NEURAL CORRELATES FOR BODY PERCEPTION DEVELOPMENT DURING CHILDHOOD

by

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Declarations

I declare that the 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 development of the neural mechanism underlying emotional body perception, during childhood, using Event-Related Potentials (ERPs). Understanding other people's emotional status is a crucial need in children's everyday interactions. Literature suggests that children benefit from body cues as much as they do from facial cues in identifying emotion (Nelson & Russell, 2011). Moreover, bodily emotion recognition is an important indicator of children's cognitive development (Atkinson, 2009; Munoz, 2009). However, despite being such an important cue of emotion information for children, the neural mechanism behind emotional body perception, as well as its developmental pattern during childhood, remained poorly investigated.

This thesis is comprised of three studies that explored these unknown areas in the field. Paper 1 examined the developmental changes in the neural mechanism underlying body perception, by looking at the associated ERPs in response to upright and inverted bodies. Results revealed an opposite body inversion effect across 3-10-year-old children compared to that of adults, suggesting that adult-like processing is still not achieved until late childhood.

Paper 2 examined emotion processing from static body postures in 5-8-years-old children. Findings suggested from the age of 5 children show early emotion sensitivity at the body structure encoding stage. Furthermore, body representation was found to interfere with emotion perception.

Paper 3 examined emotional body perception in realistic seeting by looking at 3-6-year-old children's neural response to semantic incongruent effects of pair point-light displays of body movements and target emotional words. Results indicated that, from the age of 3, children can extract emotional information from subtle body movements and integrate semantic meaning to this.

Overall, the current work addresses the development of children's body emotion recognition in terms of the neural fundamentals of body recognition and emotion recognition from static, as well as from dynamic postures. This thesis provided essential evidence for reducing the knowledge gap in emotional body perception development.

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Dedication

For Yu Wu

The kindest woman who supported my PhD,

and a true girl who deserves a better life.

Statement of Authorship

Paper one: The development of human body perception during childhood. An ERP investigation of the body-inversion effect

Han Ke and Elena Geangu

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Paper two: Inversion effect in children's emotional body perception: an ERP investigation

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Through signing this Statement, the supervisors and co-authors agree that:

a) the student's contribution to all the papers above is correct;

b) the student can incorporate these papers within the thesis;

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Neural Correlates for Body Perception Development During Childhood: An Introduction

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Neural Correlates for Body Perception Development During Childhood: An Introduction

Thesis overview

As humans are social animals, understanding each other's emotions is a constant need in everyday interaction. Therefore, our ability to recognise emotions develops from a very early stage of life. Emotions are expressed from multiple cues such as facial expressions and vocalizations. With the development of motor ability and increasingly complicated social interactions, the body expression becomes a much more important resource of emotional information. Imagine a child playing hide and seek with a group of peers. The child has to quickly detect if they should run away from potential "danger" (i.e. the seeker) in their surroundings. When detecting their friends' sudden emotional change, their facial expressions, their screaming, or their body movements could be relevant signals. During such fast moments, a friend's face could be too small and far away to see its expression; vocal expressions might not happen every time a friend detects a threat. Among all these resources, as the physically biggest target, the moving body becomes the most reliable resource to detect emotional information.

Previously, most of the investigations into infants and children relied on only their inferring of emotion from facial expressions. However, with the increasing complexity of social interaction, starting from childhood, facial expressions are not always easy to decode. Such as in the situation described above, when facial expression is difficult to detect, or when children are in urgent situations that don't allow them to observe the face clearly, a quick glance of the body would give all the necessary information. In fact, bodily emotion recognition is found as an important indicator in cognitive development. For example, individuals with autism spectrum disorders (ASD) have difficulty in recognising emotions from body movement (Atkinson, 2009; Hubert et al., 2007; Philip et al., 2010; Nackaerts et al., 2012); impairment in detecting fearful information from the body is also found related to higher callous-unemotional traits in children (Munoz, 2009). Moreover, pre-school children's emotion knowledge from body cues are found to be associated to their social skills reported by their teachers and caregivers (Parker, Mathis & Kupersmidt, 2013). These findings suggest that studying children's emotion recognition ability from body cues can be essential in identifying children's social and behavioural functioning in practice. Evidence from recent studies from both children and adults discovered that the body's role in information delivery is as important as the face. Behavioural investigation with adults and children found that performance benefits from multiple cues when both facial and body expressions are presented; furthermore, the accuracy recognising expressions from the body is similar to that for faces (Montepare, Koff, Zaitchik, & Albert, 1999; Vieillard & Guidetti, 2009; Nelson & Russell, 2011). At the neuroscientific level, any inconsistent expression between bodies and faces is immediately recognised by the brain (Fallon & Rozin, 1985; Singh, 1993; Meeren, van Heijnsbergen & de Gelder, 2005; Nelson & Russell, 2011; Robbins & Coltheart, 2015). When detecting some extreme emotions, body cues are even more helpful than the face (Aviezer, Trope, & Todorov, 2012). Nonetheless, despite the handful of studies that have provided some rough information about the early emergence of sensitivity to emotion recognition from verbal cues and children's body perception, surprisingly, a large knowledge gap has been left in this research field from a developmental standpoint.

The current thesis aims to contribute to the missing pieces in this field by looking at the neural mechanisms underlying emotional body processing, during childhood, using event-related brain potentials (ERPs). In order to achieve this, three studies were conducted. Paper 1 aimed to reveal the neural mechanism underlying static body structure processing in children, providing fundamental knowledge for additional investigations. Based on Paper 1, Paper 2 examined the neural correlates of children's emotion processing from static body postures. Paper 3 aimed to extend our understanding of children's emotional body perception in naturalistic environment, looking at how children extract emotion from moving bodies. To be specific, in Paper 1, we investigated the neural mechanism in body representation encoding by examining the body inversion effect on 3- to 10-year-old children's ERPs responses. Further, Paper2 investigated the cognitive processing sub-serving children's emotion processing from static body postures. Finally, Paper 3 looked at the neural mechanism in extracting emotional information from dynamic body movement, using point-light displays (PLDs) of emotional body expression.

In all the studies of the current work, we measure and analyse the mean, peak amplitudes as well as the latencies of all the ERP components. The peak amplitude value is the highest voltage within a time window, and the latency is the time of this point. These two measurements are the typical ways to describe ERP components' morphology and time course. The mean amplitude is computed by taking the voltage at each sample point within a time window and averaging the voltages. The mean amplitude indicates the area of a components within a time window, which is a common alternative to peak amplitude as it's believed to be more reliable (Luck, 2014). Especially in early developmental study, the nosiness of ERP data brings great challenge in peak amplitude and latency measurement. However, the time course of cognitive processing is one of the important features we are interested in in the current work. Given the age range covered in the current work is old enough to emerge peaked adult waveform (DeBoer, Scott, & Nelson, 2007), in the current work we also look at peak amplitude and latency, with carefully computed methods explained in each paper.

In this introductory chapter I will therefore outline our current knowledge of the bodily emotion recognition in the developmental domain. We will begin by reviewing the emotion recognition development in children. In the following section, the encoding of body shape in children will be introduced as the fundamental point to the emotional body perception. When we are detecting the emotion delivered by body, we are perceiving the information from body in two ways: the peak postures of the emotion portrayal, and the dynamic process of the continuous movement. Therefore, based on the knowledge reviewed in this section, the next section will focus on the previous literature on children's perception of emotional body expressivity in terms of both static body postures; while the last section will review our current knowledge of the development of emotion perception from dynamic body movement.

Emotion processing in childhood and the neglected role of bodily expressivity

Identifying other people's emotion is an important ability for children. Emotion identification behaviours such as capturing peer's emotion during play or reading caregiver's emotion status during everyday life are adaptively meaningful for children's everyday life. Empirical evidence suggested that children's emotion knowledge is positively related to their social cognitive development. For example, children who have more emotion knowledge are better liked by their peers and teacher, they also show more prosocial responsiveness to peers (Denham, McKinley, Couchoud, & Holt, 1990). Furthermore, children who recognize emotions better also show higher frequencies of positive social behaviours and better academic competence (Channell, Conners & Barth, 2014). In this section, we will start from the basic theoretical background of emotion theories; we will then move to the development of emotion processing, and discuss the important role of body in emotion processing development.

A brief introduction of the emotion theories

Three major emotion theoretical approaches have been developed to explain the process underlying affective responses; these approaches also contribute to our understanding of the development of children's emotion processing. The first one is the discrete-category model (the basic emotion model) based on the basic emotion theories (Izard 1977; Ekman, 1993). The functional hypothesis is that there are six basic emotions (happy, sad, fear, anger, surprise, disgust) which are universal. The specific affect programme corresponding to each basic emotion is triggered by each specific type of event (Izard 1977; Ekman, 1993). The development of emotion perception under this model is suggested to be a progression of understanding emotions from the most basic level to more specific emotion categories with the maturation of processing and the experience of events (Ekman, 1992, 1993; Panksepp, 1998; see Figure 1).

Another approach to emotion investigation is the dimensional model based on the constructivist emotion theories (Russell, 2003). The constructivist emotion theories conceptualise emotion as composed of two orthogonal dimensions: one related to emotional valence (a pleasure– displeasure continuum) and the other to emotional arousal (activation–deactivation) (Posner, Russell, & Peterson, 2005). All emotions vary along these two continuous dimensions (see Figure 2). This model allows us to understand emotion processing early on in development, when a broad differentiation between positive and negative stimuli takes place, whereas appreciation of different levels of arousal occurs later in development (Widen & Russell, 2008a). The emotion categories are suggested to develop out of this initial differentiation between valance and arousal levels, with the development of the verbal labels (Russell & Bullock, 1985; Widen & Russell,2008).

The third approach is represented by appraisal theories. Similar to discrete emotion theories, appraisal theories see events as the triggers of the emotions. However, appraisal theories assume that the emotion architecture is produced by an individual’s subjective appraisal of events, instead of by the event itself (Scherer, 2009). By proposing that the individual’s appraisal precedes the emotion identification, appraisal theories address individual differences in emotion identification in response to the same trigger (Roseman, & Smith, 2001). In terms of developmental changes in emotion perception, appraisal theories propose that the same situation will be appraised differently across development, therefore leading to changes in emotion identification (Roseman, & Smith, 2001).

Although there have been ongoing debates surrounding the emotion models presented above, together these models help build up our understanding of the specific processes involved in the development of emotion processing. Therefore, the notions of the models are presented here in order to provide the foundation of understanding in the following literature. In the current section and the following chapters, when we discuss the development of children's emotions perception, we will combine and use the notions of both basic emotion model and the dimensional model. As the basic emotion models is practical in research in terms of defining the emotion categories; whereas the dimensional model provides stronger evidence on developmental approach.

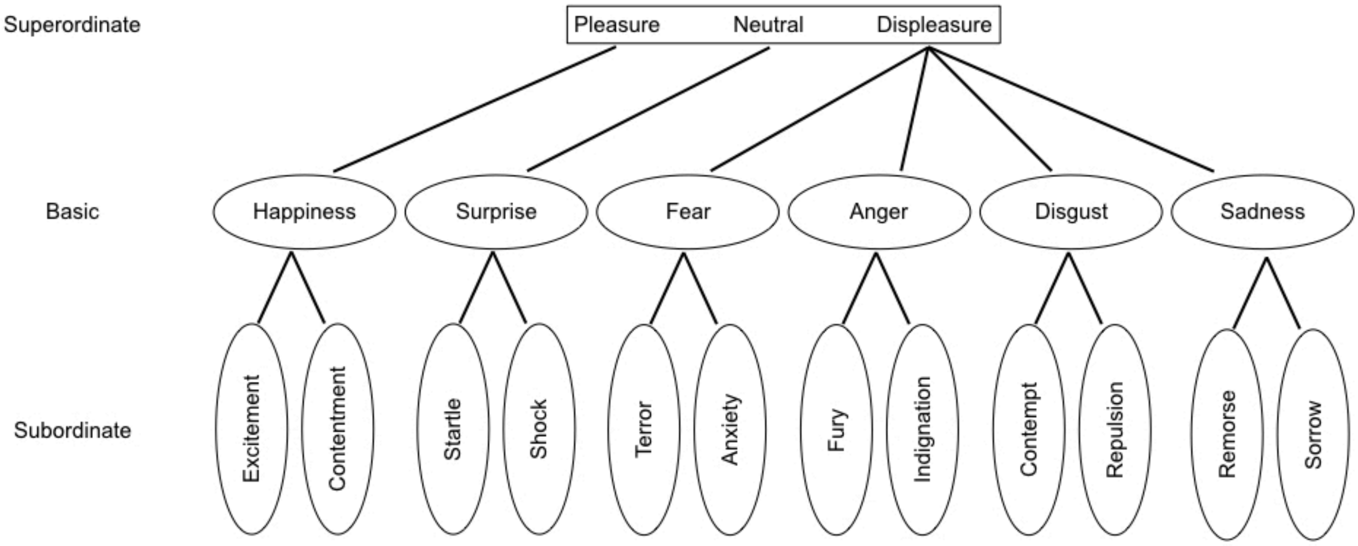

Figure 1. The discrete-category model of emotions. Adapted from *"Handbook of Emotions: Young Children's Understanding of Other's Emotions" (p.349)*, by S. C. Widen, and J. A. Russell, 2008. New York, Copyright 2008 by the Guilford Press.

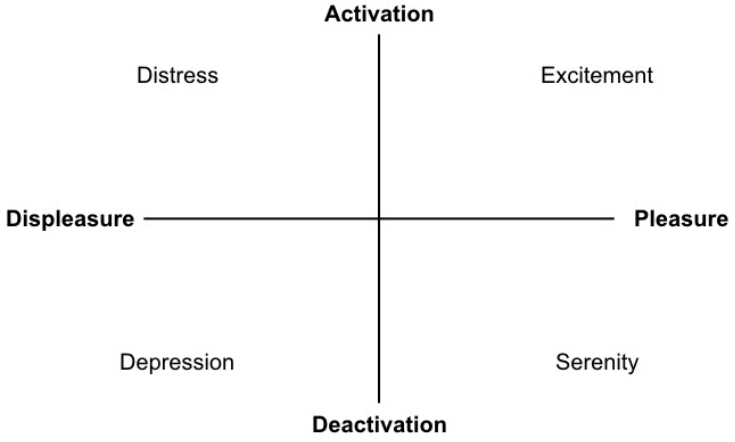

Figure 2. The circumplex model of emotions. Adapted from "*Core Affect and the Psychological Construction of Emotions*", by J. A. Russell, 2003, Psychological Review, 110(1), p.148. Copyright 2003 by the American Psychological Association, Inc.

Emotion processing development and the importance of bodily expressivity

The sensitivity to emotion starts at very early stage of life. As early as 10 weeks old infants show longer looking time to matched facial and vocal expression, they also smile more to happy facial expressions than sad ones (D'Entremont & Muir, 1999; Kahana-Kalman & Walker-Andrews, 2001). From 5-7 months old infants can match facial expression with voices of emotions in positive and negative valances (Kahana-Kalman & Walker-Andrews, 2001). However, the absence of verbal communication of emotions might lead to a possibility that the early emotion-related evidence is a result of perceptual reaction, instead of deeper emotion processing.

From approximately 2 years old, the developing of language brings our understanding of children's emotion knowledge to an advanced stage. Being able to verbally describe self and other's feeling or status promotes children to learn emotion in a more abstract way, enriching the categorising of emotions; it also allows multiple ways to investigate children's emotion recognition. Apart from parental report and observation, labelling (including force labelling and free labelling) and emotion matching (using emotional faces or stories/ events) are the two main kinds of tasks used at this developmental stage. Studies using these methods have provided rich information of the developmental trajectory of children's emotion knowledge. Matching with the importance of emotion recognition during childhood, this developmental period marks the emerging and fast improving ability of emotion identification. The ability to use verbal labels to identify emotion expressed by the faces improves fast from 3 years old, the accuracy of identifying happy and angry faces is especially good (Widen, 2013). From the age of 5 years, children are able to distinguish five emotions (happy, fear, anger distress, shame, disgust, surprised, interest) in an emotion matching task; from 7 years old, children's performance in discriminating emotions by valences in an emotion matching task becomes stable and comparable with adults (Odom & Lemond, 1972; De Sonneville et al., 2002). Research by Widen and Rusell (2008) using labelling tasks reveals that children's use of emotion categories increases in a systematic order from 3 years old to early school age: commonly starting with happy, followed by angry and sad, then fearful and surprised, and in the 6 examined emotion labels, the use of disgust develops last. Overall, previous literature using labelling and emotion matching tasks suggests that children's emotion recognition ability improves with age in terms of accuracy, precision and speed, and follows a simple-multiple pathway, starting from few basic emotions, extending to broader and more specific feelings related to more complicated situations.

However, most of the tasks used in prior investigations of children's emotion recognition use facial expression as task stimuli, as historically faces are considered as the dominant emotion carrier. The human body, which is an essential carrier of multiple information, as well as an equally frequently seen stimulus as faces in everyday life, remains poorly explored in the studies of emotion recognition. Although research shows that faces dominate human's visual field from early in life (Fausey, Jayaraman, & Smith, 2016), the existing evidence suggests that children use the information provided by the body in order to make inferences about or to detect others' emotions. In fact, infants are able to recognize body motion starts in the first couple of months of life almost as early as they react to emotion (Bertenthal, Proffitt, & Cutting, 1984; Bertenthal, Proffitt, Kramer, & Spetner, 1987). Comparable with emotion recognition from facial expression, from as early as 6.5 months old infants start to distinguish happy body movement from neutral movements, and they performed longer looking time to matched happy body expression and voice (Zieber, Kangas, Hock, & Bhatt, 2014). Body cues are found to be as important as facial cues in recognition from 8 years old, and 10-year-old children show comparable performance with adults in recognition tasks using body without head or whole-body cue (Robbins & Coltheart, 2015). This evidence allows us to address the importance of bodily expression during childhood.

How Do Children Process the Human Body?

Before understanding how emotion is encoded from body expression in children's brains, it is important to answer a more basic question: how the human body is encoded in children's brains. In this section, we will start by examining body perception in adults, because understanding the way adults perceive body representations will provide a framework for studying the development of body perception. The neural mechanism of body perception in terms of the relevant ERPs will then be discussed; and finally we will review the current knowledge of body perception development.

The mature body perception in adults

Evidence from both behavioural and neuroscientific studies suggest that the cognitive processing of bodies and faces shares some similarity. Behavioural evidence suggests that the body structure encoding involves a specialized processing strategy such as facial structure encoding does: configural processing. Configural processing refers to the cognitive processing style of perceiving the relations among all the features in a stimulus (Maurer, Grand, & Mondloch, 2002; Reed, Stone, Grubb & McGoldrick, 2006). Configural processing refers to a type of processing that perceiving the relations among the features of a stimulus. In facial structural encoding, configural processing includes three types of information, the first-order information, the holistic processing and the second order information. The first-order information refers to the structural information that is shared by all human faces: two eyes above a nose, which is above a mouth. This order helps recognition of a face from other objects. Secondly, the holistic processing helps bring up the features into a Gestalt; and lastly the second-order information describes the spatial distances between each feature, which tells the individual differences of each face (Diamond & Carey, 1986; Maurer, Grand, & Mondloch, 2002). One of the phenomena believed to reflect the activation of facial representation is the facial inversion effect. The facial inversion effect refers to people’s impaired performance in terms of reduced accuracy as well as longer reaction time when observing an inverted face in comparison to upright faces; such phenomena are usually diminished or not observed when observing inverted faces, and non-facial objects (Yin, 1969; Rossion, et al., 2002). Facial inversion also disrupts the recognition of the changes in second order information such as moving individual elements on face up and down (Friere et al., 2000). It is thus suggested that the inversion effect reflects a disruption of the cognitive processes involved in facial recognition as it impairs access to various types of facial information relevant for this task (Yin, 1969; Rossion, et al., 2002; Reed et al., 2006).

This inversion effect is also observed in body structure processing. Although very different in shapes, the human body shares a similar first-order information with faces in a sense that key elements of a body are joined in a certain way (i.e., a torso with a head above, two arms attached on both side and two legs below). Apart from the first-order information, the body also contains structural information, referring to the position of each part within the overall structural hierarchy of the body (Reed et al., 2006). Investigations using intact body images with postures show that when observing upside-down body pictures, people make more errors in recognising body posture. Their reaction time when judging inverted body images also gets delayed (Reed, Stone, Bozova & Tanaka, 2003; Reed et al., 2006). This inversion effect is also diminished for the non-body objects, suggesting the processing of body and facial representation share some similarities.

However, as discussed at the beginning, bodies are exclusive in terms of its functions in everyday life. Despite that behavioural evidence suggesting bodies are perceived configurally as faces are, neuroimaging investigations established that there is body specialized processing. Functional MRI studies demonstrated that there is a neural network functionally associated with processing human bodies. Studies revealed a distinct area in the occipito-temporal cortex (OTC) as well as the middle fusiform gyrus respond more to neutral body images and body parts than non-body objects. There are therefore named as the extrastriatal body area (EBA) and the fusiform body area (FBA) (Downing, Jiang, Shuman, & Kanwisher, 2001; Peelen & Downing, 2005); which are partially overlapped but mainly distinct with the fusiform face area (FFA).With regards to the perception of moving bodies, the posterior superior temporal sulcus (pSTS), parietal cortex and premotor cortex are found involved in biological motion perception. The STS is found to be responsive to biological motions as well as body-related stimuli such as eye gaze (Grossmann, et al., 2000; Hoffman & Haxby, 2000). These body-exclusive brain networks provide neural resources to the neurophysiological body-specific processing activities.

Neurophysiological evidence of mature body perception: N190 and P1

Neuropsychologically, event-related brain potential (ERPs) studies functionally inform specialised cognitive processes sub-serving bodily perception. Evidence from adult studies establish that body and face processing share similarities in terms of the associated ERP components: the N170 (N190 for body) and the P1.

Human faces elicit a negative going amplitude from the posterior temporal sites peaking at around 170ms after picture onset; this specific is not triggered by scrambled faces or non-face objects; further, this component can also be triggered by object forms similar to faces, such as schematic face pictures (Bentin, Allison, Puce, Perez & McCarthy, 1996; Bentin & Deouell, 2000). This component is therefore commonly agreed as a neural correlate of face recognition in high-level visual processing, sources from the posterior fusiform, the lateral occipital-temporal complex and the middle fusiform gyrus (Bentin et al., 2002; Rossion & Jacques; 2011). Especially, the N170 component is found to be sensitive to any configural change to face stimuli, such as inversion or changing of spatial distances. The N170 latency is related to the facial inversion effect, showing delayed latency to inverted faces in comparison to upright faces, similar with the behavioural findings of the facial inversion effect; this latency shift is not found on upright and inverted non-face objects (Bentin et al., 1996; Rossion et al., 1999, 2000). This effect is interpreted as a neural reflection of impaired cognitive processing of facial configuration. The information in the inverted face being more difficult to access, leads to sustained attentional processing, and this modulation effect of attention is therefore reflected by N170 amplitude/ latency (Eimer, 2000). The N170 inversion effect is therefore used to determine the perception stages of facial recognition.

The P1 component in prior to the N170 is also usually found in facial ERPs. The P1 is a positive going peak around 80-100ms after stimuli onset from occipital regions. In facial processing, some studies have found larger P1 amplitude in response to face than objects (Eimer, 1998; 2000; Itier & Taylor, 2004b), or larger amplitude and longer latency for inverted/scrambled faces than upright (Rossion et al., 1999; Itiler & Taylor, 2004b; Kuefner et al., 2010). However, these findings are not consistently observed (Sagiv & Bentin, 2001; Rossion, et al., 2002) as N170 effect does. As the P1 component is usually found sensitive to low level visual cues such as luminance, colour, contrast, or spatial frequency, but not any orientation changes (Regan, 1989), the changes of P1 amplitude and latency are considered to reflect the low-level changes between faces and non-faces stimuli (for a review, see Rossion & Jacques, 2011). The P1 is thought to originate mainly from the striate and lateral extrastriate visual areas (Clark & Hillyard, 1995; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Halgren, Raji, Marinkovic, Jousmaki, & Hari, 2000; Tanskanen et al., 2005; Tarkiainen et al., 2002).

Similarly, this P1-N170 morphology is also observed in body perception investigations. Images of intact bodies or bodies without head with different postures elicited the N170 from occipital-temporal sites of similar amplitude as faces but slightly later in latency, peaks at around 190ms (Gliga & Dehaene-Lambertz, 2005; Meeren et al., 2005; Thierry et al., 2006). Furthermore, the inversion effect is also found on the bodily N170 component, with larger amplitude and increased latency recorded in response to inverted bodies compared to upright bodies; a similar effect is not observed between upright and inverted objects (Stekeleburg & de Gelder, 2006; Righart & de Gelder, 2007; Minnebusche et la., 2009), suggesting that similar with facial perception, there is fast processing of the bodily configuration. However, as the origin of the bodily N170 is suggested being different from facial N170, having its source from the EBA (Thierry et al., 2006; Peelen & Downing, 2007). In order to discriminate these two components, the bodily N170 is also called the N190 in some literatures. In the current thesis, we will use "N190" for bodily N170 in order to distinguish these. Moreover, although there are not many studies, current evidence suggests that in body processing the P1 is also larger for bodies than non-body objects, but not sensitive to any inversion or configural changes on adults (Stekeleburg & de Gelder, 2006; Righart & de Gelder, 2007). This indicates that similarly to facial perception, the P1 in body perception is also likely associated to sensitivity to low-level visual change, and contributes ultimately to the following configural information processing.

The development of body perception

Our sensitivity to the body starts early. Eighteen-month-old infants show initial knowledge of human body structure, as they are able to discriminate scrambled body images from intact bodies by looking longer to the scrambled ones (Slaughter, Heron, & Sim, 2002). Robbin and Coltheart (2015)'s study of 8- and 10-years old children suggested that from at least the age of 8 years, children are able to use body cues to recognise people under both static and moving conditions, although their performance is significantly worse than adults. Functional MRI research also established that although bodily expression activates similar brain regions with adults and children from 6 years old, including the EBA, the FBA and the pSTS. The activity of these regions is not as mature as that in adults until 11 years old (Ross, de Gelder, Crabbe, & Grosbras, 2014). These indicate the improvement of body knowledge with age throughout childhood.

However, unlike the richness of the investigations looking at the neural mechanisms underlying facial perception in children (de Haan & Nelson, 1999; Rossion et al., 1999; Taylor, et al., 1999; Halit, de Haan, Johnson, 2003; Itlier & Taylor, 2004; Kuefner et al., 2010; Peykarjou et al., 2013; Peykarjou, et al., 2014), evidence of the development of body perception during childhood has not been extensively researched.

Neurophysiological evidence in body perception development: N290 and P400

Despite the N190 and P1 being associated with the adult body perception, two ERP components are typically reported to be associated with body perception in the developmental domain: the N290 and the P400.

The N290 and the P400 are two ERP components that are associated with visual perception of faces in 3 to 12-month-old infants. The N290 is a negative component that peaks 290 to 350ms over the midline and paramidline electrodes, and shows larger amplitude and often a shorter latency for human faces than that for other objects (Betntin et al., 1996; Taylor et al., 1999; Rossion et al., 2000). The P400 is a positive going component that occurs over posterior lateral electrodes, and peaks approximately 390-450ms in 3 to 12 months old infants. Apart from showing a similar inversion effect to that with the adult N170, the P400 also shows faster latency to human faces in comparison to objects (Halit, de Haan, & Johnson, 2003; de Haan, Johnson, Halit, 2003). The N290 is believed to reflect the structural encoding of the physical information in faces; while the P400 is suggested to be sensitive to the distortion of normal structural information (de Haan et al., 2003; Gliga, & Dehaene-Lambertz; 2005). These two components both form the developmental precursors of the adult N170 in facial perception (de Haan et al., 2003).

Only one study looked at the associated ERPs in response to body images in the early stage of life (Gliga, & Dehaene-Lambertz, 2005). It was found 3-month-old infants already show a P1 followed by a N290 from occipital-temporal sites when perceiving body postures. Although the N290 component didn't show sensitivity to any impairment of the body configuration, the distorted configurations elicited an amplitude change on the lateral positive component P400. These findings again suggested the shared similarities between body and face perception; more importantly, their findings showed that at 3 months old infant's perception of the body is far from the mature performance of adults. However, the developmental picture of the body perception cognitive process from infancy, and the mature pathway until adult-like, remains largely unknown.

Especially, face perception studies suggested there is developmental change underlying the flexible use of configural and featural processing. Although early preference to face-like stimuli is reported during the fetal and neonatal periods (Goren, Sarty, & Wu, 1975; Reid et al., 2017), and the earliest age at which the shows configural process effect is reported at 7 months old (Cohen & Cashon, 2001); the maturation of configural processing follows a long developmental path. Both configural and featural processing are used during children's facial identity recognition; however, increasing use of configural processing over featural use is reported earliest from 8-years-old

(Baenninger, 1994). Furthermore, the recognition rates to inverted faces improve with age, however always worse than upright faces, this improving curve is observed from 7 to at least 16 years old (Flin, 1985). These studies suggest the slow maturational curve of the dominant use of configural processing during childhood.

Considering the shared similarity of developmental improvement between body and face perception, this implies the numerous possibilities of the developmental variability of the body processing during childhood. However, as neuroimaging and neurophysiological evidence on adults indicated that the similar neurophysiological topography of facial and bodily perception may have different neural resources, suggesting distinct processing mechanism; we shall also predict a development pathway for body perception during childhood.

Emotion perception from static body postures in children

The static body emotion perception development

Most of the time in everyday life we see moving bodies and perceive information from them. However, when seeing the body in static pictures, or having to detect emotion from the body at a quick glance, we also perceive the emotion information using bodily expression from static body postures. The biological nature of emotion expressivity provides the fundamentals of detecting emotion from static body posture. When we are expressing emotions, the muscle changes in our face and body show matching cues. For example, when expressing anger, people will tense their eyebrows and mouth, as well as their shoulders and arms (Parjer, Methis, & Kupersmidt, 2013). This shared information gives us the possibility to process emotion from body posture in isolation from facial expression.

In fact, studies suggest that adults are able to use only static body posture to detect most of the basic emotions, and adults' responses to the static expressions of emotions are consistent. Adults are reported to be able to correctly categorise happiness, sad, anger, fear and disgust from static full-light body postures at above chance level, with the accuracy to the disgust bodies being the worst (Atkinson, Dittrich, Gemmell, & Young, 2004). Similar findings are reported in Coulson's (2004) investigation using 176 computer-generated mannequin figures expressing 6 emotions; adults correctly categorise anger, fear, happiness, sadness, and surprise. Nonetheless, intensive emotions are detected better through body postures in comparison to facial expressions (Aviezer, Trope, & Todorov, 2012). When asked to judge whether the person wins the game or not using isolated facial and body expressions, adults showed higher accuracy when basing their judgement on body postures. A possible explanation is that face muscles are not as flexible as bodies in expressing extreme emotions (Aviezer, Trope, & Todorov, 2012).

The sensitivity to the emotional information from body postures develops early. In agreement with the dimensional model of emotions (Russell, 2003), the differentiation of emotions from static body postures can only be seen between positive and negative stimuli from early ages, and becomes more specific over time in terms of the arousal level within the valences. From 6.5 months old infants show discriminative response to happy and sad body postures. Evidence from experiment examining infants' looking time suggested that by 6.5 months old they can match affective body postures to vocalizations from two opposite valences (happy and angry) (Kahana-Kalman & Waker-Andrews, 2001; Zieber. et al., 2014). Later on in childhood, children can discriminate bodily emotions not only between positive and negative valences, but also label emotions of the same valence at different arousal levels. From 4 years old, children are able to identify happy, sad and fearful emotions by isolated body posture cues in a forced labelling task (Mondloch, Horner, & Mian, 2013). Children's performance in identification accuracy also improves with age. From 6 years old children start to detect incongruent emotions from facial expression and body postures as adults do (Mondloch, Horner, & Mian, 2013). The accuracy of recognising happy and sad emotions from body postures improves significantly from 5 to 10 years old, and as early as 8 years old their performance in labelling happy and sad body postures is as good as adults (Balas, Auen, Saville, & Schmidt, 2017).

Functional MRI investigations on adults have established the neural network underlying emotional body perception shares several cortical and subcortical regions with emotional facial processing, involving amygdala, temporal gyrus, orbitofrontal cortex (OFC) and anterior cingulate cortex (ACC) (Phillips et al., 1997; Sprengelmeyer, Raush, Eysel & Przuntek, 1998; Allison, Puce & McCarthy, 2000; Morris et al., 1996; Haxby, Hoffman & Gobbini, 2002; Adolphs, 2002; Philips et al., 1998; Blair, Morris, Frith, Perrett, & Dolan, 1999). Some of those regions are involved in both body and facial emotion processing; for example, fearful bodies activate the amygdala, OFC and ACC, which are typically associated with fearful facial recognition (Hadjikhani & de Gelder, 2003). Furthermore, in comparison to facial perception, the perceived body images enhance activity in regions such as the sensorimotor and premotor cortex. fMRI studies using emotional whole body or body parts established the recruitment of additional regions such as the motor system, which is unlike the central role of the amygdala in facial perception (Grosbras & Paus, 2005; Grèzes, Pichon, & de Gelder, 2006, see de Gelder, 2006 as a review). This indicated that although there is some shared network underlying facial and bodily emotion processing, bodily emotion processing has its own selective network. In children, a fMRI study on 6- to 11-year-old children showed that when observing body movements, children from 6 years old show the same active brain regions (EBA, FBA, pSTS) as adults do, however, the strength and spatial extent of the fMRI signal is more diminished than that in adults, indicating the development of body perception is not yet complete until late childhood (Ross, de Gelder, Carbbe, & Grosbras, 2014).

