994). Temperament and the development of personality. *J Abnormal Psychology, 103*(1), 55-66.

Rothbart, M. K., Ahadi, S. A., Hershey, K. L., & Fisher, P. (2001). Investigations of temperament at three to seven years: the Children's Behavior Questionnaire. *Child Development, 72*(5), 1394-1408.

Rothbart, M. K., & Derryberry, D. (1981). Theoretical issues in temperament. In *Developmental Disabilities* (pp. 383-400). Springer Netherlands.

Sagi, A., & Hoffman, M. L. (1976). Empathic distress in the newborn. *Developmental Psychology, 12*(2), 175-176.

Sander, K., Frome, Y., & Scheich, H. (2007). FMRI activations of amygdala, cingulate cortex, and auditory cortex by infant laughing and crying. *Human brain mapping*, *28*(10), 1007-1022.

Sauter, D. A., Eisner, F., Ekman, P., & Scott, S. K. (2010). Cross-cultural recognition of basic emotions through non-verbal emotional vocalizations. *Proceedings of the National Academy of Sciences*, *107*(6), 2408-2412.

Scherer, K. R. (1986). Vocal affect expression: a review and a model for future research. *Psychol Bull, 99*(2), 143-165.

Scherer, K. R. (1995). Expression of emotion in voice and music. *Journal of voice*, *9*(3), 235-248

Schirmer, A., Chen, C. B., Ching, A., Tan, L., & Hong, R. Y. (2013). Vocal emotions influence verbal memory: neural correlates and interindividual differences. *Cognitive, Affective, & Behavioral Neuroscience*, *13*(1), 80-93.

Schirmer, A., & Kotz, S. A. (2003). ERP evidence for a sex-specific Stroop effect in emotional speech. *Journal of cognitive neuroscience*, *15*(8), 1135-1148.

Schirmer, A., & Kotz, S. A. (2006). Beyond the right hemisphere: brain mechanisms mediating vocal emotional processing. *Trends in cognitive sciences*, *10*(1), 24-30.

Schirmer, A., Kotz, S. A., & Friederici, A. D. (2005). On the role of attention for the processing of emotions in speech: Sex differences revisited, *Cognitive Brain Research, 24*(3), 442 - 452.

Scott, S. K., Lavan, N., Chen, S., & McGettigan, C. (2014). The social life of laughter. *Trends in cognitive sciences*, *18*(12), 618-620.

Shucard, J. L., Shucard, D. W., Cummins, K. R., & Campos, J. J. (1981). Auditory evoked potentials and sex-related differences in brain development. *Brain and Language*, *13*(1), 91-102.

Shucard, D. W., Shucard, J. L., & Thomas, D. G. (1987). Auditory event-related potentials in waking infants and adults: a developmental perspective. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *68*(4), 303-310.

Simner, M. (1971). Newborn's response to the cry of another infant. *Developmental psychology, 5*(1), 136-150.

Thierry, G., Vihman, M., & Roberts, M. (2003). Familiar words capture the attention of 11-month-olds in less than 250 ms. *Neuroreport*, *14*(18), 2307-2310.

Upshaw, M. B., Kaiser, C. R., & Sommerville, J. A. (2015). Parents' empathic perspective taking and altruistic behavior predicts infants' arousal to others' emotions. *Frontiers in Psychology*, *6*, 360.

Vaish, A., Grossmann, T., & Woodward, A. (2008). Not all emotions are created equal: The negativity bias in social-emotional development. *Psychological Bulletin*, *134*(3), 383–403.

Vuilleumier, P. (2005). How brains beware: neural mechanisms of emotional attention. *Trends in cognitive sciences*, *9*(12), 585-594.

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

Wildgruber, D., Ethofer, T., Grandjean, D., & Kreifelts, B. (2009). A cerebral network model of speech prosody comprehension. *International Journal of Speech-Language Pathology*, *11*(4), 277-281.

Williams, L. M. (2006). An integrative neuroscience model of" significance" processing. *Journal of integrative neuroscience*, *5*(01), 1-47.

Wolff, P. H. (1963). Observations on the early development of smiling. In B.M. Foss (Ed.), *Determinants of infant behavior. Vol. 2* (pp. 113-138). New York: Wiley.

Wunderlich, J. L., & Cone-Wesson, B. K. (2006). Maturation of CAEP in infants and children: a review. *Hearing research*, *212*(1), 212-223.

Wunderlich, J. L., Cone-Wesson, B. K., & Shepherd, R. (2006). Maturation of the cortical auditory evoked potential in infants and young children. *Hearing research*, *212*(1), 185-202.

Zhang, D., Liu, Y., Hou, X., Sun, G., Cheng, Y., & Luo, Y. (2014). Discrimination of fearful and angry emotional voices in sleeping human neonates: a study of the mismatch brain responses. *Frontiers in behavioral neuroscience*, *8*, 422.

Frontal Asymmetry Patterns and Infants' Responses to their Peers' Positive and Negative Emotions

Maria M. Crespo-Llado[1], Ross E. Vanderwert[2], Elisa Roberti[1], and Elena Geangu[1]

[1]Lancaster University, [2]Cardiff University

Author Note

A version of this paper is under review:
Crespo-Llado, M.M., Vanderwert, R.E., Roberti, E. & Geangu, E. (under review). Eight-month-old infants' behavioural responses to peers' emotions as related to the asymmetric frontal cortex activity. *Scientific Reports.*

Abstract

Although it is believed that infants' ability to share others emotions motivates the generation of other-oriented behaviors, this link has not been empirically tested. Little it is known about the neural mechanisms and motives underlying infant-oriented behaviors towards others. The present study aims at examining the neurophysiological mechanisms linked to infants' responses to a peer crying and a peer laughing by looking at frontal EEG hemispheric asymmetries. With this purpose, 8-month-old infants underwent two assessment sessions on separate days. In both sessions infants were presented with two video-films depicting a peer crying and a peer laughing each. Frontal asymmetry patterns were recorded by means of electroencephalography (EEG) during the first session while infants' other-oriented and emotional behaviors were recorded during the second visit to the lab. EEG analysis showed that distinct neural patterns were related to the observation of a peer laughing and a peer crying, with greater right frontal activation being associated with the observation of a peer crying. Furthermore, correlational analysis suggested a positive relation between left frontal cortical activation and infants' attempts to approach a peer crying or infants' attempts to engage with a peer laughing. These findings reveal that particular neurophysiological asymmetry patterns are associated with infants' motivational tendencies to approach another infant in early development.

Introduction

Empirical evidence suggests that infants in the first year of life are already socially attuned to the their peers' emotions, as shown by their ability to respond with matching vocal and facial affective states to their peers distress (Martin & Clark, 1982; Simner, 1971; Sagi & Hoffman, 1976). Notably, these findings are at least quite surprising taking into account that interactions with same-age peers are rare prior to the age of 18-months (Brownell & Brown, 1992; Eckerman & Peterman, 2001), thus suggesting the presence of an inborn ability to respond to others' emotions (Hoffman, 2000; Dondi, Simion & Caltran, 1999). In the domain of empathy, it has been argued that this early responsiveness to others' emotions, in conjunction with certain level of emotion understanding and perspective taking, may further motivate other-oriented responses, which in turn may prompt prosocial behaviors (e.g., Batson, 1991, Decety & Lamm, 2006; Eisenberg, 1997; Hoffman, 1975, 1982; Knafo & Israel, 2012; Singer, 2006). Although these links have been established at the conceptual level, it remains to be determined whether the affective responses to a peer' distress observed in the first year of life are real precursors to later forms of other-oriented responses. Furthermore, little it is known about the mechanisms involved in infants' emerging other-oriented responses, and whether they are selective to negative emotions. In light of the lack of empirical evidence, the current study aims at expanding previous behavioral research on infants' affective responsiveness to peers' emotions by exploring the link between infants' motivational responses to their peers' positive and negative emotions and the neural correlates (as reflected by EEG activity) underlying these tendencies in 8-month-old infants.

As early as few hours after birth, newborns show the ability to resonate with their peers' negative emotions as shown by contagious cry studies (Dondi et al., 1999; Field, Diego, Hernandez-Reif & Fernandez, 2007; Martin & Clark, 1982; Simner, 1971; Sagi & Hoffman, 1976). These affective resonance responses seem to persist across the first year of life (Geangu, Benga, Stahl & Striano, 2010) and when jointly presented with the corresponding facial expressions, these overt responses are accompanied by autonomic arousal changes (as reflected by larger pupil diameters) in infants as early as 6 months of age (Geangu, Hauf, Bhardwaj, & Bentz, 2011; Upshaw, Kaiser, Sommerville, Ford, & Perlman, 2015). Similar autonomic responses have been reported in infants when exposed to video-recordings of a peer laughing, yet in lower degree compared to the observation of a peer crying (Geangu et al., 2011; Upshaw et al., 2015). There is also limited ERP evidence suggesting that emotionally loaded vocalizations produced by peers modulate 8-month-old infants' brain responses (Crespo-Llado, Vanderwert, & Geangu, 2018; Missana, Alvater-Mackensen, & Grossman, 2017), with the sound of an infant crying eliciting greater sustained cognitive processing compared to both infant laughter and infant coughing sounds (Crespo-Llado et al., 2018). Notably, these initial results suggest the emergence of a differential developmental pattern in the processing of laughter and crying sounds.

The transition from these early affective matching responses to more other-oriented empathic responses remains to be determined. In juxtaposition with influential theoretical models arguing that other-oriented responses to others' negative emotions emerge beginning in the second year of life (Hoffman 2000), sparse evidence suggests that infants as young as 8 months of age already manifest other-oriented affective responses towards their peers in distress, as indexed by moderate levels of vocal and facial expressions of concern –empathic concern– and rudimentary comforting behaviors towards a peer in distress (Liddle, Bradley & MacGrath, 2015; Roth-Hanania, Davidov, & Zahn-Waxler, 2011). There is also suggestive evidence that these empathic-related responses continue to develop in the subsequent months, as shown by their gradual increase over toddlerhood (Liew et al., 2011; Nichols, Svetlova, & Brownell, 2015; Roth-Hanania et al., 2011). However, it is not until the second year of life when infants' reactions to peer emotions evolve from empathic concern and simple comforting acts to actual "prosocial" behaviors such as instrumental helping and sharing (Liew et al., 2011; Nichols, Svetlova, & Brownell, 2010, 2015; Roth-Hanania et al., 2011; Sommerville, Schmidt, Yun, & Burns, 2013; Svetlova, Nichols, & Brownell, 2010). These results are in contraposition with naturalistic studies suggesting that unprompted prosocial responding to peers in distress is rare but also quite diverse among toddlers (Demetriou & Hay, 2004; Farver & Branstetter, 1994; Howes & Farver, 1987; Lamb & Zakhireh, 1997). These differences in responsiveness may be accounted by a variety of contextual factors, such as familiarity, experience with siblings or day-care experience (Demetriou & Hay, 2004; Hay, Payne, & Chadwick, 2004; Howes & Farver, 1987; Lamb & Zakhireh, 1997) but also by individual differences in the motor and socio-cognitive skills needed to perform other-oriented responses (Paulus, 2014; Roth-Hanania et al., 2011; Svetlova et al., 2010; Walle & Campos, 2012).

As much as these findings have received attention, little is known about the motivational mechanisms involved in infants' rudimentary prosocial responses during the first year of life (Cowell & Decety, 2015; Paulus, 2014; Svetlova et al., 2010), and especially the neural mechanisms underlying infant-oriented responses towards others' happiness. The quest for the motives underlying these early empathic-related behaviors is not exempt of difficulties taking into account the inability for preverbal infants to disclose their intents. In this context, combining neuroimaging methods with behavioral measures is critical to clarify the nature of developing other-oriented behaviors in infants, often considered the precursors to later more complex prosocial behaviors.

Electroencephalography (EEG), and in particular frequency-power analysis, has been successfully used to investigate infants' motivational tendencies to approach or withdrawal emotional situations (e.g., Davidson & Fox, 1982, 1989; Fox & Davidson, 1986, 1987, 1988).

Over the last three decades, an increasing number of infant EEG research has explored the relation of frontal hemispheric asymmetries in EEG activity and developing motivational tendencies within an approach-withdraw continuum (e.g., Davidson & Fox, 1982, 1989; Dawson, 1994; Diaz & Bell, 2011; Fox & Davidson, 1986, 1987, 1988). In particular, frontal EEG asymmetry measures recorded during emotionally salient situations are considered to be a reliable index of prefrontal associations with individual motivational tendencies to either approach or avoid stimuli perceived as appetitive or aversive (e.g., Davidson & Fox, 1982, 1989; Fox & Davidson, 1986, 1987, 1988; Coan & Allen, 2004). Within this framework, greater relative left frontal activation reflects approach-related tendencies while greater relative right frontal activation reflects withdrawal-related predispositions (Fox, 1991, 1994; Harmon-Jones, Gable, & Peterson, 2010). This notion has been supported by a substantial amount of infant studies examining frontal EEG asymmetry scores during emotional tasks, which have revealed greater left frontal EEG activation in response to typically appetitive stimuli (e.g., mother approach, film of an adult displaying a happy facial expression, positively-valenced ID speech) and greater right frontal activation during the presentation of aversive stimuli (e.g., maternal distress simulation, maternal separation, stranger approach, film of an adult displaying a sad facial expression, arm restrain task, negatively-valenced ID speech) (e.g., Buss et al., 2003; Davidson & Fox, 1982, 1989; Diaz & Bell, 2011; Fox & Davidson, 1986, 1987, 1988; Killeen & Teti, 2012; LoBue, Coan, Thrasher & DeLoache, 2011; Santesso, Schmidt & Trainor, 2007).

Additionally, frontal asymmetry patterns have also been related to individual differences in social behavior. In this respect, multiple longitudinal studies have shown that early patterns of left frontal EEG asymmetry predicted higher levels of sociability during peer interactions across the toddler years. On the contrary, infants' right frontal EEG asymmetry patterns turned out to be good predictors of elevated levels of social reticence during interactions with peers in the toddler years (e.g., Calkins, Fox, & Marshall, 1996; Fox, Henderson, Rubin, Calkins, & Schmidt, 2001; Fox et al., 1995; Henderson, Fox & Rubin, 2001). There is also further evidence associating relatively left frontal activation with greater empathic responding (Paulus, Kuhn-Popp, Licata, Sodian, & Meinhardt, 2013). For instance, Paulus et al. (2013) found that greater relative left frontal activation at the age of 14 months was associated with infants' better understanding of others' distress at the age of 18 months as well as greater empathic responding during a comforting task at the age of 24 months. Similarly, Licata, Paulus, Kuhn-Popp, Meinhardt, & Sodian (2015) found a link between relative greater left frontal activation at the age of 14 months with higher frequencies of children approaching and initiating contact with their mothers during free play interactions at 50 months. Together, these studies highlight the role of frontal EEG asymmetry as a potential predictor of infants' social competence in peer settings.

For the study of empathy, infant-infant settings offer a unique window to examine early prosocial tendencies given that infants' understanding of peers' emotions do not rely on previous experiences since they have little or non exposure to peers prior to the first birthday (Nichols, Svetlova, & Brownell, 2009, 2015). Moreover, unlike adult-infant interactions, when infants are confronted with their peers in distress, normally they do not have the help of an adult to understand the scenario (Nichols et al., 2009, 2015). Hence, they must rely on their own unripe skills, without the assistance of adults, to interpret and respond appropriately to their peers' emotions. On the other hand, responding to peers' emotion may place different demands on infants' emergent social understanding skills than responding to adults' emotions. Indeed research suggests that 12-month-old infants are less skilled at interpreting other children's emotional communication than they are at understanding those of adults (Nichols et al., 2010). Altogether, child-child interactions provide a unique setting to study infants' independent motives underlying other-oriented responses to their peers' emotions.

Taking into account the aforementioned framework, the current study had three main goals. The first goal was to explore the frontal EEG asymmetry patterns elicited by the observation of a peer crying and a peer laughing in 8 month-old infants. Since increased left hemisphere activation has been associated with positive-eliciting situations while increased right hemisphere activation has been linked to negative-eliciting situations, we hypothesized that infants would exhibit greater relative right frontal activity when exposed to a crying peer as compared to a laughing peer and greater relative left frontal activity when watching a laughing peer as opposed to a crying peer.

The second major goal was to assess whether infants' responsiveness towards others' emotional states fluctuates across different valenced emotions by assessing their responses to peers experiencing distress and happiness. To capture the full range of infants' responses to peers, we distinguished vocal and facial signs of affective responding from approach-withdrawal responding, while also including measures of passive attention and general motor activation. Following the scarce pre-existing literature on the topic (Geangu et al., 2011; Roth-Hanania et al., 2011; Upshaw et al., 2015), we expected to find differences in infants' reactions due to emotion condition, with 8-month-old showing more positive affective responses and approach-related behaviors (e.g., positive vocalizations, facial expressions of joy, smiles, attempts to reach towards the stimuli) in front of a peer laughing and more negative affective responses (e.g., negative vocalizations, facial expressions of anger, attempts to escape from chair) in front of a peer crying. Because the behavioral evidence is mixed for infant-oriented responses to peers in distress during the first two years of life, we had no strong expectations about the crying peer condition eliciting more approach than withdrawal behaviors. Additionally, we had not strong predictions regarding motor activation measures. Regarding the attentional measures, in agreement with the literature on negativity bias in the processing of emotional cues (see Vaish, Grossman, & Woodward, 2008), we expected 8-month-old infants to look longer at a peer crying than a peer laughing.

The third and final goal was to investigate the relationship between behavioral responses and concurrent measures of frontal EEG asymmetry, both when infants were exposed to a peer's crying and a peer's laughter. Following previous infant EEG studies on emotion reactivity (e.g., Buss et al., 2003; Davidson & Fox, 1982, 1898; Fox & Davidson, 1986, 1988), we hypothesized that those infants who show greater relative right frontal activation when observing a peer crying would respond with more negative affective responses and withdrawal-related behaviors (e.g., negative vocalizations, facial expressions of anger, attempts to escape from chair) to the presentation of a peer crying. In the same vein, we hypothesised that infants who show greater relative left frontal activation when observing a peer laughing would respond with more positive affective responses and approach-related behaviors (e.g., positive vocalizations, facial expressions of joy, attempts to reach towards the stimuli) in response to a peer laughing. Therefore, we expected individual changes in frontal EEG asymmetry to be associated with specific affective and behavioral patterns of responding during a peer emotion task.

Methods

Participants

Forty 8-months-old infants responded to the invitation to participate in this study. Out of this sample, 32 infants (15 females, M_{age} = 254.16 days, SD_{age} = 9.36 days) provided analysable data for the EEG peer emotion task (Session 1) based on the criteria described below. For the behavioral peer emotion task (Session 2), 22 infants (13 females, M_{age} = 254.45 days, SD_{age} = 9.68 days) provided analysable data based on the criteria described below. A total of 18 infants (12 females, M_{age} = 252.61 days, SD_{age} = 8.93 days) contributed analysable data for both session 1 and Task 2. From the sample participating in Session 1, 9 participants did not return to the lab for Session 2 because the parents found it difficult to fit another visit in their schedule. More information about attrition rates for each session is presented in the following sections. All participants were recruited from a small urban area in North West England, did not suffer from any neurological or other medical condition, and were observed to have a normal vision and audition for their age.

Prior to both sessions, all parents were informed that at the end of the experiment they would receive £10 in order to cover traveling expenses and that the infant will be rewarded with a book for their participation. Informed consent was obtained from all parents and the study was approved by the Faculty Ethics Committee.

Procedure and Measures

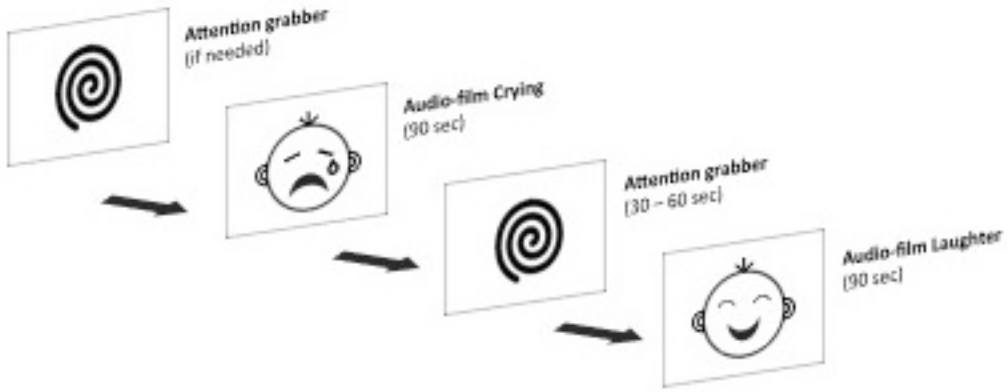
The procedure unfolded across two sessions, approximately one week apart from each other (M = 6.52 days; SD = 3.55 days). This strategy was adopted in order to accommodate infants' reduced attention span and maximize attendance to the tasks and good data quality, as well as to account for any potential carry over effects from one task to another.

EEG recording (*Session 1*)

Stimuli and procedure

The stimuli consisted of audio-video recordings of a peer infant crying and of a peer infant laughing, adapted from Geangu et al. (2011). The infants depicted in the stimuli were 8- to 9-months-old at the time of the recording. Each video recording had a sound average intensity of 70dB and duration of 90 seconds. Stimuli were presented at a size of 24x16cm on 17-inch CRT computer monitor using MATLAB R2012b (MathWorks, Natick, MA). The order of presentation of the stimuli was counterbalanced across participants. The stimulus presentation began with the display of a dynamic non-social attention grabber, which varied in duration as a function of participant's attention to the screen. Whenever the experimenter judged that the participants are attentively watching the screen, the first stimulus was presented. Between first and second stimulus, an attention grabber was always displayed with a duration that varied randomly between 30 sec and 60 sec. If infants became distressed during the stimulus presentation, max 30-sec was allowed for spontaneous recovery before the procedure was stopped and mothers were invited to comfort their infants. During the entire task, infants sat on their parent's lap at a distance of approximately 70 cm from the monitor in a dimly lit room. Figure 1 illustrates the stimulus presentation. In order to minimize the possibility that mothers could influence infants' responses to the stimuli, mothers were instructed not to interact with their infant (e.g., talk with, draw attention to the stimuli, display emotional expressions). Cases where these instructions were not followed, were excluded from further analysis.

A) SESSION 1: Electrophysiological assessment



B) SESSION 2: Behavioral assessment

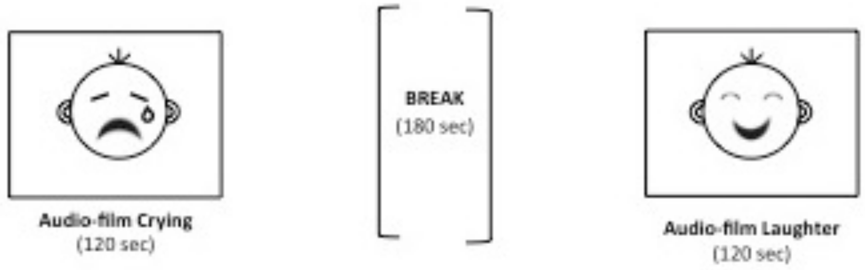


Figure 1. Example of trial structure for Task 1 (A) and Task 2 (B).

EEG recording and analysis

EEG was recorded continuously using a 128-electrode HydroCel Geodesic Sensor Net (Electrical Geodesic Inc., Eugene, OR) and amplified using an EGI NetAmps 300 amplifier. On-line recordings were referenced to the vertex electrode (Cz), and then off-line re-referenced to an average reference. The signal was band-pass filtered at .1 - 100 Hz. EEG data were digitized on-line at a sampling rate of 500 Hz per channel. Electrode impedances were checked prior to the beginning of the recording and considered acceptable if lower than 50 KΩ, which is a conservative threshold for infants and in accordance with the methodological recommendations for this age group (Johnson et al., 2001; Ferree, Luu, Russell, & Tucker, 2001). EEG data were further processed offline using NetStation v4.6.4 (Eugene, OR). EEG data were band-pass filtered (0.3-30 Hz), and segmented according to recording condition (cry film and laughter film), arising 1.5-min epochs for each task for participant. Next, the segments were checked through visual inspection for eye-movements, eye-blinks and other body movement artifacts. Segments with more than 8 bad channels (besides the 11 marked as bad eye-leads) were manually rejected. For the remaining segments, individual bad channels were replaced using spherical spline interpolation. EEG data were then processed in Matlab R2012b (Mathworks Inc., Natick, MA) for artifact rejection and power analysis. EEG segments showing amplitudes greater than +/-175 μV were marked as bad. The artefact-free segments were analysed with a Fast Fourier transform (FFT) with a 1-s Hanning window and 50% overlap with a frequency bin of 0.25 Hz. Participants with less than 10 free-artifact epochs of the 179 one-second overlapping epochs were removed from further analysis to ensure a stable estimate of alpha activity (*n* = 4). Another 4 participants were removed from further analysis because the EEG recording was stopped early due to their distress, failing to provide sufficient data points. The final sample had an average of 67.53 epochs (*min* = 10, *max* = 179) in the laugh and 70.41 epochs (*min* = 11; *max* = 156) in the cry conditions. Absolute power spectral density (psd) values for each segment were computed for the 4 - 7 Hz frequency band for two reasons: 1) majority of the EEG power was represented within this frequency band; 2) previous studies have associated this frequency with emotion reactivity and emotion regulation during infancy (e.g., Calkins et al., 1996; Santeso et al., 2007; Schmidt, 2008). Alpha power spectral density values were analysed after being natural log (ln) transformed to normalize the distribution.

Frontal asymmetry scores for each infant in each condition (cry video - $\mathrm{ASYM}_{\mathrm{cry}}$; laugh video - $\mathrm{ASYM}_{\mathrm{laugh}}$) were obtained by subtracting the left frontal hemisphere (F3) log-transformed alpha power from the right frontal hemisphere (F4) log-transformed alpha power values (i.e., ln(F4) – ln(F3)). Therefore, positive scores correspond to greater alpha power in the right hemisphere (or increase left activity interpreted as approach-oriented activity) while negative scores correspond to greater alpha power in the left hemisphere (or increased right activity interpreted as withdrawal-oriented activity).

Behavioral recordings (*Session 2*)

Stimuli and procedure

The stimuli were equivalent to those used in Session 1, although they differed with respect to length (120 seconds) and the identity of the infant peer displaying crying and laughing. The video recordings were sourced from a professional online database (www.istockphoto.com) and were edited to the required duration and an average sound intensity of 70dB. Each stimulus was displayed at 43 x 27 cm on a 17" computer monitor. The procedure begun with the presentation of a non-social attention grabber, to ensure that the participants are attending to the screen. During the entire procedure, the infant was seated in an age appropriate chair (Bumbo), at the same height and approximately 70 cm away from the screen. The participants' behavior was recorded by 4 cameras, three located in corners of the room and one placed above the monitor, allowing a close view of the face. Between the stimuli, a 180 seconds break was introduced, during which the experimenter came back to the room and played with the infant. During the break, an animation film was played on the screen. For the entire duration of the task, the parents were instructed to sit approximately 2 meters behind the infant, reading a magazine, and without engaging through eye contact or voice with the infant. See Figure 1 for an illustration of the stimulus presentation.

Behavior coding criteria

Based on previous research (e.g., Gill & Calkins, 2003; Markova & Legerstee, 2006; Spinrad & Stifter, 2006) and a preliminary inspection of the recordings, several empathy-related responses were coded: a) visual engagement; b) negative emotional vocalizations; c) positive emotional vocalizations; d) emotionally neutral vocalizations; e) positive facial expressions; f) negative facial expressions; h) approach behaviors; and i) withdraw behaviors. The coding criteria were adapted from the Laboratory Temperament Assessment Battery (Lab-TAB; Goldsmith & Rothbart, 1999). In terms of negative facial expressivity, our aim was to capture facial responses which may suggest that infants respond to their peers with emotionally congruent expressions. Thus, we opted for a more generic category, which includes displays of anger, sadness, and fear, as they might be present during infant cry. Table 1 provides a detailed description of the coding criteria for each type of behavior, together with the reliability coefficients. A second observer coded 20% of the recordings in order to establish reliability (intraclass correlation coefficient for absolute agreement).

For coding purposes, all video recordings were divided in 10-sec units. Some of the behaviors (b-i) were coded as present or absent for each unit. In order to account for variations in stimulus duration length caused by participant's emotional state, a percentage of units with behavior present was calculated from the total number of units coded for each participant. For visual engagement, the duration of looking time towards the screen was coded for the entire stimulus presentation. In order to account for variations in stimulus duration, a percentage looking time was calculated out of the entire duration of the stimulus presentation. The behaviors were tagged on the recording using Datavyu 1.3 coding software (http://datavyu.org). A total of 9 infants were removed from the final dataset for Session 2 due to excessive movement resulting in the impossibility to code their faces (*n* = 8), and lack of responses (*n* = 1).

Table 1.

Coding Criteria for the Infant-Oriented and Emotional Responses coded during the Peer Empathy Task.

Behavioral response	*Coding Criteria*
Visual engagement (.981)	The duration of infant looking towards the stimulus. NOTE: Blinks were considered as part of a continuous fixation to the stimulus.
Positive Facial Expression (.973)	Facial expression indicative of positive affect. Specific movements in both of the following face regions should be displayed. *Upper Face* (eyes, brows, forehead): eyes are squinted or do not change, furrow below the eyes deepens. *Lower Face*: cheeks are raise, lip corners are raised (either unilaterally or bilaterally) NOTE: When a brow movement was originated as a consequence of an eye/head movement (i.e. infant looking up/down), the action was not coded as brow movement.
Negative Facial Expression (1.000)	Facial expression indicative of negative affect. Specific movements in both of the following face regions should be displayed. *Upper Face* (eyes, brows, forehead): inner corner of the eyebrows are lowered and drawn together resulting in furrows between the eyes, inner corners of the eyebrows are raised and drawn together resulting in furrows in the middle of forehead, squinted eyes, furrow below the eyes deepens. *Lower Face*: Wide-opened square mouth specific for cry, sad pout, lips pressed together. NOTE: When a brow movement was originated as a consequence of an eye/head movement (i.e. infant looking up/down), the action was not coded as brow movement.
Positive Vocalizations (.976)	Any vocal production that can be identified as being positively toned, including laughter, positively toned babbling, and squealing.

Negative Vocalizations (1.000)	Any vocal production that can be identified as being negatively toned, including whimpering, whining, mild protest, crying /scream.
Neutral Vocalizations (.982)	Any vocal production that cannot be evaluated as having neither positive nor negative emotional intonation (e.g., emotionally neutral babbling).
Approach (.976)	Changes in the upper body position which reduce the distance between the participant and the screen. In order to be coded as approach, these responses need to be associated by visual engagement with the stimulus.
Withdraw (.978)	Changes in the upper body position which increase the distance between the participant and the screen. Attempts to escape from the chair, including turning away, leaning away, arching back, or twisting in the chair were also coded as withdraw behaviors. Some of these behaviors may be associated with visual disengagement from the stimulus, although this was not mandatory. Head turning in the absence of the upper body turning away was not coded as withdraw behavior.

Other behavioural variables were coded but not included in this study such as smiling, strong motor activation, self-soothing and social reference. Smiling responses were clustered together with positive facial expressions. Strong motor movements resulted to be a redundant measure that overlapped quite often with approach-withdrawal behaviours. In order to avoid redundancy, we decided to remove this measure. With respect to self-soothing and social reference behaviours, these two measures revealed interesting results regarding infants' emotional regulation skills. Thus, we decided not to report them in this manuscript in order to explore them further in relation with temperamental traits as well as frontal EEG alpha asymmetry scores recorded at resting states.

Results

Frontal EEG Asymmetry Results (Session 1)

In order to analyze whether the exposure to peer emotions elicited asymmetric frontal EEG activity, separate one sample t-tests (*n* = 32) were performed on the frontal EEG asymmetry score obtained during each condition (i.e. laughing and crying). Observing a peer crying elicited an increased left relative to right absolute alpha power (*M* = -.077, *SD* = .178), which was significantly different from 0 (*t(31)* = -2.451; *p* = .020). Observing a peer laughing elicited some increased right relative to left absolute alpha power (*M* = .015, *SD* = .216), but the difference from 0 did not reach statistical significance (*p* = .700).

Additionally, in order to disentangle the separate contributions of the absolute alpha power recorded on the left and right hemisphere to differences in asymmetry scores recorded for each condition, a 2 (condition: laughing vs. crying) x 2 (hemisphere: right vs. left) within-subjects ANOVA was performed on the log-transformed alpha power values. A significant Emotion x Hemisphere interaction was obtained (*F(1,31)* = 5.787; *p* = .022; η^2 = .157). Post-hoc pairwise comparisons showed that when infants were exposed to a peer crying, higher absolute alpha power was recorded in the left (*M* = 3.513 µV; *SE* = .086 µV) compared to the right hemisphere (*M* = 3.436 µV; *SE* = .086 µV), *p* = .020. Moreover, exposure to a laughing peer elicited higher absolute alpha power (*M* = 3.518 µV; *SE* = .083 µV) in the right hemisphere compared to when participants observed a crying peer (*M* = 3.436 µV; *SE* = .086 µV), *p* = .047. All other comparisons were not significant (*p* > .391) (See Figure 2). No gender effects were found. For further information see Appendix B.