Neurophysiological findings associated with emotional body posture perception

Despite the typical visual components associated with body perception – the N190, P1, and the N290, P400 – an infant component Nc (the negative central) is also found to be typically involved in emotion perception from the body. As its name indicates, the infant Nc is a negative going ERP component usually occurring around the 400-800ms time window after stimulus onset over the midline area, and reflects the direction of attention to unfamiliar objects (de Hann & Nelson, 1997; 1999). In facial emotion perception, the Nc is reported to show larger amplitude in response to fearful faces than happy faces in infants from 6 and 7 months old (Nelson, & de Haan, 1996; de Haan, Belsky, Reid, Volein & Johnson, 2004; Kobiella et al., 2008), indicating the emergence of the attentional response to emotions of two valences.

There are hardly any electroencephalography investigations of static body emotion processing in children. Studies on adults found that fearful body postures elicited a faster P1 latency from occipital sites to fearful body postures in comparison to neutral ones, showing emotion sensitivities from body expression are encoded from an early visual stage (Heijnsbergen et al., 2007). This emotion response elicited by fearful bodies is also found in the VPP (vertex positive potential, which in facial studies is seen as a positive counterpart of N170) at early stage, as well as on sustained potential in frontal-central sites at a later processing stage (Stekelenburg & de Gelder, 2004). Although their findings indicated a prolonged processing of emotion information from static body postures, more investigations are needed to clarify the potential reasons of the prolonged processing. One investigation looked at 8-month-old infants' neuropsychological response to fearful and happy body postures, and reported more negative N290 as well as Nc (negative central) mean amplitude to fearful bodies than happy bodies (Missana, Rajhans, Atkinson, & Grossmann, 2014), similar to the Nc emotion effect found in 6-7-month-olds in facial perception investigations (Nelson, & de Haan, 1996; de Haan et al., 2004; Kobiella et al., 2008). Taking the findings of the Nc in facial perception as well as the role of the N290 in infants' body perception, this indicated there is some level of attentional response to emotions of different valences from body postures early at 8 months old. However, between the early neural response and the mature performance indicated by investigations of the infant and adult emotional body perception investigation, brain markers of the cognitive function across childhood are largely unexplored.

Given the described similarity of body and face perception, the knowledge about the ERP correlates of face perception development would be a starting point to build up the understanding of the body perception development. Emotion processing using pictures of emotional face expression and the passive viewing paradigm have provided the developmental pathway of the neural physiological change in children. After the findings of early emerging emotion sensitivity at 6 months old (Nelson, & de Haan, 1996; de Haan, Belsky, Reid, Volein & Johnson, 2004; Kobiella et al., 2008), from 7 to 32 months old, instead of the Nc, an earlier negative component peaks between 90-250ms from fronto-central sites showing greater amplitude to sadness in comparison to fear (Parker & Neslon, 2005). This shows that young children can at least perceptually distinguish emotions in the same valences from the body as from the face. Adult-like P1-N170 morphology in facial perception emerges from preschool age, and shows an emotion effect: an early response to emotional information from bodily expression is found in 4- to 7-year-old children; fearful faces elicit slower P1 latency than happy, surprised and emotional neutral faces. However, the emotion effect is found moved to the following facial structural encoding component N170 when children get older; negative faces overall elicit larger N170 amplitude than positive faces (Batty & Taylor, 2006). Moreover, an emotion sensitive ERP response in 4- to 15-year-old children is derived from occipito-parietal sites, different from the fronto-central and midline response in infants (de Hann & Nelson, 1997; 1999; Parker & Neslon, 2005; Batty & Taylor, 2006). As discussed before, the P1 is an early component sensitive to low-level feature change but not any configural information in faces (Mercure, Dick &

Johnson, 2008), while the N170 is suggested to be a neutral representation of the facial structural encoding process. Hence, the emotion effect moving from P1 to N170 during childhood is suggested to reflect the developmental change of emotional facial encoding. With the increasing reliance of configural information in facial perception, the early global response to emotion on P1 is replaced by the using of second-order information that discriminates the emotional gestural on the face (Batty & Taylor, 2003). Furthermore, the adult-like emotional sensitivity on the facial selective component N170 is still not clearly observed until adolescence, suggesting that children use different strategies in facial emotion recognition, as well as the protracted matureness of the processing lasting until late adolescence (Batty & Taylor, 2003; Ashley, Vuilleumier & Swick, 2004; Batty & Taylor, 2006).

Considering that bodies and faces share similar structural encoding processes (i.e. the configural processing) discussed previously, and usually carry similar social behavioural information, we would expect that similarly with facial emotion perception development, the ERP morphology changes as well as the protracted matureness of the processing mechanism during childhood will also be observed in emotional body posture recognition. However, dissociation between the similarities of body and facial perception has been indicated at least in adults. For example, different brain region sources are found to subserve the same ERP components. The N170 elicited by human faces was reported to have its source from the brain areas selectively involved in processing faces, such as the fusiform face area (FFA) and the posterior superior temporal sulcus (pSTS) (Mnatsakanian & Tarkka, 2004; Rossion & Jacques, 2011; Itier & Taylor, 2004; Watanabe et al., 2003; Rossion & Jacques, 2011), whereas the N170 in response to human bodies was suggested to originate from the extrastriate body area (EBA) (Thierry et al., 2006; Peelen & Downing, 2007). Therefore, instead of generalising the electrophysiological evidence of face perception to body perception development, investigations that particularly aim to address the developmental details specific to static emotion expression from the body are highly necessary.

The processing of structure information in emotional static body processing

One potential difference between body and facial emotion perception is that unlike emotion recognition from faces, which may rely on featural and second-order information, detecting emotion through body postures would depend more on the processing of structural information.

Coulson's (2004) study used body images posting different postures to express anger, disgust, fear, happiness, sadness and surprise. Sixty-one adult participants labelled each body posture from given emotional labels. Results showed that people show high concordance on relating certain body postures with six basic emotions. For example, head and chest bending forward with shoulder swinging backward and elbow holding tight are most likely to be labelled as angry, whereas upper body leaning backwards with elbow bending straight is highly likely to be perceived as happy. Although the concordance of the emotions depends on viewing the postures from front, side or rear angle, the detection of emotions also relies on some other perceptual variables such as the context (Carroll & Russell, 1996). Findings of this investigation still established the importance of perceiving bodily structural information in emotion recognition (Coulson, 2004). This brings the possibility that different types of information such as the bending degree of the body elements, or viewing the body postures from different viewing angles might interfere with emotion perception.

In fact, both behavioural and neurophysiological evidence indicate that impairing body configural information interferes the emotion processing of both adults and infants. In adults, upright-down body movements significantly reduce their accuracy in recognising emotions in comparison to upright condition, although their recognition of emotion is not completely abolished, still show performance at above chance level

(Atkinson, Tunstall, & Dittrich, 2007). Similarly, Missana and colleagues' (2014) neurophysiological investigation report that the greater N290 mean amplitude for fearful in comparison to happy bodies in infants is only shown when the body images are presented upright but not inverted, suggesting infants' neural response discriminates emotions from body posture only in the upright condition. As previous works show that the perception of body expression is impaired by the body inversion, when investigating children's neural correlates of static emotion perception from bodies, it's necessary to take into account the possibility that the body inversion interferes with emotion perception.

Emotion perception from dynamic body movement

Although both adults and children can encode emotion from static body postures (Montepare, Koff, Zaitchik, & Albert, 1999; Vieillard & Guidetti, 2008; Nelson & Russell, 2011), in everyday life, moving bodies are still the most common source of bodily emotion information. Adults can accurately identify emotions when briefly viewing moving bodies (Montepare et al., 1999; Volkova et al., 2014). The early emergence of the sensitivity to body movement indicates the importance of this information to us. 3-month-old infants look longer at a point-light display (PLDs) of a human body walking towards them compared to random moving dots, suggesting that at least from this age they are sensitive to the biological motion of the body (Bertenthal, 1993). Interestingly, not until 18 months old do infants start to be able to distinguish intact body images and scrambled body images (Slaughter, Heron, & Sim, 2002); this indicates that infants develop sensitivities to moving bodies even before they learn the notion of body structure. Moreover, the dynamic information helps to improve preschool children's recognition of emotions (Nelson & Russell, 2011b; Vieillard & Guidetti, 2008; Nelson & Mondloch, 2017).

Evidence provided by multiple kinds of behavioral measurements indicates the improvement in development of emotion encoding from moving bodies. The very early sensitivity to emotion sensitivities from body movements is found in infants from 6.5 months old. Again the differentiation emerges from broad valence levels; they show a visual preference for happy bodies over neutral ones (Zieber et al., 2014). This also implies that infants from this age can discriminate emotion from moving bodies at least at a perceptual level; however, evidence at this stage cannot lead to a conclusion of emotion recognition yet. The earliest age that children are found to be able to identify emotions from body movements is 3 years; children from 3 to 5 years old can verbally label four emotions which vary between valence and arousal levels (happy, sad, angry and scared) from body movement video clips, with an accuracy rate of 72%, only slightly lower than recognition from facial expression (80%) (Nelson & Russell, 2011a). Furthermore, although by the age of 5 years their accuracy is still not as good as the adults, their performance continuously improves with age (Nelson & Russell, 2011a). Five-year-old children's emotion identification performance is significantly worse than that of 8-year-old children; by 8 years old children's accuracy is quite comparable with adults (Boone & Cunningham, 1988; Nelson, & Mondloch, 2017). However, in comparison to the rich behavioural findings of emotion recognition from facial expression which provide a detailed image of development in terms of recognizing emotions based on valence and arousal (Dunn, 1994; Odom & Lemond, 1972; De Sonneville et al., 2002; Widen & Russell, 2003; Widen & Russell, 2008; Widen, 2013), the behavioural evidence only offers limited information about the development of children's emotion recognition from body movements.

Further, the fact that emotions are expressed in multiple ways, leads to the multiple cognitive approach (i.e., recognizing facial/bodily expression, understanding emotional words) of emotion identification; therefore, different behavioural methods may only tap certain aspects of the emotion recognition ability. For example, a verbal labelling task requires a certain language ability and lexical understanding of emotions, thus, behavioral evidence of children's improving performance in verbal labeling tasks may reflect the increasing familiarity of perceiving matching emotional situations with words, but may not be able to reflect the nonverbal understanding of emotions before language ability was fully matured. Moreover, the sorting task or non-verbal labelling task will leave the question of how well the children understand the emotional expression or labels they sorted in the experiment. In fact, behavioural investigation using a sorting task shows that children have different understanding of emotion categories than adults. When asked to sort the same emotional faces into one box, 2-year-old children put other negative emotional faces (sad, fearful) into the angry box as well (Russell & Widen, 2002).

In comparison to behavioural evidence, neuroimaging and neurophysiology investigations using fMRI or ERPs can help provide more direct measures of children's neural response to different emotions, without being mediated by language ability. Evidence from fMRI on adults reveals that observing emotional bodies actives brain regions that are specifically related to emotion processing, such as the amygdala, OFC, ACC and anterior insula (Damasio, 1999; Hadjikhani & de Gelder, 2003; de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004); moreover, the biological movements of bodies also elicit the activities of STS, parietal cortex and premotor cortex (see de Gelder, 2006 for a review). However, few studies have looked at the developmental domain. Evidence from neurophysiology suggests that the perceptual discrimination of emotions from moving bodies is shown in the early ages. ERP investigations of emotional body perception establish that by 8 months old infants show a more positive amplitude over the late components to happy PLDs of bodies than fearful ones, suggesting an early sensitivity to positive emotions from body movements (Missana, Atkinson, & Grossmann, 2015). However, fMRI studies on 6- to 11-year-old children and adults find that when observing video-clips of emotional body movements, children show brain activity in similar regions as those reported for adults (EBA, pSTS, FBA, amygdala and precentral gyrus); however, in response to emotional body movements, adults' brains activate across a broader network, and the fMRI signal shows better strength (Ross et al., 2014). This suggests the ability of emotion body perception is still developing during the second decade of life. Nevertheless, in terms of the neural mechanism of the emotional body movements during childhood, a large blank has been left in the domain.

Thesis outline

This review highlighted the importance of the ability to process emotion from the body (both from static postures and dynamic movements) during childhood, along with the theoretical and knowledge gaps currently present in the field; especially the neural mechanism underlying this ability. From what have been discussed above, we can now clearly see several gaps in this field that are particularly essential but haven't been investigated. For example, we do not know about the neural mechanism of body structure perception throughout the entire childhood, nor the mechanism underlying emotion perception from body static and dynamic perception. Although some behavioural studies have been done, to understand the neural mechanism behind the behavioural evidence can help us to reveal the reasons behind the changes, as well as the nature of the emotion perception development. Therefore, this thesis aims to address these knowledge gaps by investigating the neural correlates of children's emotion perception from static and dynamic body information, and therefore, to contribute to a more coherent understanding of the big map.

In order to reveal the development of the neural mechanism underlying children's bodily emotion recognition, key aspects have to be addressed. Therefore, the current work will first investigate the cognitive processing of body shape perception in children. Paper 1 will address this issue by looking at the developmental changes in the ERP responses to body structure processing in children age from 3 to 10 years old, and compare this with the neural response in adults. We chose to start with this specific age range for two main reasons: first, as discussed at the beginning, we consider children from 3 years old have sufficient motor ability and social needs for perceiving bodily information; second, from the practical perspective 3 years old is the earliest age during childhood that is more likely to guarantee data of good quality. We are interested in the existence and possible developmental changes of the P1 and N170 ERP components in response to bodies in comparison to objects. We are also interested in the emerging and changing of the N170 inversion effect during childhood, also its possible difference with the adult N170 inversion effect. These findings would help in describing when children start to show the adult-like perception of body shape.

By knowing how the visual presented body is processed in children's brains, Paper 2 will examine children's emotion perception from static body postures with the predictions based on the findings of Paper 1, also using ERPs. We will look at the ERP responses to happiness, sadness and fear from static body postures on children aged from 5 to 8 years old, as previous findings suggest that children at this age should be able to process those basic emotions at different valence and arousal levels, following the predictions of the dimensional model (Russell, 2003). The reason of choosing this specific age range is that previous behavioural evidence suggested children from 5 years old performed above-chance level accuracy in decoding emotions from bodily expression for basic emotions such as sad, happy and fearful; and by 8 years old their performance are improved quickly, and as good as adults (Boone & Cunningham, 1998; Balas, et l., 2017). We are particularly interested in the role of body configural information in emotion encoding. The findings of this study will provide preliminary evidences of how body posture cues are relevant for emotion perception in children.

As the last step of this investigation, Paper 3 aims to reveal the neural correlates as well as their development of emotion processing from moving bodies and their development. Ideally, we would like to directly measure the ERP response towards emotional body motions. However, to present a body motion that is long enough for children to extract emotional meaning will not be practical for ERP measurement. Therefore, to achieve the research question, we will use an affective priming paradigm, and will be looking at the incongruence effect between the priming of emotional body movements and the target emotion words in children's ERP response. We will compare 3- and 6-year-old children's neural response to the words describing two basic emotions from different valence ("happy" and "angry") primed by either semantically congruent or incongruent dynamic body motions. The findings of this study will reveal whether children from 3 years old are able to extract the emotional information from dynamic expressions from body.

Overall, this thesis investigates the neural correlates of emotion body perception during childhood, in terms of the processing of body structure, as well as the perception of emotion expressivity from both static and dynamic body. By achieving these research aims, the current work will provide valuable information with regards to the development of emotional body perception during the very important childhood period.

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The Development of Human Body Perception During Childhood. An ERP Investigation of The Body-Inversion Effect.

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Abstract

Body perception plays a crucial role in our everyday social life. Nevertheless, in contrast to faces, research on the development of body perception remains limited. This study investigated the configural processing of the human body during childhood by using a body inversion event-related potentials (ERPs) paradigm. ERPs were recorded while 3-, 4-, 10-year-old children and adults viewed human bodies and objects presented either with upright or inverted orientation. The P1 and N190 components were examined to determine whether configural information is related to body perception during childhood in comparison to adulthood, and whether any developmental changes occur in this respect. The results revealed a paradoxical body inversion effect on the N190 in children. In contrast with the finding on adults, inverted bodies evoked a less negative N190 than their upright versions, and this effect was not found for structurally similar objects. Thus, although configural information may be integral to human body representations during childhood, the extent and the conditions under which such diagnostic information is used remain to be established. Significant developmental changes could also be observed in the early ERP components typically associated with the processing of low-level visual information which is relevant for the perception of complex visual social stimuli. Taken together, these findings suggest that body perception continues to develop well into childhood and further research is required in order to specify the exact nature of this process.

Keywords: body perception, body inversion, configural processing, development, childhood, N190, P1.

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Introduction

Facial expressions are often regarded as the main channel for social information. However, in everyday life, the human body also provides rich information relevant to social communication and interaction, such as identity, sex, intentions, and emotions (Cutting & Kozlowski, 1977; Kozlowski & Cutting, 1977; Hadjikhani & de Gelder, 2003). Especially when the face is not visible or when the facial features are difficult to detect, the body posture becomes much more informative. Recent evidence indicates that the information provided by the body postures is integral to social perception. For example, the incongruence between the body and face emotional expression is quickly detected by the human brain (Meeren, van Heijnsbergen & de Gelder, 2005), while the presence of the body significantly improves the recognition of a person (Robbins & Coltheart, 2015). However, compared to faces, the development of body perception is largely understudied. Characterizing the typical ontogenetic trajectory of human body processing is highly relevant not only to understand typical social development, but also for the timely detection and intervention in developmental disorders where processing the information conveyed by human bodies appears to be impaired, such as in autism spectrum disorders (Atkinson, 2009; Hubert et al., 2007; Philip et al., 2010; Nackaerts et al., 2012), aggression (Munoz, 2009), and anorexia nervosa (Urgesi et al., 2012). In order to reduce this gap, our study aims to investigate the development of the neural correlates of human body perception using a cross sectional design spanning the early and mid-childhood (3- to 10-year-old).

Body and face perception share some similarities (de Gelder, 2006; Downing, Peelen, Wiggett, & Tew, 2006; Minnebusch & Daum, 2009). Human faces, as highly-observed stimuli, involve different perceptual strategies, some of which focus more on processing its individual elements, while others on the relations between these elements that specify the facial configurations (Maurer, le Grand, & Mondloch, 2002; Yin, 1969). The types of configural relations between the face elements can be seen on a continuum (Leder & Bruce, 2000). The most basic, first-order relations refer to the fact that faces always have two eyes above a nose, and that all are located above a mouth. Another aspect of facial configurations is the structural information about the organization of parts in terms of the overall object as well as the spatial relationship between parts (Marr, 1982). More detailed relational information (i.e., second-order), such as the exact metric distance between different face parts, was also shown to be relevant for processing faces as configurations (e.g., Carey, 1992). Similar configural information can be established for bodies as well (Reed, Stone, Grubb, & McGoldrick, 2006). Changing the orientation of faces and bodies by presenting them upside down appears to interfere with the extraction of the configural information, with faces and bodies being more difficult to be perceived as such. Consequently, this inversion effect has been widely used to investigate the perceptual strategies involved in face and body processing (see Valentine, 2013 for a review). Although objects can also be specified in terms of their characteristic configurations, such information appears not to be as readily used by adults (Song et al., 2017; Rossion & Jacques, 2011; Stekelenburg & de Gelder, 2004). This is reflected by the reduction or absence of an inversion effect for objects compared to faces and bodies (Maurer, le Grand, & Mondloch, 2002; Yin, 1969; Reed et al., 2006; Reed, Stone, Bozova, & Tanaka, 2003).

The use of high temporal resolution electrophysiology methods (e.g. EEG) and the inversion paradigm have shown that the extraction of the configural information of visual stimuli such as faces and bodies is fast. Moreover, body and face processing show similarities in the chronology of the underlying neurocognitive mechanisms. One of the most established ERP components associated with both the face and body processing is the N170 (N190 for bodies), a negative deflection that peaks around 170ms (190ms for bodies) after the stimulus onset at occipito-temporal sites. The N170 shows systematically larger amplitudes for human faces compared to non-face objects (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000; Sagiv & Bentin, 2001; Rossion & Jacques, 2011). The broad consensus is that the larger amplitude of the N170 for faces is primarily driven by the early activation of their neural representation in the high-level visual cortex, the perception of a stimulus as a face (Rossion & Jacques, 2011; Bentin, Sagiv, Mecklinger, Friederici, & von Cramon, 2002). The more a stimulus is perceived as a face, the larger the amplitude of the N170 (Bentin et al., 2002). When the diagnostic information used to perceive a stimulus as a face is more difficult to process, the N170 can be delayed or its amplitude increased, most likely reflecting a slowed down and more effortful processing in the neural population coding for faces (Bentin et al., 1996; Rossion et al., 1999; Jacques & Rossion, 2007; Perrett et al., 1998). For example, rendering the configural information more difficult to access by presenting faces up-side down leads to larger amplitude and delayed N170 compared to up-right oriented faces (Bentin et al., 1996; Rossion et al., 1999). When the diagnostic information is too distorted, and the stimulus is not perceived anymore as being a face, the amplitude of the N170 is usually significantly attenuated (Rossion & Caharel, 2011). A larger N190 is also recorded for the inverted compared to the upright bodies, showing that the relation between the parts specific to body configurations is processed fast and contributes to the activation of the corresponding neural representations (Righart & de Gelder, 2008; Stekelenburg & de Gelder, 2004; Minnebusch et al., 2008; Minnebusch et al., 2010).

Although the N170/N190 was shown to be particularly sensitive to the perception of configural information characteristic to human faces and bodies, the extraction of the low-level visual properties of the stimuli which ultimately contribute to the perception of configural information happens chronologically earlier in the processing stream. The positive ERP component peaking around 100ms from stimulus onset (P1) was shown to be sensitive to the low-level visual properties of the stimuli such as luminance, color, contrast, or spatial frequency (Regan, 1989) and it is thought to originate mainly from the striate and lateral extrastriate visual areas (Clark & Hillyard, 1995; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Halgren, Raji, Marinkovic, Jousmaki, & Hari, 2000; Tanskanen et al., 2005; Tarkiainen et al., 2002). The P1 is not usually modulated by the orientation of the stimuli. Thus, differences in the P1 between stimuli are regarded as reflecting their low-level visual properties (Rousselet et al., 2005).

While many investigations documented the development of face perception and the associated ERP components throughout childhood (de Haan & Nelson, 1999; Taylor, et al., 1999; Halit, de Hann, Johnson, 2003; Itlier & Taylor, 2004; Kuefner et al., 2010; Peykarjou, Westerlund, Cassia, Kuefner, & Nelson, 2013), less than a handful provided similar evidence for body perception (Gliga, & Dehaene-Lambertz, 2005). One could suggest that given their described similarity, the knowledge about the ERP correlates of face perception development could be extrapolated to human bodies. However, at least in adults, the cortical sources of the N170 elicited by faces and bodies are partially distinct (Thierry et al., 2006; Taylor et al., 2010; Itier & Taylor, 2004; Rossion & Jacques, 2011). While the N170 in response to human faces was associated with the activation of brain areas selectively involved in processing this type of stimuli (e.g., the fusiform face area (FFA) - Mnatsakanian & Tarkka, 2004; Rossion & Jacques, 2011; the posterior superior temporal sulcus (pSTS) - Itier & Taylor, 2004; Watanabe et al., 2003; Rossion & Jacques, 2011), it is possible to trace the source of the N190 to regions corresponding to the extrastriate body area (EBA – Thierry et al., 2006; Peelen & Downing, 2007) which is particularly responsive to this type of stimuli. Such a dissociation in the cortical sources for the N170/N190 prevents the generalization of the findings from the electrophysiological investigations into face perception to understanding body perception development, and recommends further investigation. In the current experiment, we studied the development of human body perception by analyzing the effect of orientation inversion on the N190 ERP component.

Behavioral and functional neuroimaging evidence indicates that human body perception development follows a protracted trajectory spanning across the entire childhood. Soon after birth, infants appear to be sensitive to the biophysical properties of the body. For example, neonates visually discriminate between biomechanically possible and impossible hand movements (Longhi et al., 2015). Using looking time paradigms which manipulate the body orientation, Zieber and colleagues (2010, 2015) showed that at the age of 3-months, infants visually discriminate changes in human body shape, size, and the organization of the body parts when the bodies are presented upright but not when inverted (Zieber et al., 2010; Zieber et al., 2015). Only one study analyzed infants' ERP responses at this age in order to explore potential similarities with adults in the chronology of the underlying processing stream (Gliga & Dehaene-Lambertz, 2005). Three-month-old's ERP responses to images of typical upright human bodies were contrasted to images of human bodies in which the structural information was altered by relocating the limbs in relation to the body trunk. Although the infant corresponding N190 (N290) was elicited by the perception of human bodies, this component was not sensitive to manipulations of structural information as it was shown for adults. Rather, sensitivity to configural information was shown for 3-months-old infants only at a later stage of processing, indexed by the positive ERP component P400. These results suggest that at this age the behavioral discrimination between manipulations of different body properties relies on immature perceptual representations of human bodies. Later on, around the age of 6-8- months, infants seem to extract more complex social information from body postures, such as emotional expressions, which may rely on processing the relations between body parts (Zieber et al., 2014a; Zieber et al, 2014b; Missana et al., 2014). The ERP investigations conducted at this age show that the infant correspondent N190 (N290) is sensitive to variations in emotional body postures (Missana et al., 2014), but no systematic experimental manipulations (e.g., inversion of orientation) were conducted to help understanding at which level of processing are the aspects of human body configuration taken into account.

Behavioral evidence indicates that the incipient abilities to process human bodies described in infancy continue to mature well beyond this age. For example, 8- to 10-year- old children are less accurate and slower than adults in recognizing people based on their bodies (Robbins & Coltheart, 2015). Nevertheless, the exact nature of this development is unclear. fMRI studies show that the neural network functionally associated with human body processing in adults (i.e., the fusiform body area - FBA, the superior temporal sulcus - STS, the amygdala, the inferior parietal lobule - IPL, and the extrastriata body area – EBA; Downing et al., 2001; Peelen & Downing, 2007; Pitcher et al., 2009; de Gelder & de Borst, 2015) is selectively responsive to static and dynamic human bodies by the age of 6- years (Ross et al., 2014; Peelen et al., 2009). This indicates that some degree of cortical specialization for processing human bodies has been reached. However, this may not be fully mature yet, as the activation of the body circuitry in the right hemisphere continues to show an increase in activation beyond this age, and does not reach adult levels by the age of 11 years (Ross et al., 2014). These studies are important because they indicate that quantitative changes in the neural circuitry underlying body processing continue well into childhood. However, due to their limited temporal resolution, fMRI studies are less informative with regards to any potential changes in the perceptual strategies or speed of processing. For example, it is not yet clear whether at different ages children engage in the same manner in processing human bodies as configurations of elements. Thus, further investigations into the development of the neurocognitive mechanisms underlying human body processing are required.

The goal of the current study was to test age-related changes in both children’s and adults’ ERP responses to human bodies and their sensitivity to configural information. For this purpose, we randomly presented 3-, 4-, and 10-year-old children, as well as adults with static images of female and male human bodies with neutral postures and images of structurally similar objects (i.e., hat stands) in upright and 180° inverted orientation. The fact that previous studies did not find evidence for a change in the effect of face inversion on the N170 between the ages of 4 and 10 (Taylor, Batty & Itier, 2004) partially motivated the current choice of age groups. Due to the reduced ability of the very young children included in this study to follow complex instructions and to provide motor responses on request, we kept this task passive. This would also facilitate potential future comparisons with the results from infant studies. We were particularly interested in the N190 and the P1 ERP components since these were previously shown to be sensitive to potential differences in processing between human bodies and other objects (Thierry et al., 2006; Taylor et al., 2010; Stekelenburg and de Gelder, 2004). We anticipated that in both children and adults observing human bodies compared to objects will elicit an increased amplitude and earlier peak of the N190. If the N190 reflects the activation of the neural representation of bodies in high-level visual cortex based on information related to configural relations between body-parts, we anticipate an inversion effect on the N190. Specifically, a more negative N190 is expected for the inverted compared to upright bodies. An inversion effect on the N190 is not expected for objects. Shorter latencies of the P1 for human bodies compared to objects were previously reported (Thierry et al., 2006), and we anticipate to find these differences as well, most likely reflecting the extraction of the low-level visual properties relevant for later stimulus categorization (Rossion & Jacques, 2008). The comparisons across children age groups and with the adult group will allow conclusions about any potential developmental changes in the morphology of the components of interest, differences in speed of processing, and reliance on configural information.

Method

Participants

The final analysis included 45 children and 16 adults: 3-year-old, N = 16, 8 females, M_{age} = 35.25 months (SD_{age} = 4.34); 4-year-old, N = 15, 9 females, M_{age} = 54.93 months (SD_{age} = 6.65); 10-year-old, N = 14, 8 females, M_{age} = 128.29 months (SD_{age} = 6.35); adults, N =16, 5 females, M_{age}=25.13 (SD_{age} = 3.81). Additional 25 participants (3-year- old, N = 16; 4-year-old N = 8; 10-year-old, N = 1; adults, N= 1) were tested but not included in the analysis due to technical issues (N = 5) or insufficient number of artifact free trials (N =23). The participants were recruited from an urban area in North-West England. For children, parents gave informed written consent for their participation in the study before the procedure began. Children also assented for their participation in the study. Adult participants gave informed written consent before the procedure began. The procedure followed the ethical standards (the Declaration of Helsinki, BMJ 1991; 302:1194) and was approved by the University Ethic Committee.

Stimuli and procedure

The stimuli consisted of static grayscale images of human bodies and objects with similar structure (i.e., hat stands) presented in upright and inverted position (upright human bodies – UB; inverted human bodies – IB; upright objects – UO; inverted objects – IO). The human body stimuli included 10 different exemplars of both male (N = 5) and female (N = 5) bodies displaying an emotionally neutral posture. These stimuli were selected from the Bodily Expressive Action Stimulus Test (BEAST, de Gelder & Van den Stock, 2011). The object stimuli included 10 different exemplars of hat stands which were selected from images found on-line (Figure 1). Both human body and object stimuli were displayed on a grey background, with a size of 142 x 312 pixel, subtending a visual angle of 3.18°× 8.67° (horizontal × vertical and a viewing distance of 70 cm. Stimuli were also normalized for luminance (~180 cd/m^2).

Within a single trial, the stimulus was presented for 800ms, followed by a central fixation cross on a grey background with a duration varying randomly between 1200 and 1600ms. This is to avoid the participant's neural response biased by their expectation to a set interval. In order to maintain participants' attentiveness throughout the task, a black or red star on a grey background was presented randomly every 4 to 6 stimuli before the fixation cross. Participants were asked to press a button as soon as they saw a star on the screen. The presentation of the star lasted 1000ms irrespective of whether the participant pressed the button or not (see Figure 1 for an example of the trial structure).

All stimuli (upright human bodies – UB; inverted human bodies – IB; upright objects – UO; inverted objects – IO) were presented with equal frequency (20/condition) across several blocks. In order to avoid excessive movement due to limited attention span and maintain the quality of the data recording, younger children were presented with fewer maximum number of trials than the older children and adults. Three- and 4-years-old group watched a maximum of 240 trials (3 blocks, 80 trials/block). Ten-year-old children and adults watched a maximum of 320 trials (4 blocks; 80 trials/block).

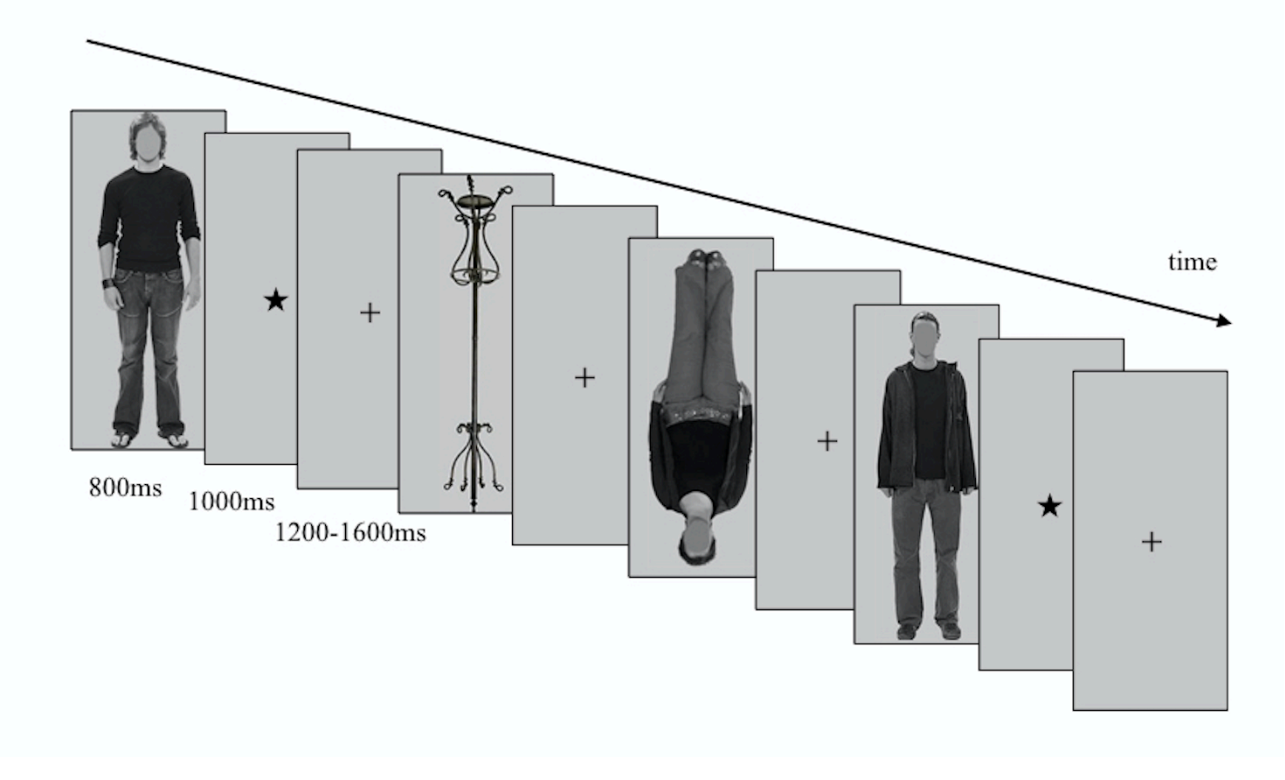

Figure 1. Example of trial structure and the stimuli used in the study: upright human body UB), inverted human body (IB), upright object (UO), inverted object (IO).

EEG Recording and Analysis

The ERPs were 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) as default for the EGI system, and a bandpass filter of 0.1–100 Hz was applied. The data were sampled at 500 Hz. Impedances were checked prior to the beginning of the recording and they were considered acceptable if lower than 50 Ω as recommended by the EGI system. A digital video of the child was recorded synchronously with the EEG, in order to identify the eye movements and visual attendance to the stimuli.

The raw EEG data were further processed offline using NetStation v4.5.4 (Eugene, OR). The signal was band-pass filtered (0.3–30Hz), and the ERP trials were segmented with a 200ms baseline and 800ms following stimulus onset. To eliminate artifacts, different methods are applied for infants' and adults' data. For adults, segmented data were automatically rejected whenever the signal exceeded ± 100 μV for eye-movement and ± 140 μV for eye-blinks 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 12 (approximate 10% for the 128-channel net) channels that the signal exceeded ± 80 μV, and also if the participant did not attend visually to the stimulus (as indicated by the digital video recording). For infants, segmented data were automatically rejected whenever the signal exceeded ± 200 μV at any electrode, due to the nature of the data. The 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 18 (approximate 14% for the 128-channel net) channels that the signal exceeded ± 80μV, and also if the participant did not attend visually to the stimulus (as indicated by the digital video recording). A minimum of 10 trials/condition was required in order to include a participant in the analysis. The average number of trail's remaining in each condition for each age group is presented in Table 1.

Table 1

Number of the trials included in the analysis for each condition across the 3 age groups

Age Group	Mean (SD) of the numbers of trials			
	UB	IB	UO	IO
3-year-old	22.69 (8.28)	22.06 (7.11)	22.56 (7.30)	22.94 (7.78)
4-year-old	32.47 (11.11)	32 (13.82)	31.13 (12.02)	31.00 (13.47)
10-year-ol	42.07 (14.42)	46.36 (15.05)	43.71 (13.61)	44.00 (14.12)
Adult	58.94 (15.08)	52.64 (14.54)	60.69 (13.50)	61.19 (12.59)

Note. UB = Upright Body, IB = Inverted Body, UO = Upright Object, IO = Inverted Object. Each condition contains 80 trials.

Based on previous literature (Stekelenburg and de Gelder, 2004; Peykarjou et al., 2013) and visual inspection of the data, we chose different regions of interests (ROIs) for children and adults for analysis. The posterior leads as ROIs for the analysis of the P1 and N190 components are: children, left - 66, 65, 69; right - 84, 90, 89 (Figure 2); adults, left - 58, 51; right - 96, 97 (Figure 3). The visual inspection of the average waveforms for each individual child participant revealed a large variability in the latency to the peak value of the N190 component. Such variability was previously reported in studies using similar paradigms for the investigation of face processing during childhood (Kuefner, Heering, Jacques, Palmero-Soler, & Rossion, 2010). In order to accommodate these individual differences, for children we followed the existent methodological guidelines (Kuefner et al, 2010), and calculated the peak of each component as the maximum voltage within a ~50ms window defined separately for each participant by visual inspection of the waveforms. The same temporal window was used for all conditions within the same participant. We further calculated the latency for the peak voltage of each component defined this way. A bifid peak on N190 was also observed for some of the participants (N = 24) across all the children groups, as it was previously reported for face processing (Hirai and Hiraki, 2015; Kuefner et al., 2010; Taylor, Batty and Itier, 2004). In these cases, the N190 was considered as the first negative deflection after the P1, even if this deflection was smaller in amplitude than the second one (Kuefner et al., 2010). For the adult group, the time windows for P1 (100-150ms) and N190 (150-200ms) were selected based on the previous literature (Stekelenburg and de Gelder, 2004) and visual inspection. The mean amplitude for each component was calculated by averaging all data points within the time window defined as described above.

Considering the differences in scalp location of the ROIs, the mean amplitude, peak amplitude, and latency to the peak were analyzed separately for children and adults. A 2 (Stimuli: human body, object) × 2 (Orientation: upright, inverted) × 2 (Hemisphere: left, right) × 3 (Age: 3-, 4-, and 10-year-old) mixed ANOVA with age as a between factor was conducted for children. A 2 (Stimuli: human body, object) × 2 (Orientation: upright, inverted) × 2 (Hemisphere: left, right) repeated measures ANOVA was conducted for adults. Holm–Bonferroni correction was used for all Post-hoc tests. The results were interpreted at the significance threshold of $p = .05$.

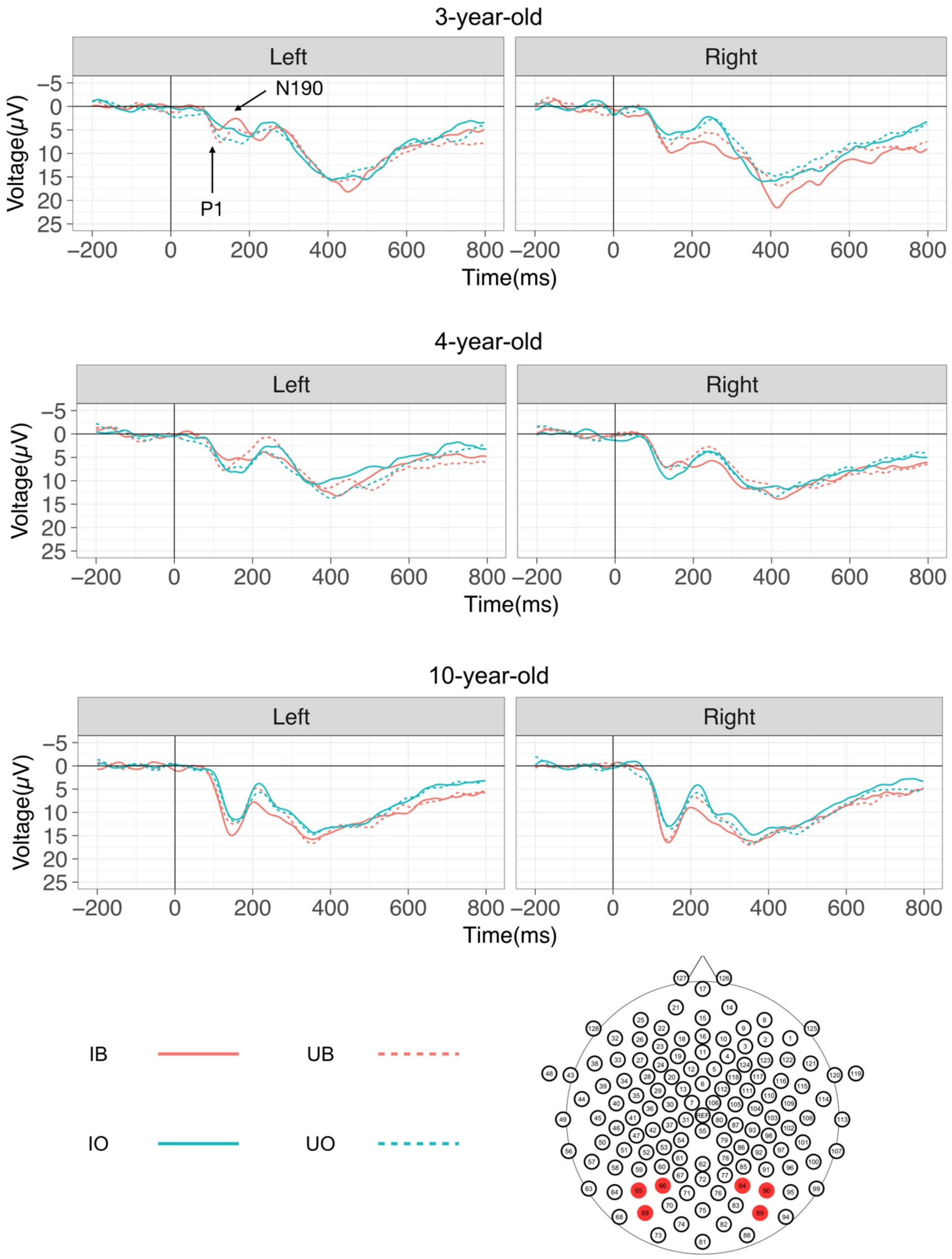
3-year-old
Left
Right
N190
P1
4-year-old
Left
Right
10-year-old
Left
Right
Voltage(μV)
−5
0
5
10
15
20
25
−200
0
200
400
600
800
Time(ms)
IB
UB
IO
UO
65
66
69
84
89
90
REF

Figure 2. Grand averaged ERPs of children for upright body (UB), inverted body (IB), upright object (UO) and inverted object (IO) from 6 electrodes (left: 66, 65, 69; right: 84, 90, 89). Please note that the negative is plotted upwards.

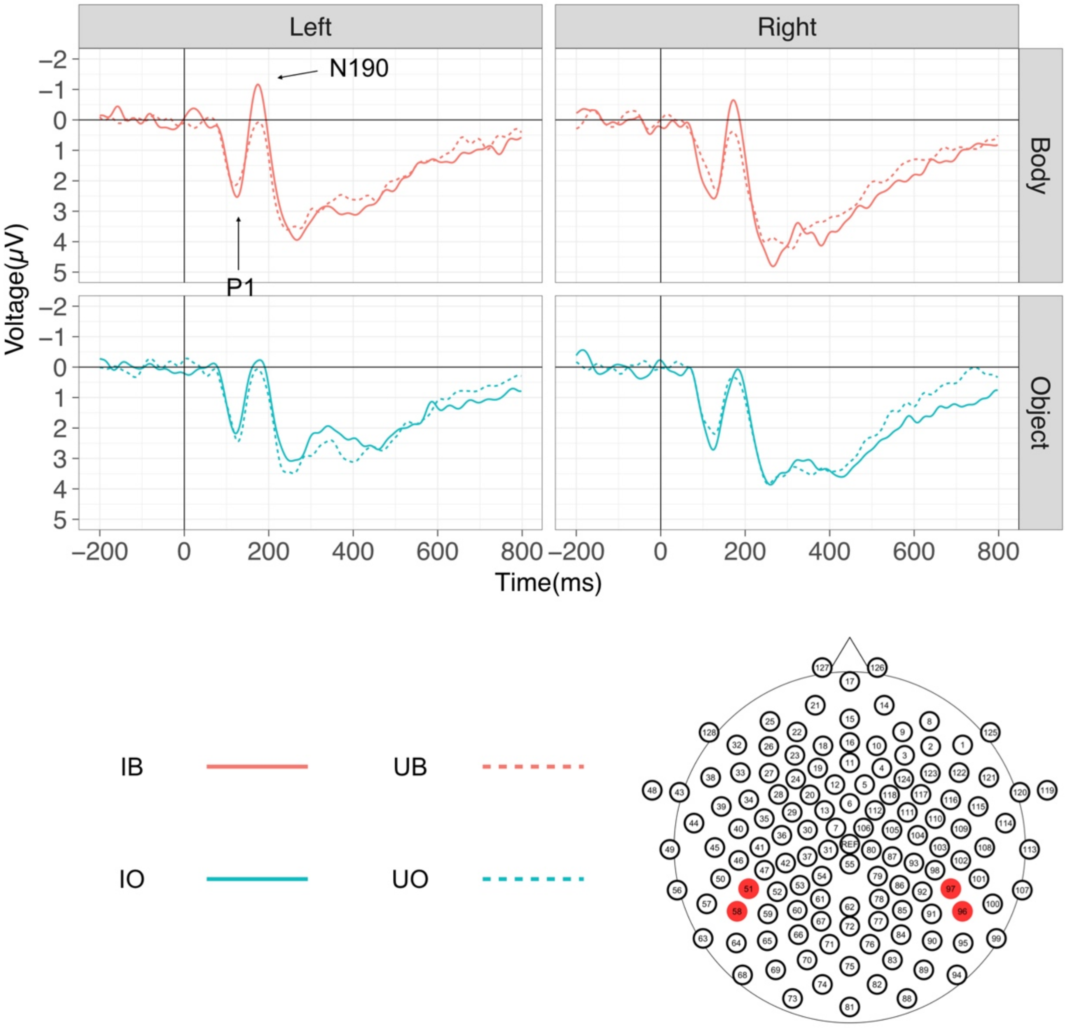

Figure 3. Grand averaged ERPs of adults for upright body (UB), inverted body (IB), upright object (UO) and inverted object (IO) from 4 electrodes (left: 58, 51; right: 96, 97). Please note that the negative is plotted upwards.

Results

Children

P1 - *Mean amplitude*

The analysis revealed a main effect of Age, $F(2, 45) = 12.76$, $p <.001$, $\eta_p^2 = .207$), showing that the mean amplitude of the P1 is larger for the 10-year-old children ($M = 10.46$ µV, $SD = 4.59$) compared to both the 3-year-olds ($M = 5.53$ µV, $SD = 4.82$, $p < .001$) and the 4-year-olds ($M = 6.08$ µV, $SD = 3.67$, $p < .001$) (See Figure 4). No significant differences were observed between the two younger age groups ($p = .320$).

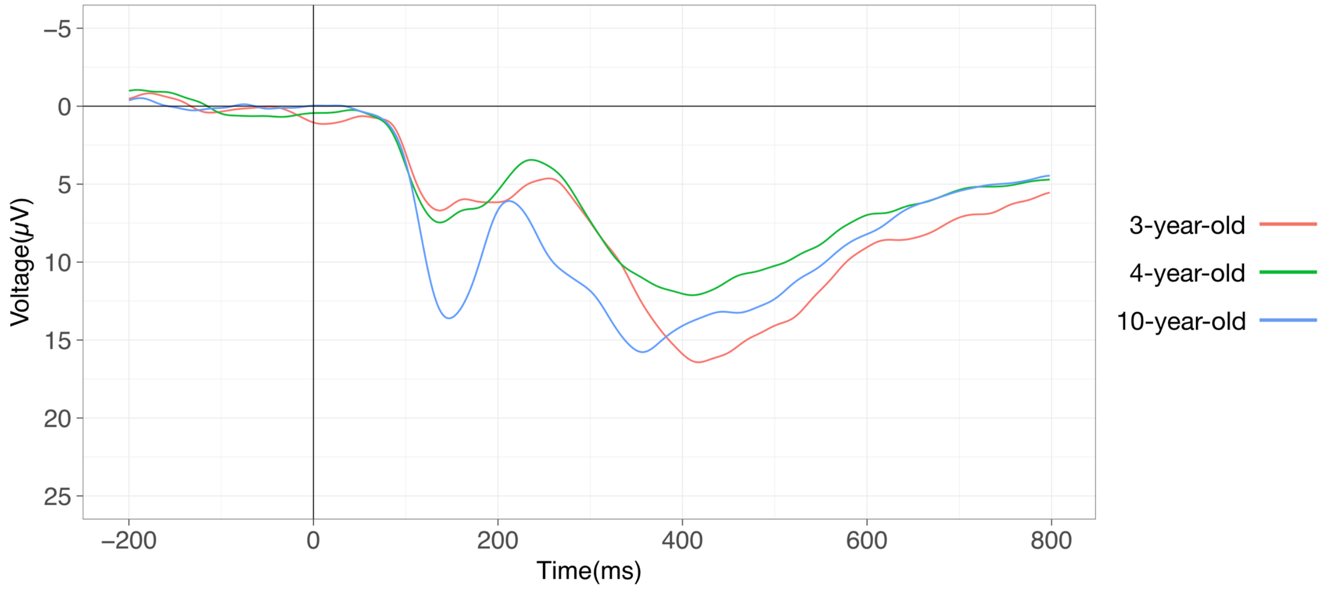

Figure 4. Grand averaged ERPs of all three age groups across all conditions. Please note that the negative is plotted upwards

We also found significant interactions between Stimuli × Hemisphere, $F(1, 45) = 8.26$, $p = .006$, $\eta_p^2 = .006$); Stimuli × Age, $F(1, 45) = 4.84$, $p = .013$, $\eta_p^2 = .018$), as well as a Stimuli × Hemisphere × Age, $F(2,45) = 6.05$, $p = .005$, $\eta_p^2 = .005$). In order to disentangle this three-way interaction, Stimuli × Hemisphere repeated measures ANOVAs were performed separately for each age group. For the 3-year-old group, a significant interaction Stimuli × Hemisphere was observed, $F(1, 15) = 13.04$, $p = .003$, $\eta_p^2 = .027$. Post-hoc pairwise comparisons revealed that this interaction is driven by a difference in the P1 mean amplitude between hemispheres in response to body stimuli: the mean amplitude recorded in the right hemisphere for the body stimuli was larger ($M = 6.92$ µV, $SD = 4.55$) than in the left hemisphere

(*M* = 4.79 μV, *SD* = 5.69), *p* = .039. For the 10-year-old children, a main effect of stimulus was observed, *F*(1, 14) = 15.48. *p* = .002, η_p^2 = .047), showing that across both hemispheres, body stimuli elicited larger P1 mean amplitude (*M* = 11.4 μV, *SD* = 4.61) than the hat-stand stimuli (*M* = 9.49 μV, *SD* = 4.41). The analysis further revealed an Orientation × Hemisphere interaction, *F*(1, 45) = 6.08, *p* = .018, η_p^2 = .002), which was further qualified by an interaction with age: Orientation × Hemisphere × Age, *F*(2, 45) = 4.62, *p* = .015, η_p^2 = .015. In order to disentangle this interaction, Orientation × Hemispheres repeated measures ANOVAs were performed separately for each age group. For the 3-year-old age group, a significant Orientation × Hemisphere interaction was found, *F*(1, 15) = 6.54, *p* = .022, η_p^2 = .010, but no significant pairwise comparisons emerged. No significant effects were found for the older age groups (*p*s > .062).

P1 - *Peak amplitude*

The analysis revealed a main effect of Age (*F*(2, 45) = 10.54, *p* = .001, η_p^2 = .189), Stimuli (*F*(1, 45) = 4.77, *p* = .035, η_p^2 = .008), and their interaction Stimuli × Age (*F*(2, 45) = 4.54, *p* = .016, η_p^2 = .016). Overall, 10-year-olds recorded larger P1 peak amplitude (*M* = 15.12 μV, *SD* = 5.73) than the younger 3- (*M* = 9.97 μV, *SD* = 5.65) and 4-year-old (*M* = 9.73 μV, *SD* = 4.14) children, *p*s < .001 (See Figure 5). For the 10-year-old children *F*(1, 14) = 15.18, *p* = .002, η_p^2 = .048), but not for the younger age groups (*p*s > .223), the peak P1 amplitude elicited by body images (*M* = 16.35 μV, *SD* = 5.76) is larger than that elicited by object images, *M* = 13.88 μV, *SD* = 5.48 (Figure 5).

The main effect of Stimuli was also qualified by a further interaction with Hemisphere, *F*(1, 45) = 5.71, *p* = .021, η_p^2= .004. The Post-hoc analysis shows that the peak P1 amplitude elicited by body images is larger over the right (*M* = 12.86 μV, *SD* = 6.22) than over the left hemisphere (*M* = 11.05 μV, *SD* = 5.82), *p* = .010. Moreover, on the right hemisphere, the peak P1 amplitude is larger for bodies (*M* = 12.86 μV; *SD* = 6.22) than for objects (*M* = 11.26 μV, *SD* = 5.94), *p* = .010.

We also observed an Orientation × Hemisphere × Age interaction, $F(2, 45) = 5.53$, $p = .007$, $\eta_p^2 = .003$. An Orientation × Hemisphere interaction was found for the 4-year-old group ($F(1, 15) = 5.81$, $p = .03$, $\eta_p^2 = .007$) and 10-year-old group ($F(1, 14) = 6.73$, $p = .022$, $\eta_p^2 = .003$), but no significant pairwise comparisons emerged (ps > .051).

P1 - *Latency*

The analysis revealed a Stimuli × Orientation interaction, $F(1, 45) = 5.68$, $p = .022$, $\eta_p^2 = .008$**,** which was further qualified by an interaction with age: Stimuli × Orientation × Age interaction, $F(2,45) = 5.61$, $p = .007$, $\eta_p^2 = .015$, see Figure 6. This interaction was followed up by Stimuli × Orientation repeated measures ANOVAs of each age group. A significant Stimuli × Orientation interaction was observed for the 3-year-old children, $F(1, 16) = 12.14$, $p = .003$, $\eta_p^2 = .035$, but not for the older age groups, ps > .859. The post-hoc analysis showed that for the 3-year-old children, the latency to the peak P1 amplitude is longer ($p = .002$) for the inverted ($M = 175.5$ ms, $SD = 36.72$) than for the upright bodies ($M = 158.52$ ms, $SD = 37.98$), and longer ($p = .011$) for the inverted bodies than for the inverted objects ($M = 154.65$ ms, $SD = 37.15$). No significant differences were recorded in terms of the latency to the peak P1 amplitude between upright and inverted objects ($p = .124$). An Orientation × Hemisphere interaction ($F(1, 45) = 5.75$, $p = .021$, $\eta_p^2 = .005$) was also observed, but the pairwise comparisons failed to show any significant differences (ps > .101).

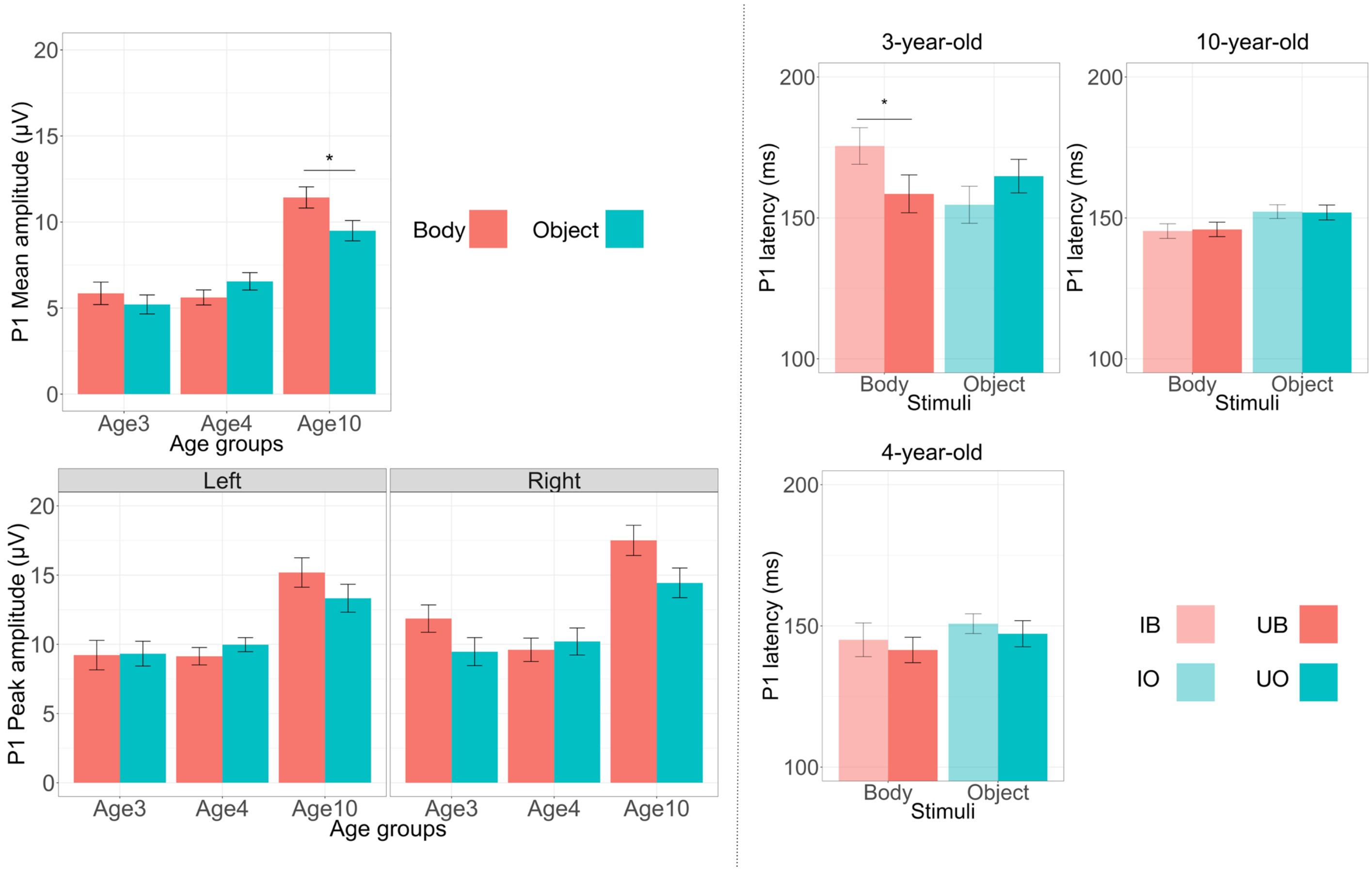

Figure 5. Left: Mean and peak amplitude of the P1 component in response to Bodies and Objects for all three age groups. Right: Latency of the P1 peak amplitude in response to Bodies and Objects in Inverted and Upright conditions.

N190 - *Mean amplitude*

The analysis of the N190 mean amplitude revealed a main effect of Age, $F(2, 45) = 4.26$, $p = .021$, $\eta_p^2 = .086$, showing that the 10-year-old children manifest a larger mean amplitude ($M = 8.39$µV, $SD = 4.82$) for this component in comparison to both 3- ($M = 5.79$ µV, $SD = 5.85$; $p < .001$) and 4-year-old children ($M = 4.64$ µV, $SD = 4.71$; $p < .001$) (See Figure 4). The mean N190 amplitude was similar for the two younger age groups ($p = .096$).

The N190 mean amplitude was also found to vary as a function of stimulus type and orientation (Stimuli × Orientation, $F(1, 45) = 5.07$, $p = .030$, $\eta_p^2 = .009$). Across all age groups included in the analysis, inverted bodies elicited greater mean N190 amplitude ($M = 7.00$ µV, *SD* = 5.63) than the upright bodies (*M* = 5.48 µV, *SD* = 5.65), *p* = .028, while this differentiation was not observed for the hat-stands (*p* = .498) (See Figure 6 and 7).

We also observed a Stimuli × Hemisphere interaction, *F*(1, 45) = 12.98, *p* = .001, η_p^2= .009, which was further qualified by an interaction with age: Stimuli × Hemisphere × Age, *F*(2, 45) = 4.63, *p* = .015, η_p^2= .006. To disentangle these effects, the three-way interaction was followed up by Stimuli × Hemispheres repeated measures ANOVAs performed separately for each age group. A significant Stimuli × Hemisphere interaction was found for 3-year-old children, *F*(1, 16) = 15.05, *p* = .001, η_p^2= .030) but not for the two older age groups (*p* > .119). Pair-wise comparisons revealed that for 3-year-old group, the mean N170 amplitude elicited by body stimuli over the right hemisphere (*M* = 7.54, *SD* = 5.70) is larger than that over the left hemisphere (*M* = 4.15µV, *SD* = 6.45), *p* = .010.

N190 - *Peak amplitude*

Similar with the results obtained for the mean amplitude, the peak N190 amplitude also varied with Age, *F*(2, 45) = 4.08, *p* =.024, η_p^2 =.074. Post-hoc comparisons showed that the peak N170 amplitude recorded for 10-year-old children is greater (*M* = 4.47 µV, *SD* = 4.73) than the one recorded for 3-year-old (*M* = 1.54 µV, *SD* = 6.28, *p* < .001) and 4-year-old (*M* = 1.07µV, *SD* = 5.09, *p* <.001) children. No significant differences emerged between the peak N170 amplitude recorded for the two younger age groups (*p* = .510).

The analysis revealed a Stimuli × Orientation interaction, *F* (1, 45) = 6.58, *p* = .014, η_p^2=.014. Irrespective of the age group, the inverted bodies elicit higher peak N170 amplitude (*M* = 3.10µV, *SD* = 6.06) than the one elicited by the upright bodies (*M* = 1.33µV, *SD* = 5.85), *p* = .014. No other significant differences were observed (*p*s > .112) (See Figure 6 and 7)

An interaction between Stimuli × Hemisphere, *F* (1, 45) = 22.70, *p* < .001, η_p^2 =.016, was also observed, which was qualified by a further interaction with age, Stimuli × Hemisphere × Age, F(2, 45) = 8.08, *p* = .001, η_p^2 =.012. This three-way interaction was followed up by Stimuli × Hemisphere ANOVA performed separately for each age group. A significant interaction Stimuli × Hemisphere was obtained only for the 3-year-old children, $F(1,16) = 27.8$, $p < .001$, $\eta_p^2 = .054$). Pair-wise comparisons suggested that the peak N190 amplitude elicited by body images is greater over right hemisphere ($M = 3.09$ µV, $SD = 6.29$) than left hemisphere ($M = -0.95$ µV, $SD = 6.93$), $p = .003$. Moreover, on the left hemisphere, the peak N190 amplitude elicited by object images ($M = 2.86$ µV, $SD = 5.50$) is more positive than that recorded in response to body images ($p = .011$). Other comparisons failed to show significance ($ps > .110$).

N190 - *Latency*

In terms of latency to the peak N190 amplitude, the analysis showed a main effect of Orientation, $F(1, 45) = 8.36$, $p = .006$, $\eta_p^2 = .006$). Irrespective of age group, all stimuli presented in the inverted orientation elicited faster latency of N190 ($M = 212.10$ ms, $SD = 41.10$) than the stimuli presented with upright orientation ($M = 218.10$ ms, $SD = 38.99$) (See Figure 7).

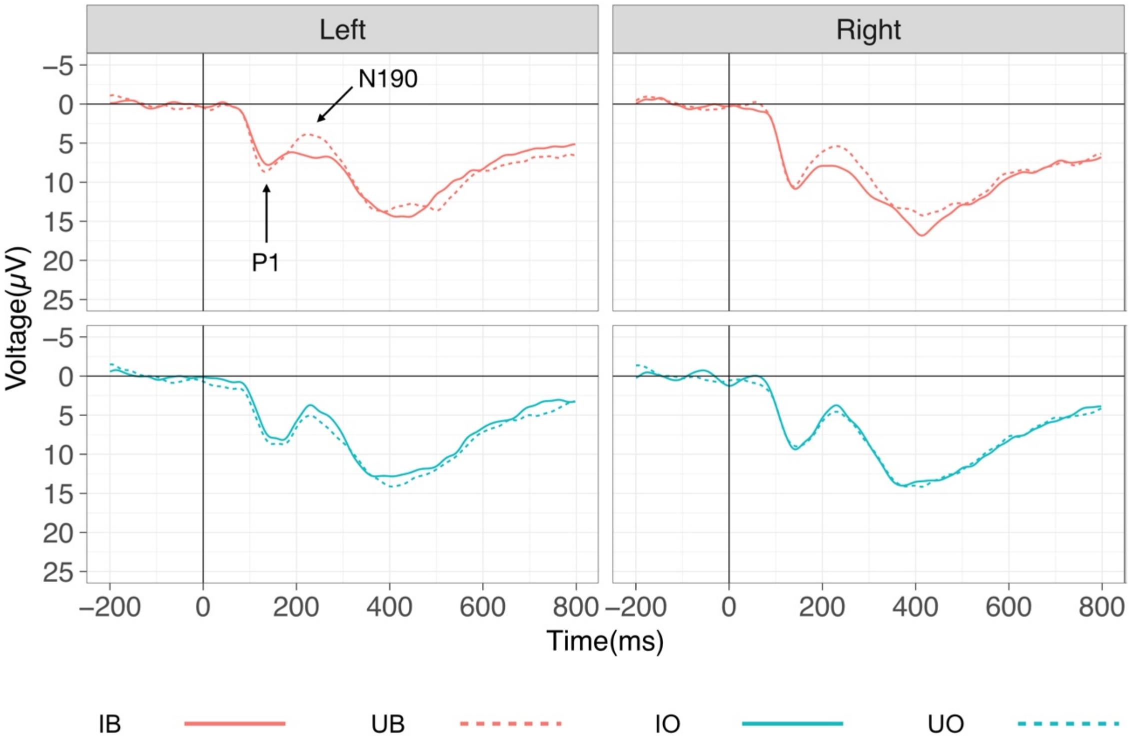

Figure 6. Grand averaged ERPs of the N190 and P1 components for body and object in upright and inverted conditions across all 3 age groups.