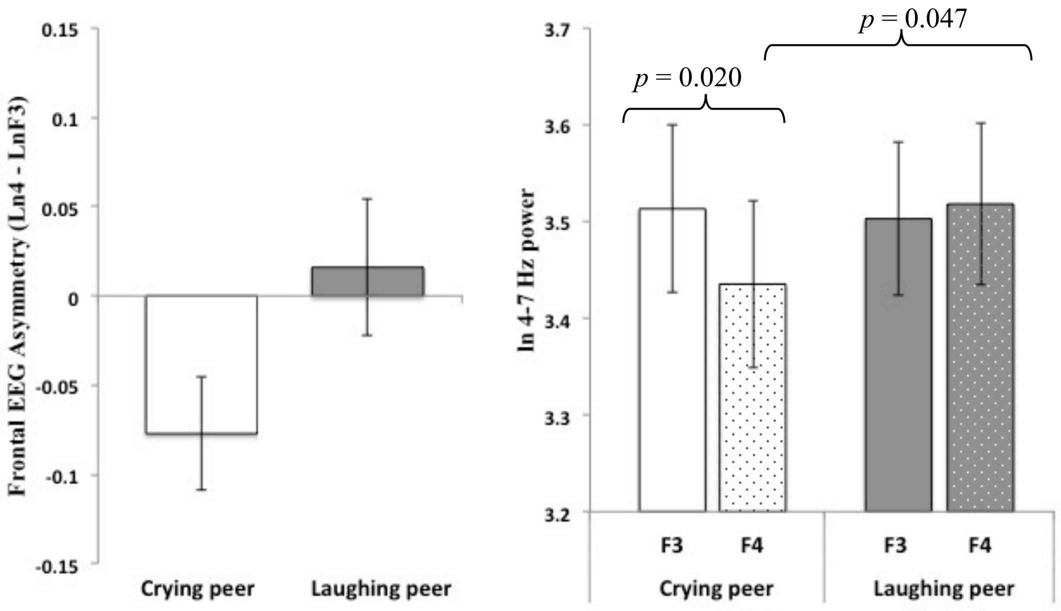


Figure 2. A) Means and standard errors for frontal alpha asymmetry scores collected during the two affective conditions; and B) Means and standard errors for the EEG ln alpha power (4-7Hz) recorded at frontal sensors F3 (left) and F4 (right) during the two affective conditions. Note: EEG power is inversely related to activity, so high power is thought to reflect lower activity.

Behavioral Results (Session 2)

Table 2 provides an overview of infants' responses to their peer emotions ($n = 22$). Repeated measures ANOVAs were conducted in order to analyze the differences between the stimuli in terms of facial and vocal expressivity. Greenhouse-Geisser corrections were applied whenever the assumptions of sphericity were violated. For looking time, approach and withdraw behaviors, repeated measures t-tests were performed. All tests were interpreted at a significance threshold of $p = .05$.

The 2 (Condition: Cry, Laughter) x 2 (Emotion: Positive, Negative) repeated measures ANOVA for facial expressivity revealed a significant interaction between stimulus and emotion, $F(1,21) = 16.353$; $p = .001$, $\eta^2 = .438$. Post-hoc pairwise comparisons indicated that infants responded with more negative facial expressions to the crying peer than to the laughing one, and with more positive facial expressions to the laughing peer than the crying one (Table 2). Also, infants displayed more positive than negative facial expressions while observing the laughing peer (p = .008). No other significant differences were observed (p > .304). The 2 (Condition: Cry, Laughter) x 3 (Emotion: Positive, Negative, Neutral) repeated measures ANOVA for vocal expressivity revealed a significant main effect of condition, $F(1,21)$ = 7.727; p = .011, η^2 = .269, which was qualified by a significant interaction with emotion, $F(1.31,21)$ = 4.724; p = .030, η^2 = .184. Post-hoc pairwise comparisons showed that infants manifested more emotionally negative vocalizations while observing the crying peer than the laughing one. Observing the crying peer also elicited more negative (p = .029) and neutral (p = .015) vocalizations than the positive ones. In response to the laughing peer, infants manifested more emotionally neutral vocalizations than negative (p = .007) and positive (p = .021) ones. No other significant differences were observed (p > .432).

Infants looked longer at the crying than at the laughing peer, $t(21)$ = 2.449; p = .023. Interestingly, gender differences were observed on infants' looking time scores during the laughter condition (p = .014), such that females tended to look longer than males to a peer laughing (Females: M = 67.13%, SD = 16.69; Males: M = 49.21%, SD = 13.03). No other gender effects were found for behavioural measures (See Appendix B). No significant differences between the stimuli emerged for the approach and withdraw behaviors (p > .607).

Table 2.

Descriptive statistics for infants' behavioral responses during Session 2 and the results of comparisons between stimuli (N = 22)

	Peer Crying			Peer Laughing			
	M	*SE*	%	*M*	*SE*	%	*p*
Looking time[a]	68.88	4.16	NA	59.80	3.73	NA	.02
Vocalizations[b]							
Negative	24.62	8.12	50.0	6.16	2.74	27.3	.01
Positive	3.79	2.10	18.2	6.44	2.68	31.8	.43
Neutral	18.18	5.10	59.1	20.90	5.05	54.5	.57
Facial expressions[b]							
Negative	21.21	7.61	45.5	6.29	3.28	27.3	.02
Positive	11.36	3.36	50.0	28.74	6.27	72.7	.00
Approach[b]	24.62	5.04	72.7	27.55	6.19	68.2	.61
Withdrawal[b]	51.52	6.41	91.9	47.74	5.33	95.5	.52

Note. % Refers to the percentage of infants displaying the behavioral response; [a]Percentage of absolute duration from the stimulation duration; [b]Percentage of 10-seconds units for which the behavior was present from the total number of units.

Relation between Frontal EEG Asymmetry and Behavioral Responses to Peers' Emotions (Session 1&2)

Pearson's correlations among frontal EEG asymmetry scores (Session 1) and the behavioral responses (Session 2) to peers' emotions were performed (*n* = 18). The number of correlations were kept to a minimum, strictly following the predictions formulated based on previous literature. Because of the small sample size, we did not correct the results for multiple comparisons to avoid inflating Type II error and thereby obscuring expected results (Rothman, 1990, 2014).

Infants' frontal asymmetry scores recorded in response to the peer crying (i.e. crying LnF4-LnF3 = ASYMcry) were negatively correlated with the percentage of time infants spent looking at a peer crying during the second session ($r = -.528$; $p = .024$) (See Figure 3A). This indicates that infants who showed a greater degree of right frontal asymmetry when observing a peer crying spent more time visually engaging with their peer distress in separate occasion. Furthermore, ASYMcry was positively correlated with the proportion of approach behaviors (*r* = .472; *p* = .048) and neutral vocalizations (*r* = .490; *p* = .039) displayed when watching a peer crying in the second session. In other words, infants who displayed greater degree of left frontal asymmetry when watching a peer crying spent more time exhibiting approach behaviors and neutral vocalizations when exposed to the peer crying film in the second session.

Infants' frontal EEG asymmetry scores recorded in response to the laughing peer (i.e. laughter LnF4-LnF3 = ASYMlaugh) were positively correlated with the amount of time infants visually engaged with a happy peer (*r* = .507; *p* = .032) in the second session (See Figure 3B). That is, infants who exhibited more left frontal asymmetry during the laughter film spent more time looking at a peer laughing. Additionally, AYMlaugh was positively correlated with the proportion of neutral vocalizations emitted in response to the sound of a peer laughing (*r* = 0.466; *p* = 0.051), with greater degree of left frontal asymmetry being linked to greater emission of neutral vocalizations during the laughter condition. No other significant correlations between the frontal EEG asymmetry scores (Session 1) and the behavioral responses (Session 2) to peers' emotions were found (*p* > .240).

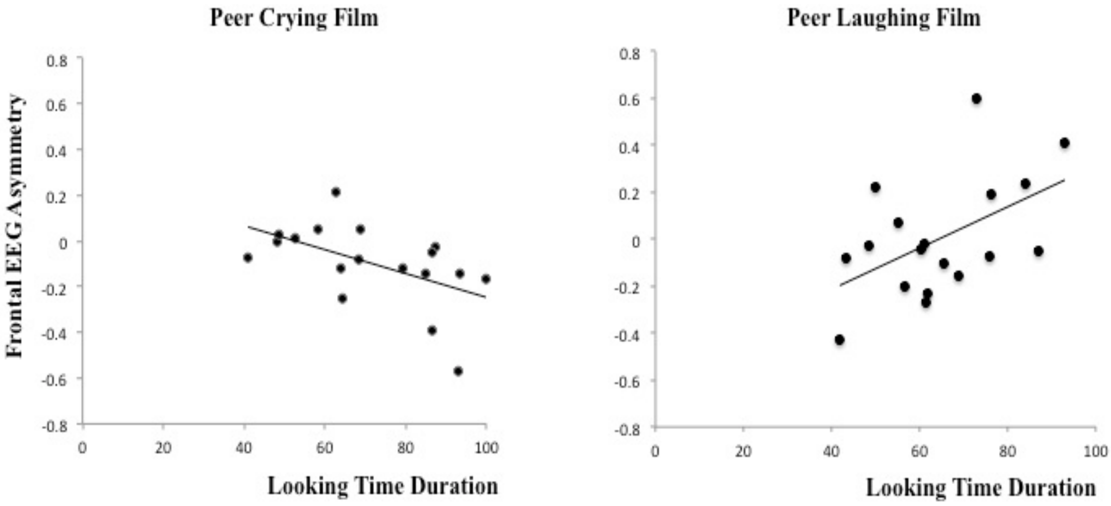


Figure 3. Correlations for frontal EEG asymmetry and looking time scores**.** This figure shows the correlation between frontal EEG asymmetry observed in infants during the presentation of video-films of a peer crying (A) and a peer laughing (B) with their looking time scores. Note: Correlations were significant on the $p < .05$ level.

Discussion

The main goal of this study was to investigate infants' brain responses to peers' emotional states, and their relation to simple behavioral manifestations of social approach and disengagement. To this end, we assessed 8-month-old infants' frontal EEG alpha power as well as infants' empathic-related behaviors when exposed to a peer laughing and a peer crying. In line with the approach-withdrawal motivational model, the current study shows that observing peers' positive and negative emotions induces distinctive patterns of brain activation and behavioral manifestations in 8-month-old infants.

In line with current models of frontal asymmetry, our EEG analyses demonstrated that the processing of positive and negative affective stimuli elicited different patterns of frontal EEG asymmetry, probably reflecting current emotional and behavioral tendencies. In particular, we found that the observation of a peer crying (negative affective stimuli) was associated with greater relative right frontal brain activation in 8-

month-olds. This distinct pattern of frontal brain activation has been previously linked to the tendency to display negative emotions (e.g. sadness, fear) during the processing of negative-eliciting situations in children and infants. For example, Fox and Davidson (1987, 1988) found that 10-month-old infants who displayed greater relative right frontal activation during a series of negative-related tasks (i.e. maternal separation and stranger approach) were more likely to exhibit behaviors reflecting active withdrawal (e.g. distress, gaze aversion). Likewise, Buss et al. (2003) reported that 6-month-old infants who showed greater right frontal asymmetry during a stranger approach task also displayed more expressions of fear and sadness. Similar association was also reported in 10 month-old infants during a stranger approach task, but also across other contexts involving non-social fearful-related situations (e.g. presentation of a toy spider and masks) (Diaz & Bell, 2012). Therefore, we suggest that our EEG finding reflects infants' tendency to respond with withdrawal behaviors and negative affect in front of a peer crying.

Contrary to our expectations and previous findings (e.g. Buss et al., 2003; Fox and Davidson, 1987, 1988; LoBue et al., 2011; Santesso et al., 2007), although observing a peer laughing evoked greater relative activation of the left hemisphere relative to the right hemisphere, this difference was not significant and very small (*d* = .033). One possible explanation for this finding is linked to the feasibility of our stimuli. Multiple authors have argued that not all forms of positive affect include an approach component (e.g. Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Ekman & Friesen, 1982; Gable & Harmon-Jones, 2008; Killeen and Teti, 2012). In this respect, a recent EEG study suggests that low-level, internally focused, positive emotions without an approach-orientation are associated with shifts toward greater relative right frontal activation (Light, Coan, Frye, Goldsmith, & Davidson, 2009). Therefore, it is possible to argue that the primary positive emotion elicited by the peer laughing stimuli used in this study did not evoke sufficient approach tendencies to engage asymmetrical frontal cortical activation. Nonetheless, when looking at our behavioral data this hypothesis does not seem reasonable given that infants displayed more positive affect towards a peer laughing (i.e. greater facial expressions of happiness) than to a peer crying.

A further plausible explanation is that the infants had a generally high degree of positive affect or approach orientation and that the laughter stimuli did not generate any greater left frontal asymmetry from that baseline state. Alternatively, it could be that infants' ability to process and respond to the communicative value of their peers' laughter may be insufficiently developed before the age of 12-months (Crespo-Llado et al., 2018; Geangu et al., 2011; Upshaw et al., 2015). Although from an early age infants are able to laugh (Nwokah, Hsu, Dobrowolska, & Fogel, 1994), this emotional expression appears to be more frequently associated with the interactions with adults (Mireault et al., 2015). As a result, infants may encounter less frequently these specific facial expressions and non-verbal vocalizations when interacting with peers (Rubenstein & Howes, 1976; Vandell & Mueller, 1980), with consequences for the development of their abilities to extract the corresponding social message. In this line, recent evidence suggests that although 7 to 8 month-olds ERP responses discriminate between emotionally valenced and neutral non-verbal vocalizations at very early stages of auditory processing (Crespo-Llado et al., 2018; Missana et al., 2017), only peers' cry sounds engaged in later sustained cognitive processing compared to both infant laughter and infant coughing (Crespo-Llado et al., 2018). It is thus possible that compared to crying, the development of laughter processing is more protracted and dependent on more advanced social cognitive and communicative abilities. In this respect, several fMRI studies with adults on laughter perception suggest that the processing of emotional laughter places higher demands on social cognitive processes as indexed by the stronger activation of frontal brain areas implicated in mentalizing and affect evaluation such as the medial prefrontal cortex (MFC) (Szameitat et al., 2010; Wildgruber et al., 2013; Tschacher, Schildt, & Sander, 2010). Furthermore, behavioral research suggests that it is not until the end of the first year when infants show increased understanding of those social situations where laughter is more common (Mireault et al., 2014; Reddy, 2001, 2008).

At the behavioral level, 8-month-old infants' emotional responses tended to converge with the affect displayed by their peers. Importantly, this emotional convergence was recorded not only in response to peers' negative affect as previously shown by several studies (e.g., Dondi et al., 1999; Field, et al., 2007; Geangu et al., 2010), but also to manifestations of happiness. That is, infants tended to display more negative affect (i.e. negative vocalizations, negative facial expressions) towards a peer crying relative to a peer laughing. In turn, infants tended to display more positive affect towards a peer laughing (i.e. greater positive facial expressions) than to a peer crying. Certainly, these only represent approximations of their real encounters with peers. Nevertheless, similar video recordings of peer affect were shown to elicit sympathetic arousal in infants as reflected by changes in pupil diameter (Geangu et al., 2011; Upshaw et al., 2015), suggesting good ecological validity. Moreover, infants in our study appeared to be interested in the stimuli as they engaged visually with them for more than half of their duration. Although they did so for both emotional expressions, they tended to look more at the crying infant. This suggests that infants showed more visual interest (as indexed by their looking times) for the infant crying, supporting the emergence of a negativity bias in affective processing around the age of 7 months (see Vaish et al., 2008 for a review).

Surprinsingly, in our study 8-month-old infants exhibit similar levels of approach and withdraw-oriented responses to their peer's distress and happiness. Nonetheless, the examination of variations in the asymmetric frontal EEG alpha helped to differentiate specific behavioural responses. Specifically, infants who were more likely to respond with greater relative left frontal activation to crying were also more likely to physically approach their distressed peer and to vocalize in an emotionally neutral tone**.** These findings fit with previous EEG work with younger children showing a link between left frontal activation and empathy-related reactions (Cowell & Decety, 2015; Jones, Field, & Davalos, 2000; Jones, Field, Davalos, & Hart, 2004; Paulus et al., 2013). Similarly, infants who exhibited higher levels of relative left frontal activation when observing a peer laughing were also more likely to vocalize in an emotionally neutral tone to the cheerful peer. This finding parallels previous infant EEG studies linking left frontal asymmetry to higher levels of sociability with peers and right frontal asymmetry with higher degree of social wariness or social withdrawal. For example, Fox et al. (1995, 1996) reported that preschool and elementary school children who were more sociable and displayed more socially competent behaviors during interactions with peers exhibited increased electrical activity in the left frontal region compared with the less sociable peers. Similarly, a longitudinal study run by the same group (Calkins et al., 1996; Henderson et al., 2001; Fox et al., 2001) reported continuities between early infant EEG asymmetry patterns and later preschool social behavior. Together, these findings suggest that patterns of left frontal EEG asymmetry mediate social approach behaviors.

Finally, we also found a link between frontal EEG asymmetry patterns and visual engagement. In particular, those infants who exhibited greater relative left frontal activation when confronted with a peer laughing were the ones who spent more time looking at the peer laughing in the second session, while those who display greater levels of relative right frontal activation in response to the peer crying stimuli spent more time looking at the peer crying in session 2. These results are in line with previous studies on adults suggesting that motivational tendencies (approach vs. withdraw) elicited by the stimulus modulate attentional processes, with withdrawal motivation leading to greater attention towards threatening stimuli (Watts et al., 1986; Joormann et al., 2007; MacLeod, 2007) and approach motivation relating to attention to appetitive stimuli (Gable & Harmon-Jones, 2011, 2013). At this respect, EEG research involving measures of frontal asymmetry has already shown that right frontal asymmetry is associated with attentional biases toward withdrawal-related stimuli (e.g., Grimshaw, Foster, & Corballis, 2014; Miskovic & Schmidt, 2010; Perez-Edgar, Kujawa, Nelson, Cole, & Zapp, 2013) while enhanced left frontal brain asymmetry during the perception of anger-evoking pictures is related to enhanced motivated attention (e.g., Gable & Poole, 2014; Poole & Gable, 2014). Due to the correlational nature of the analysis it is, however, difficult to draw conclusions of the exact nature of this relation. The inclusion of a non-emotionally valenced baseline, larger sample size and a wider age range, could allow in the future a more comprehensive analysis of the relation between frontal asymmetry in response to peers and looking behavior during infant interactions.

The present study is not without limitations. Although we included a larger sample of participants to begin with, only a subset completed both testing sessions. We are confident, however, that our results are not due to the sample size. First, our findings converge in several ways with those previously reported in studies using similar paradigms (Davidson & Fox, 1982, 1989; Field et al., 1998; Geangu et al., 2011; Nichols et al., 2015) and show medium-large to large effects. Second, post-hoc power analyses confirm that our study had more than ample power to detect all the significant (large effect) results reported in this study (over 95% power). The lack of differences between emotion conditions for approach and, separately, withdrawal behaviours in this study seems particularly relevant to the overall interpretation of results. A power analysis indicated that a total sample of 1.162, for approach, and 765, for withdrawal, would be needed to detect the observed effects of *d* = .095 (approach) and *d* = .117 (avoidance), with setting power to 0.90 using paired-sample t-tests.

It is also important to highlight that the peer emotion tasks used in both sessions differed in duration and the conditions under which they were applied, which could explained some of the differences observed. On the other hand, it is possible that infants' responses have been dampened by the exposure to unfamiliar peers rather than familiar ones. In this respect, there is suggestive evidence that child-child interactions are modulated by familiarity, with infants being more likely to interact with familiar peers as opposed to unfamiliar peers (Demetriou & Hay, 2004; Howes & Farver, 1987; Stefani & Camaioni, 1983; Young & Lewis, 1979). Likewise, the presence of the caregiver in the room during the second session may have caused children to respond less. Their own mothers' unresponsiveness toward the stimuli may have prompted them to be less interested themselves in the peer or they may have been waiting for their own mothers to intervene.

In summary, the present study suggests that observing other infants crying or laughing elicits in 8-month-old infants distinct patterns of asymmetric frontal activity, as well as overt responses suggesting the presence of convergent emotional responses and social approach behaviors. These findings add valuable information to a limited body of knowledge about the potential early origins of empathy and pro-social behaviors, and their underlying neurocognitive mechanisms. The specific link between approach behaviors and variations in left frontal activity indicates the presence of a motivational dimension to infants' responses to distressed peers and emphasizes the importance of investigating the role of these simple behaviors in the ontogeny of prosocial abilities.

References

Bell, M. A. (2001a). Brain electrical activity associated with cognitive processing during a looking version of the A-not-B task. *Infancy*, *2*, 311–330.

Bell, M. A. (2001b). 6-9 Hz as an indicator of individual differences in infant spatial working memory performance. *Psychophysiology, 38*, S7-S7.

Bell, M. A. (2002). Power changes in infant EEG frequency bands during a spatial working memory task. *Psychophysiology, 39*(4), 450-458.

Bell, M. A., & Fox, N. A. (1997). Individual differences in object permanence performance at 8 months: Locomotor experience and brain electrical activity. *Developmental Psychobiology, 31*(4), 287-297.

Brownell, C. A., & Carriger, M. S. (1990). Changes in cooperation and self-other differentiation during the second year. *Child Dev, 61*(4), 1164-1174.

Buss, K. A., Schumacher, J. R., 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. *Behav Neurosci, 117*(1), 11-20.

Calkins, S. D., Fox, N. A., & Marshall, T. R. (1996). Behavioral and physiological antecedents of inhibited and uninhibited behavior. *Child Development, 67*(2), 523-540.

Cheng, Y. W., Lee, S. Y., Chen, H. Y., Wang, P. Y., & Decety, J. (2012). Voice and Emotion Processing in the Human Neonatal Brain. *Journal of Cognitive Neuroscience, 24*(6), 1411-1419.

Coan, J. A., & Allen, J. J. (2004). Frontal EEG asymmetry as a moderator and mediator of emotion. *Biol Psychol, 67*(1-2), 7-49.

Cowell, J. M., & Decety, J. (2015). Precursors to morality in development as a complex interplay between neural, socioenvironmental, and behavioral facets. *Proceedings* *of the National Academy of Sciences of the United States of America, 112*(41), 12657-12662.

Crespo-Llado, M.M., Vanderwert, R.E., & Geangu, E. (2018). Individual differences in infants' neural responses to their peers' cry and laughter. *Biological Psychology*, *135,* 117-127.

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.

Davidson, R. J., & Fox, N. A. (1982). Asymmetrical Brain Activity Discriminates between Positive and Negative Affective Stimuli in Human Infants. *Science, 218*(4578), 1235-1237.

Davidson, R. J., & Fox, N. A. (1989). Frontal Brain Asymmetry Predicts Infants Response to Maternal Separation. *Journal of Abnormal Psychology, 98*(2), 127-131.

Dawson, G. (1994). Frontal electroencephalographic correlates of individual differences in emotion expression in infants: a brain systems perspective on emotion. *Monogr Soc Res Child Dev, 59*(2-3), 135-151.

Demetriou, H., & Hay, D. F. (2004). Toddlers' reactions to the distress of familiar peers: The importance of context. *Infancy, 6*(2), 299-318.

Diaz, A., & Bell, M. A. (2012). Frontal EEG asymmetry and fear reactivity in different contexts at 10 months. *Developmental Psychobiology, 54*(5), 536-545.

Dondi, M., Simion, F., & Caltran, F. (1999). Can newborns discriminate between their own cry and the cry of another newborn infant? *Developmental Psychology, 35*(2), 418-426.

Ekman, P., & Friesen, W. V. (1982). Felt, false, and miserable smiles. *Journal of non-verbal behavior*, *6*(4), 238-252.

Eckerman, C. O., & Peterman, K. (2001). Peers and infant social/communicative development. In A. Fogel & G. Bremmer (Eds) Blackwell handbook of infant development (pp. 326 – 350). Malden, MA: Blackwell

Farver, J. A. M., & Branstetter, W. H. (1994). Preschoolers Prosocial Responses to Their Peers Distress. *Developmental Psychology, 30*(3), 334-341.

Fernald, A., Taeschner, T., Dunn, J., Papousek, M., Deboyssonbardies, B., & Fukui, I. (1989). A Cross-Language Study of Prosodic Modifications in Mothers and Fathers Speech to Preverbal Infants. *Journal of Child Language, 16*(3), 477-501.

Field, T., Diego, M., Hernandez-Reif, M., & Fernandez, M. (2007). Depressed mothers' newborns show less discrimination of other newborns' cry sounds. *Infant Behavior & Development, 30*(3), 431-435.

Field, T., Pickens, J., & Fox, N. A., Gonzalez, J., & Nawrocki, T. (1998). Facial expression and EEG responses to happy and sad faces/voices by 3-month-old infants of depressed mothers. *British Journal of Developmental Psychology, 16*, 485-494.

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

Fox, N. A. (1994). Dynamic cerebral processes underlying emotion regulation. *Monographs of the society for research in child development*, *59*(2‐3), 152-166.

Fox, N. A., & Davidson, R. J. (1986). Taste-Elicited Changes in Facial Signs of Emotion and the Asymmetry of Brain Electrical-Activity in Human Newborns. *Neuropsychologia, 24*(3), 417-422.

Fox, N. A., & Davidson, R. J. (1987). Patterns of Eeg Asymmetry Reflect the Presence of Discrete Emotions in 10-Month-Old Infants. *Journal of Clinical and Experimental Neuropsychology, 9*(1), 71-71.

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.

Fox, N. A., Henderson, H. A., Rubin, K. H., Calkins, S. D., & Schmidt, L. A. (2001). Continuity and discontinuity of behavioral inhibition and exuberance: Psychophysiological and behavioral influences across the first four years of life. *Child Development, 72*(1), 1-21.

Fox, N. A., Rubin, K. H., Calkins, S. D., Marshall, T. R., Coplan, R. J., Porges, S. W., Long, J.M., & Stewart, S. (1995). Frontal activation asymmetry and social competence at four years of age. *Child Development, 66*(6), 1770-1784.

Fox, N. A., Schmidt, L. A., Calkins, S. D., Rubin, K. H., & Coplan, R. J. (1996). The role of frontal activation in the regulation and dysregulation of social behavior during the preschool years. *Development and Psychopathology, 8*(1), 89-102.

Gable, P. A., & Harmon-Jones, E. (2008). Approach-motivated positive affect reduces breadth of attention. *Psychological Science*, *19*(5), 476-482.

Gable, P. A., & Harmon-Jones, E. (2011). Attentional states influence early neural responses associated with motivational processes: Local vs. global attentional scope and N1 amplitude to appetitive stimuli. *Biological psychology*, *87*(2), 303-305.

Gable, P. A., & Harmon-Jones, E. (2013). Trait behavioral approach sensitivity (BAS) relates to early (< 150 ms) electrocortical responses to appetitive stimuli. *Social cognitive and affective neuroscience*, *8*(7), 795-798.

Gable, P. A., & Poole, B. D. (2014). Influence of trait behavioral inhi- bition and behavioral approach motivation systems on the LPP and frontal asymmetry to anger pictures. *Social Cognitive and Affective Neuroscience, 9*(2), 182–190.

Geangu, E., Benga, O., Stahl, D. & Striano, T. (2010). Individual Differences in Infants' Emotional Resonance to a Peer in Distress: Self–Other Awareness and Emotion Regulation. *Social Development, 20*: 450–470.

Geangu, E., Hauf, P., Bhardwaj, R., & Bentz, W. (2011). Infant Pupil Diameter Changes in Response to Others' Positive and Negative Emotions. *PLoS ONE, 6*(11), e27132.

Grimshaw, G. M., Foster, J. J., & Corballis, P. M. (2014). Frontal and parietal EEG asymmetries interact to predict attentional bias to threat. *Brain and cognition*, *90*, 76-86.

Gill, K. L., & Calkins, S. D. (2003). Do aggressive/destructive toddlers lack concern for others? Behavioral and physiological indicators of empathic responding in 2-year-old children. *Development and Psychopathology*, *15*(1), 55-71.

Goldsmith, H. H., & Rothbart, M. K. (1999). The laboratory temperament assessment battery. *Locomotor version*, *3*.

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

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. *Biol Psychol, 84*(3), 451-462.

Haviland, J. M., & Lelwica, M. (1987). The Induced Affect Response - 10-Week-Old Infants Responses to 3 Emotion Expressions. *Developmental Psychology, 23*(1), 97-104.

Hay, D. F., Nash, A., & Pedersen, J. (1981). Responses of six-month-olds to the distress of their peers. *Child Dev, 52*(3), 1071-1075

Hay, D. F., Payne, A., & Chadwick, A. (2004). Peer relations in childhood. *J Child Psychol Psychiatry, 45*(1), 84-108.

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 and Adolescent Psychiatry, 40*(1), 68-74.

Hoffman, M.L. (2000). *Empathy and moral development: Implications for caring and justice*. Cambridge, UK: Cambridge University Press.

Howes, C., & Farver, J. (1987). Toddler's response to the distress of their peers. *Journal of Applied Developmental Psychology*, 8, 441-452.

Jones, N. A., Field, T., & Davalos, M. (2000). Right frontal EFG asymmetry and lack of empathy in preschool children of depressed mothers. *Child Psychiatry & Human Development, 30*(3), 189-204.

Jones, N. A., Field, T., Davalos, M., & Hart, S. (2004). Greater right frontal EEG asymmetry and nonemphathic behavior are observed in children prenatally exposed to cocaine. *International Journal of Neuroscience, 114*(4), 459-480.

Jones, N. A., Field, T., Davalos, M., & Pickens, J. (1997). EEG stability in infants/children of depressed mothers. *Child Psychiatry & Human Development, 28*(2), 59-70.

Joormann, J., Talbot, L., & Gotlib, I. H. (2007). Biased processing of emotional information in girls at risk for depression. *Journal of abnormal psychology*, *116*(1), 135.

Killeen, L. A., & Teti, D. M. (2012). Mothers' frontal EEG asymmetry in response to infant emotion states and mother-infant emotional availability, emotional experience, and internalizing symptoms. *Development and Psychopathology, 24*(1), 9-21.

Lamb, S., & Zakhireh, B. (1997). Toddler's attention to the distress of peers in a daycare setting. *Early Education & Development*, 8, 105-118.

Licata, M., Paulus, M., Kuhn-Popp, N., Meinhardt, J., & Sodian, B. (2015). Infant frontal asymmetry predicts child emotional availability. *International Journal of Behavioral Development, 39*(6), 492-496.

Liddle, M. J., Bradley, B. S., & McGrath, A. (2015). Baby Empathy: Infant Distress and Peer Prosocial Responses. *Infant Ment Health J, 36*(4), 446-458.

Liew, J., Eisenberg, N., Spinrad, T. L., Eggum, N. D., Haugen, R. G., Kupfer, A., Reiser, M.R., Smith, C.L., Lemery-Chalfant, K., & Baham, M. E. (2011). Physiological Regulation and Fearfulness as Predictors of Young Children's Empathy-related Reactions. *Social Development, 20*(1), 111-113.

Light, S. N., Coan, J. A., Frye, C., Goldsmith, H. H., & Davidson, R. J. (2009). Dynamic variation in pleasure in children predicts nonlinear change in lateral frontal brain electrical activity. *Developmental psychology*, *45*(2), 525.

LoBue, V., Coan, J. A., Thrasher, C., & DeLoache, J. S. (2011). Prefrontal Asymmetry and Parent-Rated Temperament in Infants. *PLoS One, 6*(7).

McLeod, C. M. (2007). The concept of inhibition in cognitive. In *Inhibition in Cognition, Decade of Behavior* (pp. 1-3). American Psychological Association, Washington, DC.

Markova, G., & Legerstee, M. (2006). Contingency, imitation, and affect sharing: Foundations of infants' social awareness. *Developmental Psychology*, *42*(1), 132.

Martin, G. B., & Clark, R. D. (1982). Distress crying in neonates: Species and peer specificity. *Developmental Psychology, 18*, 3–9.

Miskovic, V., & Schmidt, L. A. (2010). Frontal brain electrical asymmetry and cardiac vagal tone predict biased attention to social threat. *International Journal of Psychophysiology*, *75*(3), 332-338.

Mireault, G. C., Crockenberg, S. C., Sparrow, J. E., Pettinato, C. A., Woodard, K. C., & Malzac, K. (2014). Social looking, social referencing and humor perception in 6-and-12-month-old infants. *Infant Behavior & Development, 37*(4), 536-545.

Missana, M., Altvater-Mackensen, N., & Grossmann, T. (2017). Neural correlates of infants' sensitivity to vocal expressions of peers. *Developmental Cognitive Neuroscience, 26*, 39-44.

Nichols, S. R., Svetlova, M., & Brownell, C. A. (2009). The role of social understanding and empathic disposition in young children's responsiveness to distress in parents and peers. *Cognitive Brain Behavior, 13*(4), 449-478.

Nichols, S. R., Svetlova, M., & Brownell, C. A. (2010). Toddlers' Understanding of Peers' Emotions. *Journal of Genetic Psychology, 171*(1), 35-53.

Nichols, S. R., Svetlova, M., & Brownell, C. A. (2015). Toddlers' Responses to Infants' Negative Emotions. *Infancy, 20*(1), 70-97.

Paulus, M. (2014). The Emergence of Prosocial Behavior: Why Do Infants and Toddlers Help, Comfort, and Share? *Child Development Perspectives, 8*(2), 77-81.

Paulus, M., Kuhn-Popp, N., Licata, M., Sodian, B., & Meinhardt, J. (2013). Neural correlates of prosocial behavior in infancy: Different neurophysiological mechanisms support the emergence of helping and comforting. *Neuroimage, 66*, 522-530.

Pérez-Edgar, K., Kujawa, A., Nelson, S. K., Cole, C., & Zapp, D. J. (2013). The relation between electroencephalogram asymmetry and attention biases to threat at baseline and under stress. *Brain and cognition*, *82*(3), 337-343.

Poole, B. D., & Gable, P. A. (2014). Affective motivational direction drives asymmetric frontal hemisphere activation. *Experimental brain research*, *232*(7), 2121-2130.

Reddy, V. (2001). Infant clowns: The interpersonal creation of humour in infancy. *Enfance*, *53*(3), 247-256.

Reddy, V. (2008). *How infants know minds*. Harvard University Press.

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

Sagi, A., & Hoffman, M. L. (1976). Empathic distress in the newborn. *Developmental Psychology, 12*(2), 175-176.

Santesso, D. L., Schmidt, L. A., & Trainor, L. J. (2007). Frontal brain electrical activity (EEG) and heart rate in response to affective infant-directed (ID) speech in 9-month-old infants. *Brain and Cognition, 65*(1), 14-21.

Schmidt, L. A. (2008). Patterns of second-by-second resting frontal brain (EEG) asymmetry and their relation to heart rate and temperament in 9-month-old human infants. *Personality and Individual Differences*, *44*(1), 216-225.

Simner, M. (1971). Newborn's response to the cry of another infant. *Developmental psychology, 5*(1), 136-150.

Solomon, B., O'Toole, L., Hong, M., & Dennis, T. A. (2014). Negative affectivity and EEG asymmetry interact to predict emotional interference on attention in early school-aged children. *Brain and cognition*, *87*, 173-180.

Sommerville, J. A., Schmidt, M. F. H., Yun, J. E., & Burns, M. (2013). The Development of Fairness Expectations and Prosocial Behavior in the Second Year of Life. *Infancy, 18*(1), 40-66.

Spinrad, T. L., & Stifter, C. A. (2006). Toddlers' empathy-related responding to distress: Predictions from negative emotionality and maternal behavior in infancy. *Infancy*, *10*(2), 97-121.

Stefani, L. H., & Camaioni, L. (1983). Effects of familiarity on peer interaction in the first year of life. *Early Child Development and Care*, *11*(1), 45-54.

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

Svetlova, M., Nichols, S. R., & Brownell, C. A. (2010). Toddlers' Prosocial Behavior: From Instrumental to Empathic to Altruistic Helping. *Child Development, 81*(6), 1814-1827.

Szameitat, D. P., Kreifelts, B., Alter, K., Szameitat, A. J., Sterr, A., Grodd, W., & Wildgruber, D. (2010). It is not always tickling: distinct cerebral responses during perception of different laughter types. *Neuroimage, 53*(4), 1264-1271.

Tschacher, W., Schildt, M., & Sander, K. (2010). Brain connectivity in listening to affective stimuli: a functional magnetic resonance imaging (fMRI) study and implications for psychotherapy. *Psychotherapy research*, *20*(5), 576-588.

Upshaw, M. B., Kaiser, C. R., Sommerville, J. A. , Ford, R., & Perlman, S. B. (2015). Parents' empathic perspective taking and altruistic behavior predicts infants' arousal to others' emotions. *Frontiers in Psychology*, *6*, 360.

Vaish, A., Grossmann, T., & Woodward, A. (2008). Not all emotions are created equal: the negativity bias in social-emotional development. *Psychological bulletin*, *134*(3), 383.

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.

Watts, F. N., McKenna, F. P., Sharrock, R., & Trezise, L. (1986). Colour naming of phobia-related words. *British journal of Psychology*, *77*(1), 97-108.

Wildgruber, D., Szameitat, D. P., Ethofer, T., Bruck, C., Alter, K., Grodd, W., & Kreifelts, B. (2013). Different types of laughter modulate connectivity within distinct parts of the laughter perception network. *PLoS One, 8*(5), e63441.

Young, G., & Lewis, M. (1979). Effects of familiarity and maternal attention on infant peer relations. *Merrill-Palmer Quarterly of Behavior and Development*, *25*(2), 105-119.

Zhang, D., Liu, Y., Hou, X., Sun, G., Cheng, Y., & Luo, Y. (2014). Discrimination of fearful and angry emotional voices in sleeping human neonates: a study of the mismatch brain responses. *Front Behav Neurosci, 8*, 422.

The Development of Spontaneous Facial Responses to Others' Emotions in Infancy:

An EMG Study

Maria M. Crespo-Llado[1§], Jakob Kaiser[2§], Chiara Turati[3], and Elena Geangu[1]*

[1]Lancaster University, [2]Ludwig-Maximilians-Universitaet Muenchen, [3]Università degli Studi di Milano-Bicocca, [§]Equal first authorship

Author Note

A version of this paper is under review:
Crespo-Llado, M.M., Kaiser, J., Turati, C., & Geangu, E (under review). The Development of Spontaneous Facial Responses to Others' Emotions in Infancy: An EMG Study. *Scientific Reports.*

Abstract

Viewing facial expressions often evokes facial responses in the observer. These spontaneous facial reactions (SFRs) are believed to play an important role for social interactions. However, their developmental trajectory and the underlying neurocognitive mechanisms are still little understood. In the current study, 4- and 7-month old infants were presented with facial expressions of happiness, anger, and fear. Electromyography (EMG) was used to measure activation in muscles relevant for forming these expressions: zygomaticus major (smiling), corrugator supercilii (frowning), and frontalis (forehead raising). The results indicated no selective activation of the facial muscles for the expressions in 4-month-old infants. For 7-month-old infants, evidence for selective facial reactions was found especially for happy faces (leading to increased zygomaticus major activation) and fearful faces (leading to increased frontalis activation), while angry faces did not show a clear differential response. This suggests that emotional SFRs cannot be explained via direct mimicry alone and that they may be the result of more complex neurocognitive mechanisms. Such mechanisms seem to undergo important developments at least until the second half of the first year of life.

Introduction

Emotional facial expressions are rich and powerful means of communicating information about one's affective states, as well as about the environment in which we live in. Not surprisingly, by adulthood, we develop high expertise to process facial expressions fast and accurately. A testimony to their importance and saliency is the fact that the perception of emotional faces often elicits emotionally convergent facial responses in the observer. For example, during social interactions, we often respond rapidly with emotional facial expressions that are similar to those we observe in others, such as smiling when we see someone happy. These spontaneous facial responses (SFRs), which are sometimes covert and not visible through direct observation (Cacioppo, Petty, Losch, & Kim, 1986; Tassinary & Cacioppo, 1992), nonetheless are thought to play crucial roles in how we communicate and empathise with each other, as well as in establishing cohesive social groups (Hatfield, Cacioppo, & Rapson, 1993; Hess & Fischer, 2013). Impairments in these social abilities are usually reported in pathologies characterised by atypical social functioning like autism, conduct disorders and psychopathy (Brid & Viding, 2014; Lockwood, Bird, Bridge, & Viding, 2014), and thus understanding the extent to which they are associated with atypical manifestations of emotional SFRs is of high importance. The study of infants' spontaneous facial responses to others' emotions is essential in this respect. Infancy is a crucial time period for tuning and optimising the brain circuitry for processing stimuli with socio-emotional relevance, setting the stage for both the refinement of the early acquired social skills and the emergence of new and more complex ones later in life (Johnson, 2011; Karmiloff-Smith, 1998; Sirois et al., 2008). In addition, infancy also provides unique opportunities for studying the SFRs to others' emotions in relative isolation from the influence of cultural norms and values, as well as symbolic linguistic processing of emotional information. Despite their relevance, the systematic investigation of infants' facial responses to others' emotions is limited (Haviland & Lelwica, 1987; Isomura & Nakano, 2016; Oostenbroek et al., 2016). In order to address this developmental gap, in this study we investigated SFRs to dynamic facial expressions of emotions in 4- and 7-months-old infants using electromyography (EMG).

Different neurocognitive mechanisms have been proposed to underlie the SFRs which are congruent with others' emotional expressions. One view regards them as instances of motor mirroring or motor mimicry, where the observation of others' facial movements elicits the selective activation of the corresponding muscles in the observer. These responses are thought to be largely automatic, occurring outside the mimicker's awareness, intention and control (Campbell & Cunnington, 2017; Heyes, 2011). In light of these characteristics, Chartrand and Bargh (1999) metaphorically referred to motor mirroring as the 'chameleon effect'. Motor mimicry relies on perception-action matching mechanisms involving the shared representation of the observed and executed facial actions. At the neural level, the mirroring properties of a cortical network including the inferior frontal, premotor and inferior parietal cortex (mirror neuron system - MNS) are thought to be involved in implementing the perceived emotional facial expression onto observer's own motor representations of producing that expression (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Dapretto et al., 2006; Pfeifer, Iacoboni, Mazziotta, & Dapretto, 2008). The simple sensory input of observing another's action leads to an activation of an internal motor representation in the observer because of the similarity of the perceived action and the motor representation used to control action execution (Blakemore & Frith, 2005; Brass & Heyes, 2005). The relation between the motor cortex activation and the selective excitability of the muscles involved in performing an action has been regarded as supportive of this view (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). The re-enactment of the observed expression could, in turn, even lead to the alteration of the observer's own affective state through muscular feedback (Chartrand & Bargh, 1999; Hatfield, Cacioppo, & Rapson, 1994). Indeed, numerous studies have shown that adults and older children rapidly mimic the facial expressions displayed by the people with whom they interact (Dimberg, 1982; Dimberg, Thunberg, & Elmehed, 2000; Moody, Mcintosh, Mann, & Weisser, 2007).

However, several findings are difficult to integrate with this perception-action matching proposal. SFRs which seem to match the observed emotions have also been recorded in response to emotional cues other than faces (i.e., body postures, vocal expressions, arousing pictures (Dimberg & Karlsson, 1997; Magnée, de Gelder, van Engeland, & Kemner, 2007; Soussignan et al., 2013; Tamietto & de Gelder, 2008), thus in the absence of the corresponding motor model which is important for a simple perception-action matching account. Moreover, observing others' facial expressions does not always elicit matching SFRs in the observer. For example, observing others' angry faces elicits SFRs specific for fear rather than anger (Beall, Moody, Mcintosh, Hepburn, & Reed, 2008; Geangu, Quadrelli, Conte, Croci, & Turati, 2016; Moody et al., 2007). Angry individuals represent potential sources of threat (Adams, Gordon, Baird, Ambady, & Kleck, 2003; Frijda, 1987), and usually elicit fear in others, both at subjective and psychophysiological level (Critchley et al., 2005; Davis & Whalen, 2001). Only when angry individuals are perceived as physically weaker and threatening one's social status, their facial displays of anger elicit similar SFRs in the observer (Hess, Adams, & Kleck, 2005; Soussignan et al., 2013). Situations of competition were also shown to trigger facial responses that are incongruent with the observed emotional expressions. Instead of showing positive emotional facial expressions, adults respond with negative displays to their competitors' pleasure (Lanzetta & Englis, 1989;

Likowski, Muhlberger, Seibt, Pauli, & Weyers, 2011). In all these examples, the facial responses converge with the meaning and the informative value for the observer of the emotional signals received from others, rather than its motor characteristics. Studies have also shown that posing a certain emotional expression can alter one's subjective emotional experience (Bush, Barr, Mehugo, & Lanzetta, 1989; Laird et al., 1989; Hennenlotter et al., 2009; Soussignan, 2002). However, the causal link between emotional facial mimicry and changes in affective state lacks definitive evidence (Dezecache, Eskenazi, & Grèzes, 2016).

To account for these additional findings, it has been proposed that the SFRs which converge with the displays of affect observed in others involve emotion communicative processes (Dezecache et al., 2016; Fischer & Hess, 2017; Grèzes et al., 2013; Grèzes & Dezecache, 2014). At the heart of this emotion-communicative proposal is the idea that the evaluation of the information provided by the emotional cues for self is critical and varies as function of stimulus features and social context. The evaluation of the emotional information can occur at different levels, from relevance detection and coding the negative and positive reward value of the stimuli, to fast or more elaborate cognitive appraisal (Koelsch et al., 2015). At the neural level, the evaluation of the emotional cues involves a circuitry consistent of both subcortical and cortical structures (Adolphs, 2002; Koelsch et al., 2015; Pessoa, 2017; Vuilleumier, Armony, Driver, & Dolan, 2003), amongst which the amygdala, the brainstem, and the orbitofrontal cortex (OFC) have been extensively investigated (see Koelsch et al., 2015 for a recent review). For example, the amygdala plays a role in the fast detection and evaluation of threat (Adolphs, 2010; Hoffman, Gothard, Schmid, & Logothetis, 2007; Ledoux, 1995; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004), as well as in the processing of happy events (Sander, Grafman, & Zalla, 2003). The amygdala shows connectivity and co-activation with the motor and pre-motor cortical structures involved in preparation for action (Balconi, Grippa, & Vanutelli, 2015; Baumgartner, Willi, & Jancke, 2007; Oliveri et al., 2003; Schutter, Hofman, & Honk, 2008), suggesting that the early evaluation of emotional cues informs the behavioral responses during social interactions (Grèzes & Dezecache, 2014). The shared motor representations comprising components of the perceived action and associated predicted somatosensory consequences are also considered to be active during the perception of emotional displays. However, the attributed role has more to do with the anticipation of others' behavior and intentions (Dezecache et al., 2016; Hamilton, 2016; Kilner, Friston, & Frith, 2007). Components of neural network underlying these processes are also thought to play a role in implementing the appropriate motor responses afforded by the specific social situation (Hamilton, 2016). Recent neuroimaging investigations have shown that although the threat evaluation processes related to the amygdala slightly precede those involved in generating shared representations, these seem to interact and be integrated as soon as 200 ms after stimulus onset (Conty, Dezecache, Hugueville, & Grezes, 2012). Given the role of the amygdala in evaluating a range of emotional events, a similar sequence of operations may also be encountered for positive emotions or for other brain structures with evaluative properties (e.g., the OFC) which are functionally connected with the motor cortex (Koelsch et al., 2015; Pessoa, 2017; Sander et al., 2003).

In order to understand the factors that influence facial reactions, it is important to investigate the development of the infant SFRs to others' emotional facial expressions. Recently it was shown that 5-months-old infants selectively respond with increased activation of the zygomaticus major to audio-visual recordings of adults smiling and with increased activation of the corrugator supercilli to audio-visual recordings of adults crying. This selective muscle activation was not reported for unimodal presentations of adult expressions of cry and laughter (i.e., voice-only, face-only; Isomura & Nakano, 2016). Nonetheless, the absence of angry expressions and of contrasts between different negative emotional expressions, together with the lack of a truly developmental perspective given that only one age group was tested, highly limit the conclusions that can be drawn based on these findings.

In the current study we employed an EMG paradigm which contrasts the responses towards three dynamic facial expressions of emotion (i.e., happiness, anger, and fear) in three facial muscles that have been found to be selectively activated in these facial displays (i.e., zygomaticus major for smiling during happiness, corrugator supercilli for frowning in anger, and frontalis for forehead raising in anger displays). The study was conducted with both 4- and 7-months-old infants. The choice of these age groups was motivated by the evidence suggesting that they represent important hallmarks in the development of the ability to process emotional information from faces (Hoehl, 2014). Although even very young infants are able to discriminate between different facial expressions of emotions (Barrera & Maurer, 1981; Farroni, Menon, Rigato, & Johnson, 2007; Serrano, Iglesias, & Loeches, 1995), it seems that only beginning with the age of 7-months they rely on adults' specific emotional expressions to guide their behavior towards the stimuli in the environment (Hoehl, 2014; Hoehl & Striano, 2010; Striano & Vaish, 2006). For example, it is around this age that infants begin to perceive fearful facial expressions as specific cues for threat (Hoehl, 2014; Striano & Vaish, 2006).

If SFRs were predominantly a case of automatic perception-action matching, one would expect stronger activation in the muscle mainly involved in this expression (zygomaticus major for happy faces, corrugator supercilii for angry faces, and frontalis for fearful faces) relative to the other facial muscles. Cases where SFRs do not match facial expressions would support the view that additional mechanism to the direct mirror matching are responsible for SFRs, such as evaluative-communicative processes. From this perspective, emotion congruent SFRs are expected to occur at the age when infants are able to process the informative value of the perceived expression. In light of evidence suggesting that only towards the age of 7-months infants are more likely to process the informative value of certain emotional facial expressions, we anticipate SFRs congruent with the observed ones in 7- rather than 4-months-old infants. The comparisons across multiple emotions and multiple facial muscles at two developmental periods will allow us to draw conclusions with regard to the specificity and selectivity of the infant emotional SFRs.

Methods

Participants

Twenty seven 4-month old infants (11 females, M_{age} = 135.11 days, SD = 10.08 days) and 24 7-month old infants (14 females, M_{age} = 226.17 days, SD = 9.90 days) were included in the final analysis. An additional 5 4-months-old and 8 7-months-old infants were tested but not included in the final sample due to technical issues (n = 4) or inattentiveness resulting in less than 5 good trials per condition (n = 10). All participants were recruited from a small urban area in North West England. Informed consent was obtained from all parents prior to the beginning of the procedure. The procedure was carried out in accordance with the ethical standards of the Declaration of Helsinki (BMJ 1991; 302:1194). Ethical approval was granted by the Lancaster University Ethics Committee. Parents were reimbursed for their travel expenses (£10), while infants received a token for their participation.

Stimuli

Fifteen grey-scale dynamic female human faces displaying happiness (n = 5), anger (n = 5), and fear (n = 5) were taken from the Cohn-Kanade Expression database (Kanade & Cohn, 2000), which has become one of the most widely used stimuli for studies of facial expression analysis (Kanade & Cohn, 2000; Lucey et al., 2010). One of the main strengths of this dataset are that all facial expressions have been fully FACS coded (Lucey et al., 2010). The chosen faces were selected for their emotional valence. The selection criteria for the stimuli was that all happy facial expressions included corners of the mouth raised in a smile, all anger expressions included furrowed brows, and all fear expressions included raised eyebrows. For all stimuli, the transition between neutral and emotional expression occurred between 0 and 1000ms, while the peak expressivity was reached between 1000 and 3000ms. The exact timing of the facial movements, specific for each emotion expression, varied within and between stimulus categories. Face images were cropped using an oval frame that allowed facial features to be visible but excluded hair, ears, and any other paraphernalia.

Procedure

Participants were tested individually in a quiet and dimly lit room. Before placing the electrodes, the skin was cleaned with an alcohol-free wipe. The electrodes were attached by one of the experimenters, while the second blew soap bubbles or manipulated a rattle toy in order to maintain the participant calm and distract him/her, as needed. Once the facial electrodes were placed, the participants sat during the entire procedure on their mothers' lap approximately 70 cm away from a 24-inch monitor. Parents were instructed to hold their infants' hand as still as possible to prevent infants from pulling the facial electrodes, not to speak to them, and not to point towards the screen during the entire stimuli presentation.

Each trial started with a central fixation cross for 1000 ms, during which baseline muscle activity levels were established. Following the fixation cross, a black screen displaying the emotional facial expression appeared for 3000 ms, followed by a blank screen (see Figure 2). Between trials, a dynamic non-social attention grabber was played whenever needed in order to maintain the participants' attention to the stimuli in case they showed signs of becoming distracted. The option of having experimental controlled presentation of the attention grabber rather than an automatic presentation after each trial is common to infant psychophysiology paradigms requiring the presentation of many trials (de Haan, 2013) and capitalizes on the infants' natural bouts of attention. The procedure continued for as long as infants paid attention to the stimuli. On average, participants completed 55.12 trials (Happy faces: *M* = 18.35 trials, *Min* = 10, *Max* = 30; Angry faces: *M* = 18.12 trials, *Min* = 10, *Max* = 30; Fearful faces: *M* = 18.65 trials, *Min* = 11, *Max* = 30). The entire procedure was video recorded in order to establish whether the infants had watched the faces in each trial and to facilitate artifact detection during the data analysis. The complete experimental session took approximately 10 min.

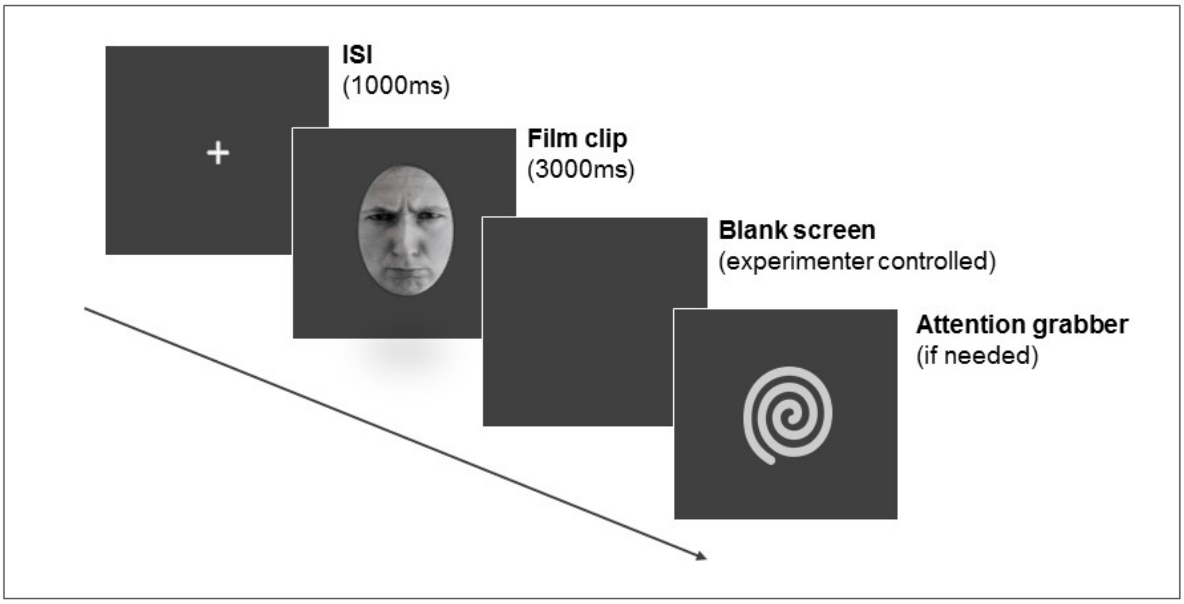


Figure 2. Example of a trial structure and stimuli used in the study. After a 1000 ms central fixation cross, the participants were presented for 3000 ms with the dynamic facial expression of either anger, happiness or fear displayed by a female adult. The emotional stimulus was followed up by a blank screen. The non-social attention grabber was presented whenever recapturing participants' attention to the screen was required. (The face picture included in the figure is for illustration purposes only and not part of the stimuli used in the study.)

EMG Data Acquisition and Analysis

Electromyography was used to record the levels of muscle activity over the zygomaticus major (raises the cheek), the medial frontalis (raises the brow), and the corrugator supercilli (knits brow). This method was extensively used to record adults' facial responses to others' emotions (Likowski et al., 2011). Although the internal consistency of the recorded EMG signal in these studies tends to be low, the test-retest reliability is good (Hess et al., 2017). Recent studies show that facial EMG is a method suitable to be used with young children and infants (Beall et al., 2008; Geangu et al., 2016; Turati et al., 2013). In the present study, a BIOPAC MP30 continuously recorded the EMG signal from the selected muscles using bipolar montages. Disposable surface adhesive 4mm Ag-AgCl EMG electrodes (Unimed) were placed on the infants' face at locations corresponding to each muscle according to the guidelines by Fridlund & Cacioppo (1986) and as previously reported in facial EMG studies with infants (Natale et al., 2014; Turati et al., 2013) and toddlers (Geangu et al., 2016). Electrodes were positioned on the left side of the face to obtain maximal reactions (Fridlund & Cacioppo, 1986). The reference electrode was positioned just below the hairline approximately 3 cm above the nasion. The EMG signal was recorded at a sampling rate of 1 kHz-filtered offline (low pass: 150 Hz; high pass: 30 Hz), and rectified. Rectified data was averaged in 200 ms time bins which where z-transformed for each muscle and participant individually. This is a standard procedure in facial EMG studies allowing for a comparison between participants and muscles. Participants' looking time toward the screen was coded offline in order to inform whether they attended the stimuli. This is common procedure in electrophysiology research with preverbal children (e.g., Lloyd-Fox et al., 2017). Trials with a looking time of less than 70 % of the stimulus duration, as well as trials with excessive movement or noise artifacts were excluded. Only children with minimum five trials per condition were included in the final statistical analyses. This criterion was informed by previous studies with infants (Isomura & Nakano, 2016), children (Beall et al., 2008; de Wied et al., 2006), and adults (Dimberg & Petterson, 2000; Dimberg et al., 2000; Hess & Blairy, 2001; Hess et al., 1998). Across participants, the mean number of trials contributing to the final statistical analyses was 33.10 (Happy faces: *M* = 11.04 trials, *Min* = 5, *Max* = 18; Angry faces: *M* = 10.18, *Min* = 5, *Max* = 17; Fearful faces: *M* = 11.88, *Min* = 5, *Max* = 19).

Previous studies with children using a similar paradigm suggest that facial reactions towards emotional expressions start to show between 500 and 1000 ms for static facial stimuli that are already fully developed in their expressivity (Beall et al., 2008; Geangu et al., 2016; Oberman et al., 2009), which is also consistent with adult studies (Dimberg, 1982; Dimberg & Petterson, 2000; Moody et al., 2007). As the dynamic stimuli in this study gradually developed over the first 1000 ms and remained at peak between the 1000 - 3000 ms, we averaged for each trial both the first onset phase (Time point 1) and the peak expression phase (Time point 2). Average activation was baseline-corrected by subtracting the 1000 ms interval immediately before stimulus onset, and the mean for trials of the same emotion was calculated.

Results

Mean amplitude values expressed as z-scores were analysed using a mixed ANOVA with Muscle (frontalis, corrugator supercilli, zygomaticus major), Emotion (happy, anger, fear), and Time window (Time 1, Time 2) as within factors and Age group (4-months-old vs. 7-months-old) as a between factor. All statistical tests were conducted at the .05 level of significance (two-tailed), with Bonferroni correction for post-hoc comparisons. The results show significant interactions between Time window x Age group ($F(1,49) = 5.466, p = .024, \eta_p^2 = .100$), Emotion x Muscle x Age group ($F(4,196) = 3.276, p = .013, \eta_p^2 = .063$), as well as Emotion x Muscle x Time window x Age group ($F(4,196) = 2.749, p = .029, \eta_p^2 = .053$). No other significant main effects or interactions were observed ($p > .052$). Furthermore, to explore the Muscle x Emotion x Age Group x Time window interaction, we proceed to perform a 3 (Muscle: frontalis, corrugator or zygomaticus) x 3 (Emotion: happy, anger or fear) x 2 (Time window: Time 1, Time 2) repeated measures ANOVAs for each age group. Also, since we transformed facial reactions to z-scores, we were able to analyse whether the reactions to each emotion differed between muscles.

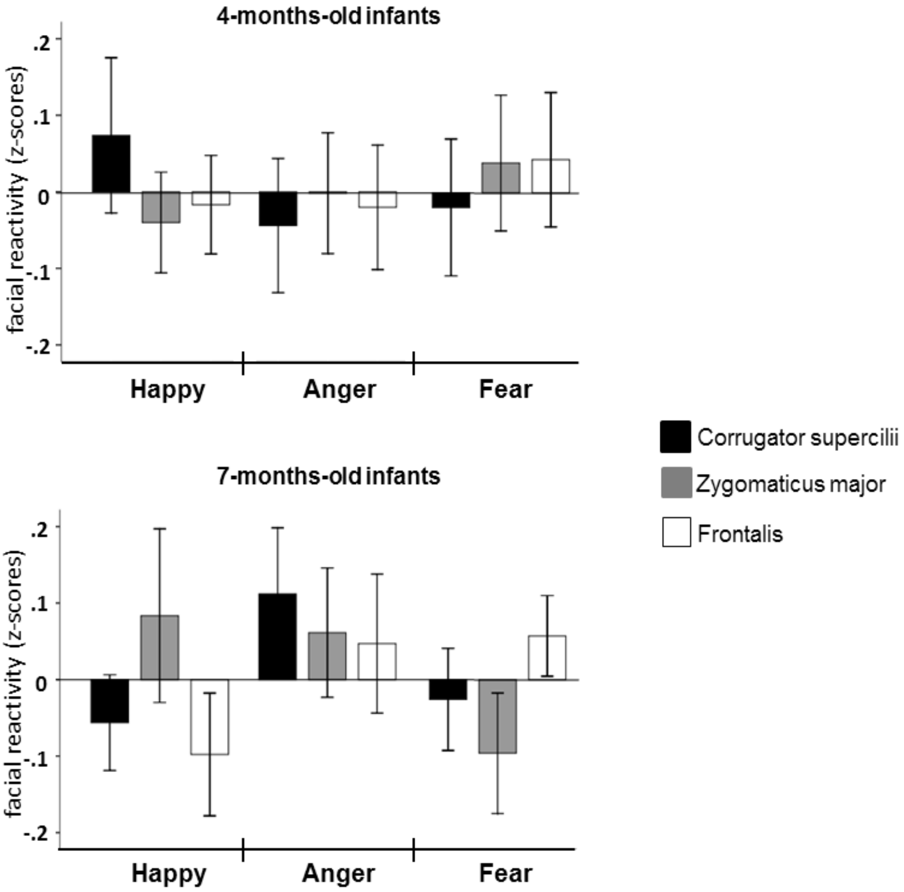


Figure 1. Means (and 95% confidence interval) of facial reactions towards the stimuli during Time 2 (1000-3000ms from onset) for different muscles (expressed as z-scores).

4-months-old infants

For the 4-months-old group an ANOVA with the factors Emotion, Muscle, and Time window revealed a significant interaction Emotion x Muscle, $F(4,104) = 3.275$, $p = .014$, $\eta_p^2 = .112$ (Figure 1). The post-hoc pairwise comparisons did not result in any significant differences in the muscle activation between emotions ($p > .261$), nor any differences in activation between muscles within emotions ($p > .054$). No other main effects or interactions were observed ($p > .088$). Thus we found no evidence of SFRs in the younger age group.

7-months-old infants

For the 7-month olds, the results show a significant interaction between Emotion, Muscle, and Time window, *F*(4, 92) = 3.451; *p* = .011; η_p^2= .130. No other main effects or interactions were observed (*p* > .052). This indicated that 7-months olds showed differential facial responses towards the emotional faces which were dependent on time. We conducted post-hoc pairwise comparisons in order to compare the effect of different emotions on each muscle. For the 0 to 1000 ms time window, no significant differences between emotions were found for any of the muscles (*p* > .213). For the 1000 to 3000 ms time window, the corrugator supercillii showed significantly stronger reactions towards angry faces (*M* = .112, *SE* = .042) than happy faces (*M* = -.056, *SE* = .030), *p* = .042. There were no significant differences between angry and fearful faces (*M* = -.026, *SE* =.032), *p* = .167, or between happy and fearful faces, *p* > .900. For the frontalis, we found significantly stronger activation for fearful (*M* = .057, *SE* = .026) than for happy faces (*M* = -.098, *SE* =.039), *p* = .023. No significant differences were found between fearful and angry faces (*M* = .047, *SE* = .044), *p* > .900, or between angry and happy faces, *p* = .213. For the zygomaticus, no significant differences emerged between the emotion categories (all p-values > .074; Figure 1). For the 0 to 1000 ms time window, no significant differences in activation between muscles were found for any emotional facial expression (*p* > .849). For the 1000 to 3000 ms time interval, happy facial expressions elicited higher zygomaticus major activation (*M* = .084, *SE* = .055) compared to the corrugator supercilii (*M* = -.056, *SE* = .030), *p* = .036, and the frontalis (*M* = -.098, *SE* = .039), *p* = .018. There was no significant difference in reaction towards happy faces between corrugator and frontalis, *p* = .783. For fearful faces, the frontalis (*M* = .057, *SE* = .026) showed a significantly higher activation than the zygomaticus (*M* = -.096, *SE* =.038), *p* = .009. There was no significant difference for fearful faces between frontalis and corrugator supercilii (*M* = -.026, *SE* = .032), *p* = .114, and no significant difference between corrugator supercilii and zygomaticus major, *p* = .316. For angry faces, no significant differences emerged between the muscles (all p-values > .849; Figure 1). Notably, no gender effects were found for this age group. For further information see Appendix C.

Discussion

Our aim was to understand the ontogeny of infants' facial response to others' emotions and how this relates to the current theoretical models regarding the role of perception-action matching mechanisms and affect processes. We therefore presented 4- and 7-months-old infants with dynamic facial expressions of happiness, fear, and anger, while we used EMG to measure the activation of the muscles specific for expressing these emotions (i.e., zygomaticus major, frontalis, and corrugator supercilli, respectively). The results show that infants' SFRs to dynamic emotional facial expressions undergo significant developmental changes towards the age of 7-months.

The 4-months-old infants in our study did not manifest selective activation of the recorded facial muscles in response to dynamic facial cues of emotions. In fact, as Figure 1 shows, very little facial responsiveness was present for this age group. These findings are in line with previous EMG studies which show that 5-months-old infants do not match their SFRs with dynamic facial expressions of cry and laughter without additional emotion-relevant auditory cues (Isomura & Nakano, 2016), as well as a series of behavioral studies which reported a lack of selective emotional facial responsiveness for 2-3-months-old infants and newborns (Kaitz, Meschulach-sarfaty, Auerbach, & Eidelman, 1988; Oostenbroek et al., 2016). Limited statistical power may have played a role in limiting the interpretation of some of the statistical comparisons conducted because of the modest sample size in this age group (*n* = 27). However, a post-hoc power analysis revealed that a total sample of 18 infants would be needed to detect a Muscle x Emotion interaction effect of $\eta^2_p = .112$ with 90% power using a repeated-measures ANOVA with alpha set to .05 level. Thus, based on power calculations, we had sufficient power to detect an effect of the magnitude observed.

Our study shows for the first time that dynamic emotional facial expressions elicit selective SFRs in 7-month-old infants. Importantly, this pattern of response was not generalizable across all emotional expressions. The comparisons of muscle activation between and within each emotion show that observing dynamic facial expressions of happiness leads to increased activation of the muscle specific for expressing this emotion (i.e., zygomaticus major) and decreased activation of the muscle involved in expressing fear (i.e., frontalis) and anger (i.e., corrugator supercilli). A similar pattern of selective SFRs was also recorded for fearful faces, with an increased activation of the frontalis and decreased activation of the muscle specific for expressing happiness (i.e., zygomaticus major). In contrast, the perception of angry faces tended to lead to a more non-differentiated pattern of facial responsiveness. While the muscle specific for expressing anger, corrugator supercilli, did record an increased activation in response to angry faces compared to the happy ones, this was not associated with a decrease in the activation of the muscle specific for smiling (i.e., the zygomaticus major) nor the muscle specific for fear (i.e., the frontalis). Similar partial selectivity of the behaviorally coded facial responsiveness has been previously reported in studies with 2- to 3-months-old and 6-months-old infants, in which responses to more than two emotional expressions during ecological mother-infant interactions were contrasted (Haviland & Lelwica, 1987; Izard et al., 1995; Walker-Andrews, 1997).