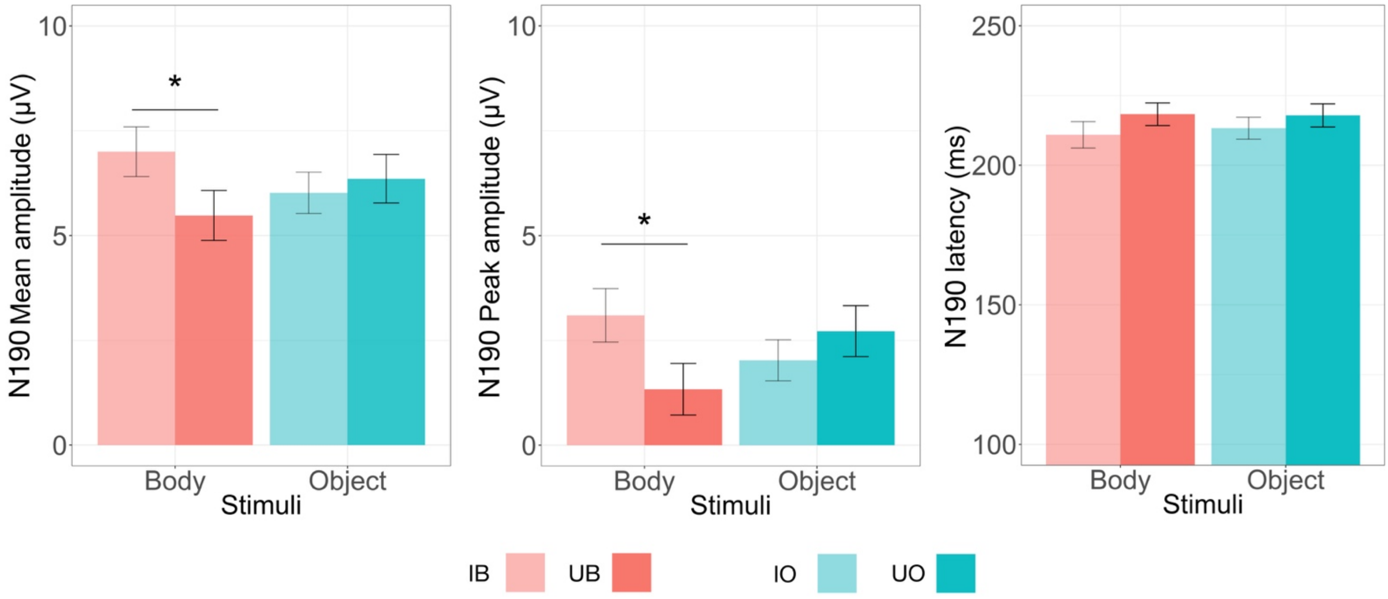

Figure 7. Mean amplitudes and peak (the most negative going), and latency to the peak amplitude of the N190 (with standard error) in response to body and object in upright and inverted conditions.

Adults P1

No significant main effects or interactions were found for the mean, peak and latency analysis (*ps* > .092).

N190 - *Mean amplitude*

The mean analysis revealed a main effect of Orientation, $F(1, 15) = 5.642$, $p = .031$, $\eta p^2 = 0.045$. The upright images ($M = 0.540$ µV, $SD = 1.792$) elicited greater mean amplitude than invert images ($M = -0.003$ µV, $SD = 1.792$) regardless of stimulus category.

N190 - *Peak amplitude*

The peak analysis revealed a main effect of Orientation, $F(1, 15) = 8.641$, $p = .010$, $\eta p^2 = 0.049$; which was further qualified by a Stimuli × Orientation interaction, $F(1, 15) = 5.795$, $p = .029$, $\eta p^2 = 0.031$. Post-hoc comparisons showed that inverted bodies elicited higher negative amplitude (*M* = -2.260 µV, *SD* = 2.664) than upright bodies (*M* = -1.100, *SD* = 1.964; $p < .001$). Furthermore, inverted object images (*M* = -1.376 µV, *SD* = 2.211) elicited greater peak amplitude than inverted body images ($p = .009$) (see Figure 3).

N190 - *Latency amplitude*

The latency analysis revealed a significant Orientation × Region interaction, $F(1, 15) = 4.673$, $p = .047$, $\eta p^2 = 0.022$. Post-hoc comparisons found that in the right hemisphere upright images (*M* = 171.313 ms, *SD* = 15.447) elicited faster latency than inverted images (*M* = 177.063 ms, *SD* = 15.854; $p = .009$), regardless of stimulus category.

Discussion

The aim of the current study was to investigate the development of human body perception in 3- to 10-year-old children, by testing the effect of stimulus orientation on the P1 and N190 ERP components. Images of human bodies and structurally similar objects – hat stands – were randomly presented to the participants in a passive paradigm. In children, both images of human bodies and hat stands elicited a positive ERP component which peaked at approximately 153ms, followed by a negative going component peaking approximately at 215ms. Given their morphology and latency, these components are most likely the correspondents of the adult P1 and N190, respectively. The analysis revealed that the N190 is particularly sensitive to manipulations of human body orientation for all age groups included in the analysis; however, the inversion effect on N190 is presented in a paradoxical way between the adults and children. Inverted body images elicited a greater N190 than upright ones in adults, whereas in children this body inversion effect performs in an opposite way. The amplitude of both P1 and N190 was found to change with age from 3-10 years; the topography of the P1 and N190 amplitude for adults and children are very different as well. These findings are discussed in terms of their implications for understanding the development of human body perception in childhood in comparison to adults.

Previous studies with adult participants provided mixed results for the presence of a body effect on the N190, as reflected in an increased amplitude and faster latencies to human bodies compared to images of objects (Stekelenburg & de Gelder, 2004; Minnebusch, Suchan, & Daum, 2008; Thierry et al., 2006; Taylor et al., 2010; Gliga & Dehaene-Lambertz, 2004). In our study, the N190 amplitude in response to the human bodies and images of objects for all age groups is in line with the findings of Stekelenburg & de Gelder (2004). However, for the P1 in children, we recorded a larger amplitude for body stimuli compared to the hat stands, and this effect tended to be lateralized to the right hemisphere. The P1 differentiation is similar to the one reported in children and adults to the different responses towards face and object stimuli (e.g., Rossion & Caharel; Itier & Taylor 2004; Itier & Taylor, 2004; Kuefner et al., 2010), as well as between non-human mammal bodies and object stimuli (e.g. Itier & Taylor, 2004). Unlike the differences in the P1 latency between human bodies and objects reported in adults (Thierry et al., 2006), the P1 in our study peaked with similar latency for both categories of stimuli across all age groups. P1 is usually sensitive to the low-level visual properties of the stimuli (Regan, 1989) and it is thought to originate mainly from the striate and lateral extrastriate visual areas (Clark et al., 1995; Di Russo et al., 2002; Halgren et al., 2000; Tanskanen et al., 2005; Tarkiainen et al., 2002). Given that the P1 differences were recorded irrespective of orientation, they most likely reflect naturally occurring variations in the low-level visual properties of the human bodies and hat-stands in children.

Inversion effect

Manipulating the orientation of human bodies by presenting them upside down interferes with the extraction of diagnostic information, such as the configuration of body. While inverted stimuli may be still perceived as human bodies (Reed et al., 2006), the activation of the specific representation is usually delayed and more effortful. The N190, which is thought to reflect the activation of the representations of the human bodies in high-level visual cortex, was previously found to be sensitive to such manipulations (Stekelenburg & de Gelder, 2004;

Minnebusch, Suchan, & Daum, 2008). Higher negative amplitudes and longer latencies of the N190 for the inverted compared to upright images of human bodies was interpreted as evidence of more effortful extraction of the configural information which is essential for the activation of the corresponding neural representations (Minnebusch, Suchan, & Daum, 2008).

In our study, the body-selective inversion sensitivity is found on the N190 peak on adult participants; inverted bodies elicited greater N190 amplitude than upright bodies, and such effect was not observed in response to objects. This finding replicated the previous literature (Stekelenburt & deGelder, 2004; Minnebusch, Suchan, & Daum, 2008; Minnebusch et al., 2010), and clarified the body inversion effect of adults' configural processing of human bodies. That is, similar to facial perception, inverting whole human bodies influenced the cognitive processing of human bodies in adults. The adult N190 latency showed general orientation sensitivity to both bodies and objects; the absence of the body-selective inversion effect here is also in agreement with the findings by Minnebusch and colleagues (2010) using similar action-neutral body images. They found the N190 latency is unaffected by the degree of the rotation of the bodies, in contrast to findings with faces (Jacques and Rossion, 2007). Therefore, our findings on adult N190 latency also indicated that different processing mechanisms are involved in body and face processing. No inversion effect was observed on P1 in adults, which is also in line with the previous adult finding that P1 is not sensitive to body inversion (Righart & de Gelder, 2007).

For the children, our findings show that children from 3- to 10-years of age recorded significant differences in the amplitude of the N190 component between the upright and inverted human bodies which was not extended to structurally similar objects. In line with some of the findings reported in adults (Minnebusch, Suchan, & Daum, 2008), but in contrast to the adult findings in the current study and other literature (Stekelenburg & de Gelder, 2004; Minnebusch, Suchan, & Daum, 2008), upright human bodies elicited a greater N190 (increased negative going amplitude) compared to their inverted presentations. Thus, for children, although the manipulation of orientation affected the amplitude of the N190 selective for the human bodies and not for the hat-stands as it was predicted, the direction of the effect is opposite to the one typically reported in adults. The child N190 for inverted bodies was also slightly faster (~ 8ms) than for upright bodies, but similar in latency with that recorded for inverted objects. A greater N190 in response to upright compared to inverted faces was also found in 4- to 10-year-old children (Taylor, Batty, & Itier, 2004). Interestingly, adults with developmental prosopagnosia show the same paradoxical inversion effect on the N170/ N190 for both face and human bodies (Righart & de Gelder, 2007). One possible explanation for these findings is that up to a certain age, children's perception of faces and bodies makes more flexible use of configural information (Campbell, 1999; Mondloch, Le Grand, & Maurer, 2002), with different perceptual strategies being equally efficient dependent on the task and context. For example, 8-to-11-year-old children recognize with similar accuracy the identity of both upright and inverted faces and the advantage for the upright faces only occurs after the age of 12-years (Mondloch et la., 2002). While behavioral responses could not be recorded in the current study due to the youngest participants' age, the similar paradoxical bodily inversion effect on N190 in children and the presence of the typical bodily inversion effect on N190 in adults suggests that such findings in faces may apply to bodies as well.

Some limited effects of body orientation were also observed at the earlier stages of processing reflected by the child P1. For the youngest 3-year-old children only, the P1 in response to inverted human bodies peaked approximately 20ms later compared to both upright bodies and inverted objects. The effect of body orientation did not extend to the P1 amplitude, which was similar for both upright and inverted presentations. Manipulations of the stimulation in the upper and lower visual field by changing the balance of simple parameters such as contrast are known to influence the latency of the P1 (Di Russo et al., 2002; Jacques & Rossion, 2009). These findings indicate that the processing of naturally occurring differences in the low level visual properties between the lower and the upper part of stimuli, and not necessarily the processing of the structured information, might drive the orientation effect on the P1 (Rossion & Caharel, 2011). One explanation for why this effect was only present in the younger children is that with increased experience in processing human bodies, children more readily detect the upper part of the torso even when the location in the visual field has changed. Further investigations on human body perception in which the visual properties are systematically manipulated and the gaze dynamic is tracked are needed in order to elucidate the significance of these findings.

Developmental effects

Both the P1 and the N170 showed more defined morphology with age, consistent with the previous reports for the face processing domain (Kuefner et al., 2010; Taylor, Batty, & Itier., 2004). The first visual evoked potential P1 did not change in latency across the 3 age groups, but its amplitude increased dramatically between the ages of 4 and 10-years. These age differences were similar for both bodies and objects. Importantly, they did not vary as a function of stimulus orientation, suggesting that they are potentially driven by the psychophysical properties of the stimuli. A sharp increase in P1 amplitude in early childhood was previously shown to be followed by a significant linear decline which continues until adulthood (van den Boomen et al., 2015). This trend can also be observed in our study. However, the exact source of these changes is not known. A decrease in EEG power, possibly due to an age-related reduction in gray matter volume (Whitford et al., 2007) and synaptic density (Huttenlocher, 1990), as well as changes in the conductivity of the underlying tissues and the general level of brain activity have all been proposed to be linked with changes in the P1 amplitude during childhood (Kuefner et al., 2010). In our study, across all children groups, the perception of bodies led to a larger P1 than the perception of objects. This effect was more specific to the right hemisphere, although the older 10-year-old children tended to record it bilaterally. Significant developments in the processing of the low-level visual properties of the stimuli occur during childhood (e.g., van den Boomen, Smagt & Kemner, 2012; van den

Boomen et al., 2015) with possible consequences on how human bodies and objects are processed. Further studies are thus needed in order to elucidate the interaction between vision development and the perception of social stimuli during childhood.

The changes with age in the amplitude of the N190 largely mirrored those found for the P1, with 10-year-old children showing less negative (higher) mean and peak amplitude than both 3- and 4-year-olds. These findings are in line with those reported for face processing (Taylor et al., 2004; Kuefner et al., 2010), and are most likely partially due to the developmental changes in the P1 amplitude (Kuefner et al., 2010). Nevertheless, despite these age differences in mean amplitude, the orientation effect on the N170 specific for human bodies was stable across children groups, suggesting that the processing of the human body configural information is present at least as early as the age of 3. In average, the N190 peaked at 218ms for upright bodies which represents a delay of approximately 46ms compared to the adult N190 (172ms). Although previous studies (Missana et al., 2014) did not quantify the exact latency of the N190 in younger age (i.e., 8-months-old infants), this seems to be slower by at least 50ms compared to the one recorded in young children. Thus, the activation of the neural representations of human bodies become faster between infancy and early childhood, followed by a period of stability at least up to the age of 10-years, before reaching adult characteristics.

One limitation of the current study, particularly in terms of analyzing the developmental changes in human body perception, is the fact that no intermediate age groups between 4- and 10-years of age were tested. It is possible that some of the changes with age in the P1 and N190 amplitude noted here may occur earlier, and that the age of 10 represents one of the points on the declining slope of a U-shape trajectory which continues into adolescence and adulthood (Kuefner et al., Taylor et al., 2004; van den Boomen et al., 2015). Future studies which include more age groups may address this limitation and would also clarify when in ontogeny the typical body inversion effect on the N190 occurs. In the face processing domain, around the age of 10-11-years, a shift occurs from the paradoxical to the typical inversion effects on the

N170 (Taylor et al., 2004). This is not the case for the perception of human bodies, which suggests different developmental trajectories. A direct comparison between the body and the face inversion effect across childhood will be especially relevant for understanding the similarities and differences in the underlying neurocognitive processes and their development. Our study is one of the few to investigate the neural correlates of social information processing using ERPs in 3-year-old children. Although the attrition rate is higher than for older children, it shows that developmental ERP research can extend to include this age group, providing unique opportunities for adopting larger scale cross-sectional or longitudinal designs which span the entire childhood, beginning with infancy.

To summarize, this study shows that human body perception is reflected in the P1 and N170 ERP components during early and middle childhood. For all age groups included in the study, the manipulation of the stimulus orientation affected predominantly the N190 in response to human bodies, but not the N190 for structurally similar objects. This body inversion effect in children is different from the one typically reported in adults, with upright bodies eliciting a more negative N190 compared to the inverted presentations. Thus, although configural information may be integral to human body representations during childhood, the extent and the conditions under which such diagnostic information is used remain to be established. Significant developmental changes were also observed in the early ERP components typically associated with the processing of low-level visual information, which is relevant for the perception of complex visual social stimuli. Taken together, these findings suggest that body perception continues to develop well into childhood and further research is required in order to specify the exact nature of this process.

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Inversion Effect in Children's Emotional Body Perception: An ERP Investigation

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Abstract

The human body provides rich emotional information in social interactions during childhood. However, so far, the investigation of the neural mechanism of processing emotional body postures received less attention than facial literatures. The present study aims to explore the neural mechanism underlying emotion perception from static body postures during childhood, using electroencephalography (EEG). Eighty emotional body images including happy, sad, fearful and emotional neutral actions were used as stimuli, half of which were presented upright and half inverted. ERPs time-locked to the stimuli onset were calculated. Twenty children aged from 5 to 7 years were tested. Results revealed a main effect of emotion on the N190 from occipito-temporal sites, as well as on the VPP from the frontal-central sites. Happy bodies elicited more negative amplitude and longer latency than the other emotional bodies. The main effect of emotion further interacted with body orientation. These findings suggest early emotional sensitivities at the body structure encoding stage in children from 5 years old; further, the emotion effect on N190 is different in upright and inverted conditions, indicating that the activation of the body representation interferes the emotion perception.

Keywords: *emotional body, invention effect, emotion, childhood, N190, VPP, EEG.*

Introduction

Sensitivity to people's emotional state is an important skill for young humans to adapt to their social environment. As children develop throughout childhood, they are exposed to an increasing variety of social situations. In order to successfully interact with others, children need to rely on multiple sources of information. For example, during play, the face, the body, and the voice may differ in terms of how informative they are with regards to peers' emotions depending on the distance between children. While at close proximity the face is clearly visible, at a distance it is more difficult to detect the changes in its expressivity. In this case, the body becomes more informative about how others feel. Moreover, the ability to recognise emotion from body images is reported to be related to 3-6-year-old children's social skills in pre-school (Parker, Mathis, & Kupersmidt, 2013). This further suggested that the ability to correctly detect emotion information from body postures is particularly important during this developmental period. Despite its importance, the study of the development of human body expressivity in children has only recently entered systematic scientific scrutiny.

Emotions are usually conveyed in multiple ways, which tend to coincide in time and share some similarities. For example, facial emotion expressions are usually associated with matching body postures. When expressing anger, the muscles tense in both face and body (Parker, Mathis, & Kupersmidt, 2013). Prior research showed that both children and adults recognize emotions better when these are expressed both in face and body in comparison to facial-only conditions, suggesting body expression is beneficial for discriminating and understanding emotions (Montepare, Koff, Zaitchik, & Albert, 1999; Vieillard & Guidetti, 2009; Nelson & Russell, 2011). From an early age, infants show discriminative response to emotions from extreme valances (happy and angry) expressed by static body postures (Zieber, Kangas, Hock, & Beat, 2014). Developing into childhood, children's performance in discriminating emotions from body postures improves. From 4 years of age, children start to show the ability to successfully sort happy and sad emotions expressed by isolated static body postures to matched context (Mondloch, Horner, & Mian, 2013). The accuracy of identifying emotions from body postures keeps developing from the age of 5 to 10 years. By the age of 8 years, children can correctly label emotions expressed by body postures from different valence (happy and sad) using given verbal labels, suggesting that the ability to understand and use emotional labels is independent of context. Further, performance of labelling happy and sad bodies at this age is also comparable to adults (Balas, Auen, Saville, & Schmidt, 2017). In terms of perceiving emotional information from dynamic body movements. Boone and Cunningham (1998)'s investigation discovered that children actually start to use the high emotional intensity movements from dancing activities to detect sadness, fear and happiness from 5 years onwards. By the age of 6, children can correctly match fearful and sad emotions expressed by isolated body postures with the appropriate emotions portrayed within the story. Further, when the bodily and facial expression was congruent, 6-year-old children showed increasing accuracy in matching emotional body expressions to the corresponding story in comparison to incongruent condition. This shows by the age of 6 there is adult-like congruency effect in detecting the mismatch information between body and facial expression. Despite this, children's accuracy is lower than adults' (Mondloch, Horner, & Mian, 2013).

Despite the behavioural findings showing an improved performance in perceiving emotions from body postures during childhood, we have limited knowledge about the neurocognitive mechanism underlying children's performance in these behavioral tasks; especially in terms of whether the behavioral improvement observed in children can reflect the development for all the sensory, perceptual and cognitive processes or only for some of them. Brain imaging fMRI studies on adults have established a body-selective brain network in the extrastriate body area (EBA), the fusiform body area (FBA), as well as the posterior superior temporal sulcus (pSTS) (Downing Jiang, Shuman, & Kanwisher, 2001; Peelen &

Downing, 2004; de Gelder, 2006). Six-year-old children show brain activation to dynamic emotional body expressions over similar brain regions (i.e. EBA, FBA and pSTS) as adults, however, until 11 years of age the strength and extent of those activities are still less mature compared to adults (Ross, de Gelder, Crabbe, & Grosbras, 2014). Apart from these findings, very few studies have investigated the developmental change of emotion perception from static body postures during childhood.

In terms of the neurophysiological evidence, previous studies employing event-related potentials (ERPs) in adults suggested that the cognitive processing underlying body perception shares some similarity with that of face perception. The facial N170 (a negative component that peaks around 170 ms after the stimulus onsets) that is larger for face than non-face objects. Similar response is also observed during this time window for body perception, a negative going component show larger amplitude for body stimuli than that for non-body objects, however, the bodily component is called N190 as it peaks slightly later than the facial one (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000; Sagiv & Bentin, 2001; Rossion & Jacques, 2011; Stekelenburg & de Gleder, 2004; Minnebusch, Suchan & Daum, 2008). The N170/N190 is preceded by a positive going component P1 that is sensitive to low-level visual information (Regan, 1989; Rousselet et al., 2005). Furthermore, presenting upside-down faces was found to lead to greater N170 amplitude and/or longer N170 latency (Bentin et al., 1996; Rossion et al., 1999, 2000). A similar inversion response is not observed for objects. This N170 facial-inversion effect is therefore interpreted as reflecting the impairment of facial structural encoding (Bentin et al., 1996; Rossion et al., 1999). Likewise, inverted body images also elicited a facial-like inversion effect, with longer latency or greater amplitude on the N190 components, thus suggesting a similar structural encoding strategy is shared by body and face perception in adults (Stekelenburg & de Gelder, 2006; Minnebusch et al., 2008). However, there are no sufficient studies for us to properly understand the development of emotion perception from static bodies neurophysiologically. First, there are very few studies provide the evidence of maturational emotional body perception. There are only less than a handful studies shows that fearful body postures elicited faster responses at early visual processing stages from the occipital-temporal electrodes and sustained neural responses at later processing stages from frontal-central electrodes (Stekelenburg & de Gelder, 2006; Heijnsbergen et al., 2007). Apart from those adult investigations, there is only one study looking at infant's neurophysiological response to emotional body postures. Results revealed that 8-month-old infants show more negative N290 (the infant N190) as well as Nc (Negative-central) mean amplitude to fearful body postures in comparison to happy ones (Missana, Rajhans, Atkinson, & Grossmann, 2014). The Nc is a negative going component peaking at approximately 600ms after stimulus onset at frontal central electrodes in infants. It is suggested that the Nc reflects attentional arousal to salient or unfamiliar stimuli (de Haan, et al., 2004; Parker & Nelson, 2005). Thus, these findings indicated that from 8 months old infants an attentional response to emotions of different valences emerges. However, apart from the early response and the mature pattern indicated by those infant and adult investigations, the neural correlates during childhood are poorly understood.

Based on the described similarity of body and face perception, one would expect the development of emotional body perception to share some similarity with that of faces; thus, looking at the development of emotional face perception can be a starting point to understand the neural processes in response to emotional body postures.

Evidence from emotional face perception ERP studies suggested that fearful faces elicit a larger Nc amplitude than happy faces in 7-month-old infants (Nelson, & de Haan, 1996; de Haan, Belsky, Reid, Volein & Johnson, 2004). Between the ages of 7 to 32 months, infants show a greater amplitude to sad and fearful faces over happy and angry on the early negative component N170 from frontal-central and occipito-parietal electrodes, instead of the attention allocation response on the Nc. It is believed that this early negative component is different from the adult N170 that is specific to the structural encoding of faces; instead, the infant N170 reflects that infants in this age range are able to distinguish facial expression of some emotions at the perceptual level (Parker & Nelson, 2005). From 4 years of age, an effect of emotion is observed on the face-selective N170 as well as on the early visual component at occipito-parietal sites. Furthermore, age related emotional changes are observed on both the N170 and P1 from 4 to 15 years (Batty & Taylor, 2006). The P1 component in 4-7-year-old children shows a longer latency to fearful faces than happy, surprised and emotionally neutral faces, while happy faces elicited shorter P1 latency than disgusted, fearful and sad faces. Considering that low-level visual differences were controlled in this study, the researchers argued that the P1 emotional sensitivity reflects young children's general processing of emotions' primary meanings at the early processing stage. Whereas, emotional effect on N170 is found in older age groups, with larger N170 amplitude for negative facial expressions than positive ones. This indicates an increasing reliance on configural processing in encoding emotional gestures in faces that replaces the early global discrimination during development (Batty & Taylor, 2006). Furthermore, findings at this age range are different from Batty and Taylor's (2003) findings on adults, showing that the N170 is sensitive to fearful and sad faces on latency, and sensitive to surprised and neutral faces on amplitude. This suggests that emotion recognition from facial expression is not fully developed until adolescence.

Moreover, we are also interested in the role of bodily configural information in children's emotion perception. People's attributing of emotions from body postures is highly associated with the biological angle and directions of the body elements; such as upper body bending backward or forwards, shoulder swinging up or down, body weight transferring backward or forward (Coulson, 2004). For example, when the upper body bends backwards with straight elbow and shoulder swing up, it will be perceived as happy, while upper body bending forwards with a tightly-bent elbow and body weight transferring forward is more likely to be recognised as angry. Further, in body structural encoding, it is suggested that similar to facial perception, all body elements and the spatial relations between them are taken into account in the structural encoding (Reed, Stone, Bozova, & Tanaka, 2003; Reed, Stone, Grubb, & McGoldrick, 2006). One of the cognitive markers of the body structure processing is the inversion effect in body perception. When presenting body images upside down, people's accuracy and reaction time in recognising the stimulus is delayed. This pattern of response is also observed in facial perception, and has been interpreted to suggest that the inversion disrupts the processing by unravelling the orders and relations among the features on body or faces (Yin, 1969; Reed et al., 2006). This leads to the hypothesis that body structural information might be necessary for emotion perception. In fact, neurophysiological evidence in infants shows that the neural responses between emotions are only observed when the static body expression is presented upright (Missana, Rajhans, Atkinson, Grossmann, 2014). Based on the previous work that adults' perception of body structure is impaired by the inversion (Stekelenburg & de Gleder, 2004; Zieber et al., 2015), we predict that the orientation of the body postures will also interfere with emotion processing in children.

The current research aims to investigate children's neural correlates of emotion perception from static body postures, as well as the influence of body inversion in emotion processing. We are particularly interested in investigating this research question in 5- to 8-year-old children, as at this age they are reported to successfully identify emotions from intense body expressions (Boone and Cunningham, 1998; Mondloch, Horner, & Mian, 2013). We use body posture pictures expressing happy, fear and sad emotions, as behavioural data suggested that children of this age range show good performance in recognising these emotions in bodies (Boone & Cunningham, 1998; Balas, Auen, Saville, & Schmidt, 2017). As the age range tested in the current study showed emotion sensitivities on both P1 and N190 in emotional facial perception investigations (Batty & Taylor, 2006), we predict that in the current study both P1 and N190 from the occipital regions will show emotion sensitivities, negative emotions might elicit larger amplitude than positive ones. Further, the VPP (vertex positive potential) component was reported to reflect the opposite side of the activity from the same generators of the N190 in facial perception investigation (Rousselet, et al., 2005; Joyce & Rossion, 2005; Rossion & Jacques, 2011). The VPP is a positive potential peak around 140 to 180ms after stimuli onset from the central sites, in facial perception it is seen as the positive counterpart of N190 (Rousselet, et al., 2005; Joyce & Rossion, 2005; Rossion & Jacques, 2011). In relation to the N190 effect and the previous finding (Stekelenburg & de Gelder, 2004), the inversion effect and emotional response is also expected to reflect on the VPP component. To be specific, we predict amplitude and/or latency differences between emotions on P1, N190, as well as VPP.

Moreover, as we hypothesised that the body structure processing may influence emotion processing, we also expect the interaction of emotion and orientation on the N190. Based on previous work in infants (Missana et al., 2014) we predict the interaction will be driven by the emotion effect in the upright condition but not the inverted. Therefore, another possible direction of the interaction would be that the emotion effect in the inverted condition is not completely absent, but shows an impaired pattern, i.e. fewer differences between emotions.

Methods

Participants

The final analysis included children aged 5-8-years (N = 20, 10 females, *Mage* = 75.5 months, *SDage* = 11.94). The participants were recruited from an urban area in the North-West, UK. Parents gave informed consent for their children to take part in the study. Children received a small gift for their participation and parents were reimbursed for the cost of their travel to the lab. The procedure followed the ethical standards (the Declaration of Helsinki, BMJ 1991; 302:1194) and was approved by the Lancaster University Ethic Committee.

Stimuli and Procedure

The stimuli were selected from the Bodily Expressive Action Stimulus Test (BEAST, de Gelder & Van den Stock, 2011) and consisted of 80 static black and white images of female bodies, displaying 3 emotional postures (Happy, Sad, Fear) and 1 emotionally neutral action (i.e., drinking water and talking on the phone). Each emotion condition contained 20 images. All stimuli were displayed on a grey background, with a size of 200 x 250 pixels, subtending a visual angle of 6.36°× 7.94° (horizontal × vertical), and were normalized for luminance (~180 cd/m^2) in Photoshop. Participants were sat in front of the monitor with a viewing distance of 70 cm.

Within a single trial, the stimulus was presented for 800ms, followed by a central fixation cross on a grey background with a duration varying randomly between 1200 and 1600 ms. This is to avoid the participant's neural response being biased by their expectation to a set interval duration. In order to maintain the participant's attentiveness throughout the task, a non-social colorful object (i.e. a star) displayed on a grey background was presented 50% of the time after the stimuli presented. Participants were asked to press a button as soon as they saw the object on the screen. The presentation of the object lasted 1000ms irrespective of whether the participant pressed the button or not (see Figure 1 for an example of the trial structure). Stimuli presentation was organized in 4 blocks (80 trials/block), maximum of 320 trials in total. Each block contained 20 trials per emotion condition, in which half of the time the image was presented upright-down.

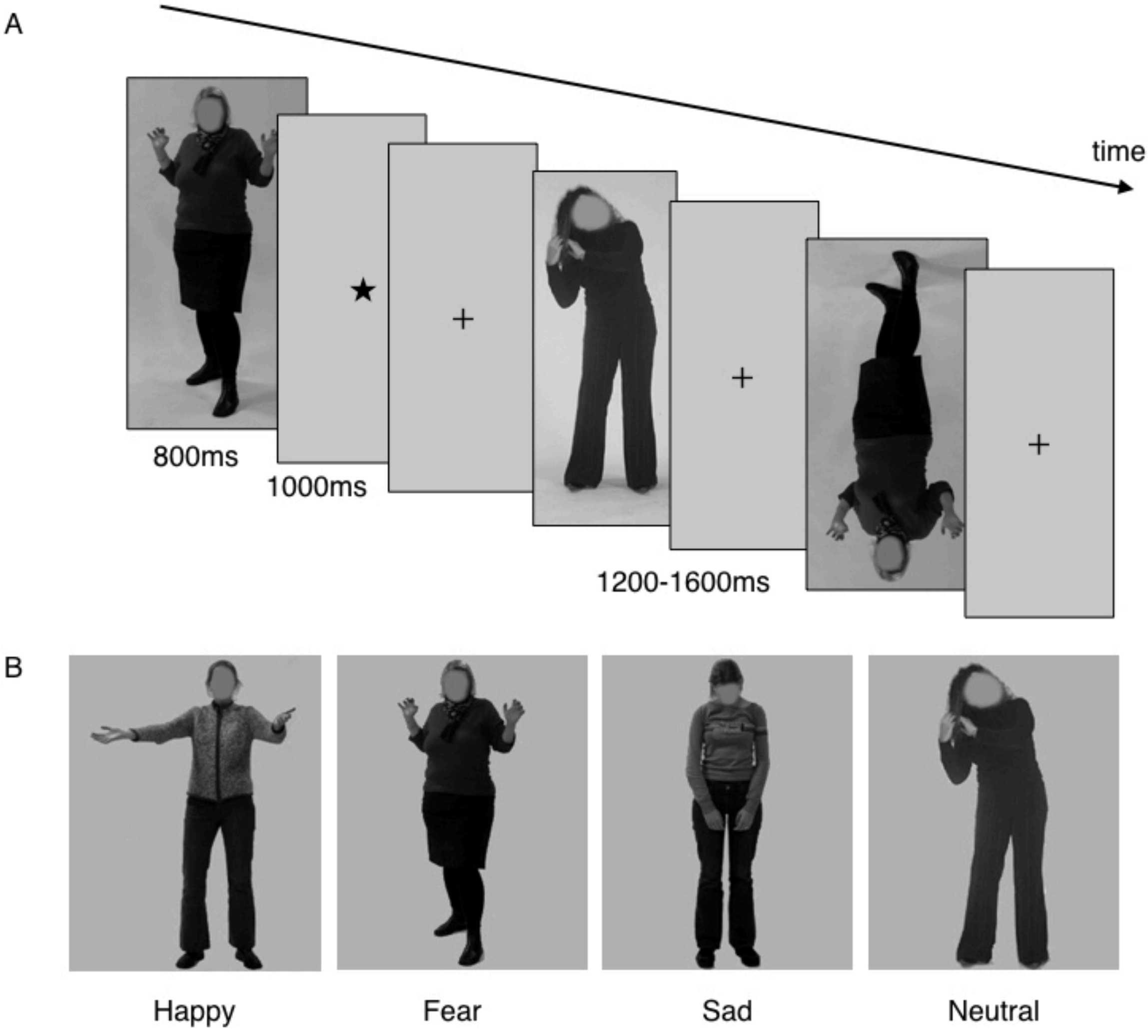

Figure 1. Example of a trial structure (A) and the stimuli used in the study (B).

EEG Recording and Analysis

The ERPs were 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 band pass filter of .1–100 Hz was applied. The data were sampled at 500 Hz. Impedances were checked prior to the beginning of the recording and they were considered acceptable if lower than 50 k. In order to identify the eye movements and visual attendance to the stimuli, a digital video of the child was recorded synchronously with the EEG.

The raw EEG data were later processed offline using NetStation 4.5.4 (Eugene, OR). The signal was band-pass filtered (0.3–30 Hz), and the ERP trials were segmented with a

200 ms baseline and 800 ms following stimulus onset. 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. For the remaining trials, individual bad channels (channels that the signal exceeded ± 200 µV) replacement was conducted using spherical spline interpolation. Individual subject averages were computed separately for each channel across all trials within each condition, and then the data was re-referenced to the average reference. Trials were excluded if more than 18 bad channels were detected and if the participant did not attend visually to the stimulus (as indicated by the digital video recording). The Means and SDs of the numbers of trials that remained in each condition are presented in Table 1.

Table 1

Means and SDs of the numbers of the trails remained out of total 80 trials in each condition.

		Emotion			
		Happy	Fear	Sad	Neutral
Orientation	Upright	22.90(6.27)	22.25(497)	23.75(5.80)	23.05(7.04)
	Inverted	25.70(5.62)	25.25(6.93)	24.55(6.15)	25.40(6.48)

Based on the previous literature (Stekelenburg and de Gelder, 2004; Taylor & Batty, 2006) and visual inspection of the data, we analyzed the VPP (vertex positive potential) from frontal-central sites (170-250ms), the P1 (100-150ms), and the N190 (150-275ms) components from occipital-temporal sites. The regions of interest (ROIs) were as follows: frontal-central (Left - 12, 20, 13, 29; Right - 5, 118, 112, 111); occipital-temporal (Left - 60, 67, 59, 66, 71, 70; Right - 85, 77, 91, 84, 76, 83), see Figure 2.

The mean amplitude, peak amplitude and latency of each component was averaged separately across each condition. Considering that the age range of the current sample could bring variations to P1 amplitude, to minimize the potential inference on the raw measurement of the follow up component N190, complementary P1-N190 peak-to-peak measurement (measurements of N190 minus P1) and analysis were performed to control for P1 variations. The same statistical analyses were performed on the mean amplitude difference between the peak of the N190 and the P1, as well as on the difference in milliseconds between the peak of the N190 and the peak of the P1. Both the analysis for the corrected and the uncorrected N190 are presented. The results were analyzed using a 3-way repeated-measure analyses of variance (ANOVAs). The factors included Emotion (Happy, Sad, Fear and Neutral), Orientation (Upright and Inverted) and Region (Left and Right). Holm-Bonferroni correction was applied for all the posthoc analysis.

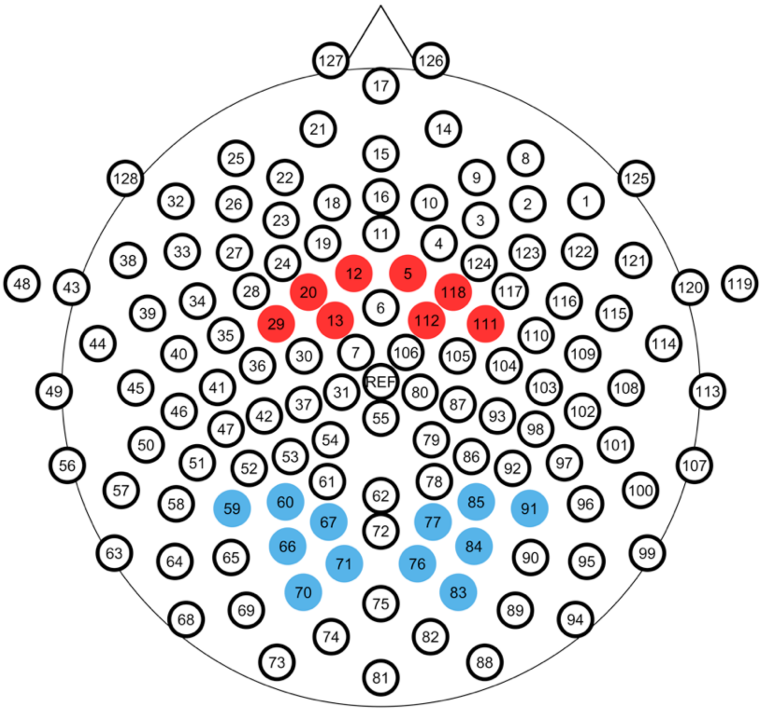

Figure 2. The regions of interest (ROIs) at frontal-central and occipital areas.

Results

VPP

Mean amplitude. The analysis revealed a main effect of Emotion, *F*(3, 57) = 4.17, *p* = .010, η_p^2 = 0.052, with happy bodies eliciting greater mean amplitude (*M* = -1.737 µV, *SD* = 3.372) than the fearful (*M* = -3.254 µV, *SD* = 3.786, *p* = .014) and sad ones (*M* = -3.102 µV, *SD* = 2.984, *p* = .036). Other comparisons failed to reach significance (*p*s > .705). A main effect of Orientation was also found, *F*(1,19) = 21.32, *p* < .001, η_p^2 = 0.121, with inverted body postures eliciting smaller mean amplitude (*M* = -3.595 µV, *SD* = 3.458) than the upright ones (*M* = -1.700 µV, *SD* = 3.175).

Peak amplitude. The analysis revealed a main effect of Emotion, F (3, 57) = 2.906, *p* =.042, η_p^2 = 0.041, and a main effect of Orientation, *F*(1,19) = 17.03, *p* < .001, η_p^2 = 0.089, which were further qualified by their interaction, *F*(3, 57) = 3.141, *p* = .032, η_p^2 = 0.037. Posthoc paired t-tests showed that when presented upright, fearful (*M* = 2.106 µV, *SD* = 3.858), happy (*M* = 3.002 µV, *SD* = 3.423) and emotionally neutral (*M* = 3.004 µV, *SD* = 4.235) body postures elicited higher peak amplitude than when presented inverted (Fear: *M* = -0.618 µV, *SD* = 4.087, *p* < .001; Happy: *M* = 1.453 µV, *SD* = 3.990, *p* = .037; Neutral: *M* =0.486 µV, *SD* = 3.312, *p* < .001) respectively). No differences were found between upright and inverted sad body postures (*p* = .977) (Figure 4). Furthermore, a higher peak VPP amplitude was recorded in response to inverted happy bodies than in response to inverted fear bodies (*p* = .033). Other comparisons failed to reach significance (*p*s > .081).

No significant main effects or interactions were observed for the latency of the VPP peak (*p*s >.060).

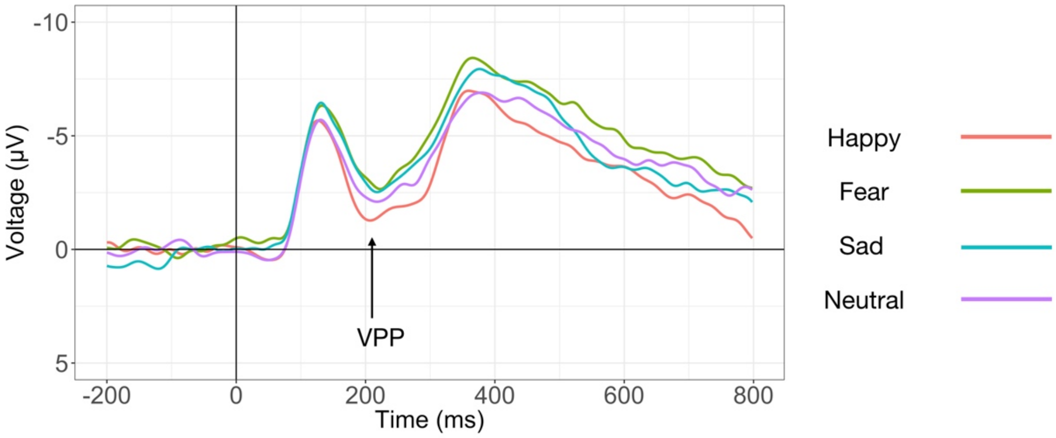

Figure 3. Grand average ERPs over frontal-central ROIs in response to body postures expressing fear, happiness, sadness and emotionally neutral actions.

P1

Mean amplitude. No significant results were found (*p*s >.106).

Peak amplitude. The analysis of the peak amplitude revealed a main effect of Orientation ($F(1, 19) = 6.173$, $p =.022$, $\eta_p^2 = 0.034$), with greater peak amplitude in response to inverted ($M = 19.782$ µV, $SD = 6.277$) compared to upright bodies ($M = 18.334$ µV, $SD = 6.014$).

Latency. No significant results were found (*p*s >.100).

N190

Mean amplitude. The analysis of the mean N190 amplitude revealed a significant main effect of Emotion ($F(3, 57) = 7.770$, $p < .001$, $\eta_p^2 = 0.077$), and a main effect of Orientation ($F(1, 19) = 41.636$, $p < .001$, $\eta_p^2 = 0.230$), which were further qualified by their interaction, $F(3, 57) = 3.331$, $p = .026$, $\eta_p^2 = 0.039$. Posthoc analyses showed significant differences between emotional postures, although the patterns differed between the two orientations (Figure 4). More specifically, when presented upright, happy ($M = 2.657$µV, $SD = 4.336$, $p = .005$) and neutral ($M = 2.837$µV, $SD = 4.724$, $p = .011$) body postures lead to increased negative amplitude compared to the sad bodies (*M* = 5.144µV, *SD* = 3.973). When presented inverted, the happy posture (*M* = 5.556µV, *SD* = 4.336, *p* < .001) elicited more negative amplitude than the fearful ones (*M* = 8.507µV, *SD* = 4.588). In addition, the mean N190 amplitude elicited by the upright bodies was significantly more negative than for the inverted ones when expressing fear (*p* < .001), happiness (*p* < .001) and emotionally neutral postures (*p* < .001; *M* and *SD* of upright neutral postures are presented before, M and SD of inverted neutral postures: *M* = 6.654 µV, *SD* = 4.850), but not when expressing sadness (*p* = .081).

Mean amplitude with respect to the P1: peak-to-peak analysis. The analysis revealed a significant main effect of Emotion (*F*(3, 57) =7.664, *p* < .001, $\mu_p^2 = 0.109$), a main effect of Orientation (*F*(1, 19) = 91.208, *p* < .001, $\eta_p^2 = 0.204$), and a main effect of Region, (*F*(1, 19) = 19.635, *p* < .001, $\eta_p^2 = 0.127$). Happy bodies (*M* = -4.524 µV, *SD* = 4.604) elicited more negative peak amplitude than fearful (*M* = -2.491 µV, *SD* = 3.899, *p* < .001), sad (*M* = -2.817 µV, *SD* = 4.035, *p* = .003) and emotional neutral bodies (*M* = -2.916 µV, *SD* = 4.098, *p* = .006); no significant effects were found between other emotions (*p*s > 1.000). The mean amplitude recorded for the upright bodies (*M* = -4.447 µV, *SD* = 4.064) was more negative than for the inverted bodies (*M* = -1.927 µV, *SD* = 4.008). The mean amplitude was more negative over the right (*M* = -4.048 µV, *SD* = 4.031) than the left hemisphere (*M* = -2.326 µV, *SD* = 4.245).

Peak amplitude. A significant main effect of Emotion (*F*(3, 57) =5.352, *p* = .003, $\eta_p^2 = 0.048$) and Orientation (*F*(1, 19) = 25.480, *p* < .001, $\eta_p^2 = 0.150$) were found, which were further qualified by their interaction, *F*(3, 57) = 5.870, *p* = .001, $\eta_p^2 = 0.057$. Posthoc analyses showed significant differentiations between emotional conditions, which varied as a function of orientation (Figure 4). More specifically, when presented upright, happy (*M* = -7.249 µV, *SD* =5.334, *p* = .003), and neutral body postures (*M* = -7.182 µV, *SD* =6.529, *p* = .004) elicited more negative mean amplitudes than the sad ones (*M* = -4.380 µV, *SD*

=4.710). For the inverted orientation, happy (*M* = -3.560µV, *SD* =5.241, $p = .041$), and sad body postures (*M* = -4.399 µV, *SD* =5.656, $p = .001$) elicited more negative mean amplitudes than the fearful ones (*M* = -1.373 µV, *SD* = 4.828). In addition, the mean N190 amplitude elicited by upright bodies was significantly more negative than the inverted ones when expressing fear (M_{up} = -5.600µV, SD_{up} = 5.633, p < .001), happiness (p < .001) and emotionally neutral postures (M_{in} = -3.415µV, SD_{in} = 5.877, p < .001), but not when expressing sadness ($p = .984$). Furthermore, a main effect of Region was observed, (F(1, 19) = 13.353, $p < .001$, $\eta_p^2 = 0.179$). Body postures elicited more negative N190 peak amplitude in the right (*M* = -6.265µV, *SD* = 5.471) compared to the left hemisphere (*M* = -3.024µV, *SD* = 5.584).

Peak amplitude with respect to the P1: peak-to-peak analysis. When taking into account the P1 peak amplitude, main effects of Orientation ($F(1, 19) = 7.487$, $p = .013$, $\eta_p^2 = 0.026$), and of Regions ($F(1, 19) = 16.690$, $p < .001$, $\eta_p^2 = 0.241$) were observed, which were further qualified by their interaction, $F(1, 19) = 4.897$, $p = .039$, $\eta_p^2 = 0.008$. Posthoc comparisons showed that the upright bodies (*M* = -27.318µV, *SD* = 7.224) elicited more negative amplitude than for the inverted bodies (*M* = -25.089µV, *SD* = 6.552) at the right hemisphere ($p < .001$). This was not the case for the left hemisphere ($p = .308$). Furthermore, irrespective of orientation, body postures elicited more negative N190 peak amplitude in the right (*M* = -26.204µV, *SD* = 6.965) compared to the left hemisphere (*M* = -21.240 µV, *SD* = 6.636).

Latency. No significant results were found (*p*s > .056).

Latency with respect to the P1: peak-to-peak analysis. The analysis revealed a significant main effect of Emotion ($F(3, 57) = 3.570$, $p = .019$, $\eta_p^2 = 0.045$). Emotional neutral bodies (*M* = 75.200ms, *SD* = 31.982) revealed shorter latency than the happy ones (*M* = 80.250ms, *SD* = 33.139, p = .042), while no significant differences were found between the other emotions (*p*s > .088). Other comparisons failed to show significance (*p*s > .057)

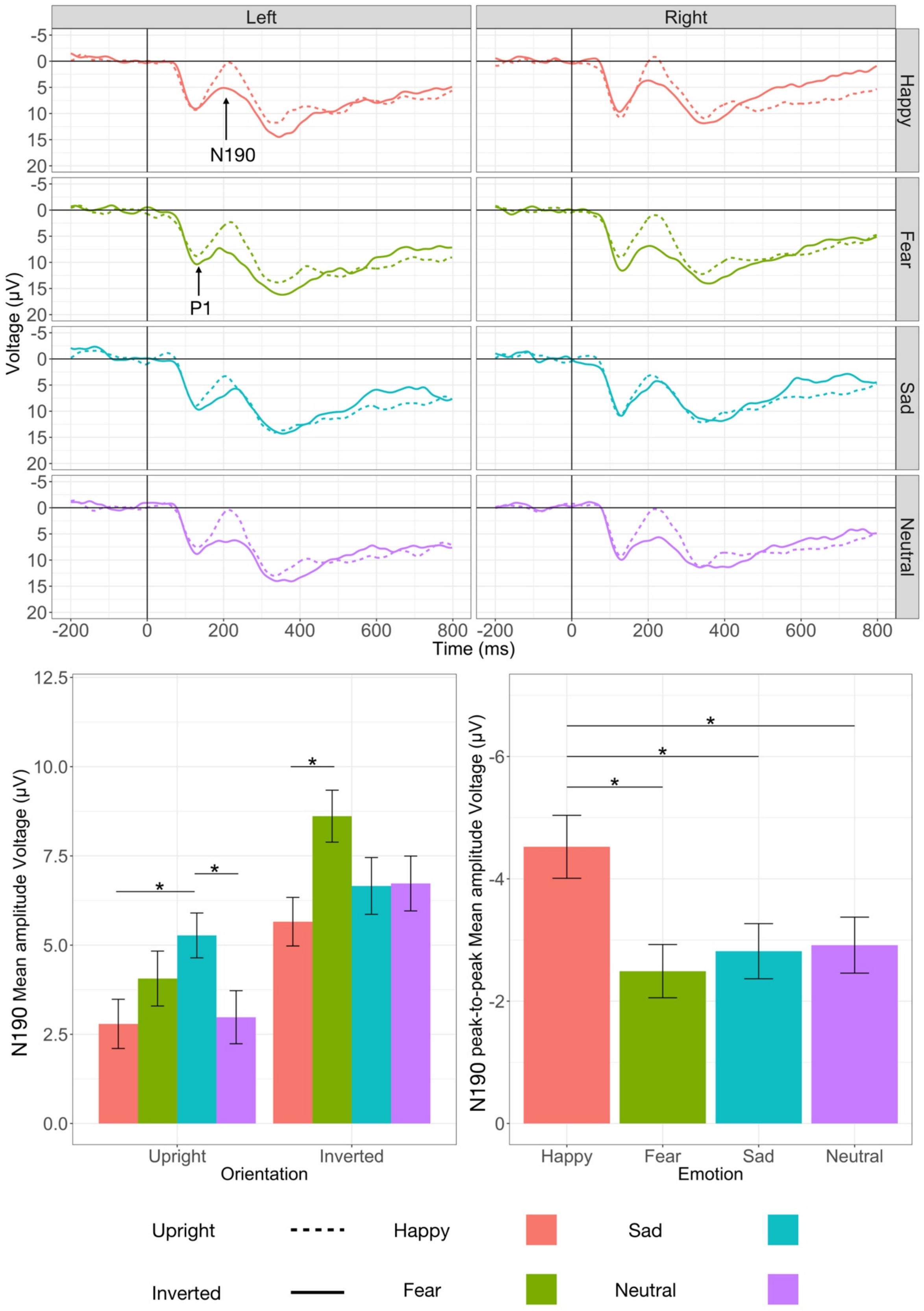
Left
Right
Happy
Fear
Sad
Neutral
N190
P1
Voltage (μV)
-5
0
5
10
15
20
-200
0
200
400
600
800
Time (ms)
N190 Mean amplitude Voltage (μV)
0.0
2.5
5.0
7.5
10.0
12.5
*
Upright
Inverted
Orientation
N190 peak-to-peak Mean amplitude Voltage (μV)
0
-2
-4
-6
Happy
Fear
Sad
Neutral
Emotion
Upright
Inverted
Happy
Fear
Sad
Neutral

Figure 4. Grand average ERPs over the occipital-temporal ROIs in responses to the bodies expressing happy, fear, sad and emotionally neutral actions when presented in upright and inverted orientation, with the bar chat representing the differences of the N190 mean amplitude Voltage (before and after peak-to-peak correction) between emotions.

Discussion

The aim of the current study was to investigate the neural underpinnings of emotional body posture processing in 5- to 8-year-old children. We analysed the ERP responses to human body postures expressing happy, sad, fearful, and neutral affective states presented either upright or inverted. We were particularly interested in ERP components typically associated with different aspects of human body processing: P1, N190, and VPP. Our results show that observing pictures of human bodies elicits these components in children and that they are modulated in different ways by the emotional expression of the bodies and their orientation.

The main effect of orientation on amplitude is the only effect revealed on the P1. Regardless of the emotional expression, inverted body images elicited greater P1 amplitude than upright bodies. Although the larger neural response to inverted face and body is considered as evidence of the impairment of configural processing on N170/N190, the inversion effect on P1 is also observed in response to non-face and non-body objects (Rossion & Caharel, 2010). The P1 is typically sensitive to the low-level visual features of the stimuli, such as luminance, color, or spatial frequency (Regan, 1989). Further, the P1 latency is found to be sensitive to manipulations of the stimulation in the upper and lower visual field, such as changing the balance of simple parameters like contrast (Di Russo et al., 2002; Jacques & Rossion, 2009). Therefore, the early sensitivity to orientation observed at the level of the P1 in our study probably originates from the low-level visual cues between the lower and the upper part the body in different orientation at this age, rather than specific to the structural encoding of bodies (Rossion & Caharel, 2011). Furthermore, this finding differs from previous findings on body perception in adults that show the P1 is not sensitive to the orientation change of bodies (Righart & de Gelder, 2007). This suggests that there are developmental differences in the body perception between 8-year-olds and adults. Interestingly, in facial perception studies, the orientation effect is observed on P1 from the temporal-occipital area from childhood until adulthood, with inverted faces eliciting greater amplitude and longer latency than upright faces (Linkenkaer-Hansen et al., 1998; Taylor et al., 2004). Therefore, the developmental differences on P1 components between bodily and facial perception support the findings of previous studies, that there are different neural resources behind similar ERP components of bodily and facial perception (Stekelenburg & de Gelder, 2004; Minnebusch et al., 2010).

Emotion is known to have an influence on the P1 in facial and bodily perception. Batty and Taylor (2003)'s investigation of adults' emotional processing of faces shows a small effect of emotion on the P1 amplitude, with neutral and surprised faces having the smallest amplitude compared to anger, disgust, fear, sadness, surprised and happy facial expressions, but the difference fails to reach significance. Their developmental findings of emotional face processing in children aged 4 to 15 years show an early emotional sensitivity on the P1. Fearful faces peak later than the neutral, happy, and surprised faces, while happy faces peak earlier than disgust, fear and sad faces. The faster neural response to happy faces in comparison to disgust, fear and sad faces is found in children from 4 to 7 years old at occipital regions (Batty & Taylor, 2006). Heijnsbergen and colleagues (2007)' study of adults processing emotion from body images found that P1 showed shorter latency to fearful bodies as compared to neutral bodies. This implies that emotion processing happens earlier than and in parallel with the structural encoding of faces from 4 years old and body processing in adults. However, the early sensitivity towards emotional information on the P1 was absent in the current study. Unlike face processing at similar ages, when observing emotional body expressions, early extraction of emotional information does not take place at this stage in 5-8-year-old children. This indicates that either emotion perception from body and facial expression involves different processing strategies, or the developmental pathway underlying the perception of emotional information in bodies and faces is different.

Both emotion and orientation and their interaction effect were observed on the N190. The typical inversion effect in body processing refers to the impaired recognition of inverted body images with correct structural hierarchy of body parts. It is believed to be an index of the activation of the body representation (Reed et al., 2003; 2006). The body inversion leads to a greater amplitude and/or longer latency of the N190 in comparison to upright body images. The N190 is associated with the body structural encoding mechanism in the fusiform cortex (Stekerlenburg & de Gelder, 2006; Minnebush et al., 2009). The N190 inversion effect is thus interpreted as the reflection of the impaired cognitive processing of the body representation (Stegelenburg & de Gleder, 2006; Minnenbush et al., 2009). In our study, we observed significant differences between upright and inverted body images on N190's amplitude (before and after peak-to-peak analysis), but in a paradoxical way. Before peak-to-peak analysis, apart from the orientation main effect, the mean amplitude of N190 showed an emotion by orientation interaction, with upright bodies evoking more negative mean amplitude than inverted bodies when expressing happy, fearful and neutral information. The sad bodies show similar amplitude differences between upright and inverted conditions, although this difference failed to reach significance. This tendency was also observed on the N190 peak before peak-to-peak analysis. After peak-to-peak analysis, with the absence of an early orientation effect driven by the P1, the emotion by orientation interaction was cancelled on both mean and peak amplitude of N190; while the inversion effect stays significant regardless of the emotions. This indicated the orientation effect is stable across all emotions after taking into account the different P1 amplitudes on the orientation. Furthermore, analysis of the N190 peak amplitude revealed that the greater responses to upright bodies over inverted bodies was stronger on right hemisphere. Although this contrasts with the body perception research in adults (Stegelenburg & de Gelder, 2006), as well as with previous face perception research (Eimer & Holmes, 2002; Ashley, Vuilleumier & Swick, 2004), the paradoxical inversion effect is consistent with our previous findings using the same paradigm with human bodies of no actions or emotional expressions in 3-, 5- and 10-year-old children, indicating the developmental differences between adults and children in their processing of human bodies with or without emotion or action information (Ke & Geangu, Study 1). Interestingly, greater N190 amplitude for upright as compared to inverted faces is also found in Taylor, Batty and Itier (2004)'s investigation of children aged 4 to 10 years. Furthermore, adults with developmental prosopagnosia also show this paradoxical inversion effect for both face and bodies (Righart & de Gelder, 2007). One possible interpretation of this paradoxical inversion effect is the immature use of configural information in face and body structural encoding. Children before a certain developmental stage rely on both feature and configural information in facial perception (Campbell, 1999; Mondloch, Le Grand, & Maurer, 2002). For instance, 8- to 11-year-old children showed similar accuracy to both upright and inverted faces, an advantage of recognizing upright faces was not observed until 12 years of age (Mondloch et la., 2002).

With regard to the emotion effect on N190 mean and peak amplitude, before correcting the orientation effect driven by P1, the emotion effect on the mean and peak of the N190 amplitude varied when the bodies were presented upright and inverted. The mean amplitude in response to happy bodies differed from that for sad bodies when the bodies were presented upright; while when presented upside-down, emotion differences were found between happy and fear on the mean amplitude; on the peak amplitude, the differences between happy and sad bodies were cancelled. Instead, fearful bodies elicited a more positive N190 peak than happy and sad bodies. This variation disappeared after P1-N190 peak to peak analysis. Therefore, the inconsistent emotion effect between upright and inverted bodies before correction was likely due to the disturbance of low-level visual cue change from the orientation driven by P1. After correction, the emotion main effect was also revealed at the N190 latency. Both the emotion differences at the mean amplitude and latency showed a consistently larger response to happy bodies in comparison to other emotions. This suggests that although previous behavioural studies showed children at this age are able to detect different negative emotions by choosing one category between the given labels (Mondloch, Horner, & Mian, 2013), they did not seem to discriminate negative emotions at the structural encoding stage, or the perception of negative emotions did not happen at this early stage. With regard to the early sensitivity to happy body postures, there are two possible inferences: first, the effect comes from low-level visual differences between happy bodies and other stimuli, as happy body postures have wider shoulder swing and elbow angle than other postures; second, the effect is actually due to perceptual sensitivities elicited by the structural differences between the emotional bodies, but takes place at the structural encoding stage. Given that there were no emotion differences found on the low-level visual component P1, we can infer that the second possibility is more likely to be the case. One explanation is that this indicates the fast detection of positive information. The early encoding of happiness was also found in a facial emotion recognition ERP study on adults (Rellecke, Palazova, Sommer, & Schacht, 2011), where a larger mean amplitude is observed in response to happy over neutral faces as early as 80-100ms after stimulus onset. Calvo and Nummenmaa (2009)'s eye tracking investigation interpreted this happy-face-advantage as a facilitated detection of certain diagnostic visual properties of happy facial expression: Happy faces are not only detected faster, but also requires less encoding effort, as indicated by shorter first fixations. They also require less cognitive effort as there were fewer refixations on happy faces than neutral faces during a recognition probe. Furthermore, investigation of the visual receptive fields found that the immature fixation pattern used to explore faces by children in comparison to adults is associated with the development of the neural receptive fields across visual cortex in childhood (Gomez et al., 2017). Therefore, another possible explanation is that given the wider span of the body elements from the central torso, the visual properties of the happy bodies may be more difficult for children to perceive at this developmental stage than for other body images, and thus requiring higher cognitive effort. Both explanations require further investigations in body perception by tracking the dynamic of the gaze.

As the positive counterpart of the N190, most of the findings on VPP mirrored the patterns of the N190 effect, suggesting the fast perceptual discrimination of happy body postures over other ones. Although few studies on emotional body image perception with adults found greater amplitude and faster latency on VPP in response to fearful bodies as compared to emotionally neutral bodies, no emotion effect is observed on N190 in these studies (Stekelenburg & de Gelder, 2006; Heijnsbergen et al., 2007). Our current finding in children seems to support the argument that VPP reflects the opposite phenomenon of the activity from the same generators of the N170 in facial perception (Rousselet, et al., 2005; Joyce & Rossion, 2005; Rossion & Jacques, 2011).

To sum up, the present study provides the first neurophysiological evidence for the mechanisms underlying the perceptual processing of emotion signals expressed by static body posture in children. Our results suggested that at least from the age of 5 years, children are able to not only extract emotion information at around 205ms after observing a body posture expressing emotion, but can also perceptually discriminate happy bodies from fearful, sad and emotionally neutral presentations at the structural encoding stage.

The current results also discovered key differences in the underlying mechanism of encoding emotion expressed by bodies and by faces. First, similar with the performance on adults (Stekenlenburg & de Gelder, 2006), at least from the age of 5 years, the perceptual processing of emotion as expressed by body posture (205ms) is not as fast as the processing of emotion expressed by face (at appropriately 80ms, Batty & Taylor, 2006). Second, consistent with our hypothesis, the inversion of the body stimuli interferes with emotion processing. Further investigation is required to clarify what type of information processing is involved in this interference on emotion perception. From the current findings we were also unable to tell whether the full meaning of the emotion expressed by body images was already processed and recognized. Although the current investigation showed children’s fast emotional signal detecting at least pf the positive emotion, these are most likely just the early stages of emotion processing. Furthermore, we should not forget that in everyday life, children process emotions from moving bodies rather than static body images. Therefore, the next stage of the investigation would be to try to reveal the perceptual processing of emotion from moving bodies.

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Three- and Six-Year-Old Children are Sensitive to Emotional Body Movements. An ERP Emotional Priming Study.

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Abstract

Body movements provide a rich source of emotional information during social interactions. Although the ability to perceive the emotional information displayed by human bodies begins to develop in infancy, processing the semantic meaning of such information may continue to develop well into childhood. The present study uses electroencephalography (EEG) to investigate the development of semantic understanding of emotions from body movements during childhood. Point-light displays (PLDs) of human adult bodies showing Happy and Angry emotional movement were used as prime stimuli, while the audio recordings of the words Happy and Angry uttered with an emotionally neutral prosody represented the targets. The aim of the study was to examine the semantic incongruency effects on N300/N400 in response to the target words that were either congruent or incongruent with the prime PLDs; such as semantic incongruent condition elicits greater N300/N400 than congruent condition. Continuous EEG was recorded with a 128 electrodes Geodesic Sensor Net (EGI). ERPs time-locked to the audio stimuli onset were calculated. 34 children aged 3 and 6-years old were tested. Results showed semantic incongruency effects on N300 and N400 for both age groups, suggesting children can process the emotional information from body movements, and are able to integrate the semantic meaning to the emotion they extracted.

Keywords: *emotional body perception, body motion, childhood, N300, N400*

Three- and Six-Year-Old Children are Sensitive to Emotional Body Movements. An ERP Emotional Priming Study.

Introduction

Appropriate social interactions require the ability to interpret the feelings and intentions of people around us. Observing the subtle movements people often unconsciously and spontaneously make, can provide a rich source of information in this respect. Extensive research has shown that adults are highly sensitive to such "biological motion" – the fine variations of body movements of humans (for a review, see Thornton, 2006). This sensitivity can be demonstrated by presenting human bodies as a small number of moving points of light corresponding to major body parts (e.g., head, wrists, ankles, and hips). Despite the absence of many visual form cues (e.g., shape, colour, etc.), adults readily perceive these point-light-displays (PLDs) as a human body when the PLDs are dynamic but not when they are static (Johansson, 1973). Importantly, adults are able to quickly extract socially-relevant information from biological motion, such as sex (Mather, & Murdoch, 1994), subtle emotional expressions (Volkova, Mohler, Dodds, Tesch, & Bülthoff, 2014b), and even psychological traits (Thoresen et al., 2012). While new-born infants show similar sensitivity to biological motion, it is less clear when the ability to extract socially-relevant information from biological-motion cues develops. Towards this aim, the current study investigated young children's processing of emotional body movements expressed during naturalistic narrative contexts and depicted as PLDs.

The results from behavioural and neuroimaging studies with infants and children suggest that both the ability to detect biological motion (e.g., from PLDs; Hadad, Maurer, & Lewis, 2011; Pavlova, 2012) and to accurately identify the emotion expressed (Ross, Polson, & Grosbras, 2012) have a protracted developmental trajectory. It is believed that for both of these functions adults integrate local motion signals from the individual dots across space and time into a global biological-motion perception (Movshon, Adelson, Gizzi, & Newsome, 1985; Smith, Snowden, & Milne, 1994; Movshon, 1990; Grossman, & Blake, 1999; Giese, & Poggio, 2003). If the local motion signals are profoundly altered, infants can discriminate above chance between coherent biological motion and non-coherent biological motion in which the individual points are temporally or spatially "scrambled" (Berthenthal et al., 1987; Moore et al., 2007), and by the age of 4- to 6-years children are as accurate as adults (Vieillard, & Guidetti, 2009). However, if the local motion signals are only slightly altered, children's sensitivity to biological motion continues to improve until adolescence although it remains particularly diminished in complex visual displays (Hadad et al., 2011, Freire et al., 2006).