Amongst the most prominent theoretical proposals for the neurocognitive mechanisms underlying the SFRs to others' emotions are those attributing a primary role to perception-action matching mechanisms (Carr et al., 2003; Hatfield et al., 1994; Pfeifer et al., 2008). The fact that 7-months-old infants do not respond to all emotional expressions included in this study with matching SFRs in a selective manner suggests that these are less likely to be simple re-enactments of the observed expressions based on perception-action matching mechanisms. Our findings are not likely to be due to an inability to perceptually discriminate or display the expressions tested. In particular, at this age infants have the ability to perceptually discriminate angry faces from various other emotional facial expressions (Grossmann, 2010; Hoehl, 2014), as well as the ability to display the facial movements specific for anger, happiness and fearfulness (Camras & Shutter, 2010; Haviland & Lelwica, 1987; Messinger, 2002; Messinger & Fogel, 2007; Walker-Andrews, 1997). Moreover, it is less likely that these results are due to differences in exposure to angry facial expressions. From around the age of 2-months, infants are exposed to parents' facial expressions of anger. Although these are not as frequent as facial expressions of happiness (Malatesta, Grigoryev, Lamb, Albin, & Culver, 1986), they are probably as frequent as those of fear (Leppänen & Nelson, 2009), for which infants show congruent SFRs.

Behavioral and neuroimaging studies have shown that the more elaborate representations of emotional expressions and their communicative value develop in infants after the age of 5-months, in an emotion dependent fashion (Grossmann, 2010; Hoehl, 2014). For example, 6-7-months-old but not younger infants show specific sensitivity to fearful faces as cues for threat and manifest increased attention towards objects that were looked at by fearful faces (Hoehl, 2014; Hoehl & Striano, 2010). This ability consolidates in the next months (Hoehl, Reid, Mooney, & Striano, 2008) and becomes more obvious in how infants interact with their environment around the age of 12-months (Campos, Thein, & Owen, 2003; Striano & Rochat, 2000; Striano & Vaish, 2006). Although emotional expressions of anger are also relevant cues for threat, infants do not seem sensitive to their specific informative value until closer to their first birthday (Grossmann, Striano, & Friederici, 2007; Missana, Grigutsch, & Grossmann, 2014). The insufficiently developed ability of 7-month-old infants to evaluate the specific informative value of angry facial expressions may partially explain their lack of selective SFRs for this expression. The immature ability of the 4-months-olds to process a variety of facial expressions may also be partially responsible for the absence of selective SFRs across all expressions included in this study. Taken together, the age differences and pattern of selective muscle activation appear to be consistent with proposals that see SFRs not as pure motor mimicry, but also see the influence of communicative processes involving the evaluation of the emotional cues (Dezecache et al., 2016; Grèzes & Dezecache, 2014; Haviland & Lelwica, 1987; Soussignan et al., 2013; Walker-Andrews, 1997).

This interpretation does not necessarily mean that instances of emotionally convergent SFRs may only be recorded in infants closer to the age of 7-months, but rather that they may be limited to those situations where infants are able to extract salient information from the perceived emotional cues. Previous behavioral studies which used more ecological adult-infant interaction paradigms showed that infants as young as 2-3-months manifest facial responses which tend to converge emotionally with the observed ones. However, these responses are specific to situations involving interactions between infants and their mothers, with whom they have had extensive experience in social exchanges (Bigelow & Rochat, 2006; Haviland & Lelwica, 1987; Izard et al., 1995; Oostenbroek et al., 2016; Walker-Andrews, 1997). In this case, infants' facial responses may reflect the appraisal of the perceived emotional cues with respect to the mother's immediate future actions that in the past elicited specific emotional responses. For example, caregivers' smiling faces are typically associated with pleasant social engagement, such as play and caring actions known to induce positive affect in the infant. In contrast, the display of negative emotional expressions is more likely to be followed by a lack of social interaction which can be distressing for the infant (Grossmann, 2010; Haviland & Lelwica, 1987; Walker-Andrews, 1997). This explanation would also account for those situations where the perception and the evaluation of others' emotions are facilitated by the presence of multiple cues (Magnée et al., 2007; Rychlowska, Zinner, Musca, & Niedenthal, 2012; Schrammel, Pannasch, Graupner, Mojzisch, & Velichkovsky, 2009; Seibt, Mühlberger, Likowski, & Weyers, 2015; Soussignan et al., 2013) or the quality of the emotional cues (e.g., static versus dynamic expressions; Rymarczyk, Biele, Grabowska, & Majczynski, 2011; Sato & Yoshikawa, 2007; Seibt et al., 2015; Weyers, Muhlberger, Hefele, & Pauli, 2006). The fact that 5-month-old infants respond with emotion convergent SFRs to audio-visual expressions of laughter and crying but not to the unimodal presentations (i.e., face-only, voice-only) of these emotional displays (Isomura & Nakano, 2016) may reflect such facilitating effect (Burnham, 1993; Flom & Bahrick, 2007; Vaillant-Molina, Bahrick, & Flom, 2013).

Although the current findings together with those previously reported (Haviland & Lelwica, 1987; Isomura & Nakano, 2016; Oostenbroek et al., 2016) are informative about the emergence of the emotion congruent SFRs in infancy and suggestive with regards to the complexity of the underlying neurocognitive mechanisms, further research is needed in order to draw firmer conclusions in this respect. For example, although the current study shows that facial EMG paradigms can be successfully used with infants of different ages, it does not allow establishing whether the observed facial responses are related to changes in autonomic arousal. Emotional expressions displayed by both adults and peers were found to elicit autonomic arousal indicative of emotional responsiveness in infants. In particular, changes in skin conductance and pupil diameter have been reported in response to expressions of happiness, fear, anger, and general distress in infants starting with the age of 4-months (Geangu, Hauf, Bhardwaj, & Bentz, 2011; Gredebäck, Eriksson, Schmitow, Laeng, & Stenberg, 2012; Jessen, Altvater-Mackensen, & Grossmann, 2016; Nava, Romano, Grassi, & Turati, 2016). Changes in autonomic arousal also seem to be significantly related to infants' facial responses in emotion elicitation situations (Emde & Campos, 1978; Lewis & Ramsay, 2005; Lewis, Ramsay, & Sullivan, 2006; Mattson et al., 2013). Concurrent facial EMG and measures of psychophysiological arousal would be particularly valuable for understanding how affect related processes contribute to the emergence of the emotionally convergent SFRs during infancy and childhood. Such knowledge is also directly relevant for studying the ontogeny of affect sharing and empathy (Decety, 2015; Decety & Michalska, 2010).

Extracting, processing, and responding to the emotional information presented by human faces relies on complex neural networks involving both sub-cortical and cortical structures, including those that are part of the emotion-related brain circuits (e.g., the amygdala and the orbito-frontal cortex (Adolphs, 2002; Pessoa, 2008; Vuilleumier et al., 2003) and those functionally linked with motor preparation for action and estimating others' immediate intent for action (Balconi & Bortolotti, 2013; Baumgartner et al., 2007; Coelho, Lipp, Marinovic, Wallis, & Riek, 2010; Coombes, Tandonnet, Cauraugh, & Summers, 2009; Grèzes & Dezecache, 2014; Hamilton, 2016; Oliveri et al., 2003; Schutter et al., 2008). Although the emotion-related brain structures are already functional at birth, and the connections with the other related cortical and subcortical areas established, these brain structures continue to mature and their pattern of connectivity refines over the course of postnatal development (Leppänen & Nelson, 2009). It is thus possible that the SFRs of the 7-months-old infants to happy and fearful facial expressions reflect, at least partially, these developmental changes in the underlying neural network (Leppänen & Nelson, 2009, 2012). Natural variations in the familiarity with different social contexts, as well as in the maturation of the relevant brain networks which are specific to the first year of life can thus provide unique opportunities for characterizing processes that would otherwise be impossible to capture in the fully mature adults (De Haan, Humphreys, & Johnson, 2002; Filippi et al., 2016).

Different experimental approaches could be adopted for further investigations into the neurocognitive mechanisms underlying emotion congruent SFRs in infancy. For example, concurrent recordings of facial EMG and EEG based measures of cortical activation would be particularly informative in understanding how neural development contributes to the emergence of emotionally convergent SFRs in infancy (Dezecache et al., 2016; Filippi et al., 2016; Hamilton, 2016), with the potential of clarifying the extent to which shared motor representations comprising components of the perceived action and associated somatosensory consequences are involved in generating emotion congruent SFRs in infants, alongside emotion evaluation and reactivity processes. Specifying the dynamic of the facial muscle activation may also be relevant in this respect, potentially reflecting the chronology of different processes. In the present study we have shown that the selective facial muscle activation specific for emotion congruent SFRs is overall recorded between 1000 and 3000ms after stimulus onset. This timing is similar to that reported in previous studies with young children (Geangu et al., 2016). Nevertheless, more subtle latency differences between emotions, and between muscles within emotion categories, may be present (Achaibou, Pourtois, Schwartz, & Vuilleumier, 2007). The stimuli used in the current study were not matched for the precise timing of facial actions, therefore not allowing a more refined time sensitive analysis. Artificially developed stimuli, such as morphed faces, or static facial expressions would be particularly suitable in this respect.

Being able to detect and respond to others' emotions is essential to our social lives. For the past decades, a large number of studies have shown that adults tend to respond with rapid facial responses which converge emotionally with the emotions they perceive in others (Seibt et al., 2015). Although much more limited, evidence also emerged in recent years to show that similar patterns of facial responsiveness can be reported during childhood (Beall et al., 2008; Deschamps, Coppes, Kenemans, Schutter, 2015; de Wied, van Boxtel, Zaalberg, Goudena, & Matthys, 2006; Oberman, Winkielman, & Ramachandran, 2009). Despite being a well-documented phenomenon in adulthood, debates regarding its early ontogeny and the underlying neurocognitive mechanisms remain open (Dezecache et al., 2016; Isomura & Nakano, 2016; Magnée et al., 2007; Oostenbroek et al., 2016). Our study shows that spontaneous facial responses which converge emotionally with the facial expressions observed in others can be recorded in 7- but not in 4-months-old infants. The pattern of infant emotional SFRs suggests that they may rely on complex neurocognitive mechanisms (Dezecache et al., 2016), which undergo important developments at least until the second half of the first year of life. The factors contributing to the development of infants' emotional SFRs remain to be established, yet continued work on this topic will be critical for better understanding the emergence of related, complex social abilities like communication and empathy.

References

Achaibou, A., Pourtois, G., Schwartz, S., & Vuilleumier, P. (2008). Simultaneous recording of EEG and facial muscle reactions during spontaneous emotional mimicry. *Neuropsychologia*, *46*(4), 1104-1113.

Adams, R. B., Gordon, H. L., Baird, A. A., Ambady, N., & Kleck, R. E. (2003). Effects of gaze on amygdala sensitivity to anger and fear faces. *Science*, *300*(5625), 1536-1536.

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

Adolphs, R. (2010). What does the amygdala contribute to social cognition?. *Annals of the New York Academy of Sciences*, *1191*(1), 42-61.

Balconi, M., & Bortolotti, A. (2013). The "simulation" of the facial expression of emotions in case of short and long stimulus duration. The effect of pre-motor cortex inhibition by rTMS. *Brain and cognition*, *83*(1), 114-120.

Balconi, M., Grippa, E., & Vanutelli, M. E. (2015). What hemodynamic (fNIRS), electrophysiological (EEG) and autonomic integrated measures can tell us about emotional processing. *Brain and cognition*, *95*, 67-76.

Barrera, M. E., & Maurer, D. (1981). The perception of facial expressions by the three-month-old. *Child development*, 203-206.

Baumgartner, T., Willi, M., & Jäncke, L. (2007). Modulation of corticospinal activity by strong emotions evoked by pictures and classical music: a transcranial magnetic stimulation study. *Neuroreport*, *18*(3), 261-265.

Beall, P. M., Moody, E. J., McIntosh, D. N., Hepburn, S. L., & Reed, C. L. (2008). Rapid facial reactions to emotional facial expressions in typically developing children and children with autism spectrum disorder. *Journal of experimental child psychology*, *101*(3), 206-223.

Bigelow, A. E., & Rochat, P. (2006). Two-month-old infants' sensitivity to social contingency in mother–infant and stranger–infant interaction. *Infancy*, *9*(3), 313-325.

Bird, G., & Viding, E. (2014). The self to other model of empathy: providing a new framework for understanding empathy impairments in psychopathy, autism, and alexithymia. *Neuroscience & Biobehavioral Reviews*, *47*, 520-532.

Blakemore, S. J., & Frith, C. (2005). The role of motor contagion in the prediction of action. *Neuropsychologia*, *43*(2), 260-267.

Brass, M., & Heyes, C. (2005). Imitation: is cognitive neuroscience solving the correspondence problem?. *Trends in cognitive sciences*, *9*(10), 489-495.

Burnham, D. (1993). Visual recognition of mother by young infants: facilitation by speech. *Perception*, *22*(10), 1133-1153.

Bush, L. K., Barr, C. L., McHugo, G. J., & Lanzetta, J. T. (1989). The effects of facial control and facial mimicry on subjective reactions to comedy routines. *Motivation and emotion*, *13*(1), 31-52.

Cacioppo, J. T., Petty, R. E., Losch, M. E., & Kim, H. S. (1986). Electromyographic activity over facial muscle regions can differentiate the valence and intensity of affective reactions. *Journal of personality and social psychology*, *50*(2), 260.

Campbell, M. E., & Cunnington, R. (2017). More than an imitation game: Top-down modulation of the human mirror system. *Neuroscience & Biobehavioral Reviews*.

Campos, J. J., Thein, S. & Owen, D. (2003). Human Infancy Emotional Expressions as Behavior Regulators. *Ann. N. Y. Acad. Sci. 134*, 110–134.

Camras, L. A., & Shutter, J. M. (2010). Emotional facial expressions in infancy. *Emotion Review*, *2*(2), 120-129.

Carr, L., Iacoboni, M., Dubeau, M. C., Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proceedings of the national Academy of Sciences*, *100*(9), 5497-5502.

Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: the perception–behavior link and social interaction. *Journal of personality and social psychology*, *76*(6), 893.

Coelho, C. M., Lipp, O. V., Marinovic, W., Wallis, G., & Riek, S. (2010). Increased corticospinal excitability induced by unpleasant visual stimuli. *Neuroscience letters*, *481*(3), 135-138.

Conty, L., Dezecache, G., Hugueville, L., & Grèzes, J. (2012). Early binding of gaze, gesture, and emotion: neural time course and correlates. *Journal of Neuroscience*, *32*(13), 4531-4539.

Coombes, S. A., Tandonnet, C., Fujiyama, H., Janelle, C. M., Cauraugh, J. H., & Summers, J. J. (2009). Emotion and motor preparation: a transcranial magnetic stimulation study of corticospinal motor tract excitability. *Cognitive, Affective, & Behavioral Neuroscience*, *9*(4), 380-388.

Critchley, H. D., Rotshtein, P., Nagai, Y., O'doherty, J., Mathias, C. J., & Dolan, R. J. (2005). Activity in the human brain predicting differential heart rate responses to emotional facial expressions. *Neuroimage*, *24*(3), 751-762.

Dapretto, M., Davies, M. S., Pfeifer, J. H., Scott, A. A., Sigman, M., Bookheimer, S. Y., & Iacoboni, M. (2006). Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders. *Nature neuroscience*, *9*(1), 28.

Davis, M., & Whalen, P. J. (2001). The amygdala: vigilance and emotion. *Molecular psychiatry*, *6*(1), 13.

De Haan, M. (2013). *Infant EEG and event-related potentials*. Psychology Press.

De Haan, M., Humphreys, K., & Johnson, M. H. (2002). Developing a brain specialized for face perception: A converging methods approach. *Developmental Psychobiology*, *40*(3), 200-212.

De Wied, M., van Boxtel, A., Zaalberg, R., Goudena, P. P., & Matthys, W. (2006). Facial EMG responses to dynamic emotional facial expressions in boys with disruptive behavior disorders. *Journal of Psychiatric research*, *40*(2), 112-121.

Decety, J. (2015). The neural pathways, development and functions of empathy. *Current Opinion in Behavioral Sciences*, *3*, 1-6.

Decety, J., & Michalska, K. J. (2010). Neurodevelopmental changes in the circuits underlying empathy and sympathy from childhood to adulthood. *Developmental science*, *13*(6), 886-899.

Deschamps, P. K., Coppes, L., Kenemans, J. L., Schutter, D. J. L. G., & Matthys, W. C. H. J. (2015). Electromyographic responses to emotional facial expressions in 6–7 year olds with autism spectrum disorders. *Journal of autism and developmental disorders*, *45*(2), 354-362.

Dezecache, G., Eskenazi, T., & Grèzes, J. (2016). Emotional Convergence: A Case of Contagion?. In S. S. Obhi & E. S. Cross (Eds.), *Shared Representations: Sensorimotor Foundations of Social Life.* Cambridge University Press.

Dimberg, U. (1982). Facial reactions to facial expressions. *Psychophysiology*, *19*, 643–647.

Dimberg, U. & Karlsson, B. (1997). Facial reactions to different emotionally relevant stimuli. *Scand. J. Psychol.*, *38*, 297–303

Dimberg, U. L. F. & Petterson, M. (2000). Facial reactions to happy and angry facial expressions: Evidence for right hemisphere dominance. *Psychophysiology*, *37*, 693–696.

Dimberg, U., Thunberg, M. & Elmehed, K. (2000). Unconscious facial reactions to emotional facial expressions. *Psychological Science, 11*, 86–89.

Emde, R. N. & Campos, J. (1978). Infant Smiling at Five and Nine Months: Analysis of Heartrate and Movement. *Infant Behav. Dev. 5*, 26–35.

Fadiga, L., Fogassi, L., Pavesi, G. & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology, 73*.

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

Filippi, C. A., Cannon, E. N., Fox, N. A., Thorpe, S. G., Ferrari, P. F., & Woodward, A. L. (2016). Motor system activation predicts goal imitation in 7-month-old infants. *Psychological science*, *27*(5), 675-684.

Fischer, A. H. & Hess, U. (2017). Mimicking emotions. *Current Opininion in Psychology, 17***,** 151–155.

Fridlund, A. & Cacioppo, J. T. (1986). Guidelines for Human Electromyographic Research. *Psychophysiology*, *23***,** 567–589.

Frijda, N. H. *The emotions (Studies in emotion and social interaction)*. (Cambridge University Press, 1987).

Flom, R. & Bahrick, L. E. (2007). The development of infant discrimination of affect in multimodal and unimodal stimulation : The role of intersensory redundancy.

Developmental Psychology, *43*, 238–252.

Geangu, E. (2015). Development of empathy during early childhood across cultures. In J. D. Wright (Ed.), *International Encyclopedia of the Social and Behavioral Sciences* (pp. 549–553). Elsevier.

Geangu, E., Hauf, P., Bhardwaj, R. & Bentz, W. (2011). Infant pupil diameter changes in response to others' positive and negative emotions. *PLoS One*, *6*, e27132.

Geangu, E., Quadrelli, E., Conte, S., Croci, E. & Turati, C. (2016). Three-year-olds' rapid facial electromyographic responses to emotional facial expressions and body postures. *Journal of Experimental Child Psychology, 144*, 1–14.

Gredebäck, G., Eriksson, M., Schmitow, C., Laeng, B. & Stenberg, G. (2012). Individual differences in face processing: Infants' scanning patterns and pupil dilations are influenced by the distribution of parental leave. *Infancy*, *17*, 79–101.

Grèzes, J. & Dezecache, G. (2014). How do shared-representations and emotional processes cooperate in response to social threat signals ?. *Neuropsychologia, 55*, 1–10.

Grèzes, J., Philip, L., Chadwick, M., Dezecache, G., Soussignan, R., & Conty, L. (2013). Self-relevance appraisal influences facial reactions to emotional body expressions. *PloS one*, *8*(2), e55885.

Grossmann, T. (2010). The development of emotion perception in face and voice during infancy. *Restorative Neurology and Neuroscience, 28*(2)**,** 219–236.

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

Hamilton, A. (2015). The social function of the human mirror system: a motor chauvinist view. In S. S. Obhi & E. S. Cross (Eds.), *Shared Representations: Sensoriomotor foundations of social life*. Cambridge University Press.

Hatfield, E., Cacioppo, J. T. & Rapson, R. L. (1993). Emotional contagion. *Current Directions in Psychological Sciences, 2*, 96–100.

Hatfield, E., Cacioppo, J. T., & Rapson, R. L. (1994). *Emotional contagion*: Cambridge studies in emotion and social interaction. Cambridge, UK: Cambridge University Press.

Haviland, J. M. & Lelwica, M. (1987).The induced affect response: 10-week-old infants' responses to three emotion expressions. *Developmental Psychology, 23*, 97–104.

Hennenlotter, A., Dresel, C., Castrop, F., Ceballos-Baumann, A. O., Wohlschläger, A. M., & Haslinger, B. (2008). The link between facial feedback and neural activity within central circuitries of emotion—New insights from Botulinum toxin–induced denervation of frown muscles. *Cerebral Cortex*, *19*(3), 537-542.

Hess, U., Adams Jr, R., & Kleck, R. (2005). Who may frown and who should smile? Dominance, affiliation, and the display of happiness and anger. *Cognition & Emotion*, *19*(4), 515-536.

Hess, U., Arslan, R., Mauersberger, H., Blaison, C., Dufner, M., Denissen, J. J., & Ziegler, M. (2017). Reliability of surface facial electromyography. *Psychophysiology*, *54*(1), 12-23.

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.

Hess, U., & Fischer, A. (2013). Emotional mimicry as social regulation. *Personality and Social Psychology Review*, *17*(2), 142-157.

Hess, U., Philippot, P., & Blairy, S. (1998). Facial reactions to emotional facial expressions: affect or cognition?. *Cognition & Emotion*, *12*(4), 509-531.

Heyes, C. (2011). Automatic imitation. *Psychological bulletin*, *137*(3), 463.

Hietanen, J. K., Surakka, V. & Linnankoski, I. (1998). Facial electromyographic responses to vocal affect expressions. *Psychophysiology*, *35*, 530–536.

Hoehl, S. (2014). Emotion processing in infancy. In K. H. Lagattuta (Ed.), *Children and Emotion. New Insights into Developmental Affective Sciences* (pp. 1–12).

Hoehl, S., Reid, V., Mooney, J. & Striano, T. (2008). What are you looking at ? Infants' neural processing of an adult' s object-directed eye gaze. *Developmental Science. 11*, 10–16.

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

Hoffman, K. L., Gothard, K. M., Schmid, M. C. & Logothetis, N. K. (2007). Facial-expression and gaze-selective responses in the monkey amygdala. *Current Biology*, *17*, 766–772.

Isomura, T., & Nakano, T. (2016, December). Automatic facial mimicry in response to dynamic emotional stimuli in five-month-old infants. In *Proc. R. Soc. B*, 283(1844).

Izard, C. E., Fantauzzo, C. A., Castle, J. M., Haynes, O. M., Rayias, M. F., & Putnam, P. H. (1995). The ontogeny and significance of infants' facial expressions in the first 9 months of life. *Developmental Psychology*, *31*(6), 997.

Jessen, S., Altvater-Mackensen, N. & Grossmann, T. (2016). Pupillary responses reveal infants' discrimination of facial emotions independent of conscious perception. *Cognition, 150*, 163–169.

Johnson, M. H. (2011). Interactive Specialization: A domain-general framework for human functional brain development? *Developmental. Cognitive Neuroscience*, *1*, 7–21.

Kaitz, M., Meschulach-sarfaty, O., Auerbach, J. & Eidelman, A. (1988).A Reexamination of Newborns' Ability to Imitate Facial Expressions. *Developmental. Psychology*, *24*, 3–7.

Kanade, T., Cohn, J. F., & Tian, Y. (2000). Comprehensive database for facial expression analysis. In *Automatic Face and Gesture Recognition, 2000. Proceedings. Fourth IEEE International Conference on* (pp. 46-53). IEEE.

Karmiloff-Smith, A. (1998). Development itself is the key to understanding developmental disorders. *Trends in Cognitive Sciences*, *2*, 389–98.

Kilner, J. M., Friston, K. J. & Frith, C. D. (2007). Predictive coding: an account of the mirror neuron system. *Cognitive Processing*, *8*(3), 159–166.

Koelsch, S., Jacobs, A. M., Menninghaus, W., Liebal, K., Klann-Delius, G., von Scheve, C., & Gebauer, G. (2015). The quartet theory of human emotions: an integrative and neurofunctional model. *Physics of life reviews*, *13*, 1-27.

Laird, J. D., Cuniff, M., Sheehan, K., Shulman, D., & Strum, G. (1989). Emotion specific effects of facial expressions on memory for life events. *Journal of Social Behavior and Personality*, *4*(2), 97.

Lanzetta, J. T. & Englis, B. G. (1989). Expectations of Cooperation and Competition and Their Effects on Observers' Vicarious Emotional Responses. *Journal of Personality and Social Psychology*,*56*, 543–554.

Ledoux, J. E. (1995). Emotion: Clues from the Brain. *Annual Review of Psychology*, *46*, 209–235.

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

Leppänen, J. M. & Nelson, C. A. (2012). Early Development of Fear Processing. *Current Directions in Psychological Science*, *21*, 200–204.

Lewis, M. & Ramsay, D. (2005). Infant Emotional and Cortisol Responses to Goal Blockage. *Child Dev.*, *76*, 518–530.

Lewis, M., Ramsay, D. S. & Sullivan, M. W. (2006). The Relation of ANS and HPA Activation to Infant Anger and Sadness Response to Goal Blockage. *Developmental Psychobiology*, *48*(5), 397–405

Likowski, K. U., Muhlberger, A., Seibt, B., Pauli, P. & Weyers, P. (2011). Processes Underlying Congruent and Incongruent Facial Reactions to Emotional Facial Expressions. *Emotion*, *11*, 457–467.

Lloyd-Fox, S., Begus, K., Halliday, D., Pirazzoli, L., Blasi, A., Papademetriou, M., ... & Elwell, C. E. (2017). Cortical specialisation to social stimuli from the first days to the second year of life: A rural Gambian cohort. *Developmental cognitive neuroscience*, *25*, 92-104.

Lockwood, P. L., Bird, G., Bridge, M. & Viding, E. (2013). Dissecting empathy: high levels of psychopathic and autistic traits are characterized by difficulties in different social information processing domains. *Front. Hum. Neurosci.*, *7*, 1–6.

Lucey, P., Cohn, J. F., Kanade, T., Saragih, J., Ambadar, Z., & Matthews, I. (2010, June). The extended cohn-kanade dataset (ck+): A complete dataset for action unit and emotion-specified expression. In *Computer Vision and Pattern Recognition Workshops (CVPRW), 2010 IEEE Computer Society Conference on* (pp. 94-101). IEEE.

Magnée, M. J. C. M., de Gelder, B., van Engeland, H. & Kemner, C. (2007). Facial electromyographic responses to emotional information from faces and voices in individuals with pervasive developmental disorder. *J. Child Psychol. Psychiatry.*, *48*, 1122–30.

Magnée, M. J. C. M., Stekelenburg, J. J., Kemner, C. & Gelder, B. De. (2007). Similar facial electromyographic responses to faces, voices, and body expressions. *Neuroreport*, *18*, 69–72.

Malatesta, Z. C., Grigoryev, P., Lamb, C., Albin, M. & Culver, C. (1986). Emotion Socialization and Expressive Development in Preterm and Full-Term Infants. *Child Development*, *57*, 316–330.

Mattson, W. I., Ekas, N. V., Lambert, B., Tronick, E., Lester, B. M., & Messinger, D. S. (2013). Emotional expression and heart rate in high-risk infants during the face-to-face/still-face. *Infant Behavior and Development*, *36*(4), 776-785.

Messinger, D. S. (2002). Positive and Negative: Infant Facial Expressions and Emotions. *Current Directions in Psychological. Science*, *11*, 1–6.

Messinger, D. & Fogel, A. (2007).The Interactive Development Of Social Smiling. *Adv. Child Dev. Behav.*, *35*, 327–366.

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.

Moody, E. J., McIntosh, D. N., Mann, L. J., & Weisser, K. R. (2007). More than mere mimicry? The influence of emotion on rapid facial reactions to faces. *Emotion*, *7*(2), 447-457.

Natale, E., Senna, I., Bolognini, N., Quadrelli, E., Addabbo, M., Cassia, V. M., & Turati, C. (2014). Predicting others' intention involves motor resonance: EMG evidence from 6-and 9-month-old infants. *Developmental cognitive neuroscience*, *7*, 23-29.

Nava, E., Romano, D., Grassi, M. & Turati, C. (2016). Skin conductance reveals the early development of the unconscious processing of emotions. *CORTEX, 84*, 124–

131.

Oberman, L. M., Winkielman, P. & Ramachandran, V. S. (2009). Slow echo: facial EMG evidence for the delay of spontaneous, but not voluntary, emotional mimicry in children with autism spectrum disorders. *Developmental Science*, *12*, 510–20.

Oliveri, M., Babiloni, C., Filippi, M. M., Caltagirone, C., Babiloni, F., Cicinelli, P., ... & Rossini, P. M. (2003). Influence of the supplementary motor area on primary motor cortex excitability during movements triggered by neutral or emotionally unpleasant visual cues. *Experimental brain research*, *149*(2), 214-221.

Oostenbroek, J., Suddendorf, T., Nielsen, M., Redshaw, J., Kennedy-Costantini, S., Davis, J., ... & Slaughter, V. (2016). Comprehensive longitudinal study challenges the existence of neonatal imitation in humans. *Current Biology*, *26*(10), 1334-1338.

Pessoa, L. (2008). On the relationship between emotion and cognition. *Nature Reviews Neuroscience*, *9,* 148–158.

Pessoa, L. (2017). Opinion a network model of the emotional brain. *Trends in Cognitve Science*, *21*, 357–371.

Pfeifer, J. H., Iacoboni, M., Mazziotta, J. C. & Dapretto, M. (2008). Mirroring others' emotions relates to empathy and interpersonal competence in children. *Neuroimage, 39*, 1–20.

Rychlowska, M., Zinner, L., Musca, S. C. & Niedenthal, P. M. (2012). From the eye to the heart: Eye contact triggers emotion simulation. In *Proceedings of the 4th Workshop on Eye Gaze in Intelligent Human Machine Interaction* 5.

Rymarczyk, K., Biele, C., Grabowska, A. & Majczynski, H. (2011). EMG activity in response to static and dynamic facial expressions. *International Journal of Psychophysiology, 79*, 330–333.

Sander, D., Grafman, J. & Zalla, T. (2003). The human amygdala: an evolved system for relevance detection. *Reviews in the Neuroscience*, *14(4)*, 303–316.

Sato, W. & Yoshikawa, S. (2007). Spontaneous facial mimicry in response to dynamic facial expressions. *Cognition*, *104*, 1–18.

Schutter, D. J. L. G., Hofman, D. & Honk, J. V. A. N. (2008). Fearful faces selectively increase corticospinal motor tract excitability: A transcranial magnetic stimulation study. *Psychophysiology*, *45*, 345–348..

Schrammel, F., Pannasch, S., Graupner, S.-T., Mojzisch, A. & Velichkovsky, B. M. (2009).Virtual friend or threat? The effects of facial expression and gaze interaction on psychophysiological responses and emotional experience. *Psychophysiology*, *46*, 922–931.

Seibt, B., Mühlberger, A., Likowski, K. U. & Weyers, P. (2015). Facial mimicry in its social setting. *Frontiers in Psychology, 6*, 1–21.

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

Sirois, S., Spratling, M., Thomas, M. S., Westermann, G., Mareschal, D., & Johnson, M. H. (2008). Précis of Neuroconstructivism: How the brain constructs cognition. *Behavioral and Brain Sciences*, *31*(3), 321-331.

Soussignan, R., Chadwick, M., Philip, L., Conty, L., Dezecache, G., & Grèzes, J. (2013). Self-relevance appraisal of gaze direction and dynamic facial expressions: effects on facial electromyographic and autonomic reactions. *Emotion*, *13*(2), 330.

Soussignan, R. (2002). Duchenne Smile, Emotional Experience, and Autonomic Reactivity. A Test of the Facial Feedback Hypothesis Duchenne Smile, Emotional Experience, and Autonomic Reactivity: A Test of the Facial Feedback Hypothesis. *Emotion, 2*, 52–74.

Striano, T. & Rochat, P. (2000). Emergence of Selective Social Referencing in Infancy. *Infancy*, *1*, 253–264.

Striano, T. & Vaish, A. (2006). Seven- to 9-month-old infants use facial expressions to interpret others' actions. *British Journal of Deelopmental. Psychology*, *24*(4), 753–760.

Tamietto, M., & de Gelder, B.. (2008). Emotional Contagion for Unseen Bodily Expressions : Evidence from Facial EMG. *2008 8th IEEE Int. Conf. Autom. Face Gesture Recognit.* 1–5.

Tassinary, L. G. & Cacioppo, J. T. (1992). Unobservable facial actions and emotion. *Psychological Science*, *3*, 28–33.

Turati, C., Natale, E., Bolognini, N., Senna, I., Picozzi, M., Longhi, E., & Cassia, V. M. (2013). The early development of human mirror mechanisms: evidence from electromyographic recordings at 3 and 6 months. *Developmental science*, *16*(6), 793-800.

Vaillant‐Molina, M., Bahrick, L. E., & Flom, R. (2013). Young infants match facial and vocal emotional expressions of other infants. *Infancy*, *18*(s1).

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

Vuilleumier, P., Richardson, M. P., Armony, J. L., Driver, J., & Dolan, R. J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature neuroscience*, *7*(11), 1271.

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

Weyers, P., Mühlberger, A., Hefele, C., & Pauli, P. (2006). Electromyographic responses to static and dynamic avatar emotional facial expressions. *Psychophysiology*, *43*(5), 450-453.

Infants' Neural Responses during a Non-verbal False Belief Task. An Event-Related Potential Study.

Maria M. Crespo-Llado and Elena Geangu

Lancaster University

Author Note

A version of this paper is under review:
Crespo-Llado, M.M., & Geangu, E. (under review). Infants' Neural Responses during a Non-verbal False Belief Task. An Event-Related Potential. *Scientific Reports.*

Abstract

Recent studies using non-verbal versions of traditional false belief tasks suggest that infants around the age of 15-18 months can already attend to others' beliefs in order to make sense of their behavior. However, there is still restricted understanding of the neurocognitive processes underlying infants' performance in these tasks and their relation to those reported in older children and adults. Our study aimed to explore the neural correlates underlying infant's false belief (FB) processing during a passive paradigm by analysing event-related potentials (ERPs). Using an adapted version of the task described by Geangu et al., (2013), 15-months-old infants were presented with sequences of images depicting a character acting congruently (FB Congruent) or incongruently (FB Incongruent) to her false belief about an object's location, while EEG was continuously recorded. ERPs analysis revealed differences between conditions at frontal leads, as indexed by modulations in the N400 component. A more negative N400 waveform was recorded for belief incongruent as compared to belief congruent trials. The sensitivity of the N400 to action sequences that were incongruent with a narrative context evocative of people's beliefs about an object location suggests that 15-monht-old infants are able to track simple forms of others' mental states embedded in goal-directed actions.