With respect to children's ability to identify emotions expressed by body movements, Ross, Polson, and Grosbras (2012) tested 4- to 17-year-old children and adults' ability to identify anger, happiness, fear, and sadness expressed by adult actors explicitly posing these emotions. The stimuli were presented as PLDs and as videos which contain both form and motion cues. Participants were asked to choose the verbal label corresponding to the posed emotion. The accuracy was significantly lower for PLDs than videos across all age groups and emotions, demonstrating that children and adults benefited from form cues in identifying emotions. Nevertheless, for both types of stimuli, accuracy improved throughout childhood and adolescence, with the steepest increase between the age of 4- and 8.5-years. Other studies suggest that children's ability to identify emotions expressed by body movements depends on various other factors. When children observe exaggerated body movements that extend over longer durations and are associated with dance narrative cues, they are able to identify the emotion at a slightly younger age (Boone, & Cunningham, 1998; Lagerlöf, & Djerf, 2009). Five- to 8-year-old children can perform above chance and at similar levels with adults in identifying happiness, sadness, anger, and fear, particularly when they benefit from training about how body movement can express different meanings

(Lagerlöf, & Djerf, 2009). Younger 2- to 4-year-old children show the lowest performance (Boone, & Cunningham, 1998; Lagerlöf, & Djerf, 2009). Sadness tends to be more consistently identified in dance movements when children are closer to the age of 2-years, while the accurate labelling of happiness, anger and fear appears to become more frequent as children reach the age of 4 years (Lagerlöf, & Djerf, 2009). These studies used explicitly posed and potentially exaggerated body movements, which are uncharacteristic of children's daily interactions. Thus, it is still unknown at which age children can identify the emotions of others from body movements which occur unconsciously and spontaneously during everyday life events.

At the neural level, event-related potential (ERP) studies suggest that changes in the speed of processing of biological motion continue to occur in 8- to 10-year-old children but do not reach adult levels at this age range (Hirai et al., 2013). More specifically, developmental changes are present both for ERP components that reflect earlier stages of processing and for those that reflect later stages of processing. The early components are most often associated with extracting low-level properties of PLDs (Hirai et al., 2013; Coch et al., 2005; Mitchell, & Neville, 2004; McCarthy et al., 1999; Jokisch et al., 2005), while the later components are often linked with attributing a meaning to the perceived biological motion (Jokisch et al., 2005; Krakowski et al., 2011). In sum, children may first be able to detect changes in posed emotional body movements when these have an exaggerated expression and benefit from additional visual and semantic/contextual information, while sensitivity to expressions which are less exaggerated continues to develop throughout childhood. These developmental changes may be detected by specific ERP components.

In the present study, we investigated 3- and 6-year-old children's processing of anger and happiness expressed by subtle body movements during story narrations (Volkova et al., 2014a, b). Unlike previous studies in which the stimuli were created by explicitly asking adult actors seated on a chair to pose distinctive emotional body expressions (e.g., Ross, Polson, & Grosbras, 2012), here we used PLDs from spontaneous body movements expressed by adult actors while they imagined telling fairy tales to children and tried to recount the emotions of the narrator and the characters in the story (Volkova, De La Rosa, Bülthoff, & Mohler, 2014a). The actors did not receive any instructions about emotional expressivity per se or about which expressions to use; thus, the body movements from this database more resemble those produced naturally during similar daily social situations. To test whether children in the two age groups could extract emotional information from biological-motion cues, we used an ERP emotional semantic priming paradigm (Deacon, Hewitt, Yang, & Nagata, 2000). In this paradigm, we presented either an "anger" or a "happy" PLD as a prime followed by the word "angry" or "happy" uttered with emotionally-neutral prosody as a target, and measured ERP responses to the auditory word *target*. Children in both age groups understand the meaning of the words (Ridgeway, Waters, & Ii,1985; Li, & Yu, 2015; Bretherton, Fritz, Zahn-Waxler, & Ridgeway, 2017). If they can extract the socially relevant emotional information from the PLD prime, then we expect differences in ERP responses to the word target when the prime-target pairs are congruent (i.e., refer to the same emotion information) versus incongruent (i.e., refer to different emotion information). Furthermore, this congruency effect may vary with age. Thus, by manipulating the emotional matching between the prime and the target, we can investigate children's processing of anger and happiness expressed through subtle biological-motion cues.

One of the reasons we chose to measure the ERP response to the emotional words as target, instead of directly measure ERPs to PLDs, is that the noisiness of the child ERPs brings practical difficulties in measure ERP response to long stimuli, such as PLDs expressing emotions. Moreover, we chose the ERP emotional semantic priming paradigm because it is well established that different ERP components can reflect different underlying perceptual and emotional relationships between prime and target. N400 and N300 are the

ERP components primarily shown to differentiate between emotional stimuli which are perceived to be semantically *congruent* or *incongruent* with the emotional context in which they appear (e.g., Bostanov, & Kotchoubey, 2004; Schirmer et al., 2002; Werheid et al., 2005; Zhang et al., 2006; Paulmann, & Pell, 2010; Goerlich et al., 2012). The N400 is a negative-going deflection in adults usually observed in the centra-parietal sites. It is a broadly observed component in language investigations that peaks at around 400ms after the target word onset in a prime-target paradigm or sentential context. A typical N400 effect refers to enhanced amplitude to the semantically incongruent condition, therefore, it's often considered as a sensitive index of semantic processing (Lau et al., 2008). However, it is also found elicited in incongruent conditions that involve any meaningful stimuli, such as story pictures, action sequences, or music and faces that contains emotional meanings (Aguado et al., 2013; West, & Holcomb, 2002; Steinbeins, & Koelsch, 2008; Reid, & Sriano, 2008). Although sometimes considered as reflecting the same processes with differences in latency due to ease of access to the semantic information (Bostanov, & Kotchoubey, 2004), N300 and N400 have also been associated with different functions. The N300 is often reported either independent of or co-occurring with the N400 (Bostanov, & Kotchoubey, 2004; Paulmann, & Pell, 2010; Nobre, & McCarthy, 1995; Friederici, 2005). In children, negativities occurring around 300ms from stimulus onset have been interpreted to index familiarity effects reflecting the fulfillment of a phonological expectation after seeing the visual depiction of an object. This slightly precedes more advanced cognitive processing of the semantic content of the word (Friedrich, & Friederici, 2004; Friederici, 2005; Torklidsen et al., 2007). N300 has also been linked to image processing when the semantic content is presented visually (e.g., West, & Holcomb; 2000). Both N300 and N400 components are present in infancy and childhood (e.g., Friedrich, & Friederici, 2004, 2005, 2008; Friederici, 2005; Parise, & Csibra, 2012; Sheehan, Namy, & Mills, 2007). As children mature, they show a reduction in amplitude, a slowing in the latency of the peak response, and a change in hemispheric distribution (Holcomb, Coffey, & Neville, 1992).

Typically, a target word which is semantically incongruent with the prime elicits more negative amplitude of N300 and N400 components compared to the words which semantically match the prime (Deacon et al., 2000; McPherson, & Holcomb, 1999; Amoruso et al., 2013; Lau et al., 2008). However, opposite effects have been reported as well (Bermeitinger, Frings, & Wentura, 2008), especially for emotional stimuli (e.g., Paulmann, & Pell, 2010; Goerlich et al., 2012; Kotz, & Paulmann, 2007; Aguado et al., 2013) and in children (Holcomb et al., 1992; Bonte, & Blomert, 2004). In addition, variations in the latency of these components, as a function of the emotional meaning of the stimuli, have been noted (Paulmann, & Pell, 2010). Thus, irrespective of its direction, a difference in the amplitude and latency of the N300 and N400 components between the congruent and incongruent emotional PLD-emotional word pairs, will suggest that children extract, to a certain degree, the emotional information conveyed by body movement and establish the semantic relation with the corresponding word. We anticipate that while children may show a smaller N400 congruency effect than the one typically reported in adults, due to poorer semantic associations between the emotional body movement and the verbal label, they may nevertheless associate them during attentive process (Rämä, Sirri, & Serres, 2013). Thus, we predict differences in amplitude and latency of the N300 between congruent and incongruent prime-target pairs in both age groups.

Methods

Participants

A total of 54 children were tested. The final analysis included 34 children, 3-year-old, *N* = 17, 8 females, *M*age = 45.82 months (*SD* = 5.60); 6-year-old, *N* = 17, 10 females, *M*age = 78.24 months (*SD* = 5.18). The remaining 20 children (3-year-old, *N* = 18; 6-year-old, *N* =2) were excluded due to either technical issues (N = 3) or insufficient number of artefact free trials (N = 17). The participants were recruited from an urban area in Northwest England. Parents gave informed written consent on behalf of their child to take part in the study. The children assented to their participation in the study and received a small gift for their participation. The procedure followed ethical standards (the Declaration of Helsinki, BMJ 1991; 302:1194) and was approved by the Lancaster University Ethic Committee.

Stimuli

The stimuli consisted of PLDs which served as primes, and auditory words that served as targets. Six PLDs were selected from the MPI Emotional Body Expression Database (Volkova et al., 2014a), the actors are in seated position, three expressing "anger" and three expressing "happiness". Each PLD consisted of 23 points located at the head, spine, and main joints, and depicted the body movements of adults while they narrated coherent emotional stories. The points were rendered as white circles against a black background. Importantly, independent observers rated the emotion expressed by the PLDs (see Volkova et al., 2014a, for details). Adult participants rated the stimuli selected for this study as expressing happiness and anger with correct valence (positive for happiness and negative for anger) and high arousal (1 as high and 0 as low) (Volkova, et al, 2014a). The average speed of the motion of the left and right wrists of the actor (as a measure of movement, speed?), along with the duration for each type of prime stimuli were presented in Table 1. As evident in the table, there are only small differences between the two types of primes.

Table 1.

Means and SDs of the measurement of the speed and duration for each type of prime

Prime type	Speed (m/s)	Duration (s)
Happy	0.34(0.02)	4.53 (0.57)
Angry	0.43(0.06)	3.85(0.53)

The two target stimuli were 505-ms audio recordings of the words "angry" or "happy" spoken in an emotionally neutral tone by a native English-speaking female adult. They were selected from a pool of 30-word utterances recorded in an anechoic chamber by 3 speakers (15 for "angry" and 15 for "happy"). Ten adult listeners rated each recording in terms of clarity (on a scale of 0-5) and prosody ("neutral", "angry" or "happy"). Both target stimuli were rated to be the clearest (clarity = 5) and having "neutral" prosody by more than half of the raters.

Apparatus

Participants were tested individually in a dimly lit room. They sat approximately 70 cm away from a CRT monitor which had a 75Hz refresh rate. The PLDs were presented on the monitor and the auditory words were presented via speakers. The PLDs covered a visual field of 22.07°× 22.07° (horizontal × vertical). The experiment was programmed in Matlab (Mathworks, Inc.). EEG was recorded with a 128-electrode HydroCel Geodesic Sensor Net (Electrical Geodesic Inc., Eugene, OR) and amplified using an EGI NetAmps 300 amplifier. A video recorder synchronized with the EEG was used to record participants during the experiment. The videos were used off-line to identify eye movements and whether or not participants were looking at the visual stimuli.

Design and Procedure

Figure 1 illustrates the experimental paradigm. The participants were presented with a PLD prime followed by an auditory word target while we continuously recorded EEG. The two PLD primes were factorially combined with the two auditory word targets, resulting in four conditions (Figure 1B): Angry Congruent (AC; Angry PLD - Angry word), Angry Incongruent (AI; Happy PLD - Angry word), Happy Congruent (HC; Happy PLD - Happy word), and Happy Incongruent (HI; Angry PLD – Happy word). Note that emotion for the condition label is with respect to the auditory word target.

The trial sequence is illustrated in Figure 1B. Each trial began with a PLD prime presented at the centre of the screen for its duration. The auditory word target was presented for its full duration 200ms after the end of the PLD. The last “frame” of the prime remained on the screen during the 200-ms interval and throughout the duration of the target (~700ms in total). After the offset of the target, a central white fixation cross was presented on a black background for a duration varying randomly between 1800 and 2000ms. This is to avoid the participant’s neural response being biased by their expectation to a set interval. To maintain participants’ attention throughout the task, a non-task-related image (a rainbow-coloured star) was presented before the fixation cross on 40% of the trials. We chose to present the attention getters in this percentage so that they are frequent enough but not too frequent that the children will lose interests. Participants were asked to press a button as soon as they saw the image. The image was presented for 2000ms irrespective of their response. Each of the four conditions was presented for a maximum of 27 times. The three different PLDs for each emotion were randomly selected on each trial with replacement.

The 200-ms interval allowed a motion-free baseline for EEG recording. Furthermore, the presentation of the last “frame” of the PLD during the 200-ms interval and target presentation ensured that the participants remained engaged on each trial and that they were less likely to look away from the screen which could increase the chance of artefacts in the EEG data.

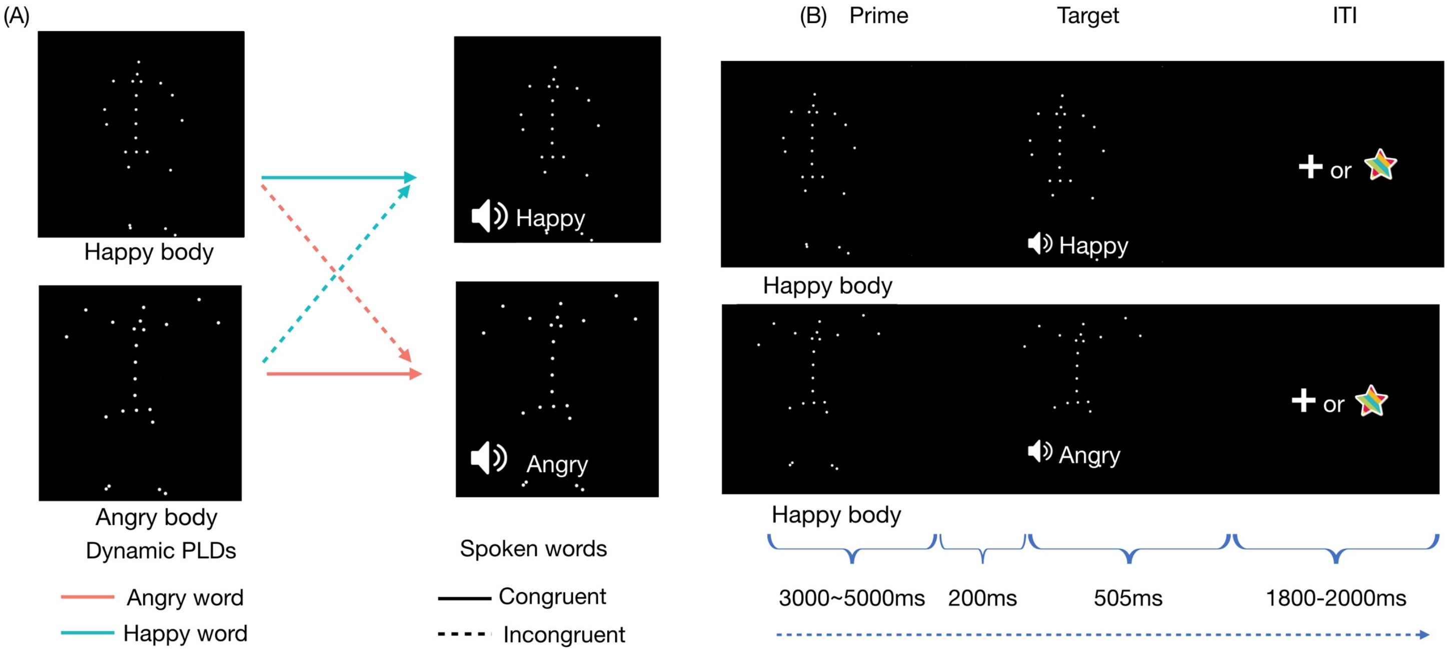

Figure 1. (A) Schematic illustration of the prime-target pairs specific for each condition. (B) Example of a trial structure. Each trial began with the prime PLDs displayed in the centre of the screen, the auditory word target followed after 200ms from the offset of the motion.

EEG Analysis

EEG was recorded continuously at a sampling rate of 500 Hz. For each electrode, the signal was referenced online to the vertex electrode (Cz) and a band-pass filter of .1–100 Hz was applied. Impedances were checked prior to the beginning of the recording and they were considered acceptable if lower than 50 *kΩ*. The EEG data were further processed off-line using NetStation v 4.5.4 (Eugene, OR). The signal was band-pass filtered (0.3–30Hz) and segmented from 100ms before the onset of the auditory word target to 1000ms after onset for each trial. To eliminate artefacts, segmented data were automatically rejected whenever the signal exceeded ± 200 µV at any electrode. The data were further checked by visual inspection for eye-movements, eye-blinks, and other body movement artefacts not detected by the automated algorithm. At this stage, trials were excluded if more than 18 bad channels were detected or if participants did not look at the PLD primes (as indicated by the video recording). For the remaining trials, after the data clearance and preparation, the individual channels that the signal exceeded ± 200 µV were replaced using spherical spline interpolation. Individual subject averages were computed separately, for each channel, across all trials within each condition, and then the data was re-referenced to the average reference. The average number of included trials, as a function of condition and age group, is presented in Table 2.

Table 2

Mean numbers of the trials (with SD) included in the analysis for each condition, separately for each age group

Age Group	Mean (*SD*) numbers of trials remains			
	Angry Congruent	Angry Incongruent	Happy Congruent	Happy Incongruent
3-year-old	13.82 (3.43)	12.82 (3.41)	12.82 (2.83)	13.35 (3.62)
6-year-old	16.24 (3.91)	15.25 (4.46)	14.35 (5.50)	15.06 (4.59)

Following pre-processing, we conducted statistical analyses on the amplitude and latency of different ERP components within regions of interest (ROIs). Figure 2 shows the two ROIs selected: central (left: 29, 35, 36; right: 104, 111, 110) and parietal (left: 42, 47, 52; right: 92, 93, 98). The components included the N300 (250-380ms) at central ROIs, and the N400 (400-550ms) at the parietal ROIs (see Figure 3). The time windows for each component and ROIs were based on previous literature using similar paradigms with children and adults (Friedrich, & Friederici, 2004; Steinbeis, & Koelsch, 2008; Henderson et al., 2011) and visual inspection of the data. The visual inspection of the data also indicated that at central ROIs, differentiations between conditions may be present during an earlier positivity (150-250ms) which precedes the N300 and corresponds to the P200 component previously described in the literature (Paulmann, Bleichner, & Kotz, 2013; Paulmann, &

Kotz, 2008; Pell et al., 2015; Schirmer, Chen, Ching, Tan, & Hong, 2013). It is possible that variations in the P200 may have affected the N300 differently across conditions. In order to test for this possibility, we analysed the central P200 as well. Whenever significant effects of Emotion, Congruence, Age, or their interaction were observed for this component, we performed complementary P200-N300 peak-to-peak measurement (that is, to minus the measurement of P200 from N300) and analyses for the N300 to control for P200 variations. For each component, we submitted the mean amplitude, peak amplitude, and the latency to the peak to a 2 Emotion (Happy word, Angry word) × 2 Congruence (Congruent, Incongruent) × 2 Hemisphere (Right, Left) × 2 Age (3-year-old, 6-year-old) mixed analysis of variance (ANOVA), with Age as a between-subjects factor, and the remaining variables as within-subjects factors. Significant interactions were further analysed by simple ANOVAs. We report Bonferroni or Tukey corrected *p*-values for post-hoc comparisons. The results were interpreted at the significance threshold of $p = .05$.

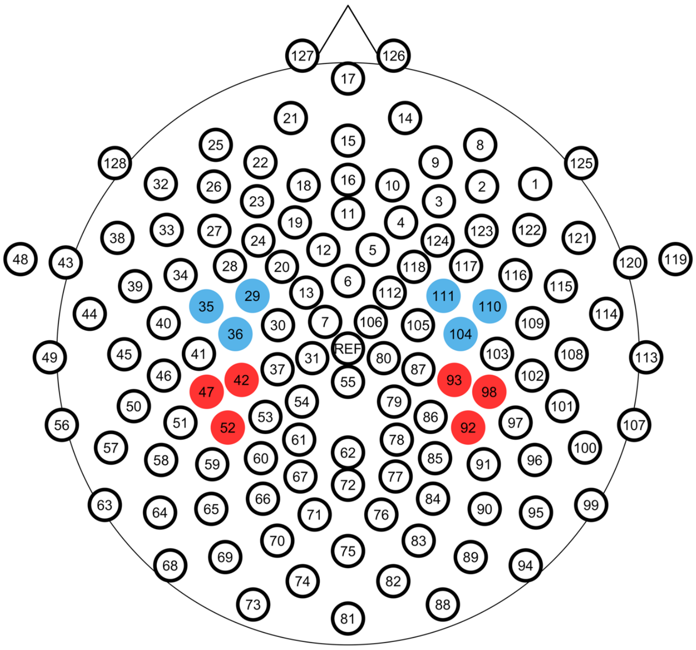

Figure 2. The location of the electrodes included in each regions of interest (ROIs)

Results

Parietal N400

Mean amplitude. The analysis revealed a significant main effect of Emotion ($F(1,32) = 6.42$, $p = .016$, $\eta_p^2 = 0.014$), with the Angry word eliciting greater mean amplitude ($M = 0.90\mu V$, $SD = 4.74$) than the Happy word ($M = -0.20\mu V$, $SD = 5.07$). A significant main effect of Hemisphere, ($F(1,32) = 7.24$, $p = .011$, $\eta_p^2 = 0.037$), showed an increased mean N400 amplitude over the left ($M = 1.26\mu V$, SD = 5.27) compared to the right region ($M = -0.56\mu V$, $SD = 4.41$). Furthermore, a significant Age × Congruence interaction emerged, $F(1,32) = 7.35$, $p = .011$, $\eta_p^2 = 0.085$. The post-hoc comparisons showed that in 3-year-old children only, the Incongruent condition elicited reduced mean amplitude ($M = 0.26\mu V$, $SD = 0.68$) compared to the Congruent one ($M = 1.22\mu V$, $SD = 0.68$, $p = .041$), see Figure 3 and 4.

Peak amplitude. No significant main effects or interactions were found (ps > .062).

N400 latency. A significant main effect of Age, $F(1,32) = 10.93$, $p = .002$, $\eta_p^2 = 0.058$, and interaction between Emotion × Congruence ($F(1,32) = 16.11$, $p = .003$, $\eta_p^2 = 0.042$), were found. These were further qualified by an Age × Emotion × Congruence interaction, ($F(1,32) = 6.02$, $p = .020$, $\eta_p^2 = 0.016$). Further analysis revealed a significant Emotion × Congruence interaction in 6-year-old children only, $F(1,16) = 21.16$, $p < .001$, $\eta_p^2 = 0.131$. Posthoc comparisons showed that the HC elicited peak N400 amplitude with longer latency ($M = 478.82$ ms, $SD = 40.04$) than the HI ($M = 453.71$ms, $SD = 43.05$, $p= .003$) and AC ($M = 447.00$ ms, $SD = 39.63$, $p < .001$). Furthermore, AI ($M = 476.47$ ms, $SD = 40.69$) elicited N400 peak amplitude with longer latency than AC ($p < .001$) and HI ($p = .009$), see Figure 4. An Emotion × Congruence × Hemisphere interaction was also found, ($F(1,32) = 6.88$, $p = .013$, $\eta_p^2 = 0.020$. Emotion × Congruence repeated measures ANOVAs performed separately for each hemisphere revealed a significant interaction in the left hemisphere only, $F(1,32) = 23.60$, $p < .001$, $\eta_p^2 = 0.111$. Posthoc comparisons showed that, for both age groups, HC ($M = 491.88$ ms, $SD = 40.05$) elicited peak N400 amplitude with longer latency than HI ($M = 462.65$ ms, $SD = 43.43$, $p=.001$) and AC ($M = 459.88$ ms, $SD = 49.23$, $p = .001$). Furthermore, AI ($M = 487.82$ ms, $SD = 41.89$) elicited peak N400 amplitude with longer latency than AC ($p = .002$) and HI ($p = .010$).

The latency analysis also revealed a significant Age × Emotion × Hemisphere interaction ($F(1,32) = 7.50$, $p = .010$, $\eta_p^2 = 0.028$). A significant Emotion × Hemisphere interaction was observed in 3-year-olds only, $F(1,16) = 7.34$, $p = .015$, $\eta_p^2 = 0.036$. The posthoc comparisons showed that over the right hemisphere, the Angry word elicits N400 peak amplitude with shorter latency ($M = 472.29$ ms, $SD = 41.51$) than the Happy word ($M = 491.59$ ms, $SD = 44.59$, $p = .047$) (Figure 4). Although a significant Age × Congruence × Hemisphere interaction was also observed, ($F(1,32) = 4.25$, $p = .048$, $\eta_p^2 = 0.017$), the posthoc analysis did not show any significant differences ($p > .130$).

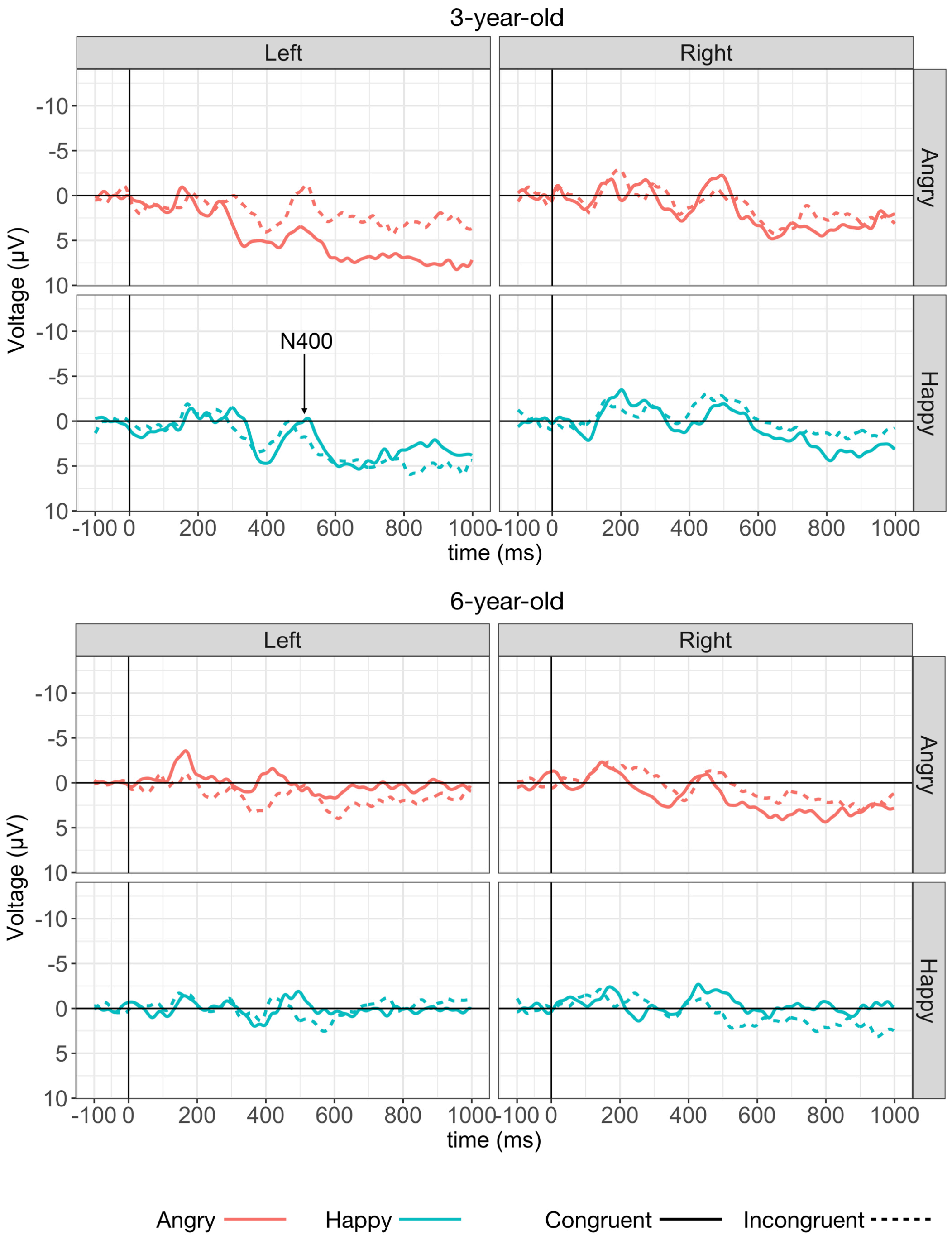

Figure 3. Grand average ERPs and topography for the Happy and Angry in Congruent and Incongruent conditions from Parietal electrodes (left: 25, 35, 36; right: 111, 110, 104) of the two age groups.

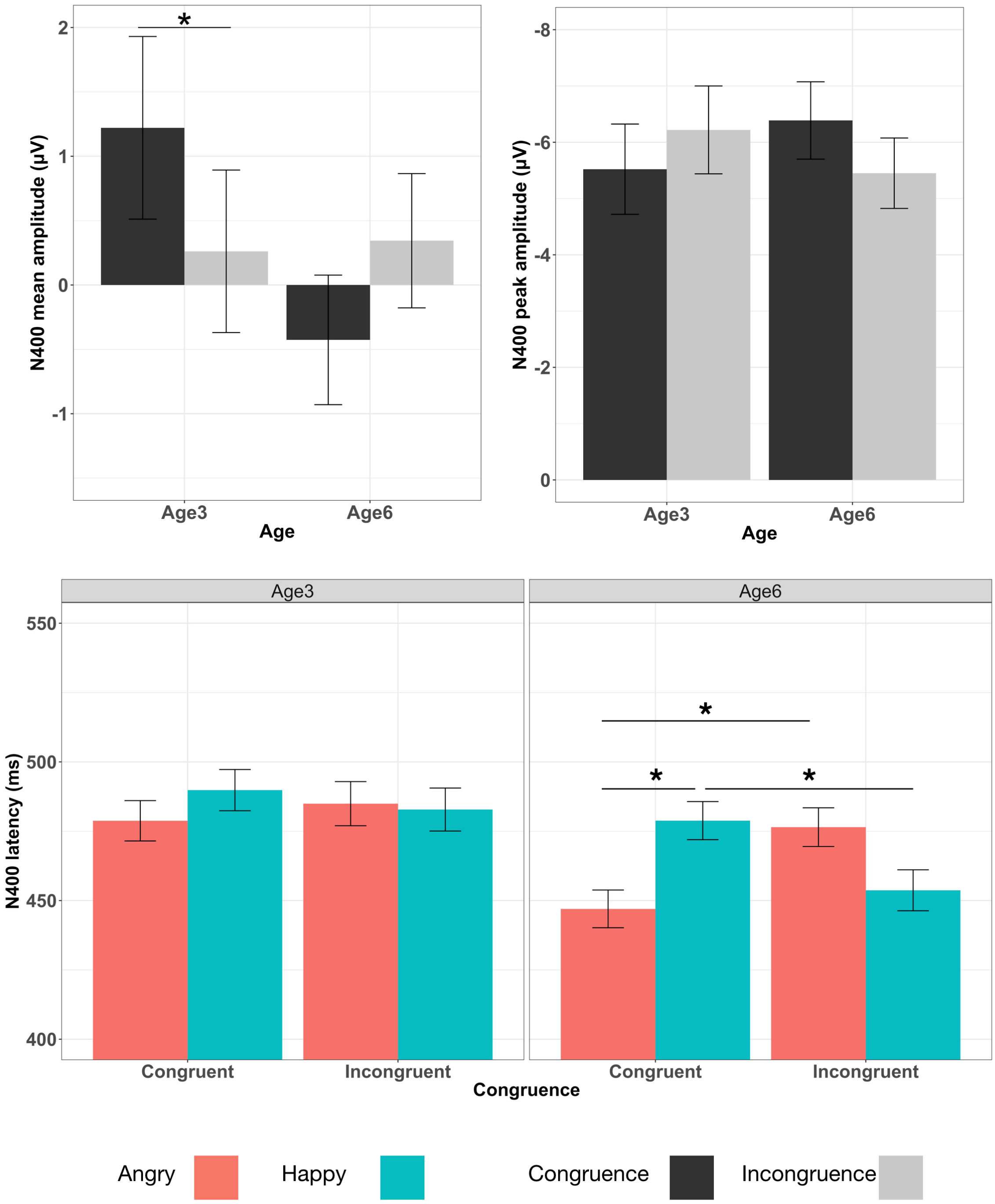

Figure 4. Bar chart of the N400 mean, peak amplitude and the latency of the two age groups across each condition.

Central P200

Mean & peak amplitude. For both the mean and the peak amplitude of the P200 recorded at central ROIs, a main effect of hemisphere was found, $F(1,32) = 4.70$, $p = .038$,

$\eta_p^2 = 0.018$ and $F(1,32) = 4.67$, $p = .038$, $\eta_p^2 = 0.016$, respectively. A higher amplitude was recorded at the left ($M = 3.10$ µV, $SD = 4.14$ and $M = 8.22$ µV, $SD = 4.52$, respectively) compared to the right hemisphere ($M = 2.01$ µV, $SD = 3.97$ and $M = 7.02$ µV, $SD = 5.01$, respectively).