Introduction

Interacting with other people is central to our lives. Recognizing and understanding that other people's behavior is driven by their mental states, like intentions, desires, emotions and beliefs, helps us to predict their behaviors and to collaboratively perform complex actions (Kuhn-Popp, Sodian, Sommer, Dohnel, & Meinhardt, 2013; Sodian, 2011; Wellman, 2011). An essential milestone in the development of these abilities is to understand that people build representations of reality, which are more or less accurate, similar or dissimilar to our own (Flavell, 1988; Luo, 2011; Rakoczy, 2012; Wellman & Bartsch, 1988). Classically, it was thought that this ability first emerges around the age of 4 years, when children can make judgements about people's false beliefs (FB) about reality and predict their behavior accordingly (Baron-Cohen, Leslie, & Frith, 1985; Flavell, 1988; Perner, 1991; Wellman, Cross, & Watson, 2001; Wellman et al., 1988; Wimmer & Perner, 1983). This evidence comes primarily from behavioral studies with pre-schoolers using standard false-belief tasks, where children are explicitly asked to reason about an agent's perception or beliefs about different aspects of reality (e.g., Wimmer & Perner, 1983; Baron-Cohen, Leslie & Frith, 1985; Wellman & Bartsch, 1988). However, more recent studies using spontaneous-response passive tasks suggest that computations about others' beliefs may be already present in infancy (Kovacs, Teglas, & Endress, 2010; Onishi & Baillargeon, 2005; Scott & Baillargeon, 2009; Song & Baillargeon, 2008; Song, Onishi, Baillargeon, & Fisher, 2008; Southgate, Senju, & Csibra, 2007; Surian, Caldi, & Sperber, 2007; Träuble, Marinović, & Pauen, 2010). Also, neuroscientific investigations point to a protracted development of belief understanding which extends well beyond the age of 4-years, reaching more mature levels of performance only towards the end of adolescence (Apperly & Butterfill, 2009; Blakemore, 2008, 2012; Chandler & Lalonde, 1996; Gweon, Dodell-Feder, Bedny, & Saxe, 2012; Johnson, 2001; Kobayashi, Glover, & Temple, 2007; Saxe, Whitfield-Gabrieli, Scholz, & Pelphrey, 2009). The present study sought to extend the knowledge about belief processing development by investigating the infant's neural responses during a passive non-verbal FB task by using event-related potentials (ERPs).

In their now well know study, Onishi and Baillargeon (2005) proposed for the first time that 15-month-old infants may present at least some incipient abilities for belief computations. Closely following the sequence of events in the classic false belief task (Wellman et al., 2001; Wimmer & Perner, 1983), in this study, infants saw a character placing an object in one of two containers. In the following sequences, the object emerges from the container where it was initially placed and moves into the second one. The character is either absent or present during the location change event, making their beliefs about reality either true (TB) or false (FB). During the test trials, infants see the character reaching in one of the two containers. The fact that infants in the TB condition looked longer when the character reached for the object in the initial location, while infants in the FB condition looked longer during the search in the final location, was interpreted as suggesting that infants make some computations about others' beliefs. Since this initial report, several other studies using similar paradigms have suggested that infants are not only sensitive to beliefs about objects' locations, but also about objects' identity, content, number, and perceptual properties (He & Baillargeon, 2007; Scott & Bailargeon, 2009; Scott, Song, Baillargeon, & Leslie, 2007; Song & Baillargeon, 2008; Song et al., 2008). Also, it has been proposed that infants integrate information about the means through which others form these representations (i.e., either through seeing or touching, Träuble et al., 2010) and that representing others' beliefs is similar to and interacts with infants' own representations of reality (Kovacs et al., 2010). Such processes seemingly influence infants' behavior in relation to other people or to the physical environment. For example, 17-month-olds reach for an object disregarding adults' ostensive cues, if the previous events suggest this person has false beliefs about the object's location (Southgate, Johnson, El Kariou, & Csibra, 2010).

To date, multiple behavioral studies suggest that from around the age of 18-months, infants also seem to be able to anticipate others' behavior based on the succession of events suggestive of their false beliefs (Southgate et al., 2007; Thoermer, Sodian, Vuori, Perst, & Kristen, 2012; Zmyj, Prinz, & Daum, 2015), which is more cognitively demanding than post-hoc evaluations of the congruency between actions and beliefs (Daum, Attig, Gunawan, Prinz, & Gredebäck, 2012;

Gredebäck, Melinder, & Daum, 2010; Verschoor, Spapé, Biro, & Hommel, 2013). Eighteen-months-olds' ability to anticipate a character's behavior based on his/her false beliefs was found to significantly predict their performance in a classic verbal false-belief reasoning at the age of 48-months (Thoermer et al., 2012). These findings provide further support for the relevance of the passive non-verbal false belief tasks in the study of the early ontogeny of the ability to infer mental states to others. Nevertheless, we still have only limited understanding of the neurocognitive processes underlying infants' performance in the passive non-verbal tasks and how they relate to those reported in older children and adults. Further knowledge of such neurocognitive processes would also bear relevance for the open theoretical debates regarding the relation between implicit and explicit inferences about others' mental states. While some authors still question whether implicit tasks reflect mentalizing processes (Heyes, 2014), others propose the presence of two distinct systems (He & Baillargeon, 2007): an implicit one which emerges early in life and operates automatically, making the processing faster and more efficient; and an explicit system that develops later and operates in a more top-down manner, leading to a slower but more deliberate processing. Finally, others have postulated the presence of a single system, which depending on the contextual demands, operates either automatically or in a more controlled way (Carruthers, 2016).

Measurements of the electrical brain activity recorded at the level of the scalp (e.g., electroencephalography – EEG, and ERPs) have proven useful in investigating the perceptual and cognitive processes involved in the social functioning of both developing and adult populations (de Haan, 2007; Luck, 2005). The crucial advantage of ERPs is the high temporal resolution, providing precise information about the chronometry of given neural responses and the associated perceptual and cognitive processes. Together with the fact that they can be used across the entire lifespan, the use of ERPs provides opportunities to tracking cognitive development from birth until adulthood (de Haan, 2007; Reid & Geangu, 2008).

ERPs have been successfully used in investigating both implicit and explicit mental state processing in adults with several components showing sensitivity to inferences about others' mental states (Ferguson, Cane, Douchkov, & Wright, 2015; Geangu, Gibson, Kaduk, & Reid, 2013; Kovacs, Kühn, Gergely, Csibra, & Brass, 2014; Liu, Meltzoff, & Wellman, 2009; Liu, Sabbagh, Gehring, & Wellman, 2004, 2009; Meinhardt, Kuhn-Popp, Sommer, & Sodian, 2012; Meinhardt, Sodian, Thoermer, Dohnel, & Sommer, 2011; Sabbagh, Moulson, & Harkness, 2004; Sabbagh & Taylor, 2000; Sommer et al., 2007). A negative ERP component recorded at frontal scalp regions, usually between 200 and 500 ms after stimulus onset (N400) was found to be modulated by whether adults judge others' mental states versus physical features (Sabbagh et al., 2004) and whether adults judge action outcomes based on the agents' beliefs or based on reality and photographs of reality (Ferguson et al., 2015; Sabbagh & Taylor, 2000). Within roughly the same time window, a positive component (LPC, 300-600 ms) recorded particularly at parietal regions of the scalp was found to show increased amplitude for belief versus reality reasoning and for FB compared to TB reasoning (Meinhardt et al., 2011; Sabbagh et al., 2000). These two components seem to have different sources of activation, with the frontal N400 being mainly generated by the orbitofrontal cortex and medial temporal lobes, while the LPC being related to the activity of the parietal cortex (Sabbagh et al., 2004) and temporal-parietal junction (TPJ; Kovacs et al., 2014; Kobayashi et al., 2007; Sommer et al., 2007). Differentiations in the brain waves slowly developing after 600 ms from stimulus onset at both parietal and frontal locations have also been reported to differentiate between false and true representations of reality (Geangu et al., 2013; Meinhardt et al., 2011) between mental and non-mental representations of reality (Liu et al., 2004; Liu, Meltzoff et al., 2009; Sabbagh et al., 2000) and between pretense and false belief reasoning (Meinhardt et al., 2012). These late slow waves (LSWs) are considered to index the decoupling between representations of and the real state of affairs, which is important for understanding FB (Geangu et al., 2013; Liu et al., 2004; Liu, Meltzoff et al., 2009; Liu, Sabbagh, et al., 2009; Meinhardt et al., 2011; Meinhardt et al., 2012; Sabbagh et al., 2000; Rösler & Heil, 1991).

The investigations on FB processing in children older than 4-years reveal similar ERP responses to the adult ones, although with some marked differences. Children ERP responses tend to be delayed, have greater duration and smaller amplitude, and may even be inverted in polarity and present different scalp distributions (Liu, Sabbagh et al., 2009; Meinhardt et al., 2011). These ERP differences are echoed by the results in functional magnetic brain imaging. When reasoning about others beliefs, children engage areas of the prefrontal cortex and the posterior cingulate, which are relevant for monitoring and regulating behavior (Amodio & Frith, 2006; Kobayashi et al., 2007; Sommer et al., 2010) to a larger extent than adults. Also, the TPJ shows an increasing selective activation with age in response to mental state information, correlating with children's performance on ToM tasks outside the scanner (Gweon et al., 2012; Saxe et al., 2009; Sommer et al., 2010). Taken together, these studies suggest that the neurocognitive processes involved in mentalizing may show some differences during childhood, and that they continue to develop long after children pass the classic behavioral FB tasks (Dumontheil, Apperly, & Blakemore, 2010; Gweon et al., 2012; Sommer et al., 2010). It is thus reasonable to enquire whether ERPs can shed some light into the neurocognitive processes underlying infants' responses to non-verbal FB tasks.

To this aim we used a passive non-verbal content transfer FB task closely derived from previous behavioral studies (e.g., Onishi & Bailargeon, 2005, as described above) and previously used with adult population (Geangu et al., 2013). Specifically, in order to differentiate between ERP responses driven by reality processing and those driven by false belief processing, we employed a match-mismatch paradigm with two FB conditions: the FB congruent condition (FBc - the character's behavior in the last scene is congruent with her belief about reality but incongruent with the current location of the object she reaches for) and the FB incongruent condition (FBi - the character's reach behavior in the last scene is congruent with the current location of the object even though she was unaware of the change in location). We were interested in finding out the extent to which the infants' brain responses are sensitive to such incongruences between the agent's actions and the visual narrative context suggestive of her false beliefs by analysing the effects on the N400 component. Outside the belief-processing domain, this component has been related to processing of semantic information (see Kutas & Federmeier, 2000, 2011, for reviews), both linguistic (Camblin, Ledoux, Boudewyn, Gordon, & Swaab, 2007; Holcomb, 1993; Kutas & Hillyard, 1980, 1984; van Berkum, Hagoort, & Brown, 1999) and related to human actions (Bach, Gunter, Knoblich, Prinz, & Friederici, 2009; Gunter & Bach, 2004; Pace, Carver, & Friend, 2013; Proverbio & Riva, 2009; Reid, Hoehl, & Striano, 2009; Shibata, Gyoba, & Suzuki, 2009). Higher amplitudes of the N400 are reported in response to linguistic and action stimuli which are semantically incongruent within a specific context compared to the congruent ones (Bach et al., 2009; Camblin et al., 2007; Gunter & Bach, 2004; Holcomb, 1993; Kutas & Hillyard, 1980, 1984; Pace et al., 2013; Proverbio & Riva, 2009; Reid et al., 2009; Shibata et., 2009; van Berkum et al., 1999). When visual stimuli are presented, such as those depicting human behavior, N400 is usually reported over anterior scalp locations (Friedrich & Friederici, 2004; Ganis, Kutas, & Sereno, 1996; McPherson & Holcomb, 1999; Proverbio, Crotti, Manfredi, Adorni, & Zani, 2012; Sheehan, Namy, & Mills, 2007; Sitnikova, Holcomb, Kiyonaga, & Kuperberg, 2008; West & Holcomb, 2002). In infants and toddlers, N400 was recorded both in response to linguistic and human action stimuli (Friedrich & Friederici, 2004; Ganis et al., 1996; Pace et al., 2013; Reid et al., 2009; Sheehan et al., 2007). We thus anticipate that if 15-month-old infants in our study process the character's actions as being related to her knowledge about object location rather their own knowledge about reality, then an increased N400 will be recorded during the last scene of the FBi compared to the FBc condition. Alternatively, if infants are more likely to process the character's actions in relation to the current reality, we expect a more negative anterior N400 to be elicited by the FBc rather than the FBi condition. Given that the stimuli included in our study are visual, in light of previous studies with both infants and adults (Friedrich & Friederici, 2004; Ganis et al., 1996; McPherson & Holcomb, 1999; Pace et al., 2013; Proverbio et al., 2012; Reid et al., 2009; Sheehan et al., 2007; Sitnikova et al., 2008; West & Holcomb, 2002), we expect to record this effect at anterior scalp locations.

Methods

Participants

Sixteen 15-month-old infants (8 girls, *M* = 470.81 days, *SD* = 6.872 days) were included in the final analysis. All participants were recruited from a small urban area in North West England. Additional 10 infants were tested, but excluded from the final analysis due inattentiveness and excessive movement resulting in less than 9 trials per condition which were both artifact free and observed. This attrition rate is similar to previous belief processing ERP studies with developing populations (Bowman, Liu, Meltzoff, & Wellman, 2012) and ERP investigations in other domains involving this age group (Hoehl & Wahl, 2012). Informed consent was obtained from all parents prior to the beginning of the procedure. Ethical approval was granted by the University Ethics Committee.

Stimuli

Using an adapted version of the visual stimuli from Geangu *et al.* (2013), infants were presented with images depicting sequences of events in which a female agent acts congruently or incongruently to her false belief (FB) about an object location (Figure 3). Across a total of 12 images, the character first reaches towards an object, then places it in one of the two boxes located to the left and right in front of her. In the next step, a black board is raised, occluding the character's view of the scene. While the character's view of the scene is occluded, the object leaves the box and, after reaching the middle of the table, moves to the other box, creating a FB condition. The last images show the occluding board being removed and the character either reaching inside the box where she has initially placed the object (FBc – false belief congruent) or reaching inside the box where the object currently is (FBi – false belief incongruent). In order to make the task interesting for the infants, the character manipulates the location of three objects (i.e., a banana, an orange, and a green pepper), which were presented alternatively across trials. The colour (i.e., red or blue) and the position (i.e., left or right) of the boxes remained constant across trials. The box in which the agent first placed the object was counterbalanced across trials. The presentation of the entire sequence of images lasted 5s. The first 10 images were presented for 350 ms each, while duration of the final image was 1000 ms. Before the last image, a 500 ms fixation cross was presented to allow correction for baseline during the EEG analysis.

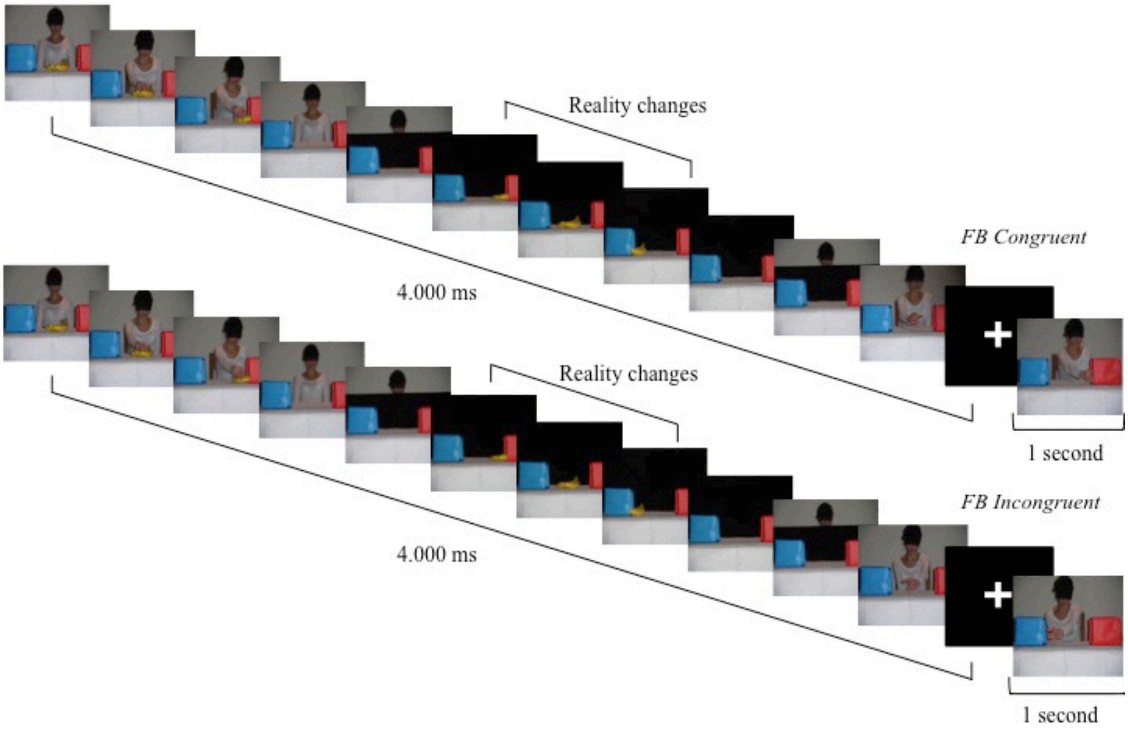


Figure 3. Illustration of the sequence of images seen by the infants during the task: (A) false belief congruent - FBc; and (B) false belief incongruent - FBi.

Procedure

Participants were tested individually in a quiet and dim lit room. Infants were seated on their mother's lap, approximately 70 cm away from a 17-inch monitor. Parents were instructed to hold their infants as still as possible to reduce artefacts in the data due to motion, not to speak to them, and not to point towards the screen during the entire stimuli presentation. The FB congruent and incongruent trials were presented in a randomized order with the constraint that the same condition did not occur three times consecutively. A trial consisted of the 12 images sequence lasting 5 seconds, followed by a fixation cross. The offset of the fixation cross was controlled by the experimenter, allowing for either the continuation of the stimulus presentation or for the display of a dynamic non-social attention grabber with the purpose of maintaining attention in case the infant became fussy or uninterested. The testing session ended when the infant's attention could no longer be attracted to the screen (FBc: *M* = 24 trials, *Min* = 18, *Max* = 32; FBi: *M* = 27 trials, *Min* = 21, *Max* = 34). The entire procedure was video recorded in order to establish whether the infants had watched all images within a trial and to facilitate artifact detection during the data analysis.

EEG Recording and Analysis

The electroencephalogram (EEG) was recorded continuously using a 128-electrode HydroCel Geodesic Sensor Net (Electrical Geodesic Inc., Eugene, OR) and amplified using an EGI NetAmps 300 amplifier. The signal was referenced online to the vertex electrode (Cz), a bandpass filter of .1 to 100Hz was applied, and the data were sampled at 500 Hz. Impedances were checked prior to the beginning of recording and considered acceptable if lower than 50KΩ. EEG data were further processed offline using NetStation v4.6.4 (Eugene, OR). The signal was band-pass filtered (0.3-30 Hz), and the ERP trials were segmented between 100 ms before and 1000 ms after the presentation of the last frame where the character reaches into the box where she initially had placed the object. Data were corrected to the average voltage during baseline and re-referenced to the algebraic mean of all channels. To eliminate artifacts, segmented data were automatically rejected whenever the signal exceeded ± 200 µV at any electrode. Data were further checked through visual inspection for eye-movements, eye-blinks and other body movement artifacts not detected by the automated algorithm. Trials were excluded if more than eighteen bad channels were detected. Of the remaining trials, individual bad channels were replaced using spherical spline interpolation. Individual subject averages were computed separately for each channel across all trials within each condition and then re-referenced to the average reference. Only those trials in which infants had looked at the full sequence of images (12 pictures) were included in the final analysis. This inclusion criteria was selected in order to avoid attentional confoundings during the interpretation of the results. Notably, this restrictive criteria is in line with previous children ERP studies on theory of mind using similar stimuli (Bowman et al., 2012; Kuhn-Popp et al., 2013; Liu et al., 2009). In order to ensure that the infants' neural reponses registered in this study were not driven by their mothers' reactions to the visual stimul, all trials included in the final analysis were further coded for child-directed interactions defined as all that instances where the mother 1) talked to the infant, 2) pointed to the screen, or 3) briefly established eye contact with the infant. As a result of this coding, an additional 12 trials (FB: 5 trials; TB: 7 trials) were removed due to parental interference. Across participants, the mean number of trials contributing to the average ERP was 13 per each condition (FBc: M = 12.5, SD = 2.805; FBi: M = 13.5, SD = 3.932). Individual ERP waveforms were created through averaging the segmented EEG data for each condition.

For the statistical analysis, in order to correct for chance capitalisation (i.e., correcting for the number of tests of significance being performed), we divided our average ERP/EEG data in intervals of 50 ms and tested for significance using a repeated measures ANOVA. Statistical analyses were performed on the mean amplitude for three clusters of electrodes: frontal (3, 4, 5, 10, 12, 18, 19, 20, 23, 24, 118, 124), central (7, 30, 31, 36, 37, 42, 80, 87, 93, 104, 105, 106), and parietal (52, 59, 60, 66, 67, 71,76, 77, 84, 85, 91, 92). Data was analysed with separated 2 (Condition: FBc, FBi) x 3 (Region: frontal, central, parietal) repeated measures ANOVAs on each 50 ms time windows. Based on this analysis, we only report results for those time windows composed by a minimum of three consecutive intervals of 50 ms with a significant Condition x Region interaction (see also Muller et al., 2016). On the basis of this information, and in consonance with prior work (Balconi & Caldiroli, 2011; Kuhn-Popp et al., 2013; McPherson & Holcomb, 1999; Meinhardt et al., 2011; Pace et al., 2013; Sheehan et al., 2007; Sitnikova et al., 2008; West & Holcomb, 2002), statistical analyses were performed in the aforementioned clusters of electrodes (at frontal, central, and parietal regions) within the time window 450-600 ms (N400).

Results

A repeated measures ANOVA with condition (FBc, FBi) and region (frontal, central, parietal) as within subject factors was conducted on the mean amplitude of the N400. Same repeated measures ANOVA was also calculated on the peak amplitude of the N400, where there was a clear peak. All ERP statistical tests were interpreted at .050 level of significance (two-tailed). No gender differences were found for the selected time window per condition neither on mean amplitude nor peak amplitude measures. Yet, the inclusion of gender lead to significant gender disparities on the N400 peak amplitude at frontal regions (p = .042), with females displaying a more negative peak than males (Females: M = -16.462 µV, SE = 2.056; Males: M = -10.533 µV, SE = 2.056). For further information see Appendix D. Additional statistical analyses conducted on the N400 component are provided in Appendix I and J. Figure 1 shows the grand-average of ERPs recorded at frontal, central and posterior sited in both conditions.

N400 (450-600 ms)

The analysis of the mean amplitude for this time window revealed a significant main effect of region, $F(2,30)$ = 46.483, p = .000, η^2 = .756. Overall, waveforms within this epoch were more negative-going at frontal (M = -8.802 µV ; SE = 1.359) and central (M = -7.351 µV ; SE = .980) locations than parietal (M = 11.638 µV ; SE = 1.802). Importantly, an interaction of Condition x Region was observed, $F(2,30)$ = 6.198, p = .006, η^2 = .292. Post-hoc pairwise comparisons showed that differences between conditions were significant in frontal areas (p = .001), with FBi trials eliciting a more negative N400 (M = -10.528 µV; SE = 1.318) compared to the FBc trials (M = -7.077 µV; SE = 1.525). There were no significant differences between conditions at either central (p > .610) or parietal regions (p > .092). The analysis of the peak amplitude for this time window resulted in similar effects. A more negative peak amplitude was recorded at frontal (M = -13.498 µV; SE = 1.600) and central areas (M = -11.279 µV; SE = 1.084) compared to the parietal areas (M = 6.068 µV; SE = 1.682), $F(2,30)$ = 41.533; p = .000; η^2 = .735. This main effect was further qualified by a significant interaction with condition, ($F(2,30)$ = 5.325; p = .010; η^2 = .262). Post-hoc pairwise comparisons revealed that FB incongruent trials elicited a more negative peak (M = -14.938 µV; SE = 1.525) than the FB congruent trials (M = -12.058 µV; SE = 1.807) at frontal locations (p = .010), but not at central (p = .405) or parietal regions of interest (p = .098).

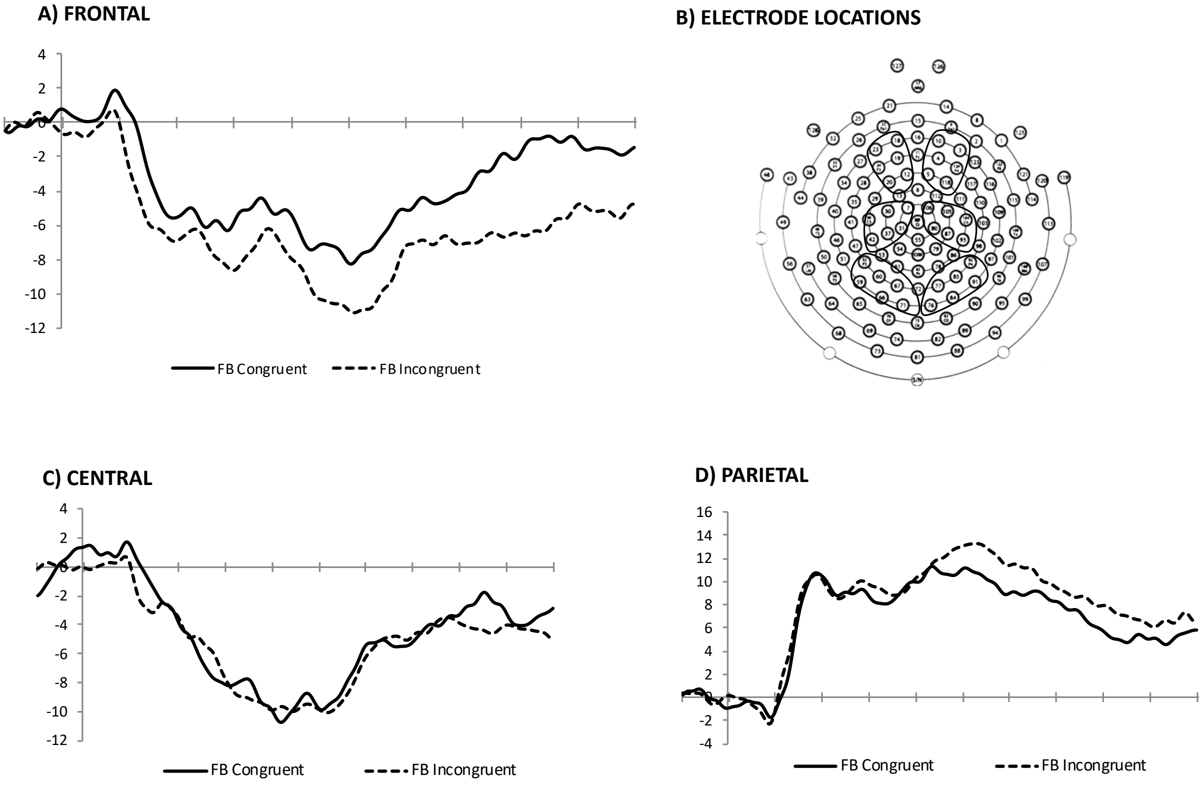


Figure 1. Grand average ERPs for the FBc and FBi conditions over frontal (A), central (C) and parietal locations (D). For the frontal areas, the electrodes included in the analysis were 3, 4, 5, 10, 12, 18, 19, 20, 23, 24, 118, 124 (B). For the central areas, the electrodes included in the analysis were 7, 30, 31, 36, 37, 42, 80, 87, 93, 104, 105, 106 while for the parietal areas the included channels were 52, 59, 60, 66, 67, 71, 76, 77, 84, 85, 91, 92 (B).

Discussion

Using a non-verbal ERP paradigm adapted from previous behavioral studies (Onishi & Bailargeon, 2005; Scott & Baillargeon, 2009; Song & Baillargeon, 2008; Träuble et al., 2010), 15-month-old infants were presented with visual narratives depicting a female adult acting congruently or incongruently with her false belief about the location of an object. Our results show that the N400 component recorded at frontal locations significantly differentiates between conditions. Watching someone searching for an object where it is currently located in the context of having the knowledge of it being somewhere else, elicited a more negative N400 compared to observing someone searching for an object where they previously placed it. This differentiation persists for most of the remaining duration of the stimulation, suggesting that 15-month-old infants engage in processing others' actions as related to their representations of reality.

Traditionally, the N400 has been shown to reflect the semantic integration in the linguistic context, where anomalous sentence endings elicit an increased negativity compared to the semantically congruent ones (Kutas & Hillyard, 1980a, 1980b). These increased negativities for semantically incongruent stimuli are thought to index the activation state of the input in semantic memory, which tends to be higher for the stimuli that violate the predictions formulated based on the preceding contextual information (Kutas & Federmeier, 2011). More recently, evidence has also accrued to show that larger N400s are evoked in both adults and infants by incongruous and/or unexpected images compared to the congruous ones in narratives presenting people and their behavior (e.g., Amoruso et al., 2013; Cohn & Kutas, 2015; Reid et al., 2008; Reid et al., 2009; Pace et al., 2013; Sitnikova, Kuperberg, & Holcomb, 2003). When these narratives are presented in images, the N400 tends to be more frontally distributed and to have shorter latencies (particularly for dynamic stimuli) compared to when the narratives are presented textually (Amoruso et al., 2013; Coch, Maron, Wolf, & Holcomb, 2002; Pace et al., 2013; Sitnikova et al. 2008). The N400 recorded in this type of paradigms tends to be preceded by an earlier negative component – N300 (Amoruso et al., 2013; Federmeier & Kutas, 2001; Hamm, Johnson, & Kirk, 2002; McPherson & Holcomb, 1999; West & Holcomb, 2002). ERP responses with morphology characteristic for the N400 have also been recorded in studies that investigate belief processing. For example, such responses are triggered while adults passively read or watch narratives describing characters who behave congruently or incongruently to their false beliefs about reality (Ferguson et al., 2015; Geangu et al., 2013) as well as when they actively engage in tasks that visually (e.g., Liu, Sabbagh et al., 2009) or audio-visually depict characters who behave incongruently with their representations of reality (e.g., Meinhardt et al., 2012). The increased negativity of the N400 for the events which are incongruent with the characters' representations of reality in these types of paradigms seems to be dependent on the individual's social competence (Ferguson et al., 2015) and perhaps the different type of processes involved in understanding others' actions as being related to their beliefs (Low, Apperly, Butterfill, & Rakoczy, 2016; Michael & Christensen, 2016). Interestingly, N400 with increased negativity has also been recorded when adults make explicit inferences about other's mental states based on eye expressivity compared to when they judge the sex of the person in the image (Sabbagh et al., 2004).

In line with these previous findings, 15-months-ols infants in our study showed a larger anterior N400 response for trials in which the agent's behavior is incongruent with her knowledge about object location (but congruent with the current reality and the participant's knowledge) compared to trials in which the observed behavior is congruent with the agent's knowledge (but incongruent with the current reality and the participants' knowledge). The N400 was preceded by an earlier negativity similar to the N300 previously reported in a variety of studies using this type of paradigm with pictorial stimuli illustrating human actions (Amoruso et al., 2013; Federmeier & Kutas, 2001; Hamm et al., 2002; McPherson & Holcomb, 1999; West & Holcomb, 2002). From a young age, infants are able to follow pictorial narratives depicting human agents in action. Certainly, by the age of 9-months infants seem to be able to encode and access the information provided through such narratives which is reflected in N400 variability to violations in goal directed action sequences (Reid et al., 2009). Our study shows that by the age of 15-months, infants are able to track the relation between human agent's actions and the present objects across a succession of events, and that they are able to detect inconsistencies between the final action and the semantic context indicative of the character's perspective of reality. The differentiation between false belief congruent and false belief incongruent trials at the level of the N400 suggests that the previously reported behavioral findings (Onishi & Bailargeon, 2005; Scott & Bailargeon, 2009; Song & Bailargeon, 2008; Southgate et al., 2007; Surian et al., 2007; Träuble et al., 2010) are less likely to be reliant on pure perceptual processes, but rather on some form of belief representation that involves semantic memory (Michael & Christensen, 2016). The processes required by 15-month-old infants to establish the congruency between the character's final action and her view of the reality seem to be more effortful and to require more time than for adults, as reflected by the N400 larger amplitude and slightly delayed latency (Ferguson et al., 2015). Similar developmental differences have been reported for linguistic processing

(Friedrich & Friederici, 2004) and goal directed action understanding (Reid et al., 2009). The current findings add to the existent literature showing that infants' anticipations of others' actions in relation to their false beliefs about reality significantly predicts their performance in explicit false-belief tasks at the age of 4-years (Thoermer et al., 2012), by providing more specific information about the neurocognitive processes underlying these early abilities. Importantly, the study presented here supports the use of ERPs in investigating the link between the early indicators of belief processing and the later development of the ability to infer mental states to others. Due to their unique high temporal resolutions, ERPs provide valuable information about the chronology of the underlying neurocognitive processes which can complement the evidence regarding the related neural networks resulted from the use of methods with high spatial resolution, such as functional near-infrared spectroscopy (Lloyd-Fox, 2017).