Latency. No significant results were found for the latency of the P200 at central ROI (*p*s > .055).

Central N300

Because no significant effect of Emotion, Congruence, Age, or their interaction were observed for the P200, we proceeded by analysing the N300 without correction.

Mean amplitude. The analysis revealed an Emotion × Congruence interaction, $F(1,32) = 5.28$, $p = .028$, $\eta_p^2 = 0.012$ (Figure 5). The posthoc comparisons showed that the AI elicited reduced mean amplitude ($M = -0.56$ µV, $SD = 4.02$) than the AC ($M = 0.60$µV, $SD = 4.86$; $p = .046$). The mean amplitude elicited by the AI was also significantly reduced compared to that triggered by the HI ($M = 0.69$ µV, $SD = 4.78$; $p= .039$), see Figure 6.

Peak amplitude. Although a significant Emotion × Congruence interaction was observed, $F(1,32) = 4.38$, $p = .044$, $\eta_p^2 = 0.010$, the posthoc comparisons failed to reach significance, see Figure 6.

Latency. A significant main effect of Age was found, $F(1,32) = 5.14$, $p = .030$, $\eta_p^2 = .037$, which was further qualified by a significant interaction with Congruence, F (1,32) = 5.11, $p = .031$, $\eta_p^2 = .009$. Posthoc pairwise comparisons showed that when the target word was incongruent with the prime, 3-year-olds ($M = 320.59$ms, $SD = 42.66$) reach the peak N300 amplitude after a longer latency than the 6-year-olds ($M = 298.91$ms, $SD = 37.03$, $p = .004$). Moreover, 6-year-olds reach the peak N300 amplitude significantly slower for the congruent ($M = 308.09$ms, $SD = 38.37$) than the incongruent condition ($M = 298.91$ms, $SD = 37.03$ms; $p= .048$). A significant Emotion × Congruence interaction was also found, F

(1,32) = 11.26, $p = .002$, $\eta_p^2 = 0.052$. Posthoc pairwise comparisons showed that the AC elicited faster latency (*M* = 300.41 ms, *SD* = 37.89) than the AI (*M* = 315.74ms, *SD* = 39.67, p = .015) or the HC (*M* = 323.15 ms, *SD* = 34.80, *p* = .003). Moreover, the peak N300 amplitude was reached significantly later for HC than for the HI (*M* = 303.76 ms, *SD* = 42.22, p = .023), see Figure 6. Other comparisons failed to show significance (ps >.106).

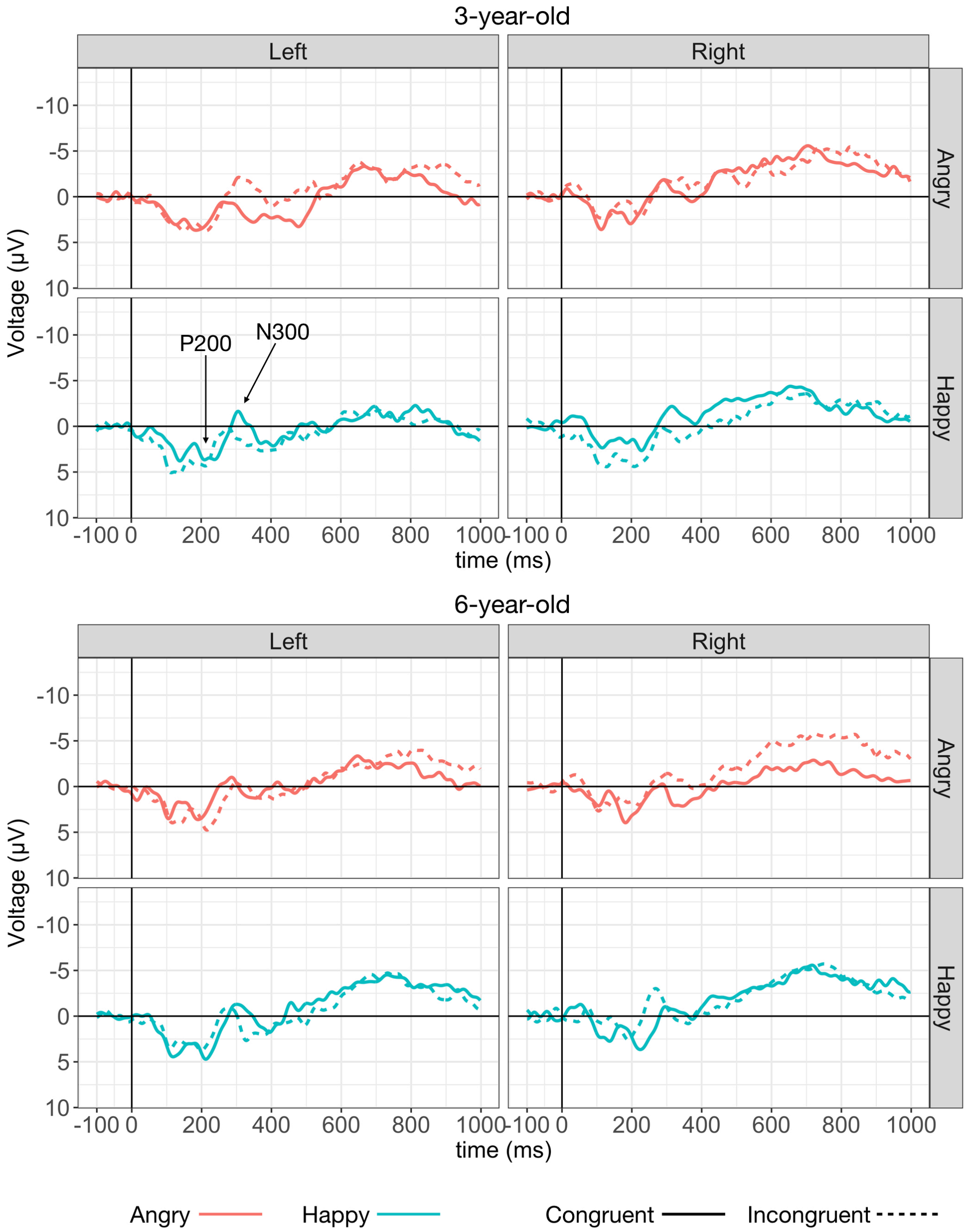

Figure 5. Grand average ERPs at Central ROI (left: 25, 35, 36; right: 111, 110, 104) for the Happy and Angry words primed congruently or incongruently by Happy and Angry PLDs.

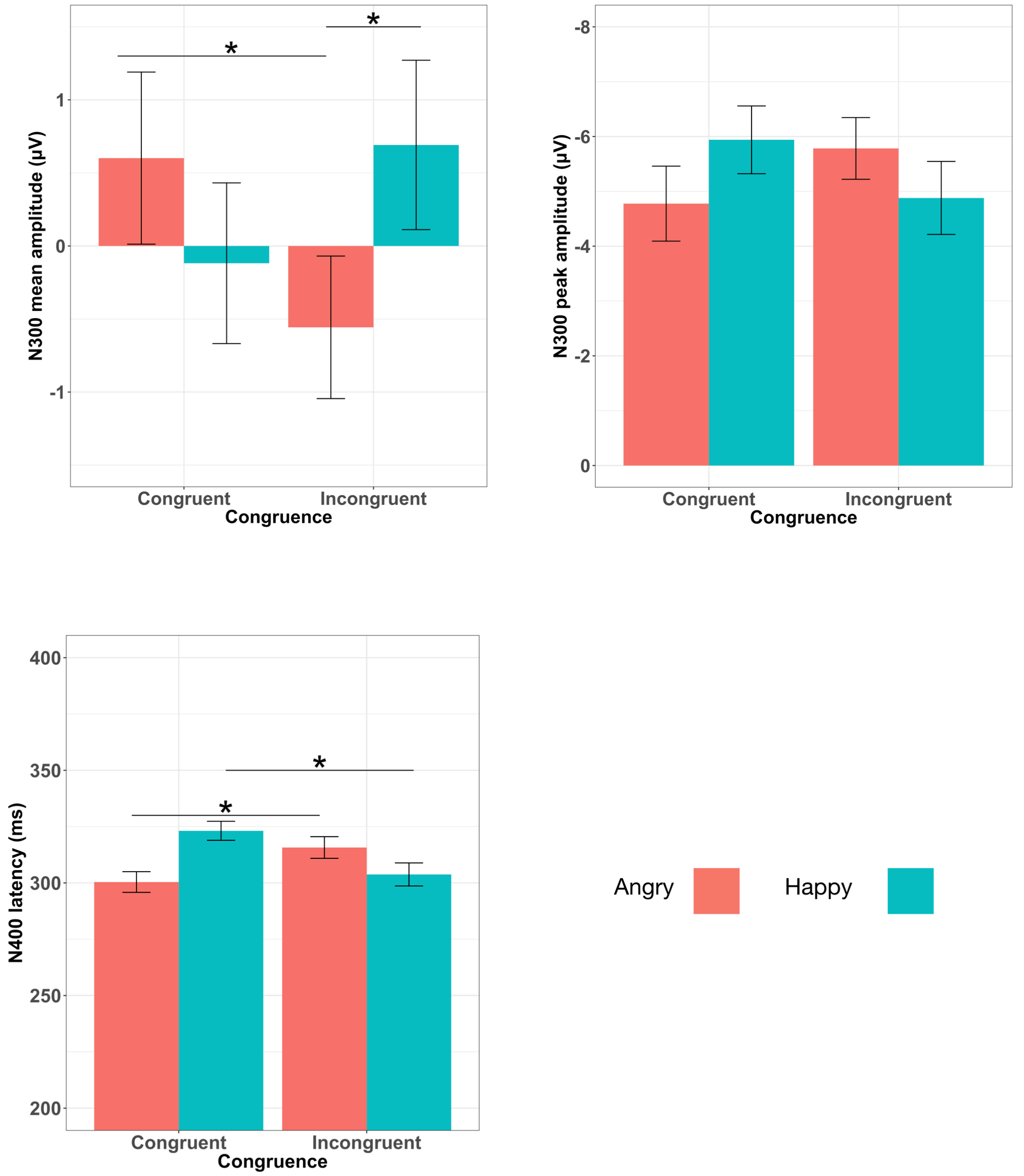

Figure 6. Bar chat of the N300 mean, peak amplitude and latency cross each condition.

Discussion

Observing the subtle movements people often unconsciously and spontaneously make can reveal their emotions or psychological traits. Body movement is thus considered a rich source of social information with high relevance for social interactions. The aim of our study was to probe 3- and 6-year-old children’s sensitivity to the emotional information expressed spontaneously by adults through subtle body movements during typical social events. Towards this aim we devised an emotional semantic priming ERP paradigm in which PLDs with angry or happy movement preceded congruently or incongruently the words 'angry' and 'happy' spoken with emotionally neutral prosody. The analysis of the ERP responses provided the opportunity to investigate the attentional and semantic functions involved in children's emotion processing. We hypothesized that if children extract the emotional information from body movement and perceive the semantic and emotional relation with the corresponding verbal label, differentiations in the latency and amplitude of the N300 and the N400 ERP components will be recorded between the congruent and incongruent conditions. Overall, the analysis of the effect of congruence between the emotional PLD and the verbal label suggests that both 3- and 6-year-old children are sensitive to the emotional information conveyed by the subtle body movements occurring during story telling situations. However, variations between age groups in the latency of the ERP components of interest, and the modulations of the congruency effect by the emotional valence, indicate that the underlying processes may undergo important developments within this age range. In what follows, we present the findings and discuss their implications for understanding the development of emotional body movement processing in childhood.

In line with previous semantic priming studies (Nobre, & McCarthy, 2003; Holcomb & Neville, 1990), for both 3- and 6-year-old children, the N300 recorded at central scalp locations reached peak amplitude faster when the words happy and angry were preceded by matching rather than mismatching emotional PLDs. As the latency to the peak amplitude of ERP components can be regarded an indicator of processing speed, it appears that watching emotional body movement facilitates the responses to the verbal label of its corresponding category. As we included different examples of happy and angry body movement, these findings suggest that children are able to extract and represent the common psychophysical properties specific to each emotional category.

The utterance of the target words 'angry' and 'happy' lasted 500ms, with the first half of this duration covering the first syllable of the word. Thus, the N300 effects are most likely due to the processing of the first syllable of the target word. Given that only two target words were used in the present study and that these have distinct first syllables, it would have been easier for children to anticipate the entire word based on this information alone. Moreover, the emotional information conveyed visually by the face and body, and auditorily by the voice are frequently associated with the corresponding emotion category label, and could be learned from very early on. Indeed, at the behavioural level, children as young as the age of 2 years can correctly choose the facial expression corresponding to the words 'happy' and 'angry' (Denham et al., 2003). One possible interpretation of the results could be that the facilitation effect observed for the N300 is due to the perceptual association between the visual information characteristic to emotional body movement and the word (Zieber, Kangas, Hock, & Bhatt, 2014).

However, previous semantic priming studies which report an N300 at anterior-central locations also describe a more negative amplitude for the congruent compared to the incongruent trials (Nobre, & McCarthy, 2003; Holcomb, & Neville, 1990; Friedrich, & Friederici, 2005; Friederici, 2005; Torklidsen et al., 2007). This increased negativity is probably the result of a sharpened time locking between the target onset and the activation of its lexical/semantic representation due to priming, leading to increased temporal summation and thus amplitude of the N300 (Nobre, & McCarthy, 2003). In our study, for both 3- and 6-year-old children, angry congruent emotional PLDs-word pairs led to a diminished N300 amplitude compared to the angry incongruent pairs, in line with typical semantic and affective priming effects (Aguado et al., 2013; West, & Holcomb, 2002; Steinbeins, & Koelsch, 2008; Reid, & Sriano, 2008; Lau et al., 2008). Moreover, the analysis shows an added effect of the emotional information in the prime and target on the N300 latency. When anger was present in both the body movement and the word, N300 peaked faster than when happy information was presented. As indicators of the motivational and emotional states of an individual, emotional expressions displayed by faces, voices, and bodies are important social signals of intentions. From an evolutionary perspective, angry expressions signal a potential threat to the individual and it would be adaptive to detect them fast and to allocate attentional resources. In adults, threat cues elicit increased attention (e.g., Öhman, Flykt, & Esteves, 2001) and undergo more elaborate and facilitated processing (e.g., Schupp et al., 2004). In children, facial expressions indicating the presence of threat were shown to trigger increased attention as reflected by the central negative ERP component peaking around 300ms (Dennis, Malone, & Chen, 2009). It is thus possible that the faster N300 recorded in the present study, in response to angry compared to the happy congruent trials, reflects the activation of threat related representations, which further facilitate the early integration of the information conveyed by body movement and the verbal label.

Although, indications of early integrating of the emotional information conveyed by body movement and the word were present for all children, age differences emerged as well. In particular, older children tended to process faster the incongruent emotion PLD – emotion word pairs compared to the younger children. Given that these differences were not observed for the congruent trials, it is possible that both 3- and 6-year-old children are able to integrate at an attentional level the emotional information extracted from the prime and target with similar speed, but may differ in terms of operating simultaneously with emotional information of different valence and detecting conflicting information (Rueda et al., 2014; Buss et al., 2011). Developmental research on conflict control suggested that children show longer reaction time as well as worse accuracy of conflict situation (such as the NoGo condition in a Go-NoGo task, or the incongruent condition in a flanker task) than adults (Jonkman, 2006). The N2 component, which is usually observed between approximately 300 to 400ms at the frontal-central sites in children, was found induced by the stimuli that require the inhibition of a prepared response, (Eimer, 1993; Rueda, Posner, Rothbart, & Davis-Stober, 2004; Jonkman, 2006; Forster, Carter, Cohen, & Cho, 2011). Therefore, the N2 is seen as the neural mark of conflict monitoring. Developmental research on N2 also suggested that its amplitude and latency show a decrease with age (Davis, Bruce, Snyder, & Nelson, 2003; Rueda et al., 2004; Jonkman, 2006; Espinet et al., 2012; Hoyniak, Petersen, Bates, & Molfese, 2017). Hence the age-related latency differences in processing incongruent information could also be the conflict monitoring process reflect on the ERP in this time window. In the current study, this indicated that it may take more time for younger children to activate the representations corresponding to an emotional target word of different valence than the prime, and this affects the speed with which they are integrated.

Research which investigates the ERP responses to affectively primed information, as well as to lexical content, provided systematic evidence which links the N400 with semantic content processing. In particular, the N400 is considered to reflect the semantic and emotional integration of the currently processed information within the existent representations. Increased negative amplitude of the N400 is usually regarded to index integration difficulty (Paulmann, & Kotz, 2008; Friedrich, & Friederici, 2004). While most often, the presence of a prime stimulus, which matches the target emotionally and semantically, is reported to elicit reduced N400 amplitude compared to incongruent prime-target pairs, the opposite effects (Bermeitinger, Frings, & Wentura, 2008) or variations, as a function of stimulus affective valence (Aguado et al., 2013), and individual characteristics (Paulmann, & Kotz, 2008; Goerlich et al., 2012; Bermeitinger et al., 2008; Schirmer et al., 2002) have been reported as well. In the present study, variations in N400 amplitude and latency were observed as a function of the congruency between the emotional PLD prime and the target verbal label in both 3- and 6-year-old children. Overall, these findings show that from as early as the age of 3-years, children extract the affective semantic information from body movement, and that this is further integrated with the emotional information conveyed at the lexical level by word labelling the corresponding affective category. However, age differences in the observed N400 effects suggest that developmental changes may also occur within this age range. In line with several semantic and emotional priming investigations (Bostanov, & Kotchoubey, 2004; Schirmer et al., 2002; Werheid et al., 2005; Zhang et al., 2006; Bermeitinger, Frings, & Wentura, 2008; Paulmann, & Pell, 2010; Goerlich et al., 2012), 3-year-old children in our study responded with increased N400 negative amplitude to the target words primed incongruently by the emotional PLD. In contrast, this effect was not observed in 6-year-old children. At a first glance these results may suggest that older children do not extract the emotional meaning from the target word and/or the body movement. However, the difference in N400 amplitude between the target words and the differences in the latency with which the N400 reaches peak amplitude in different emotional PLD – emotional word pairs, suggest that this is less likely to be the case.

Both 3- and 6-year-old children responded with increased N400 negative amplitude to the happy compared to the angry target word. This result is of particular relevance as it shows that children of both ages differentiate between these words at the semantic level. Moreover, it provides evidence to suggest that children within the 3- to 6-years age range seem to engage in deeper semantic processing of the word happy compared to the word angry. Such differentiation could be due to the fact that happy emotional information is less novel in the children's environments than the other basic emotions (Malatesta, & Haviland, 1982). As a result, the representation of happiness may be richer at this age and possibly requires more neural resources to activate compared to anger (Aguado et al., 2013). Nevertheless, 3- and 6-year-old children may differ in the processing time of the emotional meaning in the body movement prime, the word target, and how this information is integrated. These aspects are known to influence the manifestation of the affective and semantic priming effect on the N400 (Alguado, Schirmer et al., 2002; Paulmann, & Kotz, 2008; Holcomb et al., 1992; Goerlich et al., 2012). While 3-year-old children extract the emotional information from the body movement and from the word, this may be more effortful and slower compared to older children, possibly due to having less experience observing and using such information (Boone, & Cunningham, 1998; Nelson, & Russell, 2011). Also, 3-year-old children may also need more information for processing the emotional meaning of the body movement. It is thus possible that younger children need to watch the entire emotional PLD prime to extract the relevant information. In this case the corresponding representation would reach the optimal level of activation to facilitate the processing of the emotional word at the end of the emotional body movement and shortly (200ms) before the onset of the target (Steinbeis, & Koelsch, 2008; Schirmer et al., 2002; Goerlich et al., 2012; Aguado et al., 2013). Younger children have also been shown to rely more on contextual information to process the meaning of the words compared to older children (Holcomb et al., 1992). Although 3-year-old children use and understand the words 'happy' and 'angry' (Ridgeway, Waters, & Ii,1985; Li, & Yu ,2015; Bretherton, et al.,2017), they probably need, to a greater extent, the emotional information conveyed by body movement and other means of emotional expressivity (e.g., face, voice) in order to comprehend their meaning. In turn, 6-year-old children are probably able to infer emotional states based on fewer body movement cues. This leads to the activation of the corresponding representation well before the offset of the prime stimulus. With a longer delay until the perception of the target word, the activation of the emotion representation may diminish and not be sufficient to produce the typical facilitation effect reflected by the N400 amplitude (Lau et al., 2008). In addition, older children may focus more on the word itself for extracting the meaning (Holcomb et al., 1992), which may further diminish the typical semantic priming effect. The analysis of the latency with which the N400 reaches peak amplitude provides further evidence to suggest that 6-year-old children extract the emotional meaning of the body movement and the target word, despite a lack of congruency effect on the mean N400 amplitude. Similar to the N300 responses, children from both age groups tended to record peak N400 amplitude with shorter latency after watching an angry body movement. Moreover, this latency tended to be shorter when both the prime and target conveyed anger. The influence of threat on the speed with which emotional information is processed at semantic level has been previously noted in adults as well (Paulmann, & Pell, 2011), possibly reflecting the adaptive value of this type of emotional information in terms of preparing the individual to confront the danger which may potentially occur in their environment (Schupp et al., 2004). Thus, although the mean amplitude of the N400 was not sensitive to the emotional congruency between the prime PLD and the target word in 6-year-old children, our overall results suggest that they too extract and integrate the emotional meaning from the body movement and the emotional words, but that the current experimental paradigm might not be sensitive enough to capture it. Future research, in which the ERP responses to the emotional body movement are analysed and the duration of the interval between the prime and target is manipulated, would be particularly relevant for testing these possible interpretations.

In summary, the present study is one of the few that studied the development of children's neural response underlying the emotion extraction from adults' subtle body movements during typical social contexts. Current findings suggested that children from as young as 3 years old can recognise the semantic incongruity of the emotion from body movements and the emotional words, indicating that children from 3 years old can extract the emotional information from body movements, and are able to integrate the semantic meaning of the emotion they extracted. The present study also uncovered some developmental differences in this ability between 3- and 6-year-old children. Results implied that 3-year-old children are less efficient in extracting information from moving bodies than 6-year-old children. The results also indicate that threatening information enhances the processing speed of emotion information at a semantic level in children of this age range.

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Neural Correlates for Body Perception Development During Childhood: A Discussion

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Neural Correlates for Body Perception Development During Childhood: A Discussion

Summary

The current thesis aimed to reveal the neural mechanisms of the cognitive processes underlying emotional body perception in childhood, as well as their developmental pattern, using Event-Related Potentials (ERPs). We are particularly interested in these three research questions: 1) How does body structure processing develop during childhood? 2) What does the neural mechanism of emotion perception from static body postures look like? 3) How do children process emotion from dynamic body motions? In order to achieve these research aims, three studies have been conducted in order to address these issues incrementally, from the perception of body structure, to the emotion perception of static and dynamic body expressions.

Paper 1 began the investigation by examining the development of body structure perception in children three to 10 years old. In order to answer the question of the neural mechanisms underlying body perception, this study looked at the change in associated ERP components in response to upright and inverted human bodies and objects. Children of 3-, 4-10-year-old children, as well as a group of adults passively viewed pictures of human bodies and objects (e.g., hat stand) that were randomly presented in upright and inverted position. Two ERP components, P1 and N190, occurring over occipito-temporal electrodes were measured. The P1, a positive going component that peaks at 100ms after stimulus onset, has been shown to be sensitive to low-level visual properties of the stimulus including luminance, color and contrast (Regan, 1989; Rousselet et al., 2005). In contrast, the N190 is a negative going component that peaks at 170-190ms after stimulus onset. The N190 is suggested to be the neural marker of body perception in high level visual cortex (Rossion & Jacques, 2011; Watanabe et al., 2003; Itier & Taylor, 2004), and it is reported to be sensitive to any distortion of body structure information, such as inverting the body (Righart & de Gelder, 2008; Stekelenburg & de Gelder, 2004; Minnebusch, Suchan, & Daum, 2008; Minnebusch et al., 2010). The main findings of this study revealed a general change with age in terms of the neural responses on both P1 and N190 components. The P1 amplitude for both bodies and objects enhanced dramatically from 4 to 10 years old. Mirroring the P1, the N190 mean and peak amplitude was less negative in 10-year-olds in comparison to both 3- and 4-year-olds. The implication of the developmental changes will be discussed in detail in the next section. Another important finding of this study is children's paradoxical body inversion effect in comparison to adults in all age groups. Results from adults show greater N190 for inverted bodies over upright ones, and this phenomenon is not observed for objects. This inversion effect is seen as a neural marker reflecting the impairment of body processing in adults (Stekelenburg & de Gelder, 2004; Minnebusch et al., 2008; Minnebusch et al., 2010). The inversion effect in adults in our study replicated the previous adult ERP body perception studies. However, findings from Paper 1 suggested that in 3- to 10-year-old children, the N190 showed greater amplitude for upright bodies in comparison to inverted ones. This inversion effect was also absent in children for objects. This paradoxical inversion effect is reported in children of similar age (4- to 10-year-old) in ERP studies of facial perception (Taylor, Batty, & Itier, 2004), indicating that similar to facial perception development, until the later childhood the cognitive processing of body structure encoding is still developing.

Building on the findings of children's body structure perception reported in Paper 1, Paper 2 further investigated the role of emotional body postures perception in 5- to 8-year-old children. We moved to 5-year-old children because behavioural studies indicate that from this age children show above-chance level accuracy in identifying emotions from intensive body expressions (Boone & Cunningham, 1998; Mondloch, Horner, & Mian, 2013). Here, a similar paradigm was applied. Children passively viewed body images expressing happy, fearful, sad and emotionally neutral actions, and the images were presented upside-down randomly for half of the time. Again, the study measured the P1 and N190 components. The results showed a main effect of emotion on N190 mean amplitude and latency. This suggested that from five years old, children show neural responses to emotions expressed via body posture at around 205ms after stimulus onset. Furthermore, the emotion effect indicated that happy bodies elicited increased negative N190 amplitude as well as longer N190 latency over other emotional conditions, indicating that children from five years old are able to discriminate happy postures from other postures at least at a structural encoding or perceptual stage. The results also revealed that altering access to information for body structure detection influences emotion perception. The emotional body postures elicited different N190 amplitudes when the bodies were presented upright in comparison to the inverted condition. To be specific, when the bodies were presented upright, the N190 mean amplitude differed between happy and sad bodies; while in the inverted condition, the mean amplitude differed between fearful and happy bodies. This variation was cancelled after removing the influence of the orientation differences on P1, suggesting that the inconsistent emotion effect on N190 was likely due to the disturbance by the change of low-level visual cues.

To extend our investigation of children's body-based emotion perception to a realistic setting, Paper 3 investigated 3- to 6-year-old children's emotion Extraction ability from point-light displays (PLDs) of moving bodies. Stimuli included six PLDs of dynamic body video clips expressing happiness and anger, as well as two audio clips of the words "happy" and "angry" spoke in an emotionally neutral tone of voice. A semantic priming paradigm was used in the study (Deacon, Hewitt, Yang, & Nagata, 2000). In this paradigm, an "angry" or a "happy" PLD as a prime was paired with a target word ("angry" or "happy") either congruent with the previous body movements or incongruent. ERP responses to the auditory word target were measured. We anticipated different N300/N400 responses to emotional words between the congruent and incongruent conditions. N400s are negative-going deflections that peak around 400ms after the stimulus onset from the central-parietal sites. This component is reported to be sensitive to any incongruency in meaning, showing variations in the amplitude and latency between the congruent and incongruent conditions (Lau et al., 2008; Aguado et al., 2013; West & Holcomb, 2002; Steinbeins & Koelsch, 2008; Reid & Sriano, 2008; Bermeitinger, Frings, & Wentura, 2008). The semantic incongruency effect is therefore interpreted as a neural marker of impaired processing of post-attempt to integrate the target with the prior context (Sereno, Rayner, & Posner, 1998; Hauk, Davis, Ford, Pulvermuller, & Marslen-Wilson, 2006). Therefore, any differences in the N400 amplitude and latency in congruent and incongruent conditions suggest that children can extract the emotional information conveyed by body movement and establish the semantic relation with the corresponding word. The N300 component is a negativity occurring around 300ms after stimulus onset. It is often reported as being independent from or co-occurring with the N400 (Bostanov & Kotchoubey, 2004; Paulmann & Pell, 2010; Nobre & McCarthy, 1995; Friederici, 2005). Analogous to N400, N300 is suggested to be sensitive to incongruity between sounds and prevous visual objects in emotion context (Bostanov & Kotchoubey, 2004; Paulman & Pell, 2010). The results of Paper 3 showed that both 3- and 6-year-old children show different latency N300/ N400 responses in congruent and incongruent conditions, suggesting that children from 3 years old can detect the incongruence of the emotion expressed by a moving body and the following lexical meaning. Thus, from as early as 3 years children may extract information with affective information from dynamic bodily expressions.

Overall, the work presented in the current thesis addressed the development of bodily emotion perception in children in terms of the neural fundamentals of body perception, emotion perception from static postures, and emotion perception from dynamic displays. In the following section, we will further discuss the important developmental traits revealed by the current work, in terms of the neural mechanisms underlying body structure perception as well as emotion processing from body expressions. Finally, based on previous studies along with the contribution of the current work, we will discuss a temporal model of the neural mechanisms underlying emotion perception from bodily expression throughout childhood.

Development of Body Perception During Childhood

As important as faces, human bodies also deliver various types of information such as the emotion status of the person (Meeren, van Heijnsbergen & de Gelder, 2005; Robbins & Coltheart, 2015). In particular, understanding the neural mechanisms of body perception is crucial in childhood. From toddlerhood children develop increasing needs to processing emotions from bodily expression, especially when faces are invisible or too far to see. Few studies summarised models of visual body perception as well as emotion perception from bodily expression based on the findings in adults (de Gelder, 2006; Minnebusch & Daum, 2009). However, we are lacking a comprehensive understanding of the development of emotion perception from the body due to lack of evidence. The current work therefore provided important evidence to close the gap in the developmental domain. In the following section we will first go through the important findings of the current work, then consolidate the current findings with previous evidence, to reveal a possible model of information-processing of body along a developmental timeline during childhood.

Important findings of the current work

Paper 1 presented a cross-sectional investigation of the developmental change in the neural responses to body structure by contrasting four age groups: 3-, 4-, and 10-year-olds, as well as adults. The results reported in Paper 1 revealed for the first time dramatic developmental changes of relevant ERPs of body structural processing (the P1 and N190) from 4- to 10-year olds. A decrease in N190 amplitude with the increase in age was observed. This finding mirrored the effect of the increasing on P1 amplitude, in which 10-year-old children showed greater mean and peak amplitude than younger children. These findings are consistent with the findings in facial perception studies (Taylor et al., 2004; Kuefner et al., 2010), implying the general development of visual social stimulus perception reflected in P1. Furthermore, a paradoxical inversion effect in contrast with the adult group was shown on the N190 amplitude throughout the 3 children groups, revealing that the immature pattern of body perception lasted until late childhood. Based on the findings of Paper 1, Paper 2 investigated the neural mechanism underlying the emotion perception from static body postures from 5-8 years old. In order to achieve this research aim, Paper 2 also measured the P1 and N190. One strength of this work is that both Paper 1 and 2 involve examinations of the associated ERPs (P1 and N190) of static body structures, so that we can present an integral perspective of the developmental change of neural physiological response underlying body perception throughout childhood.

In order to describe the developmental trajectory of the neural mechanism underlying body structure perception across childhood, we combined the amplitude of the P1 and N190 from Paper 1 and 2 from all age groups (see Figure 1). Bearing in mind the variability due to the use of individual peaks in Paper 1, in order to deliver better elucidate developmental changes, only the results of mean amplitudes from all age groups are presented here. Furthermore, Paper 2 tested children age from 5- to 8 years old. However, as there was an insufficient number of children to conduct between age group comparisons, we did not compare across ages in the analysis for Paper 2. Here, in order to get a clear understanding of the developmental traits throughout childhood, the children tested in Paper 2 were divided into two age groups: 5-6 years old (age = < 77 months, N = 11) and 7-8 years old (age > 78 months, N = 9). Msean amplitudes were averaged separately across these two age groups, and presented in Figure 1 with the mean amplitudes of the other three age groups tested in Paper 1. As any conclusions regarding developmental change in ERPs between these two age groups should only be made when there is a sufficient number to conduct the statistical analysis, here in the current section, we will only discuss the potential tendency that is shown in the graphs.