One could argue that the N400 differences reported here are due to the perceptual differences between frame 3 and 12 in the FBi condition presenting different hand movements, without any need for understanding the preceding action events. If perceptual differences between the two conditions would drive the observed responses, one would expect to find differences between conditions at the level of the earlier ERP components, shown to reflect brain activity governed by perceptual processing (see Thierry, 2005, for a review). Nevertheless, the waveform morphology and the differentiation between conditions recorded in this study do not support such interpretation. Furthermore, a number of studies have shown that infants younger than 15-months are able to establish clear relations between a specific agent and his/her action goal (Buresh & Woodward, 2007; Kuhlmeier, Wynn, & Bloom, 2003), which persists across perceptual variations in the context, such as the location of the goal (Robson, Lee, Kuhlmeier, & Rutherford, 2014) or the paths and direction of the action involved (Biro & Leslie, 2007; Csibra, 2011; Luo, 2011) as long as the equifinality principles are respected. Also, by the end of the first year infants are able to detect goal changes (Biro & Leslie, 2007; Sodian & Thoermer, 2004) and track a person's attention towards an object in order to infer next actions (e.g., Onishi & Bailargeon, 2005; Southgate et al., 2007). Therefore, there is clear evidence that by the age of

15-months infants have the ability to formulate expectations about other people's actions, which can support further inferences about their mental states.

Different engagement of attentional processes could also potentially drive the observed responses. In particular, previous studies have argued that the frontal N400 can also reflect the influence of attentional components like the Nc when the stimuli depict actions with different degree of saliency for infants (e.g., feeding vs. non-feeding; Reid et al., 2009). The strength of our study is that the stimuli in both conditions are equally salient, thus unlikely to elicit differences in attention allocation due to this property. Modulations in attention have been reported when infants process human hand grasps oriented congruently or incongruently with respect to the previous location of an object. Nevertheless, the ERP component reflecting such differences is a posterior P400 (Bakker et al., 2014), which in our study does not differentiate between conditions. This could be due to the fact that the direction of the grasp is present and processed earlier in the sequence of events included in our stimuli, prior to the one we analysed. The gradual completion of an action is the norm in ecological situations, potentially engaging attention to a different extent while observing its earlier stages rather than the later ones. Thus, the presentation of more ecologic information about the gradual completion of an action can represent an advantage in studying infant complex processing of others' behaviors in relation to their representations of reality, and should not be omitted.

Different theoretical accounts have been proposed for how humans mindread others and how this ability develops. While some fall closer to the extremes of the deflationary (Perner & Ruffman, 2005; Ruffman, 2014) and the nativist (Kovacs et al., 2010; Baillargeon et al., 2010; Leslie, 2005) views, others try to provide a reconciliatory approach, which takes into account the rich and predominantly behavioral empirical evidence (Apperly & Butterfill, 2009; Low et al., 2016; Michael et al., 2016). With respect to these theoretical accounts, the present findings with 15-monts-old infants seem to support the presence of some basic form of mentalistic processing (as opposed to a mere physical processing). The sensitivity of the 15-month-old N400 to action sequences which are congruent or incongruent with a narrative context suggestive of people's beliefs about the reality indicates that deeper meaning processing is already present at this age. Although infants probably do not represent beliefs in the same way that older children and adults do, our results seem to support the view that their processing of others' belief-based actions involves access to more generalized semantic memory which probably supports the later emergence of more sophisticated forms of belief representations (Michael et al., 2016). Beyond providing substantive data, we also provide a platform for future research of the early development of mentalizing as ERP paradigms are affordable to use throughout ontogeny.

References

Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: the medial frontal cortex and social cognition. *Nature Reviews Neuroscience, 7*(4), 268-277.

Amoruso, L., Gelormini, C., Aboitiz, F., Gonzalez, M.A., Manes, F., Cardona, J.F., & Ibanez, A. (2013). N400 ERPs for actions: building meaning in context. *Frontiers in Human Neuroscience, 7*, 57.

Apperly, I. A., & Butterfill, S. A. (2009). Do Humans Have Two Systems to Track Beliefs and Belief-Like States? *Psychological Review, 116*(4), 953-970.

Aschersleben, G., Hofer, T., & Jovanovic, B. (2008). The link between infant attention to goal-directed action and later theory of mind abilities. *Developmental Science, 11*(6), 862-868.

Bach, P., Gunter, T. C., Knoblich, G., Prinz, W., & Friederici, A. D. (2009). N400- like negativities in action perception reflect the activation of two components of an action representation. *Social Neuroscience*, *4*, 212–232.

Baillargeon, Scott, & He (2011). False-belief understanding in infants. *Trends in Cognitive Sciences, 14*(3), 110-118

Balconi, M., & Caldiroli, C. (2011). Semantic violation effect on object-related action comprehension. N400-like event-related potentials for unusual and incorrect use. *Neuroscience, 197*, 191-199.

Bardi, L., Desmet, C., Nijhof, A., Wiersema, J.R., & Brass, M. (2016). Brain activation for spontaneous and explicit false belief tasks: new fMRI evidence on belief processing and violation of expectation. Social Cognitive and Affective Neuroscience, nsw143.

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

Biro, S., & Leslie, A.M. (2007). Infants' perception of goal-directed actions: development through cue-based bootstrapping. *Developmental science, 10*(3), 379-398.

Blakemore, S. J. (2008). Development of the social brain during adolescence. *Quarterly Journal of Experimental Psychology, 61*(1), 40-49.

Blakemore, S. J. (2012). Imaging brain development: The adolescent brain. *Neuroimage, 61*(2), 397-406.

Bowman, L. C., Liu, D., Meltzoff, A. N., & Wellman, H. M. (2012). Neural correlates of belief- and desire-reasoning in 7- and 8-year-old children: an event-related potential study. *Developmental Science, 15*(5), 618-632.

Buresh, J.S., & Woodward, A.L. (2007). Infants track action goals within and across agents. *Cognition, 104*, 287-314.

Camblin, C. C., Ledoux, K., Boudewyn, M., Gordon, P. C., & Swaab, T. Y. (2007). Processing new and repeated names: Effects of co-reference on repetition priming with speech and fast RSVP. *Brain Research*, *1146*, 172–84.

Carruthers, P. (2016). Two systems for mindreading? *Philosophy and Psychology*, *7*, 141-162.

Chandler, M.J., & Lalonde, C. (1996). Shifting to an interpretative theory of mind: 5- to 7-year-olds' changing conception of mental life. In Sameroff, A., & Haith, M. (Eds.), *Reason and Responsibility: The Passage Through Childhood* (pp. 11-139). Chicago, IL: University of Chicago Press.

Cohn, N., & Kutas, M. (2015). Getting a cue before getting a clue: Event-related potentials to inference in visual narrative comprehension. *Neuropsychologia, 77*, 267-278.

Csibra, G. (2011). Recognizing communicative intentions in infancy. *Mind & Language, 25*(2), 141-168.

Daum, M., Attig, M., Gunawan, R., Prinz, W., & Gredebäck, G. (2012). Actions seen through Babies' eyes: a dissociation between looking time and predictive gaze. *Frontiers in Psychology*, *3*, 1-13.

de Haan, M. (2007). Infant EEG and event-related potentials. Sussex, UK: Psychology Press.

Dumontheil, I., Apperly, I. A., & Blakemore, S. J. (2010). Online usage of theory of mind continues to develop in late adolescence. *Developmental Science, 13*(2), 331-338.

Ferguson, H.J., Cane, J.E., Douchkov, M., & Wright, D. (2015). Empathy predicts false belief reasoning ability: evidence from the N400. *Social Cognitive and Affective Neuroscience, 10*(6), 848-855.

Flavell, J. H. (1988). The development of children's knowledge about the mind: From cognitive connections to mental representations. In J. W. Astington, P.L. Harris, & D.R. Olson (Eds.), *Developing theories of mind* (pp. 244-267). New York: Cambridge University Press.

Friedrich, M., & Friederici, A. (2004). N400-like semantic incongruity effect in 19-month-olds: processing known words in picture contexts. *Journal of Cognitive Neuroscience, 16*(8), 1465-1477.

Ganis, G., Kutas, M., & Sereno, M. I. (1996). The search for "common sense": an electrophysiological study of the comprehension of words and pictures in reading. *Journal of Cognitive Neuroscience*, *8*(2), 89-106.

Geangu, E., Gibson, A., Kaduk, K., & Reid, V. M. (2013). The neural correlates of passively viewed sequences of true and false beliefs. *Social Cognitive and Affective Neuroscience, 8*(4), 432-437.

Gilbert, S. J., Simons, J. S., Frith, C. D., & Burgess, P. W. (2006). Performance-related activity in medial rostral prefrontal cortex (area 10) during low-demand tasks. *Journal of Experimental Psychology: Human Perception and Performance*, *32*(1), 45.

Gredebäck, G., & Daum, M.M. (2015). The microstructure of action perception in infancy: decomposing the temporal structure of social information processing. *Child Development Perspectives, 9*(2), 79-83.

Gunter, T. C. & Bach, P. (2004). Communicating hands: ERPs elicited by meaningful symbolic hand postures, *Neuroscience Letters*, *372*, 52–56.

Gweon, H., Dodell-Feder, D., Bedny, M., & Saxe, R. (2012). Theory of mind performance in children correlates with functional specialization of a brain region for thinking about thoughts. *Child Development, 83*(6), 1853-1868.

Hamm, J. P., Johnson, B. W. & Kirk, I. J. (2002). Comparison of the N300 and N400 ERPs to picture stimuli in congruent and incongruent contexts. *Clinical Neurophysiology, 113,* 1339–1350.

He, Z., & Baillargeon, R. (2007). *Understanding of false belief in 11-month-old infants*. Paper presented at the Biennial meeting of the society for research in child development, Boston, MA.

Heyes, C. (2014). False belief in infancy: a fresh look. *Developmental Science, 17*(5), 647-659.

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

Holcomb, P. J. (1993). Semantic priming and stimulus degradation: Implications for the role of the N400 in language processing. *Psychophysiology*, *30*, 47–61.

Huttenlocher, P. R., & Dabholkar, A. S. (1997). Developmental anatomy of prefrontal cortex. *Development of the prefrontal cortex: Evolution, neurobiology, and behavior*, 69-83.

Hyde. D.C., Aparicio Betancourt, M., & Simon, C.E. (2015). Human temporal-parietal junction spontaneously tracks others' beliefs: A functional near-infrared spectroscopy study. *Human Brain Mapping, 36*(12), 4831-4836.

Jackson, I., & Sirois, S. (2009). Infant cognition: going full factorial with pupil dilation. *Developmental Science, 12*(4), 670-679.

Kobayashi, C., Glover, G. H., & Temple, E. (2007). Children's and adults' neural bases of verbal and non-verbal 'theory of mind'. *Neuropsychologia, 45*(7), 1522-1532.

Kovacs, A. M., Kühn, S., Gergely, G., Csibra, G., & Brass, M. (2014). Are all beliefs equal? Implicit belief attributions recruiting core brain regions of theory of mind. *Plos One, 9*(9), E106558.

Kovacs, A. M., Teglas, E., & Endress, A. D. (2010). The Social Sense: Susceptibility to Others' Beliefs in Human Infants and Adults. *Science, 330*(6012), 1830-1834.

Kuhlmeier, V., Wynn, K., & Bloom, P. (2003). Attribution of dispositional states by 12-month-olds. *Psychological Science, 14*(5), 402-408.

Kuhn-Popp, N., Sodian, B., Sommer, M., Dohnel, K., & Meinhardt, J. (2013). Same or different? ERP correlates of pretense and false belief reasoning in children. *Neuroscience, 248*, 488-498.

Kutas, M., & Federmeier, K.D. (2011). Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology, 62*, 621-647.

Kutas, M., & Hillyard, S.A. (1980a). Event-related brain potentials to semantically inappropriate and surprisingly large words. *Biological Psychology,11*(2), 99-116.

Kutas, M., & Hillyard, S.A. (1980b). Reading senseless sentences: Brain potentials reflect semantic incongruity. *Science, 207*(4427), 203-205.

Leslie, A. M. (2005). Developmental parallels in understanding minds and bodies. *Trends in Cognitive Sciences, 9*(10): 459-462.

Liu, D., Meltzoff, A.N., & Wellman, H.M. (2009). Neural correlates of belief- and desire-reasoning. *Child Development, 80*(4), 1163-1171.

Liu, D., Sabbagh, M. A., Gehring, W. J., & Wellman, H. M. (2004). Decoupling beliefs from reality in the brain: an ERP study of theory of mind. *Neuroreport, 15*(6), 991-995.

Liu, D., Sabbagh, M. A., Gehring, W. J., & Wellman, H. M. (2009). Neural correlates of children's theory of mind development. *Child Development, 80*(2), 318-326.

Lloyd-Fox, S. (2017). Functional infrared spectroscopy – fNIRS. In Hopkins, B., Geangu, E., & Linkenauger, S. (Eds.). *The Cambridge encyclopedia of child development* (pp. 130-137). Cambridge, UK: Cambridge University Press.

Low, J., Apperly, I.A., Butterfill, S.A., & Rakoczy, H. (2016). Cognitive architecture of belief reasoning in children and adults: A primer on the two-systems account. *Child Development Perspectives, 10*(3), 184-189.

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

Luo, Y. (2011). Do 10-month-old infants understand others' false beliefs? *Cognition, 121*(3), 289-298

McCleery, J. P., Surtees, A. D., Graham, K. A., Richards, J. E., & Apperly, I. A. (2011). The neural and cognitive time course of theory of mind. *Journal of Neuroscience, 31*(36), 12849-12854.

McPherson, W. B. & Holcomb, P. J. (1999). An electrophysiological investigation of semantic priming with pictures of real objects. *Psychophysiology*, *36*, 53–65.

Meinhardt, J., Kuhn-Popp, N., Sommer, M., & Sodian, B. (2012). Distinct neural correlates underlying pretense and false belief reasoning: evidence from ERPs. *Neuroimage, 63*(2), 623-631.

Meinhardt, J., Sodian, B., Thoermer, C., Dohnel, K., & Sommer, M. (2011). True- and false-belief reasoning in children and adults: an event-related potential study of theory of mind. *Developmental Cognitive Neuroscience, 1*(1), 67-76.

Michael, J., & Christensen, W. (2016). Flexible goal attribution in early mindreading. *Psychological Review, 123*(2), 219-227.

Müller, B. C., Tsalas, N. R., van Schie, H. T., Meinhardt, J., Proust, J., Sodian, B., & Paulus, M. (2016). Neural correlates of judgments of learning–An ERP study on metacognition. *Brain research*, *1652*, 170-177.

Onishi, K. H., & Baillargeon, R. (2005). Do 15-month-old infants understand false beliefs? *Science, 308*(5719), 255-258.

Pace, A., Carver, L. J. & Friend, M. (2013). Event-related potentials to intact and disrupted actions in children and adults. *Journal of Experimental Child Psychology, 116*(2), 453-470.

Perner, J. (1991). Understanding the representational mind. Cambridge, MA: The MIT Press.

Perner, J., & Ruffman, T. (2005). Infants' insight into the mind: How deep?. *Science, 308*, 214–216.

Proverbio, A. M., Crotti, N., Manfredi, M., Adorni, R. & Zani, A. (2012). Who needs a referee? How incorrect basketball actions are automatically detected by basketball players' brain. *Scientific Reports*, *2*: 883.

Proverbio, A. M. & Riva, F. (2009). RP and N400 ERP components reflect semantic violations in visual processing of human actions. *Neuroscience Letter*, *459*, 142–6.

Rakoczy, H. (2012). Do infants have a theory of mind? *British Journal of Developmental Psychology, 30*(1), 59-74.

Reid, V.M., & Geangu, E. (2008). Research methodology and social cognition. In Striano, T., & Reid, V. (Eds.), *Social cognition: Development, Neuroscience and Autism* (pp. 17-35). Oxford, UK: Wiley-Blackwell.

Reid, V.M., Hoehl, S., Grigutsch, M., Groendahl, A., Parise, E., & Striano, T., (2009). The neural correlates of infant and adult goal prediction: evidence for semantic processing systems. *Developmental Psychology, 45*(3), 620-629.

Reid, V.M., & Striano, T. (2008). N400 involvement in the processing of action sequences. *Neuroscience Letters, 433*, 93-97.

Reynolds, G. D., & Guy, M. W. (2012). Brain-behavior relations in infancy: integrative approaches to examining infant looking behavior and event-related potentials. *Developmental Neuropsychology, 37*(3), 210-225.

Robson, S.J., Lee, V., Kuhlmeier, V.A., & Rutherford, M.D. (2014). Infants use contextual contingency to guide their interpretation of others' goal-directed behavior. *Cognitive Development, 31*, 69-78.

Rosler, F., & Heil, M. (1991). Toward a functional categorization of slow waves: taking into account past and future events. *Psychophysiology, 28*(3), 344-358.

Ruffman, T. (2014). To belief or not belief: Children's theory of mind. *Developmental Review, 34*(3), 3265-293.

Sabbagh, M. A., Moulson, M. C., & Harkness, K. L. (2004). Neural correlates of mental state decoding in human adults: An event-related potential study. *Journal of Cognitive Neuroscience, 16*(3), 415-426.

Sabbagh, M. A., & Taylor, M. (2000). Neural correlates of theory-of-mind reasoning: an event-related potential study. *Psychological Science, 11*(1), 46-50.

Saxe, R. R., Whitfield-Gabrieli, S., Scholz, J., & Pelphrey, K. A. (2009). Brain regions for perceiving and reasoning about other people in school-aged children. *Child Development, 80*(4), 1197-1209.

Scott, R. M., & Baillargeon, R. (2009). Which Penguin Is This? Attributing False Beliefs About Object Identity at 18 Months. *Child Development, 80*(4), 1172-1196.

Scott, R., Song, H., Baillargeon, R., & Leslie, A. M. (2007). 18.5-month-old infants attribute to others false beliefs about objects' internal properties. Paper presented at the Biennial meeting of the society for research in child development, Boston, MA.

Sheehan, E.A., Namy, L.L., & Mills, D.L. (2007). Developmental changes in neural activity to familiar words and gestures. *Brain and Language*, 101, 246-259.

Shibata, H., Gyoba, J. & Suzuki, Y. (2009). Event-related potentials during the evaluation of the appropriateness of cooperative actions. *Neuroscience Letter*, *452*, 189–93.

Sirois, S., & Jackson, L. (2007). *Pupil dilation and infant cognition*. Paper presented at IEEE 6th International Conference on Development and Learning, London, UK.

Sitnikova, T., Holcomb, P.J., Kiyonaga, K.A., & Kuperberg, G.R. (2008). Two neurocognitive mechanisms of semantic integration during the comprehension of visual real-world events. *Journal of Cognitive Neuroscience, 20*(11), 2037-2057.

Sitnikova, T., Kuperberg, G., & Holcomb, P. J. (2003). Semantic integration in videos of real-world events: an electrophysiological investigation. *Psychophysiology, 40*(1), 160-164.

Sodian, B. (2011). Theory of mind in infancy. *Child development perspective, 5*(1), 39-43.

Sodian, B., & Thoermer, C. (2004). Infants' understanding of looking, pointing and reaching as cues to goal-directed action. *Journal of Cognitive Development, 53*, 289–316.

Sommer, M., Dohnel, K., Sodian, B., Meinhardt, J., Thoermer, C., & Hajak, G. (2007). Neural correlates of true and false belief reasoning. *Neuroimage, 35*(3), 1378-1384.

Sommer, M., Meinhardt, J., Eichenmuller, K., Sodian, B., Dohnel, K., & Hajak, G. (2010). Modulation of the cortical false belief network during development. *Brain Research, 1354*, 123-131.

Song, H. J., & Baillargeon, R. (2008). Infants' Reasoning About Others' False Perceptions. *Developmental Psychology, 44*(6), 1789-1795.

Song, H. J., Onishi, K. H., Baillargeon, R., & Fisher, C. (2008). Can an agent's false belief be corrected by an appropriate communication? Psychological reasoning in 18-month-old infants. *Cognition, 109*(3), 295-315.

Southgate, V., Johnson, M.H., El Kariou, I., & Csibra, G. (2010). Motor system activation revelas infants' on-line prediction of others' goals. *Psychological Science, 21*(3) 355-359.

Southgate, V., Senju, A., & Csibra, G. (2007). Action anticipation through attribution of false belief by 2-year-olds. *Psychological Science, 18*(7), 587-592.

Surian, L., Caldi, S., & Sperber, D. (2007). Attribution of beliefs by 13-month-old infants. *Psychological Science, 18*(7), 580-586.

Thierry, G. (2005). The use of event-related potentials in the study of early cognitive development. *Infant and Child Development*, *14*, 85–94 (2005).

Thoermer, C., Sodian, B., Vuori, M., Perst, H. & Kristen, S. Continuity from an implicit to an explicit understanding of false belief from infancy to preschool age. *British Journal of Developmental Psychology, 30*, 172-187 (2012).

Träuble, B., Marinović, V., & Pauen, S. (2010). Early theory of mind competencies: do infants understand others' beliefs? *Infancy, 15*(4), 434-444.

van Berkum, J. J., Hagoort, P., & Brown, C. M. (1999). Semantic integration in sentences and discourse: Evidence from the N400. *Journal of Cognitive Neuroscience*, *11*, 657–671.

Verschoor, S. A., Spapé, M., Biro, S., & Hommel, B. (2013). From outcome prediction to action selection: developmental change in the role of action-effect bindings. *Developmental Science*, *16*(6), 801-814.

Wellman, H.M. (2011). Developing a theory of mind. In Goswami, U. (Ed.). *The Wiley-Blackwell handbook of childhood cognitive development* (pp. 258-284). Chichester, UK: Wiley-Blackwell.

Wellman, H. M., & Bartsch, K. (1988). Young children's reasoning about beliefs. *Cognition, 30*(3), 239-277.

Wellman, H. M., Cross, D., & Watson, J. (2001). Meta-analysis of theory-of-mind development: the truth about false belief. *Child Development, 72*(3), 655-684.

West, W. C. & Holcomb, P. J. (2002). Event-related potentials during dis-course-level semantic integration of complex pictures. *Cognitive Brain Research*, *13*, 363-375.

Wimmer, H., & Perner, J. (1983). Beliefs about beliefs: representation and constraining function of wrong beliefs in young children's understanding of deception*.* *Cognition, 13*, 41-68.

Zmyj, N., Prinz, W., & Daum, M. M. (2015). Eighteen-month-olds' memory interference and distraction in a modified A-not-B task is not associated with their anticipatory looking in a false-belief task. *Frontiers in Psychology*, *6*(857).

General Discussion

Maria M. Crespo Llado

Lancaster University

Summary of Findings

The current thesis examined early precursors of empathy development in infancy. Because of the complexity of this psychological construct and the limitations involved in its evaluation within developing populations we used a multi-method approach. The four studies within this thesis have explored the two main components of empathy, affective and cognitive, by investigating the neural mechanisms underlying infants' perception of peers' non-verbal vocalizations and the role of temperament as a modulator of these responses (Paper 1), the neural indices of motivational tendencies underpinning infants' affective and behavioral responses to their peers' negative and positive emotions (Paper 2), the developmental trajectory and mechanisms underlying infants' spontaneous facial reactions (SFRs) to others' emotional facial expressions (Paper 3), and the neurocognitive processes underlying early forms of belief processing that are thought to support the later emergence of more mature forms of mentalizing and empathy responses (Paper 4).

In Paper 1, 8-month-old infants were exposed to the sounds of another peer crying, laughing and coughing while their EEG activity was recorded online. Further, parent filled in a questionnaire about their infants' temperamental traits. Results showed that the processing of emotional non-verbal vocalizations produced by peers (i.e. laughter and crying) elicited differential event-related potential (ERP) activity at frontal locations, as indexed by differences in the N100, P200 and late positive component (LPC). Specifically, N100 amplitudes were more negative for peers' crying sounds relative to positive and neutral peers' non-verbal vocalizations of emotions, whereas P200 amplitudes did not show any differentiation between conditions. Peers' crying elicited higher LPC amplitudes compared to laughing or coughing sounds. Importantly, these neural responses were modulated by temperamental differences. Infants with better abilities to regulate their own arousal and low in negative emotionality showed more differentiated ERP responses between emotional and neutral vocalizations as well as between threatening (crying) and non-threatening vocalizations (laughing and coughing). Taken together, this study adds novel information to an increasing body of knowledge suggesting important links between temperament and emotion information processing development, which might help to predict later individual predispositions to experience greater or lesser empathy.

In Paper 2 we presented 8-month-old infants with the audio-video recordings of a peer laughing and a peer crying. The stimuli were displayed twice on separate sessions. Frontal asymmetry patterns were recorded by means of electroencephalography (EEG) during the first session while infants' other-oriented and emotional behaviors were recorded during the second visit to the lab. This study demonstrated that observing a peer crying was accompanied by greater relative right frontal activity while the observation of a peer laughing elicited greater relative activity in the left frontal region compared to the right region, yet the difference was not significant for this condition. During the second session, we found that infants resonated with their peers' emotions. That is, they tended to display more positive affect (i.e. greater facial expressions of happiness) in response to a peer laughing as compared to a peer crying, and more negative affect (i.e. negative vocalizations, facial expressions of distress) in response to a peer crying as opposed to a peer laughing. Although we observed approach-oriented responses to peers' distress and happiness in 8-month-old infants, overall they tended to display more withdrawal than approach behaviors for both peer affective conditions. Notably, we also found a significant link between early measures of frontal asymmetry activation and later infants' empathic-related responses. Increased electrical activity in the left frontal region was associated with the occurrence of more approach-oriented behaviors towards a peer crying and laughing. These findings are crucial since for first time they reveal a link between particular neurophysiological asymmetry patterns reflecting motivational tendencies and infants' approach-oriented behaviors to their peers in early development.

For Paper 3 we presented 4- and 7-month-old infants with dynamic facial expressions of happiness, fear, and anger, while we used electromyography (EMG) to measure the activation of the facial muscles specific for expressing these emotions (i.e. zygomaticus major (smiling), corrugator supercilii (frowning), and frontalis (forehead raising). Seven-month-old infants exhibited selective muscle activation patterns but not across all facial emotional expressions. In particular, the observation of happy and fearful faces in 7-month-old infants lead to increased activation of the muscles specific for expressing these emotions, with increased zygomaticus major activation for happy faces and increased frontalis activation for fearful faces. In contrast, the perception of angry faces lead to a more non-differentiated pattern of facial responsiveness. Although the muscle specific for expressing anger, corrugator supercilli, did record an increased activation in response to angry faces, this was not associated with a decrease in the activation of the muscle specific for smiling (i.e., the zygomaticus major) nor the muscle specific for fear (i.e., the frontalis). Unlike the older age group, 4-months old infants did not manifest selective activation of the recorded facial muscles in response to the facial cues of emotion. These findings are of crucial relevance since they suggest that motor mimicry alone is not sufficient to explain infants' spontaneous facial reactions (SFRs) to others' dynamic facial expressions of emotions, and that other mechanisms are likely to play an important role. Furthermore, the absence of emotionally matched facial expression in 4-month-old infants as compared to the oldest age group, suggests that the neurocognitive mechanisms underlying SFRs undergo important changes during the second half of the first year of life.

Finally, for Paper 4, 15-month-old infants were presented with a non-verbal false belief task consisting of visual narratives depicting a female agent acting congruently or incongruently with her false belief about the location of an object. During the whole session, infants' EEG activity was recorded online. Our analyses revealed that ERP responses at frontal locations significantly differentiated between conditions, with the false belief incongruent condition (belief incongruent – reality congruent) evoking the largest N400. In line with previous behavioral studies, this finding suggests that at the age of 15 months infants are able to track other people's actions, and detect inconsistencies between human agents' final actions and their mental states. In the context of empathy development, these results are relevant since they set the basis for future research to explore the link between neural correlates underlying implicit forms of mentalizing and other-oriented responses (i.e. affective concern and approach-related behaviors) during toddlerhood and early childhood.

Overall, this thesis demonstrated that during the second half of the first year the infant's brain is already sensitive to their crying and laughing peers, which fits with the behavioral evidence provided by cry contagion studies (e.g., Martin & Clark, 1982; Sagi & Hoffman, 1976; Simner, 1971) and previous infant ERP studies on face and speech emotional processing (e.g., Cheng, Lee, Chen, Wang, & Decety, 2014; de Haan, Belsky, Reid, Volein & Johnson, 2004; Grossman, Striano, & Friederici, 2005; Nelson & de Haan, 1996). The novel aspect of these findings is the discovery that infants' brain responses to their peers' non-verbal emotional vocalizations were modulated by individual differences in their tendency to express negative affect (IBQ-R Negative Emotionality factor) and their ability to regulate one's own arousal (IBQ-R Fall

Reactivity scale). This relation is relevant given that negative emotionality and self-regulation have been previously linked to empathy-related responses during childhood (e.g., Eisenberg et al., 1996; Eisenberg et al., 1998; Murphy, Shepard, Eisenberg, Fabes, & Guthrie, 1999). Remarkably, the perception of a peer crying and laughing not only elicited differentiated ERP responses, but also led to different EEG frontal asymmetry patterns, with the observation of a peer crying being associated with withdrawal tendencies (i.e. greater relative right frontal activation). Interestingly, these neural indices of motivational tendencies were related to infants' later affective and behavioral responses to their peers, revealing a positive relation between left frontal activation and infants' attempts to approach a peer crying and laughing. In other words, infants who exhibited higher relative left frontal activity during the observation of a peer crying displayed more attempts to approach the peer in distress during the second session. Likewise, infants who displayed higher relative left frontal activity during the observation of a peer laughing exhibited more attempts to engage vocally with the cheerful peer during the second visit.

Notably, the current work also demonstrates for the first time that infants were able to respond with matching emotional responses to peers' positive affect. This highlights that emotional resonance in infancy is not specific to negative emotions. Additionally, this thesis shows that infants' facial responsiveness to others' facial expressions of emotions do not solely rely on pure motor mimicry and that they may be the result of more complex neurocognitive mechanisms linked to a broad set of affective, cognitive and physiological processes. Additionally, the presence of age differences in SFRs suggests that the mechanisms underlying these responses undergo significant developmental changes between 4 and 7 months of age. Finally, this thesis also provides the basis for further research on the relationship between theory of mind and empathy development by indicating that infants by the second year of life area able to run some neural computations of others' beliefs, computations that are thought to underline the later emergence of affective concern and approach-related behaviors towards others' in distress.

Theoretical Implications

Individual Differences in Infants' Neural Responses to their Peers' Non-verbal Vocalizations

Infants' ability to detect, discriminate and recognize others' emotional expressions through vocalizations, facial expressions or body postures is fundamental for the later development of children's interpersonal and social skills (e.g., Grossmann, 2010; Walker-Andrews, 1997), and may be crucial for the development of empathy (Decety, 2015; Decety & Howard, 2013; Geangu, 2015; Hoffmann, 2001). Although non-verbal vocalizations are produced by pre-verbal infants from an early age and are thought to communicate pure emotional states, infants' ability to process, respond, and use non-verbal vocalizations of emotions remains understudied (Dunbar et al., 2012; Geangu, 2015; Pell et al., 2015; Provine, 1996). The current thesis provides novel and valuable insights into the early development of emotion processing, with important implications for the study of empathy. Notably, the ERP components (N100, P200, LPC) sensitive to emotional vocalizations of peers in this study suggests that vocal emotional processing in infancy follows a multistep process, in a similar way to the one proposed for adults (see Schirmer & Kotz, 2006 for a review). Specifically, in adults the processing of vocal emotional information has been associated with three main processes, which are differentially represented in the brain (Schirmer & Kotz, 2006). These processes has been described as follows: (1) analysis of the acoustic cues of vocalizations, (2) extraction of the emotional signals conveyed within the set of acoustic cues, and (3) deployment of higher order cognitive processes to decode emotional significant vocalizations. Importantly, this multistep account proposes that contextual or individual factors might facilitate or enhance processing at any of the three stages, which is partially corroborated by our study. In this respect, we showed that individual differences in the temperamental dimension of negative emotionality modulated the mean amplitude of the P200 and LPC responses to peers' emotional non-verbal vocalizations. Nonetheless, further research is needed in order to clarify the developmental trajectory of these ERP components and how they relate to the ones described in adults.

Importantly, our ERP results underscored a preferential processing of crying sounds at early (as indexed by an enhanced N100) and later stages (as indexed by an enhanced LPC). This selective enhancement for crying sounds in auditory processing is in line with a substantial body of evidence suggesting the emergence of a negativity bias in the processing of emotional information at the age of 7 months, with enhanced allocation of attention and sensorial processing for negative emotions rather than positive (see Vaish, Grossman, & Woodward, 2008 for a review). ERP studies on infants' perception of emotional faces and voices have provided some indirect evidence in this respect. For instance, the perception of angry and fearful prosodies embedded in speech has been associated with larger ERP amplitudes than happy or neutral prosodies, suggesting increased attention for negative emotional expressions (Cheng et al., 2014; Grossman et al., 2005). In the visual domain, infants tend to display stronger ERP responses when watching a fearful face than neutral or happy faces, suggesting the recruitment for more attentional resources for negative-valenced information (e.g., Nelson & de Haan, 1996; de Haan et al., 2004; Leppänen, Moulson, Vogel-Farley, & Nelson, 2007; Peltola, Leppänen, Mäki, & Hietanen, 2009). Notably, these ERP findings are in agreement with behavioral evidence showing that infants use negative cues more successfully than positive cues to efficiently guide their own behavior in new or ambiguous situations (e.g., Hertenstein & Campos, 2001; Hornik, Risenhoover, & Gunnar, 1987; Mumme & Fernald, 2003; Mumme, Fernald, & Herrera, 1996).

One potential explanation is that infants are born with a predisposition to primarily attend and process aversive events given its potential threat to survival (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; Cacioppo & Berntson, 1999; Rozin & Royzman, 2001; Taylor, 1991). Indeed, threat-related emotions are hypothesized to carry greater informational value, develop more rapidly and require a faster reaction than positive ones, which in turn translates into the recruitment of more resources (e.g., Cacioppo & Berntson, 1999; Peeters & Czapinski, 1990; Vuilleumier, 2005; Williams, 2006). Based on this evolutionary premise, throughout generations, those organisms who were better attuned to negative events had a better chance to survive threats and therefore to pass their genes onto next generations. Thus, negative events would operate as a sign for behavioural change while positive emotions would allow us for consistency and stability (Baumeister et al., 2001; Rozin & Royzman, 2001; Taylor, 1991). Notably, behavioural adjustment to the environment is seen by some as the best mechanism to increase the likelihood for survival (Cacioppo et al., 1999; Baumeister et al., 2001).

Although these models are informative, they are unable to account for the whole phenomenon (Rozin & Royzman, 2001). At this respect, some studies have already reported that infants do not show a negativity bias in the first few months after birth (Aldrige, 1994; Fernald, 1993; Singh, Morgan, & Best, 2002), which calls into question the credibility of an innate predisposition to negative events. Furthermore, even if the bias was an artefact of evolution, one would expect early experiences to play an essential role in its ontogenetic emergence (Johnson, 2005; Vaish, Grossman, & Woodward, 2008). Mechanistic theories such as the range-frequency theory have incorporated the nature of this early experiences to explain the emergence of the negativity bias (Helson, 1964; Parducci, 1995). According to these theories, it is the novelty of negative events what leads to a negativity bias rather the negative valence per se. Support for this account comes from multiple behavioural studies showing that from early on infants are more frequently expose to positive interactions than negative (Malatesta & Haviland, 1982; Malatesta, Grigoryev, Lamb, Albin, & Culver, 1986). This early predominance of positive events may positively skew infants so that later on, negative events stand out and demand more attentional resources (Fiske, 1980; Peeters & Czapinski, 1990). This hypothesis does not necessarily conflict with evolutionary accounts. Rather, they can be seen as complementary, where ultimately the negativity bias serves the adaptive purpose of helping us to avoid harmful situations.

Finally and more importantly, our results showed for first time that later auditory processing stages were modulated by individual differences, in particular by variations in the tendency to express negative affect (IBQ-R Negative Emotionality factor) and the ability to regulate one's own arousal (IBQ-R Fall Reactivity scale). This is particularly important given the high relevance of negative emotionality and emotion regulation in the production of empathic responses (Eisenberg & Fabes, 1992). Specifically, Eisenberg & Fabes (1992) model on empathy suggests that the interaction of the temperamental factors emotional reactivity (affective and motoric arousal) and self-regulation modulates the expression of empathy. This model assumes that people who are able to regulate their own emotions would be prone to experience less personal distress when exposed to another person's suffering, regardless of their dispositional emotionality. In contrast, people who tend to experience emotions more intensely (display higher arousal) would be more likely to show personal distress if they lack the ability to regulate themselves. All these assumptions have received some empirical support in research with children (e.g., Eisenberg et al., 1996; Eisenberg et al., 1998; Murphy et al., 1999; Rothbart, Ahadi, & Hershey, 1994; Ungerer et al., 1990). In relation with this model, our results suggest that those infants who were better at self-regulation and low in negative emotionality were the ones who exhibited a more accurate processing of emotional cues, which in turn might promote the expression of more other-oriented responses to others' emotions. Taken together, our findings add novel information to an increasing body of knowledge suggesting important links between infant temperament and emotion information processing development, with potential implications for understanding the ontogeny of empathy.

Neural Indices of Infants' Motivational Tendencies to Approach their Peers

In the domain of empathy, it has been argued that infants' early responsiveness to others' emotions, in conjunction with certain levels of emotion understanding and perspective taking, may further motivate other-oriented responses like prosocial behaviors (e.g., Batson, 1991, Decety & Lamm, 2006; Eisenberg, Losoya, & Guthrie, 1997; Hoffman, 1975, 1982; Knafo & Israel, 2012; Singer, 2006). Nevertheless, until now these links had only been established at a theoretical level. This thesis provides significant data in relation to the neurocognitive mechanisms underlying infants' motivational tendencies to approach or avoid peers experiencing distress or happiness, with potential implications for understanding the ontogeny of prosocial behaviors.

In line with contemporary models of frontal EEG asymmetry (Davidson & Fox, 1982, 1989), Paper 2 found that the observation of peers' positive and negative emotions elicited distinctive patterns of brain activation and affective responding. In particular, the observation of a peer crying was associated with greater relative right frontal activation in 8-month-old infants. This result fits with a series of previous studies linking right frontal cortical activity to the tendency to display negative emotions and withdrawal behaviors (e.g., Buss et al., 2003; Diaz & Bell, 2012; Fox & Davidson, 1987, 1988). Although observing a peer laughing evoked relative greater activation of the left hemisphere than the right hemisphere, this difference was not significant. A possible explanation for this finding is that the more generalized pattern of brain activity observed for a peer laughing reflects higher cognitive demands. This hypothesis is consistent with recent studies suggesting that generalized increases in alpha frontal EEG power are associated with higher levels of performance on memory and attentional task (Bell, 2001, 2002; Bell & Fox, 1997; Santesso, Schmidt, & Trainor, 2007; Stroganova, Orekhova, & Posikera, 1999). It is thus possible that by the age of 8 months the laughter of a peer is not yet especially meaningful, thus leading infants to recruit extra cognitive resources to extract the emotional information conveyed. In this respect, it is important to bear in mind that this thesis (Paper 1) has also shown that only the sound of a peer crying engages in later sustained cognitive processing compared to both infants laughter and infant coughing vocalizations. It is thus possible that compared to crying, the development of laughter follows a different course and relies on more sophisticated social cognition abilities that develop later. Supporting this view, several fMRI studies with adults suggest that the processing of emotional laughter places higher demands on frontal brain areas implicated in theory of mind and emotion evaluation (Szameitat et al., 2010; Tschacher, Schidt, & Sander, 2010; Wildgruber et al., 2013).

Additionally, the current work extends the existing developmental literature by showing that emotional resonance in infancy is not only limited to negative emotions (e.g., Dondi, Simion, & Caltran, 1999; Sagi & Hoffman, 1976; Simner, 1971). Our behavioral data suggests that by the age of 8 months infants respond with distinctive matching affective behaviors to a crying and laughing peer, which goes in consonance with previous findings indicating differences in physiological measures of arousal among 6- to 12-months-old infants in response to other infants' happiness and distress (Geangu, Hauf, Bhardwaj, & Bentz, 2011; Upshaw, Kaiser, & Sommerville, 2015).

To finalize, it is important to outline that the current work provided support for an incipient body of research suggesting important links between left frontal activity and approach-related responses towards others' in distress, with potential implications for understanding the ontogeny of prosocial behaviors. In agreement with previous research (Hay, Nash, & Pedersen, 1981; Liddle, Bradley & MacGrath, 2015; Roth-Hanania, Davidov, & Zahn-Waxler, 2011), our study showed that infants are able to display very simple forms of approach towards others in distress, and that these behaviors are mediated by specific frontal asymmetry patterns indexing motivation to approach. In particular, we found a positive relation between left frontal asymmetry and infants' approach-related behaviors to their peers crying and laughing. These findings fit with previous EEG work with younger children showing a link between left frontal activation and empathy-related reactions (Jones, Field, & Davalos, 2000; Jones, Field, Davalos & Hart, 2004; Paulus, Kuhn-Popp, Licata, Sodian, & Meinhardt, 2013) as well as previous infant EEG studies linking left frontal activation to higher levels of sociability with peers (Calkins, Fox, & Marshall, 1996; Fox, Henderson, Rubin, Calkins, & Schmidt,, 2001; Henderson, Fox, & Rubin, 2001). Thus, this study adds to the literature on social neuroscience and developmental psychology by providing evidence that frontal asymmetries are important markers for motivational processes and social behaviors (e.g., Fox, 1991, 1994; Harmon-Jones, Gable, & Peterson, 2010) and by supporting current frontal EEG asymmetry models of motivational tendencies (Davidson & Fox, 1982, 1989).

The role of Motor Mimicry in Empathy

Traditionally, motor mimicry and matching mechanisms have been proposed as primary mechanisms underlying affect sharing in preverbal infants (e.g. Hatfield, Cacioppo, & Rapson, 1994; Hoffman, 2001; Meltzoff & Decety, 2003; Preston & de Waal, 2002). This idea goes in line with the theoretical account of the automatic transmission of emotions, according to which humans tend to automatically mimic other's facial, vocal or postural expressions of emotions and that such motor mimicry evokes the same emotions in the observer through perception-action matching (e.g. de Waal, 2009; Hatfield et al., 1994; Lipps, 1907). The idea that motor mimicry and matching mechanisms are causally related in the generation of emotional contagion responses mostly comes from a series of studies exploring spontaneous facial responses (SFRs) by using facial electromyography (EMG). Nonetheless, there is a large controversy about whether SFRs commonly seen after the exposure to facial expressions are triggered by perception-action matching mechanisms, bypassing emotional systems or, conversely, whether they are they result of an affective response (e.g. Beall, Moody, McIntosh, Hepburn, & Reed, 2008; Hess, Philippot, & Blairy, 1998; Moody, McIntosh, Mann, & Weisser, 2007).

The current thesis contributes to this old debate by challenging the perception-action matching proposal. Taken together, the age differences and pattern of selective muscle activation found in Paper 3 suggest that motor mimicry alone is not sufficient for explaining spontaneous facial reaction since according to the perception-action assumption facial actions should have led to matching expression for every emotion. Rather they appear to be consistent with proposals that see SFRs not as pure motor mimicry, but the result of complex neurocognitive mechanisms allowing both evaluative processes and shared motor representations (e.g., Dezecache et al., 2016; Grèzes & Dezecache, 2013). Specifically, the results suggest that infants' SFRs to dynamic emotional facial expressions undergo significant developmental changes towards the age of 7 months and that motor mimicry is not always present (as in the case of anger). Therefore, it is plausible to argue that infants' reactions to others' facial emotional displays may be influenced by early and quick evaluations of the emotional signal (Dezecache et al., 2016; Grèzes & Dezecache, 2013; Soussignan et al., 2013). In support of this view, there is evidence suggesting that the processing of emotional cues from faces not only recruits neural networks linked to shared motor representations but also emotion-related brain networks such as the amygdala and the orbitofrontal cortex in adults (Adolphs, 2002; Carr, Iacobini, Dubeau, Mazziotta, & Lenzi, 2003; Pessoa, 2008; Vuilleumier, Armony, Driver, & Dolan, 2003) and infants (Minagawa-Kawai et al., 2009). Overall, it is possible to suggest that infants' ability to share emotions with others during the first year of life may not rely on motor mimicry alone, but the combination of multiple complex neurocognitive mechanisms with direct relevance for the emergence of more mature empathy-related responses.

The Role of Theory of Mind in Empathy

The capacity for two people to resonate with each other emotionally, prior to any cognitive understanding, is the basis for developing shared emotional representations, but is not enough to account for more mature forms of empathic understanding. Such a comprehension requires the ability to understand the emotions and feelings of others in relation to oneself, which is commonly known as cognitive empathy. In turn, this cognitive aspect of empathy is thought to rely on the gradual emergence of theory of mind (ToM) processes implemented by a decoupling computational mechanism that allow the individual to generate second-order representations of the feelings of another person, while regulating the own emotional arousal response to avoid personal distress (e.g., Decety, 2010; Decety & Meyer, 2008; Decety & Michalska, 2010; Decety & Svetlova, 2012). Therefore, in order to understand the developmental course of empathy, it is important to elucidate when and how ToM develops. Once having a starting point, we can further investigate when and how ToM begins to shape early forms of empathy into more complex ones.

For many years it has been thought that the ability to represent other people's false beliefs (FBs) first emerges around the age of 4 years (Baron-Cohen, Leslie, & Frith, 1985; Flavell, 1988; Perner, 1991; Wellman, Cross, & Watson, 2001; Wellman & Bartsch, 1988). This evidence comes primarily from behavioral studies with preschoolers using standard FB tasks, where children were explicitly asked to reason about an agent's perception or belief about different aspects of reality (e.g. Baron-Cohen et al., 1985; Wellman & Bartsch, 1988; Wimmer & Perner, 1983). However, an increasing number of studies using non-verbal tasks based on looking-time measures suggest that computations about others' beliefs may be already present around the age of 15-18 months (e.g., Onishi & Baillargeon, 2005; Scott & Baillargeon, 2009; Song, Onishi, Baillargeon & Fisher, 2008; Träuble, Marinović, & Pauen, 2010). Interestingly, it is around the same age when infants also begin to display more mature forms of empathy like affect concern, attention to the distress of the other, cognitive exploration of the event and approach-oriented behaviors towards the other in distress (e.g., Knafo, Zahn-Waxler, Van Hulle, Robinson, & Rhee, 2008; Zahn-Waxler, Radke-Yarrow, Wagner, & Chapman, 1992). Although the emergence of implicit forms of ToM and more mature empathy-related behaviors occur around the same period, no studies have empirically examined the link between these two constructs in infants. The lack of studies on the topic might be due to the methodological difficulties associated with the evaluation of implicit (non-verbal) forms of ToM in infants and the old notion that this ability is not present until the age of 4 years. Critically, the investigation of the neural mechanisms underlying ToM in infancy is central to elucidating the developmental course of empathy since it has the potential to inform about the nature of the relation. Furthermore, by using brain measures it is possible to overcome the interpretational issues associated with looking time results, and specifically provide more certainty about the nature of the processes measured (Aschersleben, Hofer, & Jovanic, 2008; Gredebäck & Daum, 2015; Jackson & Sirois, 2009; Reynolds & Guy, 2012; Sirois & Jackson, 2007).

The current thesis contributes to the developmental literature by providing empirical evidence suggesting the presence of some basic form of mentalistic processing as opposed to mere physical processing at the age of 15 months. Notably, these findings support previous looking time measure studies suggesting that infants in the first half of the second year of life correctly anticipate the actions of agents holding a false belief, and, consequently, have an implicit understanding of others' false beliefs (e.g., Onishi & Baillargeon, 2005; Scott & Baillargeon, 2009; Song et al., 2008; Song & Baillargeon, 2008; Träuble et al., 2010). Although our results support the view that computations about others' belief-based actions may be already present in infancy, the nature of the cognitive abilities measured in this task and how they relate to those measured in verbal (explicit) false belief tasks remains unclear. Research is therefore needed to investigate the relation between these two types of false belief tasks in development.

In the domain of empathy, this finding is crucial given the relevance of mentalizing skills in the modulation of empathic responses through top-down processes.

Interestingly, the positive link between ToM and empathy development has been already reported by few fMRI studies in younger children (Decety, Michalska, & Akitsuki, 2008) and adolescents (Decety, Michalska, Akitsuki, & Lahey, 2009). These studies show that mentalizing about the pain of others when it has been intentionally caused recruits brain regions linked to the ToM network network as compared to situations in which the pain was caused accidentally. Despite these positive findings, there is still some controversies regarding the link between FB understanding (ToM) and empathy since not all developmental studies have succeeded in finding a link between these constructs (Astington & Jenkins, 1995; Hugues, White, Sharpen, & Dunn, 2000) or have failed to report age effects on the development of cognitive empathy (Garaigordobil, 2009). The current thesis sets the basis for further studies to explore the link between infants' empathic responses and their neural correlates underlying others' belief processing at early stages. For instance, this study may encourage future research to investigate whether the neural correlates of preverbal infants in non-verbal FB tasks are related to infants' ability to appropriately match others' emotions or infants' ability to respond with approach behavior to others' in distress during the second year of life.

Limitations and Future Studies

This thesis is not without limitations. Regarding the study presented in Paper 1 aimed at exploring individual differences in infants' neural correlates to their peers' laughter and crying, it is important to highlight two main limitations. The first limitation is linked to our stimuli. In particular, 25% of the adult raters judged the neutral sounds as something other than neutral. This may mean that any contrast involving the neutral stimuli was not as robust as one would hope. Interestingly, similar data has been obtained with visual stimuli, indicating that neutral faces may be interpreted as potentially negative or threatening given their ambiguity and lack of clear approach signals (Lee, Kang, Park, Kim, & An, 2008; Wieser & Brosch, 2012). This constrain seems to be an inherent problem given that we tend to attribute emotional and mental states to neutral and facial vocal expressions. Therefore, it would be important for future research to elucidate the emotional significance of neutral stimuli in infancy. Additionally, it is possible that the use of only vocal information (without the convergent presentation of facial cues) may have muted infants' ERP responses, especially those to laughter sounds, whose successful processing may depend on the presence of other emotional social cues (e.g., face and body posture) during the first year of life (Provine, 2004; Scott, Lavan, Chen, & McGettigan, 2014). Finally, it is important to bear in mind that the measures used to evaluate infants' temperament relied on parental reports, which is an indirect measure of individual differences and is prone to rater bias or distortion. It would thus be important to further investigate individual differences by using more direct measures of temperament such as structured observations (e.g., Laboratory Temperament Assessment Battery – LabTab). Certainly, longitudinal or cross-sectional studies would provide further information about how the ERP components observed in this study mature across time and how they link with the adult ones.

There are also few limitations in the study presented in Paper 2 that require discussion. First, although the peer emotion tasks used in both sessions were similar, they differed in duration and the conditions under which they were applied, which could explain some of the differences observed. In addition, it is possible that infants' responses were dampened by the exposure to unfamiliar peers rather than familiar ones. In this respect, there is suggestive evidence that child-child interactions are modulated by familiarity, with infants being more likely to interact with familiar peers as opposed to unfamiliar peers (Demetriou & Hay, 2004; Howes & Farver, 1987; Stefani & Camaioni, 1983; Young & Lewis, 1979). Likewise, the presence of the caregiver in the room during the second session may have caused children to respond less. Their own mothers' unresponsiveness toward the stimuli may have prompted them to be less interested themselves in the peers. It is also possible that infants responded less because they were waiting for their own mothers to intervene. In the future, it would be important to study the links between frontal EEG asymmetry and infants' approach-related responses towards their peers in more natural settings. It would also be relevant to study the neural indices of motivational tendencies of infants' approach-related responses towards their caregivers.

Regarding Paper 3, there are some constrains regarding the stimuli. Most notably, the emotional cues were only conveyed visually, which it may have been an issue for 4-month-old infants. In this respect, there is suggestive evidence that infants are able to discriminate emotional expressions conveyed visually around the age of 7 months but not earlier (Bahrick, Lickliter, & Flom, 2004; Flom & Bahrick, 2007). Thus, the use of audio-visual stimuli could have been more effective in order to capture spontaneous facial reactions (SFRs) in 4-month-old infants as previously illustrated by Isomura and Nakano (2016). Future studies would need to clarify the details of the emergence and development of infants' emotional SFRs by directly investigating the links between motor mimicry and emotion recognition abilities. In addition, we only included emotional facial expressions produced by strange female actresses, which might have weakened the infants' responses. Previous studies suggest that infants exhibit more emotional resonance to their own mothers' vocal and facial displays of emotions than towards an unfamiliar female (Kahana-Kalman & Walker-Andrews, 2001; Montague & Walker-Andrews, 2002). Therefore, we do not know whether the observed effects are induced by characteristics such as sex or degree of familiarity. Finally and most importantly, because this study did not use stimuli that were carefully matched in terms of the timing of the facial movements and peak intensity for the different emotional expressions, we cannot draw conclusions about the dynamic changes of the EMG signal across time. Further research should explore this question by creating artificial faces through morphing. The analysis of the dynamic changes across time would provide additional information about different underlying mechanisms and their interaction. In future studies, it would be important to use concurrent recordings of facial EMG and measures of psychophysiological arousal or electrical brain activity to better understand how affect related processes and neural correlates contribute to the emergence of the emotionally convergent SFRs during infancy.

Finally, there are some limitations linked to the interpretation of the results described in Paper 4. Although this study shows that by the age of 15 months infants are able to distinguish between conditions (as indexed by differences in the N400 component), and these differences may be suggestive of the presence of some basic form of mentalistic processing, there are some controversies regarding the interpretation of these results. One could argue that amplitude differences in the N400 between false belief congruent (FBc) and false belief incongruent (FBi) conditions were due to infants' expectations on the retrieval of an object. That is, in the FBi condition, there is an object that could be retrieved, so the 'incongruency' indexed with a greater N400 for this condition could be because infants expected the actor to pull her hand of the box once she grasp the object, creating confusion of why she does not pull her hand out. On the contrary, in the FBc condition, there is no object to retrieve, so the fact that the actor does not pull her hand out of the box is congruent with the idea that she may be still exploring around for her object in the box, trying to find it. One way to address this issue would be by modifying the existing stimuli such that for both conditions in the target stimulus the actress pulls her hand out of the box. Certainly, longitudinal designs correlating infants' brain responses with later behavioral measures of performance in false belief tasks would be important to clarify the interpretation of results.

Conclusions

This thesis provides a substantial body of empirical evidence in relation to the affective and cognitive processes underlying the development of empathy during infancy. Despite the relevance of empathy for the development of healthy social interactions (Blair, 2001, 2005), this topic has remained largely unexplored throughout infancy. Undoubtedly, empathy is a complex phenomenon whose examination is not exempt of difficulties, mostly within preverbal infants. Nonetheless, recent advances in neuroimaging and psychophysiological techniques have provided a new venue to explore the processes underlying empathy without the need to rely on introspective data. The main objective of the current thesis was to contribute to the existing limited literature on empathy by adopting an multi-method approach to shed new light into the neural processes that underpin infants' responses to others' emotional states as well as the neural processes underlying infants' responses to others' false beliefs.

The evidence presented in this thesis expands upon previous studies from developmental psychology and social cognitive neuroscience while raising new questions to be investigated by future studies. Importantly, this thesis demonstrates the advantages that developmental neuroscience can offer to the study of social cognition. Despite being a young discipline, there is no doubt that future infant research will greatly benefit from the combination of neuroimaging (e.g. EEG, fMRI, diffusion tensor imaging, optical imaging), hormonal and genetic methodologies. Finally, the findings reported in the current work might help to improve early diagnosis of children with atypical social development and contribute to the development of more efficient prevention and intervention programmes for these populations.

References

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

Aldridge, M. (1994). Newborns' perception of emotion in voices. In *International Conference on Infant Studies, Paris, France*.

Aschersleben, G., Hofer, T., & Jovanovic, B. (2008). The link between infant attention to goal-directed action and later theory of mind abilities. *Developmental Science, 11*(6), 862-868.

Astington, J. W., & Jenkins, J. M. (1995). Theory of mind development and social understanding. *Cognition & Emotion*, *9*(2-3), 151-165.

Bahrick, L. E., Lickliter, R., & Flom, R. (2004). Intersensory redundancy guides the development of selective attention, perception, and cognition in infancy. *Current Directions in Psychological Science*, *13*(3), 99-102.

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

Batson, C.D. (1991). *The altruism question: Toward a social psychological answer*. Hillsdale, NJ: Erlbaum

Baumeister, R. F., Bratslavsky, E., Finkenauer, C., & Vohs, K. D. (2001). Bad is stronger than good. *Review of general psychology*, *5*(4), 323.

Beall, P. M., Moody, E. J., McIntosh, D. N., Hepburn, S. L., & Reed, C. L. (2008). Rapid facial reactions to emotional facial expressions in typically developing children and children with autism spectrum disorder. *Journal of experimental child psychology*, *101*(3), 206-223.

Bell, M. A. (2001). 6-9 Hz as an indicator of individual differences in infant spatial working memory performance. *Psychophysiology, 38*, S7-S7.

Bell, M. A. (2002). Power changes in infant EEG frequency bands during a spatial working memory task. *Psychophysiology, 39*(4), 450-458.

Bell, M. A., & Fox, N. A. (1997). Individual differences in object permanence performance at 8 months: Locomotor experience and brain electrical activity. *Developmental Psychobiology, 31*(4), 287-297.

Blair, R. J. R. (2001). Neuro-cognitive models of aggression, the antisocial personality disorders and psychopathy. *Journal of Neurology, Neurosurgery & Psychiatry*, 71, 727–731.

Blair, R. J. R. (2005). Responding to the emotions of others: Dissociating forms of empathy through the study of typical and psychiatric populations. *Consciousness and Cognition, 14*(4), 698-718.

Buss, K. A., Schumacher, J. R., 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. *Behav Neurosci, 117*(1), 11-20.

Cacioppo, J. T., & Berntson, G. G. (1999). The affect system: Architecture and operating characteristics. *Current directions in psychological science*, *8*(5), 133-137.

Carr, L., Iacoboni, M., Dubeau, M. C., Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proceedings of the national Academy of Sciences*, *100*(9), 5497-5502.

Cheng, Y., Lee, S. Y., Chen, H. Y., Wang, P. Y., & Decety, J. (2012). Voice and emotion processing in the human neonatal brain. *Journal of cognitive neuroscience*, *24*(6), 1411-1419.

Calkins, S. D., Fox, N. A., & Marshall, T. R. (1996). Behavioral and physiological antecedents of inhibited and uninhibited behavior. *Child Development, 67*(2), 523-540.

Davidson, R. J., & Fox, N. A. (1982). Asymmetrical Brain Activity Discriminates between Positive and Negative Affective Stimuli in Human Infants. *Science, 218*(4578), 1235-1237.

Davidson, R. J., & Fox, N. A. (1989). Frontal Brain Asymmetry Predicts Infants Response to Maternal Separation. *Journal of Abnormal Psychology, 98*(2), 127-131.

De Haan, M., Belsky, J., Reid, V., Volein, A., & Johnson, M. H. (2004). Maternal personality and infants' neural and visual responsivity to facial expressions of emotion. *Journal of Child Psychology and Psychiatry*, *45*(7), 1209-1218.

De Waal, F. (2009). *Primates and philosophers: How morality evolved.* Princeton University Press.

Decety, J. (2015). The neural pathways, development and functions of empathy. *Current Opinion in Behavioral Sciences*, *3*, 1-6.

Decety, J. (2010). The neurodevelopment of empathy in humans. *Dev Neurosci, 32*(4), 257-267.

Decety, J., & Howard, L. H. (2013). The role of affect in the neurodevelopment of morality. *Child Development Perspectives*, *7*(1), 49-54.

Decety, J., & Lamm, C. (2006). Human empathy through the lens of social neuroscience. *ScientificWorldJournal, 6*, 1146-1163.

Decety, J., & Meyer, M. (2008). From emotion resonance to empathic understanding: A social developmental neuroscience account. *Development and Psychopathology, 20*(4), 1053-1080.

Decety, J., & Michalska, K. J. (2010). Neurodevelopmental changes in the circuits underlying empathy and sympathy from childhood to adulthood. *Developmental Science, 13*(6), 886-899.

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., Michalska, K. J., Akitsuki, Y., & Lahey, B. B. (2009). Atypical empathic responses in adolescents with aggressive conduct disorder: a functional MRI investigation. *Biological psychology*, *80*(2), 203-211.

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

Demetriou, H., & Hay, D. F. (2004). Toddlers' reactions to the distress of familiar peers: The importance of context. *Infancy, 6*(2), 299-318.

Dezecache, G., Eskenazi, T., & Grèzes, J. (2016). Emotional Convergence: A Case of Contagion?. In S. S. Obhi & E. S. Cross (Eds.), *Shared Representations: Sensorimotor Foundations of Social Life.* Cambridge University Press.

Diaz, A., & Bell, M. A. (2012). Frontal EEG asymmetry and fear reactivity in different contexts at 10 months. *Developmental Psychobiology, 54*(5), 536-545.

Dondi, M., Simion, F., & Caltran, F. (1999). Can newborns discriminate between their own cry and the cry of another newborn infant? *Developmental Psychology, 35*(2), 418-426.

Dunbar, R. I., Baron, R., Frangou, A., Pearce, E., van Leeuwin, E. J., Stow, J., ... & Van Vugt, M. (2011). Social laughter is correlated with an elevated pain threshold. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20111373.

Eisenberg, N., & Fabes, R. A. (1992). Emotion, regulation, and the development of social competence. In M. S. Clark (Ed.), *Review of Personality and Social Psychology: Emotion and Social Behavior* (pp.119-150). Newbury Park, CA: Sage.

Eisenberg, N., Fabes, R. A., Murphy, B., Karbon, M., Smith, M., & Maszk, P. (1996). The relations of children's dispositional empathy-related responding to their emotionality, regulation, and social functioning. *Developmental psychology*, *32*(2), 195.

Eisenberg, N., Fabes, R. A., Shepard, S. A., Murphy, B. C., Jones, S., & Guthrie, I. K. (1998). Contemporaneous and longitudinal prediction of children's sympathy from dispositional regulation and emotionality. *Developmental Psychology*, *34*, 910.

Eisenberg, N., Losoya, S., & Guthrie, I. K. (1997). Social cognition and prosocial development. *The development of social cognition*, 329-363.

Fernald, A. (1993). Approval and disapproval: Infant responsiveness to vocal affect in familiar and unfamiliar languages. *Child development*, *64*(3), 657-674.

Fischer, A. H. & Hess, U. (2017). Mimicking emotions. *Current Opininion in Psychology, 17*, 151–155.

Fiske, S. T. (1980). Attention and weight in person perception: The impact of negative and extreme behavior. *Journal of personality and Social Psychology*, *38*(6), 889.

Flavell, J. H. (1988). The development of children’s knowledge about the mind: From cognitive connections to mental representations. In J. W. Astington, P.L. Harris, & D.R. Olson (Eds.), *Developing theories of mind* (pp. 244-267). New York: Cambridge University Press.

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

Fox, N. A. (1994). Dynamic cerebral processes underlying emotion regulation. *Monographs of the society for research in child development*, *59*(2-3), 152-166.

Fox, N. A., & Davidson, R. J. (1987). Patterns of Eeg Asymmetry Reflect the Presence of Discrete Emotions in 10-Month-Old Infants. *Journal of Clinical and Experimental Neuropsychology, 9*(1), 71-71.

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.

Fox, N. A., Henderson, H. A., Rubin, K. H., Calkins, S. D., & Schmidt, L. A. (2001). Continuity and discontinuity of behavioral inhibition and exuberance: Psychophysiological and behavioral influences across the first four years of life. *Child Development, 72*(1), 1-21.

Garaigordobil, M. (2009). A comparative analysis of empathy in childhood and adolescence: Gender differences and associated socio-emotional variables. *International Journal of Psychology and psychological therapy*, *9*(2).

Geangu, E. (2015). Development of empathy furing early childhood across cultures. In J. D. Wright (Ed.), *International Encyclopedia of the Social and Behavioral Sciences* (pp. 549–553). Elsevier.

Geangu, E., Hauf, P., Bhardwaj, R., & Bentz, W. (2011). Infant Pupil Diameter Changes in Response to Others' Positive and Negative Emotions. *PLoS ONE, 6*(11), e27132.

Gredebäck, G., & Daum, M.M. (2015). The microstructure of action perception in infancy: decomposing the temporal structure of social information processing. *Child Development Perspectives, 9*(2), 79-83.

Grèzes, J. & Dezecache, G. (2014). How do shared-representations and emotional processes cooperate in response to social threat signals ?. *Neuropsychologia, 55*, 1–10.

Grèzes, J., Philip, L., Chadwick, M., Dezecache, G., Soussignan, R., & Conty, L. (2013). Self-relevance appraisal influences facial reactions to emotional body expressions. *PloS one*, *8*(2), e55885.

Grossmann, T. (2010). The development of emotion perception in face and voice during infancy. *Restorative neurology and neuroscience*, *28*(2), 219-236.

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

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. *Biol Psychol, 84*(3), 451-462.

Hatfield, E., Cacioppo, J. T., & Rapson, R. L. (1994). *Emotional contagion*: Cambridge studies in emotion and social interaction. Cambridge, UK: Cambridge University Press.

Hay, D. F., Nash, A., & Pedersen, J. (1981). Responses of six-month-olds to the distress of their peers. *Child Dev, 52*(3), 1071-1075.

Helson, H. (1964). Adaptation-level theory: an experimental and systematic approach to behavior.

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 and Adolescent Psychiatry, 40(1), 68-74.

Hertenstein, M. J., & Campos, J. J. (2001). Emotion regulation via maternal touch. *Infancy*, *2*(4), 549-566.

Hess, U., Philippot, P., & Blairy, S. (1998). Facial reactions to emotional facial expressions: affect or cognition?. *Cognition & Emotion*, *12*(4), 509-531.

Hoffman, M. (1975). Development synthesis of affect and cognition and its implications of altruistic motivation. *Developmental Psychology, 23*, 97-104.

Hoffman, M. (1982). Development of prosocial motivation: Empathy and guilt. In N. Eisenberg (Ed.), *The development of prosocial behavior* (pp. 281-313). New York: Academic Press.

Hoffman, M. L. (2001). *Empathy and moral development: Implications for caring and justice*. Cambridge University Press.

Hornik, R., Risenhoover, N., & Gunnar, M. (1987). The effects of maternal positive, neutral, and negative affective communications on infant responses to new toys. *Child development*, 937-944.

Howes, C., & Farver, J. (1987). Toddler's response to the distress of their peers. *Journal of Applied Developmental Psychology*, 8, 441-452.

Hughes, C., White, A., Sharpen, J., & Dunn, J. (2000). Antisocial, angry, and unsympathetic:"Hard-to-manage" preschoolers' peer problems and possible cognitive influences. *The Journal of Child Psychology and Psychiatry and Allied Disciplines*, *41*(2), 169-179.

Jackson, I., & Sirois, S. (2009). Infant cognition: going full factorial with pupil dilation. *Developmental Science, 12*(4), 670-679.

Johnson MH. (2005). Developmental cognitive neuroscience. Oxford: Blackwell Publishing.

Jones, N. A., Field, T., & Davalos, M. (2000). Right frontal EFG asymmetry and lack of empathy in preschool children of depressed mothers. *Child Psychiatry & Human Development, 30*(3), 189-204.

Jones, N. A., Field, T., Davalos, M., & Hart, S. (2004). Greater right frontal EEG asymmetry and nonemphathic behavior are observed in children prenatally exposed to cocaine. *International Journal of Neuroscience, 114*(4), 459-480.

Kahana-Kalman, R., & Walker-Andrews, A. S. (2001). The role of person familiarity in young infants' perception of emotional expressions. *Child Development, 72*(2), 352-369.

Knafo, A., & Israel, S. (2012). Empathy, prosocial behavior, and other aspects of kindness. In M. Zentner & R. L. Shiner (Eds.), The *Handbook of temperament* (pp. 168-182). New York: Guilford Press.

Knafo, A., Zahn-Waxler, C., Van Hulle, C., Robinson, J. L., & Rhee, S. H. (2008). The developmental origins of a disposition toward empathy: Genetic and environmental contributions. *Emotion*, *8*(6), 737.

Koelsch, S., Jacobs, A. M., Menninghaus, W., Liebal, K., Klann-Delius, G., von Scheve, C., & Gebauer, G. (2015). The quartet theory of human emotions: an integrative and neurofunctional model. *Physics of life reviews*, *13*, 1-27.