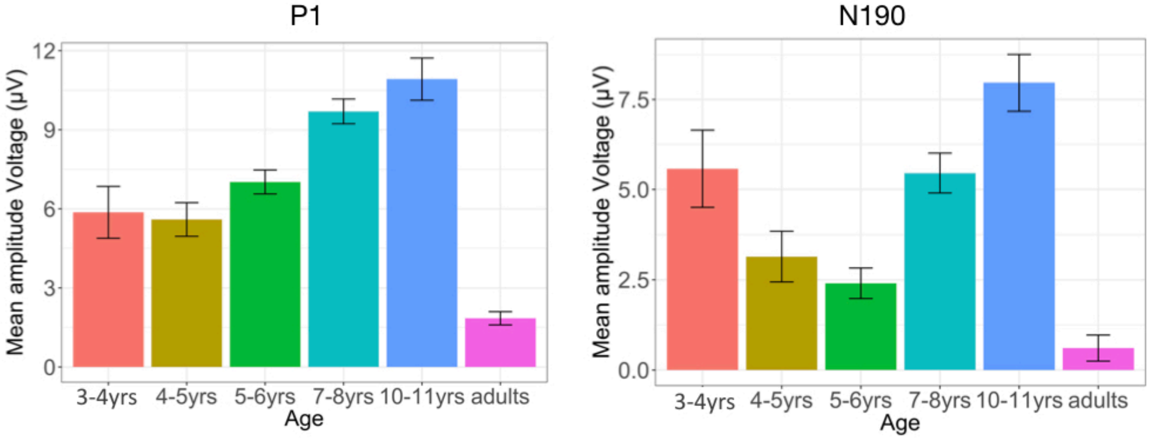


Figure 1 Mean amplitude of P1 and N190 to upright bodies across all age groups from Paper 1(3-, 4-, 10-years-old, and adults) and 2 (5- and 7-year-old).

Overall, across age groups, the P1 and N190 components show more defined morphology, and a general tendency to decrease from 3 to 4-5 years old, followed by a tendency to increase from 5 to 10 years old (see Figures 1, 2, 3). This result was similar to findings from previous developmental studies on face perception (Taylor, Batty & Itier, 2004; Kuefner et al., 2010). In Paper 1, the P1 amplitude showed a dramatic increase in 10- compared to 4- year-old children regardless of the type of stimuli (i.e., bodies, objects, up-right orientation, inverted orientation) the participants watched, most likely reflecting the development of processing of the psychophysical properties of the stimuli. Findings from Paper 2 showed that this increase tended to be linear when taking into account the intermediate age range (5-8 years old). This is probably followed by a large decrease of mean amplitude in adulthood. This is consistent with the previous developmental findings that P1 amplitude sharply increases towards the age of 7-8 years, followed by a decline towards adulthood (van den Boomen et al., 2015). There are several possible explanations for these developmental changes in the P1, such as the reduction of gray matter volume and synaptic density (Huttenlocher, 1990; Whitford et al., 2007), changes in the conductivity of the underlying tissues, increasing of the head size and the general level of brain activity reflected in the electronical signals (Kuefner et al., 2010). However, to elucidate the interaction between development of visual processing and the perception of social stimuli during childhood we need further investigations.

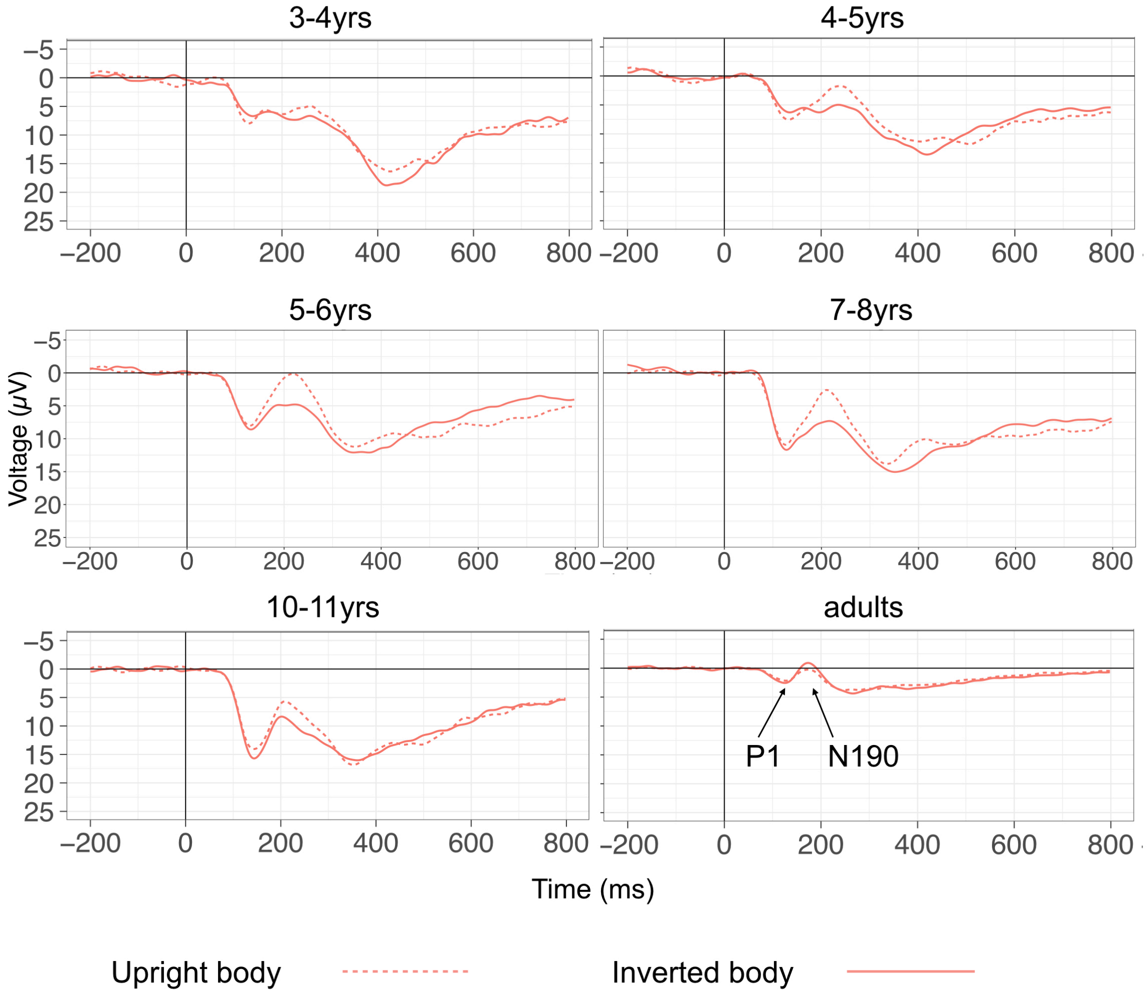


Figure 2 Grand average ERPs in response to upright and inverted bodies from 3 years old until adult.

The developmental changes in N190 mirrored the P1 in Paper 1. From the information Paper 2 contributed to Figure 1 we can observe that by 8 years old, both the N190 and the P1 mean amplitude showed a tendency to increase towards 10 years old. These findings together indicate that both N190 and P1 in response to body structure decreases in early childhood, followed by an increase towards late childhood. This tendency was also in line with the developmental findings reported for face processing (Taylor et al., 2004; Kuefner et al., 2010).

The delay of the N190 peak between 10-year-old children and adults (46ms) further suggested that the processing speed of body perception in 10-year-old children is still not comparable with that in adults.

Furthermore, both body inversion effects on the N190 observed in Paper 1 and Paper 2 suggested a paradoxical inversion effect throughout early childhood to late childhood compared to the typical inversion effect found in adults (see Figure 3). This was in contrast to the inversion effect found for adults in the current thesis, as well as that found in adult body perception studies (Stekelenburg & de Gelder, 2004; Minnebusch et al., 2008; Minnebusch et al., 2010). In Taylor and colleagues' (2004) investigation of children's facial perception, children from 4 to 10 years old also showed this reversed inversion effect in relation to that observed previously in adults. The typical inversion effect in the N190 response to bodies is considered a neural marker of body perception. Therefore, one possible interpretation is that until a certain age, children apply a more flexible use of information in both body and face perception (Itier & Taylor, 2004; Taylor et al., 2016; Colombatto & McCarthy, 2017). The slow developmental pattern shown in the current work is also consistent with previous findings relating to facial perception; that is, the adult-like characteristics of the N190 are more likely to be manifest until early adolescence (Taylor et al., 2004).

To sum up, papers 1 and 2 provided evidence that is important for describing the developmental changes in the neural mechanisms underlying body perception throughout childhood, as well as how these components differ from the one typically reported in adults.

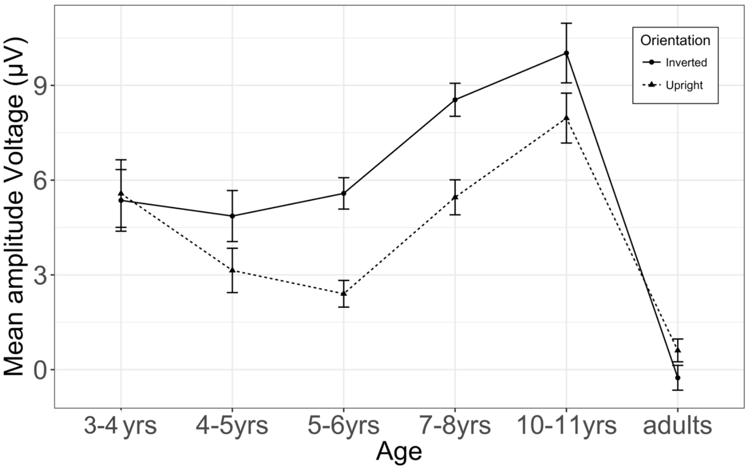


Figure 3 Mean amplitude of the N190 to upright and inverted bodies from 3 years old until adulthood.

A tentative time line of body perception development

Above, we have summarised previous studies' findings relating to body perception from 3-month-olds to adulthood and incorporated these with findings from current work. Below we list the findings we now have from behavioural and ERP studies as well as fMRI measurements by age (Table 1). Based on these findings, we depict a developmental time line of body structure processing in Figure 4. Although the current work focused on childhood, for the timeline we propose we also present findings from infancy to provide a complete developmental pathway. We highlight our findings in grey in both tables, to help capture an intuition regarding how the current work contributes to the broader research landscape.

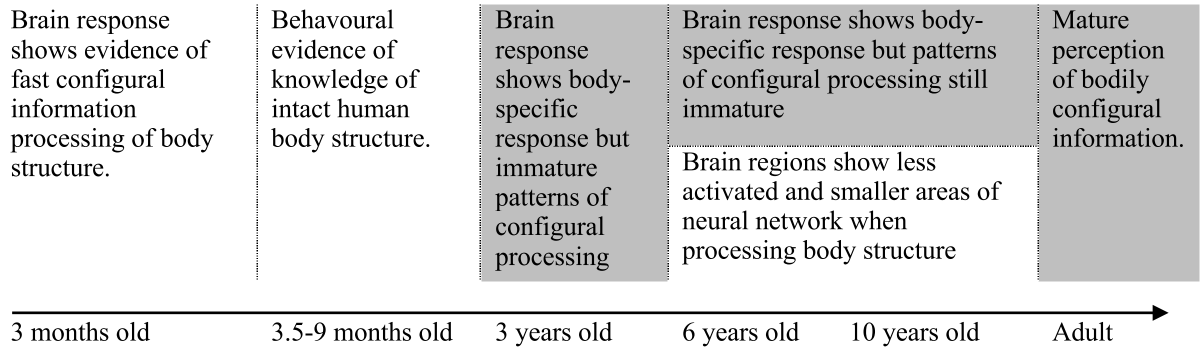
Table 1

Findings relating to the development of body perception from previous studies and the current work.

Age	Behavioural performance	ERP evidence	fMRI evidence	Study
3 months	-	Larger P400 mean amplitude to scrambled bodies than intact bodies	-	Gliga & Dehaene-Lambertz, 2005
3.5-9 months	Preferences for normal body to scrambled and/or distorted bodies only when images were presented upright.	-	-	Zieber et al., 2010; Zieber et al., 2014a
9-18 months	Distinct patterns of responding to typical bodies and scrambled bodies	-	-	Heron & Slaughter, 2010
3-4 years	-	Reversed inversion effect in N190. Greater N190 mean and peak amplitude for upright bodies than inverted ones. Larger P1 peak amplitude for bodies than objects. Faster P1 latency for upright bodies than inverted.	-	**Ke & Geangu, Paper1**
4-5 years	-	Reversed inversion effect in N190. Greater N190 mean and peak amplitude for upright bodies than inverted ones. Larger P1 peak amplitude for bodies than objects.	-	**Ke & Geangu, Paper1**
5-6 years	-	Larger N190 mean and peak amplitude to upright bodies than inverted bodies.	Six to 11 years old show bilateral activity in right hemisphere of occipitotemporal regions, such as	Ross et al., 2014; **Ke & Geangu, Paper2**

7-8 years	-		pSTS, amygdala, fusiform gyrus and percentral gyrus. Also show significant less activation in those regions.	Ross et al., 2014; **Ke & Geangu, Paper2**
10-11 years	-	Reversed inversion effect in N190. Greater N190 mean and peak amplitude for upright bodies than inverted ones. Larger P1 peak amplitude for bodies than objects.		Ross et al., 2014; **Ke & Geangu, Paper1**
Adult	Recognition of body structure is diminished by inversion.	Greater N190 peak amplitude for inverted bodies than upright.	Neural networks of extrastriate body area (EBA) and Fusiform body area (FBA) active when observing body parts and whole bodies.	Reed et al., 2003; Stekelenburg & de Gelder, 2004; Righart & de Gelder. 2007; Minnebusch et al., 2009; de Gelder, 2010; **Ke & Geangu, Paper 1**

Note. In order to be consistent with the current work, we only include studies using real body images. Findings contributed by the current work are highlighted in grey.



Brain response shows evidence of fast configural information processing of body structure.

Behavioural evidence of knowledge of intact human body structure.

Brain response shows body-specific response but immature patterns of configural processing

Brain response shows body-specific response but patterns of configural processing still immature

Brain regions show less activated and smaller areas of neural network when processing body structure

Mature perception of bodily configural information.

Figure 4. Developmental time line of body structure perception based on known findings.

The above time lines indicate clearly that the findings of the current work close a substantial gap in the developmental time line of the body structure processing. Previously we only had evidence for the immature pattern of body structure recognition in late infancy and the mature processing pattern in adults. The current work provided evidence of the neural mechanisms of the development of body structure processing during the early developmental stages. It revealed a possible pattern of flexible use of configural information during childhood, which is similar to facial perception development, indicating a prolonged maturation of configural information processing of both facial and bodily information. The contribution of the current work in childhood development also indicates a connection with findings from early developmental stages. Gliga and colleagues (2005) found sensitivity to impaired configural bodily information in P400 but not N290 in 3-month-olds. In the current work this sensitivity is found on the N190 component from 3 years. A similar developmental tendency is also observed in facial perception, with the N290 and P400 developing to become the N170 (Halit, de Haan, & Johnson, 2003; de Haan, Johnson, Halit, 2003; Gliga, & Dehaene-Lambertz; 2005). However, due to an insufficient number of studies, whether the N290 and P400 in early body perception also form the precursors of the N190 in children remains to be clarified.

Bodily Emotion Perception in Childhood

Another main aim of the current work is to close the gap in affective neuroscience in emotional body perception from the developmental point of view. Recent years have seen a number of studies revealing new understanding of emotion perception from bodies in childhood, as well as the possible important role of emotional body perception ability in social emotional development (Barth, & Bastiani, 1997; Atkinson, 2009; Muñoz, 2009). However, the affective neuroscience field has been dominated by studies of facial expression. To contribute to the largely unknown field of emotion body perception during childhood, the second and third paper in the current work examined the neural mechanism of children's perception of emotion from bodies, particularly from two typical situations: through static posture, and from body movements.

To better understand the current status of what we know and what remains to be done, we will again first present the crucial contributions of the current work, then sum up previous findings and the current work into a tentative time line of emotion body perception development.

Contributions of the current work

An early stage in development of emotion discrimination from static postures is reported at 6.5 months, when infants can relate positive and negative body postures to matched vocalizations (Zieber, Kangas, Hock, & Beat, 2014). Certainly, this ability shows some early signs of emotion processing at a perceptual level at this age; however, performance could be due to infants' familiarity with the matching of body postures with vocal cues in everyday life, rather than showing evidence of extracting the meaning of the body postures. Behavioural evidence indicating the ability to label emotions expressed by body postures is reported for 5-year-old children (Boone and Cunningham, 1998; Mondloch, Horner, & Mian, 2013).

Paper 2 enriched our understanding of emotion perception from static body posture in 5- to 8-year-old children. Findings reported in Paper 2 revealed that there was no emotion sensitivity shown on P1, but emotion was found to have an impact on the N190 mean amplitude as well as latency. Happy bodies elicited more negative N190 mean amplitude than fearful, sad and emotionally neutral bodies. Happy bodies also triggered longer latencies than emotionally neutral bodies. This suggested that 5-year-old children are able to discriminate happy body postures from sad, fearful and emotionally neutral ones at around 205ms after onset of static body postures. The fact that body posture images did not trigger any emotion effect on the low-level visual component P1 suggested that the emotion effect was not due to differences in the visual properties of the emotional body postures (e.g. the direction of the upper bodies, or the angle of the hands or the legs). Therefore, the discriminative ERP response towards happy body postures in comparison to other body postures in this study indicated extraction of emotional information from static bodies. Another important finding is the interaction between the encoding of bodies and the perception of emotion. In Paper 2, the interpretation of this interaction focused on the processing of the visual properties of the body images. This is consistent with previous findings demonstrating that when judging emotions from static bodies, adults reply based on various body structure cues, such as the positioning of each element relative to the torso (Coulson, 2004; Mondloch et al., 2013). Further research is needed in order to investigate how impairment of information leads to this interference effect on emotion perception in children. For example, does the impairment of bodily configural information or posture perception influence emotion perception? Furthermore, it will also be interesting to see whether this interference effect will be observed in adults. Comparing the potential differences between adults and children will provide us with further information about the maturation of the use of bodily information in emotion perception.

Analysing the perception of dynamic body movements in 3- and 6-year-old children, Paper 3 established that from at least 3 years children are sensitive to the incongruence of information from moving bodies and subsequent lexical meanings. For both 3- and 6-year-old children, the N300 from the central scalp locations showed shorter latency when the target words were congruent with the previous emotional PLDs than when they were incongruent. Variations in N400 amplitude and latency between congruent and incongruent conditions were also observed in both 3- and 6-year-old children. Furthermore, faster N400 latency to target words primed by angry bodies was observed in both age groups. Also, response latency tended to increase when the target word and the PLDs were both angry. This suggested that children of both age groups can extract and integrate emotional meaning from body movement. Overall, Paper 3's findings suggested that from at least 3 years, children can extract emotion information from moving bodies, even when that information is expressed in highly abstract form such as point-light displays of body movements.

Development time line of emotion perception from bodily expression

As above, we summarise the previous findings relating to emotion perception from bodily expression, consolidate these with our findings, and list them by age. As we looked at emotion perception from both static and dynamic expressions, findings of studies using both expressions are included. Again, our findings are highlighted in grey.

Table 2.

Findings of the development of emotion perception from bodily expressions, from previous studies as well as the current work.

Age	Behavioural performance	ERP evidence	fMRI evidence	Study
3.5 months	Failed to match happy and angry bodily expression (both static and *dynamic*) to corresponding vocalizations	-	-	Zeiber et al., 2014b; Missana et al., 2015
4 months	-	*Failed to show any significant ERP response to emotions from dynamic bodily expressions.*	-	Missana et al., 2015
5 months	*Looked longer at matched dynamic body movements and voices when the movements were present upright but not inverted.*	-	-	Missana et al., 2015
6.5 months	Able to match happy and angry static bodily expression to corresponding	-	-	Zeiber et al., 2014b; 2014c

	vocalizations when they were upright but not inverted. *Showed preference for happy over angry dynamic bodily expressions in upright but not in inverted condition*			
8 months	-	N290 and Nc showed significantly more negative mean amplitude to fearful bodies than happy bodies from static expressions. *Larger Pc for happy bodies than fearful bodies in right hemisphere when PLDs were presented upright.*	-	Missana et al., 2014; 2015
3 years		*Incongruency effect on N300 and N400 when processing unmatched emotional words and body movements.*		Ke & Vuong, Geangu, Paper 3
5 years	*Could correctly label Happy, Sad, Angry and Scared from dynamic bodily expressions at above chance level. Performance increased with age.*		-	Nelson & Russell, 2011
	-	Showed emotion effect on N190 in response to static bodily expressions. Happy bodies elicited more negative amplitude and longer latency than the other emotional bodies.	-	Ke & Geangu, Paper 2

6 years	-	*Incongruency effect on N300 and N400 when processing unmatched emotional words and body movements.*	-	Ke & Vuong, Geangu, Paper 3
7-8 years	-	Showed emotion effect on N190 in response to static bodily expressions. Happy bodies elicited more negative amplitude and longer latency than the other emotional bodies.	-	Ke & Geangu, Paper 2
Adults	*Could accurately identify emotions from only 3s long dynamic bodily expression.* Detected extreme emotions better from static body postures than static facial expression.	Enhanced response to fearful static bodily expression than neutral ones on frontal vertex positive potential (VPP) and sustained potential.	FFA and FG more activated when observing fearful bodies than instrumental ones.	Montepare, Koff, Zaitchik, & Albert, 1999; Hadjikhnani & de Gelder, 2003; Stenkerlenburg & de Gelder, 2004; de Gelder et al., 2004; Aviezer, Trope, & Todorov, 2012;

Note. Studies using both static and dynamic bodily expression as stimuli are included. Findings from dynamic expression are presented in italics. Findings contributed by the current work are highlighted in grey.

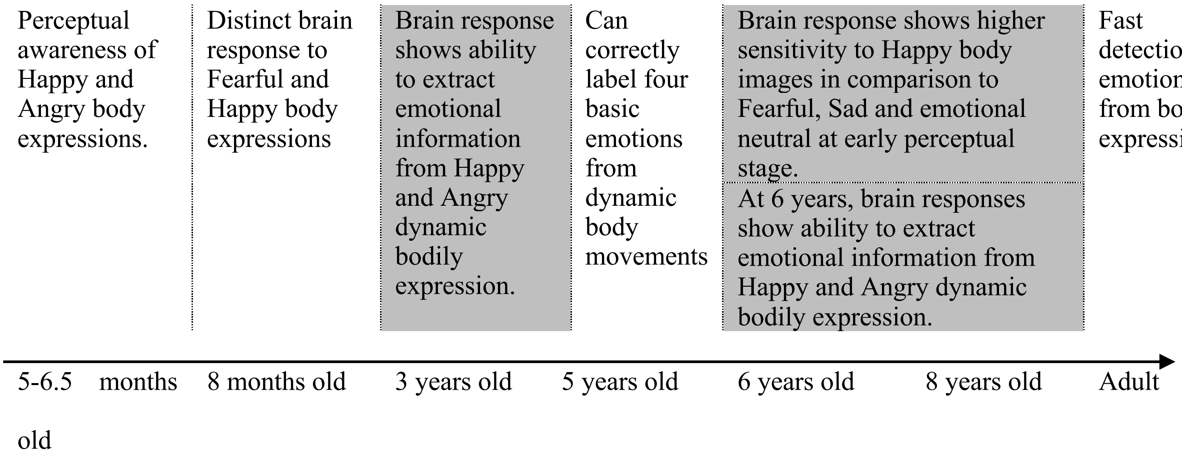


Figure 5. Developmental time line of emotion perception from both static and dynamic bodily expressions. The contribution of the current work is highlighted in grey.

A tentative model of bodily information processing in immature brain

By conducting three carefully designed and connected EEG investigations, the current work provided fundamental evidence towards a comprehensive understanding of the developmental time line of the emotional body perception; further, the findings of this work reveal information processing in emotion body perception in children. Therefore, based on previous neuroimaging findings, as well as the three interrelated brain network models in emotional body perception by de Gelder (2006), here we propose a tentative neural network of information processing in emotional body perception in children.

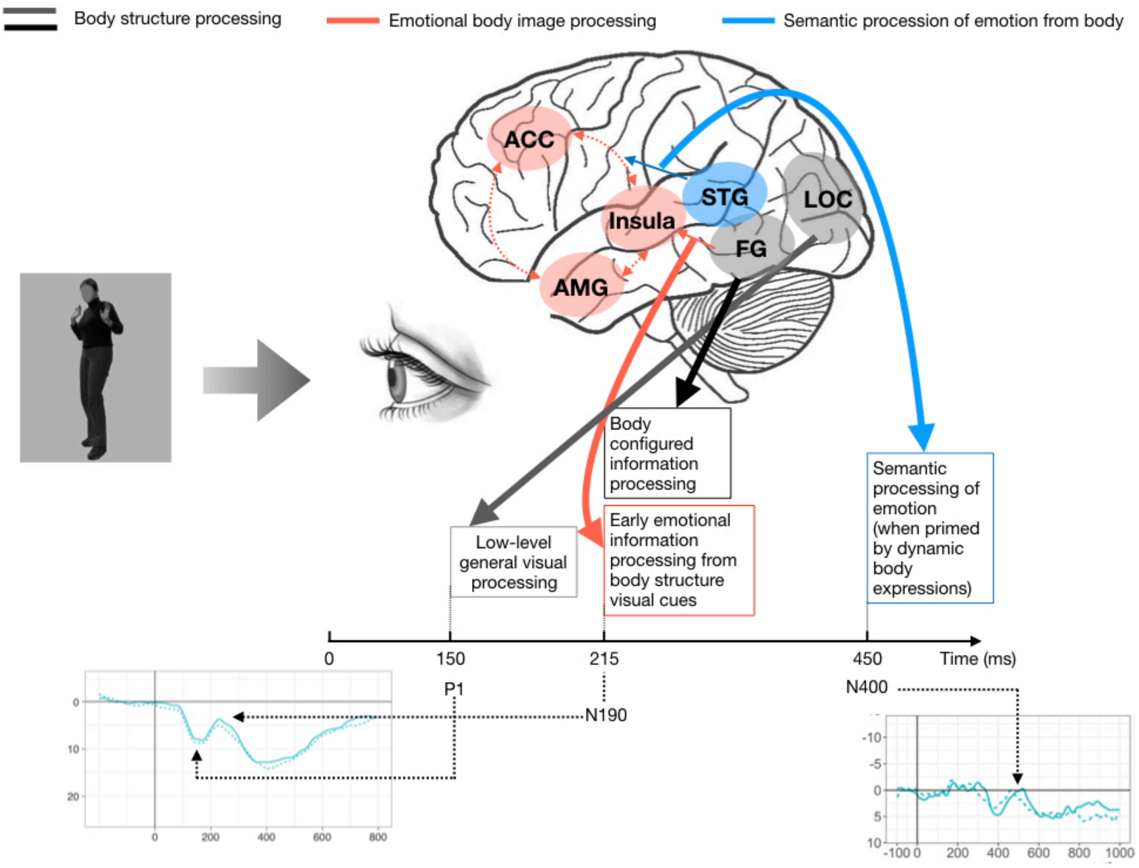


Figure 6. A network of the information processing in emotional body perception for children.

The network of information processing from bodily expressions (see Figure 6) proposed here, involves brain regions including the visual system, motion perception system and the amygdala circuit for emotion processing. The first response reflecting the visual processing starts at approximately 150ms after stimulus onset, which is the low-level visual processing reflected on P1 component. It is suggested to stem from the lateral occipital cortex (LOC; Di Russo et al., 2002; Ke & Geangu, Paper 1). Around 215ms, bodily configural information processing emerges, based in the fusiform gyrus (FG; Stekelenburg & de Gelder; 2004; Ke & Geangu, Paper 1). Early emotional information perception from body structure clue also happens at this stage (Ke & Geangu, Paper 2). To complete this network, the emotion processing network (amygdala (AMG), insula and anterior cingulate cortex (ACC); de Gelder et al., 2004) is possibly involved at this stage.

Processing emotional information from dynamic expression involves both the emotion and the motion perception network. Human body motion perception activates the body-selective regions located in the posterior fusiform gyrus, overlapping with the motion-selective regions (Peelen, Wiggett, & Downing, 2006). Although the current work did not directly examine the neural response to emotional body motion, we looked at the semantic incongruency effect on N400 peaks around 450ms in the children we tested. N400 is commonly believed to origin from a highly distributed neural source (Kutas & Federmeier, 2011). In our study, semantic in/congruency processing involved integrating auditory lexical items with the emotion information extracted previously seen body motions. The superior temporal gyrus (STG) is responsible for auditory language processing (Bigler et al., 2007). Hence, this high-level cognition reflected in the N400 likely involves the network between the STG and the emotion system during information integration.

Taken together, the current work contributes crucial evidence for emotion perception from both static body postures and dynamic body movements during childhood at the neurophysiological level. Previously there were limited numbers of behavioural findings relating to 3-year-old children's ability to identify emotion from others' body movements. Adding to this literature, our findings revealed that at least from 3 years, children can extract emotion information from abstract body movements. Furthermore, extending existing knowledge that before 5 years children can accurately match verbal labels to corresponding body postures (Mondloch et al., 2013), our findings suggest that from 5 years, children can perceptually discriminate happy body posture from sad, fearful and emotionally neural body postures at very early processing stages. Overall, based on the new findings in this work, the current timeline provides a more comprehensive understanding of the development of body perception and emotion perception from bodily expression and signposts important directions for future work, which will be further discussed in the final section.

The outlook and limitations of this work

The current work closes an important gap in our understanding of emotion perception from bodily expression as well as body perception *per se* during childhood. Based on the tentative models and developmental time lines presented above, various further investigations can be conducted to address the remaining gaps in terms of details of the maturational pattern. For example, although there are some behavioural findings in emotional body perception during childhood, collecting behavioural data with corresponding tasks would provide an important behavioural counterpoint to the ERP results. Moreover, investigations examining the development of the bodily inversion effect from late childhood into adolescence may enrich our understanding of the difference between children and adults in terms of the inversion effect.

The current work also highlights essential possibilities for future social emotional developmental research. As discussed, a poor ability to recognise emotions from bodies is reported to be associated with higher levels of callous-unemotional traits and violent behaviour in 8- to 16-year-old children, as well as their social behavioural performance in the classroom as rated by teachers at school (Barth & Bastiani, 1997; Muñoz, 2009). Building on the characterisation of the neural mechanisms of body perception presented in the current work, future investigations can further examine the mechanisms underlying the impairment of recognition of body and behavioural performance, in terms of whether the nature of the impairment comes from the processing of bodies, emotional information, or the interactive effect of both.

Another insight revealed in the current work is the affective bias on emotion processing. Previous literature has shown that the impact of affective bias on emotion perception emerges early in facial emotion perception, and becomes established with development. Infants from 8 to 14 months old respond faster to angry faces compared to happy faces (LoBue and DeLoache, 2010, LoBue, 2010). The current work cross referenced this impact by revealing a negative emotion bias in body perception in the age range of 3 to 6 years. As affect bias could also be shaped by differences in children's environment (Morales, Fu, & Pérez-Edgar, 2016), further investigations can be directed towards the potential role of individual differences in emotional body perception.

As discussed above, one unexpected result in Paper 2 is that previous behavioural studies showed children from 4 years old can accurately identify fear and sadness from body posture by matching the verbal label to corresponding bodies (Mondloch, Horner, & Mian, 2013). However, no difference was observed in the N190 in response to fear versus sad body postures. One limitation of the study is the short presentation of each stimulus (800ms), which may have restricted the options for examining the potential emotion information processing at a later cognitive stage, such as those reflected by the late positive potential (LPP). The LPP is a broadly superior posterior-distributed ERP component evident after approximately 300ms in adults. It is reported to be sensitive to affective valence and emotion regulation capacity, suggesting a facilitated attention to emotional information at the lateral processing stage (Dennis, & Hajcak, 2009; Aguado, Dieguez-Risco, Méndez-Bértolo, Pozo, &Hinojosa, 2013; DeCicco, O'Toole, & Dennis, 2014). Emotion arousal could have a prolonged effect on LPP amplitude after 300-400ms. For example, the amplitude of LPP reduced in response to emotionally negative pictures in comparison to neutral ones between 400-1000ms time window (Foti & Hajcak, 2008). Therefore, future studies that include longer stimulus presentations may address this limitation, and help clarify the time course of emotion perception from static body postures.

Some additional limitations of the current work are about Paper 3. First of all, in Paper 3 we did not analyse the relation between the neural response and language comprehension information. Paper 3 used two emotional words, "happy" and "angry", as the targets. These two words were previously reported to be understood and used by children aged 3 to 6 years (Ridgeway, Waters, & Ii,1985; Li & Yu ,2015; Bretherton, Fritz, Zahn-Waxler, & Ridgeway, 2017). However, evidence suggested that the N400 effect is related to listening and reading comprehension performance in children. The incongruency effects on N400 amplitude were found to be correlated positively with listening comprehension (Henderson, Baseler, Clarke, Watson, & Snowling, 2011). Therefore, the relationship of language comprehension and children's neural response when extracting emotions from body movements is worth investigating as a possible future direction. Further related to Paper 2 as well as Paper 3, a follow-up study looking at the inversion effect in emotion perception from dynamic body perception would be ideal. However, due to time constraints of PhD work, the practical reason we explained in Paper 3 about the potential difficulties of recoding EEG response to long stimuli in good quality, as well as that we try to out our focus on the emotional body perception instead of just body perception, we decided to leave this question for future investigation.

In summary, the current thesis is one of the few works that provide essential evidence for reducing the knowledge gap in emotional body perception development. By focusing specifically on understanding the associated neural correlates, this work reveals the developmental traits of body structure perception in 3- to 10-year-old children for the first time, establishing the protracted progression of the perception of this type of stimuli. This thesis further provides neurophysiological evidence of emotion processing from static body expressions in childhood (in 5- to 8-year-olds), as well as establishing the ability of children as young as 3 years old to extract emotion from dynamic body motions. Although the developmental pattern at later ages, as well as various relations between emotional body processing and social emotional development, still remain to be investigated, the insights provided here provide essential foundational knowledge of the development of emotional body perception and establish multiple avenues for future investigations.

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