Lee, E., Kang, J. I., Park, I. H., Kim, J. J., & An, S. K. (2008). Is a neutral face really evaluated as being emotionally neutral?. *Psychiatry Research*, *157*(1), 77-85.

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.

Liddle, M. J., Bradley, B. S., & McGrath, A. (2015). Baby Empathy: Infant Distress and Peer Prosocial Responses. *Infant Ment Health J, 36*(4), 446-458.

Lipps, T. (1907). Das wissen von fremden Ichen. *Psychologische untersuchungen*, *1*(4), 694-722.

Malatesta, C. Z., Grigoryev, P., Lamb, C., Albin, M., & Culver, C. (1986). Emotion socialization and expressive development in preterm and full-term infants. *Child development*, 316-330.

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

Martin, G. B., & Clark, R. D. (1982). Distress crying in neonates: Species and peer specificity. *Developmental psychology*, *18*(1), 3.

Meltzoff, A. N., & Decety, J. (2003). What imitation tells us about social cognition: a rapprochement between developmental psychology and cognitive neuroscience. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *358*(1431), 491-500.

Minagawa-Kawai, Y., Matsuoka, S., Dan, I., Naoi, N., Nakamura, K., & Kojima, S. (2008). Prefrontal activation associated with social attachment: facial-emotion recognition in mothers and infants. *Cerebral Cortex*, *19*(2), 284-292.

Montague, D. P., & Walker–Andrews, A. S. (2002). Mothers, fathers, and infants: The role of person familiarity and parental involvement in infants' perception of emotion expressions. *Child development*, *73*(5), 1339-1352.

Moody, E. J., McIntosh, D. N., Mann, L. J., & Weisser, K. R. (2007). More than mere mimicry? The influence of emotion on rapid facial reactions to faces. *Emotion*, *7*(2), 447-457.

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.

Murphy, B. C., Shepard, S. A., Eisenberg, N., Fabes, R. A., & Guthrie, I. K. (1999). Contemporaneous and longitudinal relations of dispositional sympathy to emotionality, regulation, and social functioning. *The Journal of Early Adolescence*, *19*(1), 66-97.

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

Onishi, K. H., & Baillargeon, R. (2005). Do 15-month-old infants understand false beliefs?. *Science*, *308*(5719), 255-258.

Parducci G. (1995). *Happiness, pleasure, and judgment: The contextual theory and its applications*. Mahwah, NJ: Lawrence Erlbaum Associates.

Paulus, M., Kuhn-Popp, N., Licata, M., Sodian, B., & Meinhardt, J. (2013). Neural correlates of prosocial behavior in infancy: Different neurophysiological mechanisms support the emergence of helping and comforting. *Neuroimage, 66*, 522-530.

Peeters, G., & Czapinski, J. (1990). Positive-negative asymmetry in evaluations: The distinction between affective and informational negativity effects. *European review of social psychology*, *1*(1), 33-60.

Pell, M. D., Rothermich, K., Liu, P., Paulmann, S., Sethi, S., & Rigoulot, S. (2015). Preferential decoding of emotion from human non-linguistic vocalizations versus speech prosody. *Biological psychology*, *111*, 14-25.

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.

Perner, J. (1991). Understanding the representational mind. Cambridge, MA: The MIT Press.

Pessoa, L. (2008). On the relationship between emotion and cognition. *Nature Reviews Neuroscience*, *9,* 148–158.

Preston, S. D., & De Waal, F. B. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and brain sciences*, *25*(1), 1-20.

Provine, R. R. (1996). Laughter. *American scientist*, *84*(1), 38-45.

Provine, R. R. (2004). Laughing, tickling, and the evolution of speech and self. *Current Directions in Psychological Science*, *13*(6), 215-218.

Reynolds, G. D., & Guy, M. W. (2012). Brain-behavior relations in infancy: integrative approaches to examining infant looking behavior and event-related potentials. *Developmental Neuropsychology, 37*(3), 210-225.

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

Rothbart, M. K., Ahadi, S. A., & Hershey, K. L. (1994). Temperament and social behavior in childhood. *Merrill-Palmer Quarterly (1982-)*, 21-39.

Rozin, P., & Royzman, E. B. (2001). Negativity bias, negativity dominance, and contagion. *Personality and social psychology review*, *5*(4), 296-320.

Sagi, A., & Hoffman, M. L. (1976). Empathic Distress in Newborn. *Developmental Psychology, 12*(2), 175-176.

Santesso, D. L., Schmidt, L. A., & Trainor, L. J. (2007). Frontal brain electrical activity (EEG) and heart rate in response to affective infant-directed (ID) speech in 9-month-old infants. *Brain and Cognition, 65*(1), 14-21.

Schirmer, A., & Kotz, S. A. (2006). Beyond the right hemisphere: brain mechanisms mediating vocal emotional processing. *Trends in cognitive sciences*, *10*(1), 24-30.

Scott, R. M., & Baillargeon, R. (2009). Which penguin is this? Attributing false beliefs about object identity at 18 months. *Child development*, *80*(4), 1172-1196.

Scott, S. K., Lavan, N., Chen, S., & McGettigan, C. (2014). The social life of laughter. *Trends in cognitive sciences*, *18*(12), 618-620.

Simner, M. L. (1971). Newborns Response to Cry of Another Infant. *Developmental Psychology, 5*(1), 136-150.

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

Singh, L., Morgan, J. L., & Best, C. T. (2002). Infants' listening preferences: Baby talk or happy talk?. *Infancy*, *3*(3), 365-394.

Sirois, S., & Jackson, L. (2007). *Pupil dilation and infant cognition*. Paper presented at IEEE 6th International Conference on Development and Learning, London, UK.

Song, H. J., Onishi, K. H., Baillargeon, R., & Fisher, C. (2008). Can an agent's false belief be corrected by an appropriate communication? Psychological reasoning in 18-month-old infants. *Cognition*, *109*(3), 295-315.

Soussignan, R., Chadwick, M., Philip, L., Conty, L., Dezecache, G., & Grèzes, J.

(2013). Self-relevance appraisal of gaze direction and dynamic facial expressions: effects on facial electromyographic and autonomic reactions. *Emotion*, *13*(2), 330.

Stefani, L. H., & Camaioni, L. (1983). Effects of familiarity on peer interaction in the first year of life. *Early Child Development and Care*, *11*(1), 45-54.

Stets, M., Stahl, D., & Reid, V. M. (2012). A meta-analysis investigating factors underlying attrition rates in infant ERP studies. *Developmental Neuropsychology*, *37*(3), 226-252.

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

Szameitat, D. P., Kreifelts, B., Alter, K., Szameitat, A. J., Sterr, A., Grodd, W., & Wildgruber, D. (2010). It is not always tickling: distinct cerebral responses during perception of different laughter types. *Neuroimage, 53*(4), 1264-1271.

Taylor, S. E. (1991). Asymmetrical effects of positive and negative events: the mobilization-minimization hypothesis. *Psychological bulletin*, *110*(1), 67.

Träuble, B., Marinović, V., & Pauen, S. (2010). Early theory of mind competencies: do infants understand others' beliefs?. *Infancy*, *15*(4), 434-444.

Tschacher, W., Schildt, M., & Sander, K. (2010). Brain connectivity in listening to affective stimuli: a functional magnetic resonance imaging (fMRI) study and implications for psychotherapy. *Psychotherapy research*, *20*(5), 576-588.

Ungerer, J. A., Dolby, R., Waters, B., Barnett, B., Kelk, N., & Lewin, V. (1990). The early development of empathy: Self-regulation and individual differences in the first year. *Motivation and emotion*, *14*(2), 93-106.

Upshaw, M. B., Kaiser, C. R., & Sommerville, J. A. (2015). Parents’ empathic perspective taking and altruistic behavior predicts infants’ arousal to others’ emotions. *Frontiers in Psychology*, *6*, 360.

Vaish, A., Grossmann, T., & Woodward, A. (2008). Not all emotions are created equal: the negativity bias in social-emotional development. *Psychological bulletin*, *134*(3), 383.

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. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature neuroscience*, *6*(6), 624.

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

Wellman, H. M., & Bartsch, K. (1988). Young children's reasoning about beliefs. *Cognition, 30*(3), 239-277.

Wellman, H. M., Cross, D., & Watson, J. (2001). Meta-analysis of theory-of-mind development: the truth about false belief. *Child Development, 72*(3), 655-684.

Wieser, M. J., & Brosch, T. (2012). Faces in context: a review and systematization of contextual influences on affective face processing. *Frontiers in psychology*, *3*.

Wildgruber, D., Szameitat, D. P., Ethofer, T., Bruck, C., Alter, K., Grodd, W., & Kreifelts, B. (2013). Different types of laughter modulate connectivity within distinct parts of the laughter perception network. *PLoS One, 8*(5), e63441.

Williams, L. M. (2006). An integrative neuroscience model of" significance" processing. *Journal of integrative neuroscience*, *5*(01), 1-47.

Wimmer, H., & Perner, J. (1983). Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition*, *13*(1), 103-128.

Young, G., & Lewis, M. (1979). Effects of familiarity and maternal attention on infant peer relations. *Merrill-Palmer Quarterly of Behavior and Development*, *25*(2), 105-119.

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

Appendix A

Gender Difference Analyses for Paper 1

Table 1.

Principal statistics for the 3 (Emotion) x 2 (Hemisphere) repeated measures ANOVA conducted on N100 mean amplitudes including gender as a between-subjects factor (N = 30)

Source	ANOVA Parameter Estimates
Emotion	$F(2,56) = 6.639$; $p = .003$, $\eta^2_p = .192$
Emotion*Gender	$F(2,56) = 2.529$; $p = .089$, $\eta^2_p = .083$
Hemisphere	$F(1,28) = 1.402$; $p = .246$, $\eta^2_p = .048$
Hemisphere*Gender	$F(1,28) = .236$; $p = .631$, $\eta^2_p = .008$
Emotion*Hemisphere	$F(2,56) = .595$; $p = .555$, $\eta^2_p = .021$
Emotion*Hemisphere*Gender	$F(2,56) = 2.157$; $p = .125$, $\eta^2_p = .072$

Note: $N_{female} = 13$; $N_{male} = 17$

Table 2.

Principal statistics for the 3 (Emotion) x 2 (Hemisphere) repeated measures ANOVA conducted on P200 mean amplitudes including gender as a between-subjects factor (N = 30)

Source	ANOVA Parameter Estimates
Emotion	$F(2,56) = 4.993$; $p = .010$, $\eta^2_p = .151$
Emotion*Gender	$F(2,56) = 2.257$; $p = .114$, $\eta^2_p = .075$
Hemisphere	$F(1,28) = .488$; $p = .490$, $\eta^2_p = .017$
Hemisphere*Gender	$F(1,28) = .039$; $p = .845$, $\eta^2_p = .001$
Emotion*Hemisphere	$F(2,56) = .566$; $p = .571$, $\eta^2_p = .020$
Emotion*Hemisphere*Gender	$F(2,56) = .688$; $p = .507$, $\eta^2_p = .072$

Note: $N_{female} = 13$; $N_{male} = 17$

Table 3.

Principal statistics for the 3 (Emotion) x 2 (Hemisphere) repeated measures ANOVA conducted on LPC mean amplitudes including gender as a between-subjects factor (N = 30)

Source	ANOVA Parameter Estimates
Emotion	$F(2,56) = 3.731; p = .030, \eta^2_p = .118$
Emotion*Gender	$F(2,56) = .459; p = .634, \eta^2_p = .016$
Hemisphere	$F(1,28) = .057; p = .813, \eta^2_p = .002$
Hemisphere*Gender	$F(1,28) = 2.335; p = .138, \eta^2_p = .077$
Emotion*Hemisphere	$F(2,56) = .950; p = .393, \eta^2_p = .033$
Emotion*Hemisphere*Gender	$F(2,56) = 1.355; p = .266, \eta^2_p = .046$

Note: $N_{female} = 13$; $N_{male} = 17$

Appendix B

Gender Difference Analyses for Paper 2

Table 1.
Principal statistics for the 2 (Condition) x 2 (Hemisphere) repeated measures ANOVA performed on the log-transformed alpha power values including gender as a between-subjects factor (N =32)

Source	ANOVA Parameter Estimates
Condition	$F(1,30) = .711$; $p = .406$, $\eta^2_p = .023$
Condition*Gender	$F(1,30) = .031$; $p = .862$, $\eta^2_p = .001$
Hemisphere	$F(1,30) = .995$; $p = .327$, $\eta^2_p = .032$
Hemisphere*Gender	$F(1,30) = 1.028$; $p = .319$, $\eta^2_p = .033$
Condition*Hemisphere	$F(1,30) = 6.029$; $p = .020$, $\eta^2_p = .167$
Condition*Hemisphere*Gender	$F(1,30) = .889$; $p = .353$, $\eta^2_p = .029$

Note: $N_{female} = 15$; $N_{male} = 17$

Table 2.
Principal statistics for the 2 (Condition) x 2 (Emotion facial expressions) repeated measures ANOVA performed on the percentages of emotional facial expressions including gender as a between-subjects factor (N = 22)

Source	ANOVA Parameter Estimates
Condition	$F(1,20) = .104$; $p = .750$, $\eta^2_p = .005$
Condition*Gender	$F(1,20) = .552$; $p = .466$, $\eta^2_p = .027$
Emotion	$F(1,20) = 3.152$; $p = .091$, $\eta^2_p = .136$
Emotion*Gender	$F(1,20) = .660$; $p = .426$, $\eta^2_p = .032$
Condition*Emotion	$F(1,20) = 16.450$; $p = .001$, $\eta^2_p = .451$
Condition*Emotion*Gender	$F(1,20) = .493$; $p = .491$, $\eta^2_p = .024$

Note: $N_{female} = 13$; $N_{male} = 9$

Table 3.

Principal statistics for the 2 (Condition) x 3 (Emotion vocal expressions) repeated measures ANOVA for emotional vocalizations percentages including gender as a between-subjects factor (N = 22)

Source	ANOVA Parameter Estimates
Condition	$F(1,20) = 7.044$; $p = .015$, $\eta^2_p = .260$
Condition*Gender	$F(1,20) = .006$; $p = .941$, $\eta^2_p = .000$
Emotion	$F(2,40) = 3.071$; $p = .057$, $\eta^2_p = .133$
Emotion*Gender	$F(2,40) = .332$; $p = .720$, $\eta^2_p = .016$
Condition*Emotion	$F(2,40) = 5.248$; $p = .009$, $\eta^2_p = .208$
Condition*Emotion*Gender	$F(2,40) = 1.143$; $p = .329$, $\eta^2_p = .054$

Note: $N_{female} = 13$; $N_{male} = 9$

Table 4.

Principal statistics for paired-sample t-tests performed on looking time, withdrawal and approach behaviours percentages for each condition including gender as a between-subjects factor (N = 22)

Source	Paired-Sample T-Tests Parameters
% Looking Time_Cry	$t(20) = 1.444$; $p = .164$
% Looking Time_Laughter	$t(20) = 2.695$; $p = .014$
% Withdraw_Cry	$t(20) = -1.133$; $p = .271$
% Withdraw_Laughter	$t(20) = .221$; $p = .827$
% Approach_Cry	$t(20) = .238$; $p = .814$
% Approach_Laughter	$t(20) = 1.956$; $p = .065$

Note: $N_{female} = 13$; $N_{male} = 9$

Appendix C

Gender Difference Analyses for Paper 3

Table 1.
Principal statistics for the 3 *(Muscle) x 3 (Emotion) x 2 (Time Window) repeated measures ANOVA conducted on the muscle mean amplitude z-scores including gender as a between-subjects factor for the 7-month-old group (N = 24)*

Source	ANOVA Parameter Estimates
Muscle	$F(2,44) = 2.021$; $p = .145$, $\eta^2_p = .084$
Muscle*Gender	$F(2,44) = 1.449$; $p = .246$, $\eta^2_p = .062$
Emotion	$F(2,44) = 1.937$; $p = .156$, $\eta^2_p = .081$
Emotion*Gender	$F(2,44) = .073$; $p = .930$, $\eta^2_p = .003$
Time Window	$F(1,22) = 1.889$; $p = .183$, $\eta^2_p = .079$
Time Window*Gender	$F(1,22) = .787$; $p = .385$, $\eta^2_p = .035$
Muscle*Emotion	$F(4,88) = 2.133$; $p = .083$, $\eta^2_p = .088$
Muscle*Emotion*Gender	$F(4,88) = 1.019$; $p = .402$, $\eta^2_p = .044$
Muscle*Time Window	$F(2,44) = .116$; $p = .890$, $\eta^2_p = .005$
Muscle*Time Window*Gender	$F(2,44) = .360$; $p = .699$, $\eta^2_p = .016$
Emotion*Time Window	$\mathrm{F}(2,44) = 3.600$; $p = .036$, $\eta^2_p = .141$
Emotion*Time Window*Gender	$F(2,44) = 1.019$; $p = .339$, $\eta^2_p = .048$
Muscle*Emotion*Time Window	$F(4,88) = 3.081$; $p = .020$, $\eta^2_p = .123$
Muscle*Emotion*Time Window*Gender	$F(4,88) = .468$; $p = .759$, $\eta^2_p = .021$

Note: $\mathrm{N}_{\mathrm{female}} = 14$; $\mathrm{N}_{\mathrm{male}} = 10$

Appendix D

Gender Difference Analyses for Paper 4

Table 1.
Principal statistics for the 2 (Belief) x 3 (Region) repeated measures ANOVA conducted on N400 mean amplitude including gender as a between-subjects factor (N =16)

Source	ANOVA Parameter Estimates
Belief	$F(1,14) = .040$; $p = .844$, $\eta^2_p = .003$
Belief*Gender	$F(1,14) = .411$; $p = .532$, $\eta^2_p = .028$
Region	$F(2,28) = 53.021$; $p = .000$, $\eta^2_p = .791$
Region*Gender	$F(2,28) = 3.110$; $p = .060$, $\eta^2_p = .182$
Belief*Region	$F(2,28) = 6.719$; $p = .004$, $\eta^2_p = .324$
Belief*Region*Gender	$F(2,28) = 2.262$; $p = .123$, $\eta^2_p = .139$

Note: $N_{female} = 8$; $N_{male} = 8$

Table 2.
Principal statistics for the 2 (Belief) x 3 (Region) repeated measures ANOVA conducted on N400 peak amplitude including gender as a between-subjects factor (N = 16)

Source	ANOVA Parameter Estimates
Belief	$F(1,14) = .131$; $p = .723$, $\eta^2_p = .009$
Belief*Gender	$F(1,14) = .327$; $p = .576$, $\eta^2_p = .023$
Region	$F(2,28) = 48.608$; $p = .000$, $\eta^2_p = .776$
Region*Gender	$F(2,28) = 3.555$; $p = .042$, $\eta^2_p = .203$
Belief*Region	$F(2,28) = 5.779$; $p = .008$, $\eta^2_p = .292$
Belief*Region*Gender	$F(2,28) = 2.279$; $p = .121$, $\eta^2_p = .140$

Note: $N_{female} = 8$; $N_{male} = 8$

Appendix E

Power Analyses for Paper 1

The sample size of 30 was used to run post-hoc power analyses for the entire data set. For this study, separated 3 (Emotion: laughter, crying, coughing) x 2 (Hemisphere: left , right) repeated measures ANOVAs were conducted on the mean amplitude of different ERP components at frontal locations (i.e. N100, P200 and LPC). Power estimates are reported for the main effects and interaction of all the ANOVAs. The analyses were performed using the program GPower[1].

Frontal N100

This study had more than ample power to detect an effect of emotion, hemisphere and their interaction, at the observed magnitude, given that such effects truly exist in the population. Power analyses are shown in Table 1.

Table 1.
Power statistics for the N100 component (N = 30)

Source	Effect size	# Groups	# Measurements	Power
Main effect Emotion	.168	3	46	>.95
Main effect Hemisphere	.043	2	138	>.95
Interaction	.021	6	138	>.95

Note. Effect size refers to η^2_p

Frontal P200 (corrected)

This study did not have sufficient power to determine whether there actually exists effects of this magnitude in the population. Power analyses are shown in Table 2.

Table 2.
Power statistics for the P200 (corrected) component (N = 30)

Source	Effect size	# Groups	# Measurements	Power
Main effect Emotion	.003	3	46	.159
Main effect Hemisphere	.001	2	138	.054
Interaction	.017	6	138	.154

Note. Effect size refers to η^2_p

Frontal LPC

This study had more than ample power to detect the effect of emotion at the observed level given that one actually exists. Same for the interaction. However, it did not have sufficient power to be confident that there truly is no effect in the population for hemisphere (5% power). Power analyses are shown in Table 3.

Table 3.
Power statistics for the LPC component (N = 30)

Source	Effect size	# Groups	# Measurements	Power
Main effect Emotion	.125	3	46	>.95
Main effect Hemisphere	.000	2	138	.050
Interaction	.036	6	138	>.95

Note. Effect size refers to η^2_p

---

[1] Erdfelder, E., Faul, F., & Buchner, A. (1996). GPOWER: A general power analysis program. *Behavior research methods, instruments, & computers*, *28*(1), 1-11.

Appendix F

Power Analyses for Paper 2

Frontal Asymmetry measures

The sample size of 32 was used to run a post-hoc power analysis for the EEG dataset. Specifically, one 2 (Condition: peer laughing film, peer crying film) x 2 (Hemisphere: left, right) repeated measures ANOVA was conducted on the log-transformed alpha power values. Power estimates for the main effects and interaction of this ANOVA are shown in Table 1. The analyses were performed using the program GPower[1].

Table 1.
Power statistics for log-transformed alpha power values (N = 32)

Source	Effect size	# Groups	# Measurements	Power
Main effect Condition	.024	2	179	>.95
Main effect Hemisphere	.035	2	358	>.95
Interaction	.157	6	358	>.95

Note. Effect size refers to η^2_p

This study had more than ample power to detect effects of condition, hemisphere and interaction of this magnitude given that one truly exists in the population.

Behavioural measures

For infants' emotional facial expressivity, the sample size of 22 was used to run a post-hoc power analysis. One 2 (Condition: peer laughing film, peer crying film) x 2 (Emotion expression: positive, negative) repeated measures ANOVA was conducted on the percentage of emotional facial expressions coded. Power estimates for each main effect and interaction of the ANOVA are illustrated in Table 2.

Table 2.
Power statistics for facial expressions of affect (N = 22)

Source	Effect size	# Groups	# Measurements	Power
Main effect Condition	.010	2	12	.289
Main effect Emotion	.156	2	24	>.95
Interaction	.438	4	24	>.95

Note. Effect size refers to η^2_p

This study did not have sufficient power to determine whether there actually exists an effect of condition of this magnitude in the population (28.9% chance). Yet, it had ample power to detect the observed effect of emotion and interaction effect, assuming that these effects truly exist.

For infants' emotional vocalisations, the sample size of 22 was used to run a post-hoc power analysis. One 2 (Condition: peer laughing film, peer crying film) x 3 (Emotion expression: positive, negative, neutral) repeated measures ANOVA was conducted on the percentage of emotional vocal expressions coded. Power estimates for the main effects and interaction of the ANOVA are illustrated in Table 3.

Table 3.
Power statistics for vocal expressions of affect (N = 22)

Source	Effect size	# Groups	# Measurements	Power
Main effect Condition	.269	2	12	>.95
Main effect Emotion	.128	3	24	>.95
Interaction	.184	6	24	>.95

Note. Effect size refers to η^2_p

This study had more than ample power to detect an effect of emotion, vocalisation and their interaction at the observed magnitude, given that such effects truly exist in the population.

Further post-hoc power analyses were conducted across a series of paired-sample t-tests run for withdrawal, approach and looking time measures with condition as independent variable. These results are reported in Table 4.

Table 4.
Power statistics for approach/withdrawal behaviours and looking time measures (N = 22)

Source	Effect size	# Groups	# Measurements	Power
Approach	.095	2	12	.071
Withdrawal	.115	2	12	.082
Looking time	.422	2	12	.473

Note. Effect size refers to Cohen's *d*

Overall, this study did not have enough power to detect an effect of emotion for approach/withdrawal behaviours, assuming that such effects truly exist in the population. Nonetheless, it had low to medium power (47.3% power) to detect an effect of emotion for looking time measures at the observed size.

---

[1] Erdfelder, E., Faul, F., & Buchner, A. (1996). GPOWER: A general power analysis program. *Behavior research methods, instruments, & computers*, *28*(1), 1-11.

Appendix G

Power Analyses for Paper 3

The sample size of 24 7-month-old infants and 27 4-month-old infants were used respectively to run post-hoc power analyses for the key main effects and contrasts. For this study, separated 3 (Emotion: happiness, anger, fear) x 3 (Muscle: zygomaticus, corrugator, frontalis) x 2 (Time Window: 0-1 sec, 1-3 sec) repeated measures ANOVAs were conducted on the z scores of muscle activity mean amplitude for each age group. Power estimates are reported for the main effects and key interactions of all ANOVAs. The analyses were performed using the program GPower[1].

EMG Results for 7-month-old infants

This study had ample power to detect all of the observed effects in 7-month-old infants, given that these effects truly exist at the reported level (see Table 1 for more details).

Table 1.
Power statistics for the EMG results on 7-month-old infants (N = 24)

Source	Effect size	# Groups	# Measurements	Power
Main effect Emotion	.088	3	20	>.95
Main effect Muscle	.099	3	60	>.95
Main effect Time Window	.095	2	60	>.95
Emotion*Muscle	.085	9	60	>.95
Emotion*Muscle*Time Window	.130	18	60	>.95

Note. Effect size refers to η^2_p

EMG Results for 4-month-old infants

This study had sufficient power to detect all of the observed effects, given that these effects truly exist in the population. Yet, it is important to highlight that there was only a 46.6% chance of detecting the observed effect size of emotion for this age group. Power estimates are presented in Table 2.

Table 2.
Power statistics for the EMG results on the 4-month-old infants (N = 27)

Source	Effect size	# Groups	# Measurements	Power
Main effect Emotion	.016	3	20	.466
Main effect Muscle	.031	3	60	>.95
Main effect Time Window	.108	2	60	>.95
Emotion*Muscle	.112	9	60	>.95
Emotion*Muscle*Time Window	.063	18	60	>.95

Note. Effect size refers to η^2_p

---

[1] Erdfelder, E., Faul, F., & Buchner, A. (1996). GPOWER: A general power analysis program. *Behavior research methods, instruments, & computers*, *28*(1), 1-11.

Appendix H

Power Analyses for Paper 4

The sample size of 16 was used to run post-hoc power analyses for the entire data set. For this study, separated 2 (Belief: FB congruent, FB incongruent) x 3 (Region: frontal, central, parietal) repeated measures ANOVA were conducted on the mean and peak amplitude of the N400 component. Power estimates are reported for each main effect and interaction of the corresponding ANOVAs. The analyses were performed using the program GPower[1].

For the N400 mean amplitude, this study had the highest level of power to detect all (but one) of the observed effects, given that these effects truly exist at the level observed. Specifically, this study had lower power (8% chance) to detect an effect of condition at the observed size. For further details, see Table 1.

Table 1.
Power statistics for the N400 mean amplitude (N = 16)

Source	Effect size	# Groups	# Measurements	Power
Main effect Belief	.003	2	20	.080
Main effect Region	.756	3	60	>.95
Interaction	.292	6	60	>.95

Note. Effect size refers to η^2_p

Similarly, for the N400 peak amplitude, this study had the highest level of power to detect all (but one) of the observed effects, given that these effects truly exist at the level we reported. Specifically, this study had lower power (1.65% chance) to detect an effect of condition at the observed size. Power estimates are presented in Table 2.

Table 2.
Power statistics for the N400 peak amplitude (N = 16)

Source	Effect size	# Groups	# Measurements	Power
Main effect Belief	.009	2	20	.165
Main effect Region	.735	3	60	>.95
Interaction	.262	6	60	>.95

Note. Effect size refers to η^2_p

---

[1] Erdfelder, E., Faul, F., & Buchner, A. (1996). GPOWER: A general power analysis program. *Behavior research methods, instruments, & computers*, *28*(1), 1-11.

Appendix I

Peak-to-Peak Analysis for Paper 4

Given the temporal proximity between the N400 (450 – 600 ms) component and the N300 (250 – 350 ms) at frontal locations, it is possible that variations in the N300 parameters may have affected the N400 component differently across conditions. Thus, complementary peak-to-peak measurements and analyses were performed to control for N300 variations. With this purpose, same statistical analyses were performed on the measure of the mean amplitude difference between the peak of the N400 and the N300 (i.e. N400-N300). These analyses revealed non-significant main effects or interactions ($p < .067$). Therefore, when accounting for peak-to-peak amplitude differences, the Belief x Region interaction disappears. Table 1 illustrates the 2 (Belief: FB congruent, FB incongruent) x 3 (Region: frontal, central, parietal) repeated measures ANOVA results for the corrected N400.

Table 1.
Principal statistics for the 2 (Belief) x 3 (Region) repeated measures ANOVA conducted on the mean amplitude difference between the peak of the N400 and the N300 (N = 16)

Source	ANOVA Parameter Estimates
Belief	$F(1,15) = .225$; $p = .642$, $\eta^2_p = .015$
Region	$F(2,30) = 2.956$; $p = .067$, $\eta^2_p = .165$
Belief*Region	$F(2,30) = 1.516$; $p = .236$, $\eta^2_p = .092$

Appendix J

Repeated-Measures ANOVA with Hemisphere as a Factor for Paper 4

An increasing amount of fMRI studies emphasizes the dominant role of the right hemisphere in mentalizing tasks[1,2,3]. These results go in line with lesion studies reporting Theory of Mind (TOM) impairments in patients with right hemispheric lesions[4,5]. Nonetheless, the literature contains opposing results with other studies depicting a higher activation of the left hemisphere during TOM tasks. Certainly, such disparities could be explained by differences in the task and stimuli used among studies.

Following the empirical evidence pointing towards a differential involvement of the left and right hemisphere on TOM processing, the emergence of hemispheric differences on the N400 component was explored. With this purpose, independent 2 (Belief: FB congruent, FB incongruent) x 3 (Region: frontal, central, parietal) x 2 (Hemisphere: left, right) repeated measures ANOVAs were conducted on the N400 mean and peak amplitude (see Table 1 and 2 for full parameters).

Notably, the addition of hemisphere did not to provide any valuable information. Specifically, the analysis of the mean amplitude for this time window did not reveal neither a significant Belief x Hemisphere interaction ($F(1,15) = .089$, $p = .769$, $\eta^2_p = .006$) nor a significant Belief x Hemisphere x Region interaction ($F(1,15) = 1.109$, $p = .343$, $\eta^2_p = .069$). Similar results were found for the peak amplitude, where the analysis failed to find a significant Belief x Hemipshere interaction ($F(1,15) = .211$, $p = .652$, $\eta^2_p = .014$) as well as a significant Belief x Hemisphere x Region interaction ($F(1,15) = .552$, $p = .581$, $\eta^2_p = .036$).

Notably, post-hoc power analyses indicated that this study had ample power (>.095 power) to detect both interaction effects at the observed size, assuming that such effects exist in the population. Thus, based on power calculations, we had sufficient power to detect a Belief x Hemisphere and a Belief x Hemisphere x Region interaction effects of the magnitude observed, if such effects really exist.

Altogehter, this study has failed to report hemispheric differences on the morphology of the N400 component as a function of belief (i.e. FBc, FBi).

Table 1.
Principal statistics for the 2 (Belief) x 3 (Region) x 2 (Hemisphere) repeated measures ANOVA conducted on the N400 mean amplitude (N = 16)

Source	ANOVA Parameter Estimates
Belief	$F(1,15) = .042$; $p = .841$, $\eta^2_p = .003$
Region	$F(2,30) = 46.483$; $p = .000$, $\eta^2_p = .756$
Hemisphere	$F(1,15) = 4.069$; $p = .062$, $\eta^2_p = .213$
Belief*Region	$F(2,30) = 6.198$; $p = .006$, $\eta^2_p = .292$
Belief*Hemipshere	$F(1,15) = .089$; $p = .769$, $\eta^2_p = .006$
Region*Hemisphere	$F(2,30) = 1.771$; $p = .187$, $\eta^2_p = .106$
Belief*Region*Hemisphere	$F(2,30) = 1.109$; $p = .343$, $\eta^2_p = .069$

Table 2.
Principal statistics for the 2 (Belief) x 3 (Region) x 2 (Hemisphere) repeated measures ANOVA conducted on the N400 peak amplitude (N = 16)

Source	ANOVA Parameter Estimates
Belief	$F(1,15) = .137$; $p = .716$, $\eta^2_p = .009$
Region	$F(2,30) = 41.533$; $p = .000$, $\eta^2_p = .735$
Hemisphere	$F(1,15) = 3.832$; $p = .069$, $\eta^2_p = .203$
Belief*Region	$F(2,30) = 5.325$; $p = .010$, $\eta^2_p = .262$
Belief*Hemipshere	$F(1,15) = .211$; $p = .652$, $\eta^2_p = .014$
Region*Hemisphere	$F(2,30) = 1.973$; $p = .157$, $\eta^2_p = .116$
Belief*Region*Hemisphere	$F(2,30) = .552$; $p = .581$, $\eta^2_p = .036$

[1] Gallagher, H. L., Happé, F., Brunswick, N., Fletcher, P. C., Frith, U., & Frith, C. D. (2000). Reading the mind in cartoons and stories: an fMRI study of 'theory of mind'in verbal and nonverbal tasks. *Neuropsychologia*, *38*(1), 11-21.

[2] Saxe, R., & Wexler, A. (2005). Making sense of another mind: the role of the right temporo-parietal junction. *Neuropsychologia*, *43*(10), 1391-1399.

[3] Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happé, F., Falkai, P., ... & Zilles, K. (2001). Mind reading: neural mechanisms of theory of mind and self-perspective. *Neuroimage*, *14*(1), 170-181.

[4] Happé, F., Brownell, H., & Winner, E. (1999). Acquiredtheory of mind'impairments following stroke. *Cognition*, *70*(3), 211-240.

[5] Weed, E., McGregor, W., Nielsen, J. F., Roepstorff, A., & Frith, U. (2010). Theory of Mind in adults with right hemisphere damage: What's the story?. *Brain and Language*, *113*(2), 65-72.