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UNDERSTANDING OTHERS' ACTIONS AND EMOTIONS: ELECTROPHYSIOLOGICAL EVIDENCE IN INFANCY AND EARLY CHILDHOOD

PhD candidate

Ermanno Quadrelli

Supervisor

Prof. Chiara Turati

Co-supervisor

Prof. Viola Macchi Cassia

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ABSTRACT

The research presented in the current dissertation investigates two of the most intriguing topics pertaining to the field of developmental cognitive neuroscience, namely, the development of the ability to understand others' actions and the ability to comprehend others' emotions. Recent research suggests that the human brain is equipped with structures that are active both during first- and third-person experience of actions and emotions. These structures, known as the mirror neuron system (MNS), were originally discovered in monkeys. They have been proposed as a neural mechanism through which others' actions, intentions, and emotions can be directly understood by bridging the gap between self and others. In fact, when we perceive someone else's action or emotion expression we activate a network that is also active during action execution or expression of emotions. Despite recent advances in the study of the development of action and emotion processing, the neuro-cognitive correlates of these abilities in infants and children are far from being fully understood. Studies described in this dissertation attempt to fill this gap by investigating the neural correlates of the ability to perceive and understand others' actions and emotions in preverbal infants and older children.

Chapter 1 provides a review of existing models developed to tackle the developmental origins of mirroring mechanisms, and a discussion of the existing debate about the role of the motor system in action and emotion understanding. The studies reported in Chapter 2 and 3, respectively, focus on the neural correlates of 7-month-olds' processing of human action sounds, as measured through event-related potentials (ERPs), and the neural mechanisms driving toddlers' ability to understand others' actions, as assessed by frequency oscillation through time-frequency analysis. Furthermore, the development of the ability to understand others' emotions and the role played by the motor

system in such an understanding across development will also be explored. The study described in Chapter 4 explores the neural correlates of 7-month-old infants' capability to process static and dynamic facial expressions of emotions, whereas Chapter 5 is dedicated to the investigation of the mechanisms underlying covert facial muscle reactions, as measured through surface electromyography (sEMG), elicited by the observation of emotional expressions in 3-years-old children. Results of the presented research will be discussed in Chapter 6 to provide an integrated picture of the early stages of the development of action and emotion understanding. The existing theoretical debate about the role of the motor system in action and emotion understanding processes will be addressed by proposing a developmental viewpoint.

INTRODUCTION

Humans are inherently social animals. Despite sharing some social behaviours with other species –e.g., affiliation, aggression or establishment of hierarchy (Ragen, Mendoza, Mason & Bales, 2012), human social life is far more complex. We spend a great deal of time attending to other faces, bodies and actions, thus being by and large experts in reading information about who people are and what people do and managing multifaceted social interactions. Moreover, we seek company of others, share emotions with conspecifics and generally cooperate to reach a common goal (Tomasello & Vaish, 2013). As we enter a room full of people, we immediately have a number of social perceptions: at first hearing we are able to recognize who is talking to whom or if someone is walking towards or away from us. Likewise, at a glance we can deduce intentionality in others' actions and, from a continuous stream of behaviours, we can extract goals, desires and emotions or dispositions. It is evident that social perception and interpretation about others' faces, body postures and actions is foundational to how we communicate, learn about the social and physical world, regulate our emotions and develop relationships with others (Pelphrey & Carter, 2008). Adult humans seem to be experts at developing strategies to create and maintain social relationships and manage complex interactions. Therefore, it is not surprising that the human brain is highly capable to solve social situations, such as anticipating other people's behaviours or recognizing and reading others' emotion. However, how do we understand the actions, emotions and intentions of others and what are the neural mechanisms mediating these abilities? It is generally acknowledged that, as adults, we have areas of the brain specialized for processing and integrating sensory information about the appearance, behaviours and intentions of other humans. These cortical areas are part of a complex network of interconnected subcortical and cortical brain structures, known as the *social brain*, which includes the superior temporal sulcus (STS), the fusiform face area (FFA), the orbitofrontal and the sensori-motor cortices (Adolphs, 1999). Additionally, the discovery of mirror neurons in monkeys has had a revolutionary impact on the neuroscientific world, leading to a great deal of research looking for an equivalent system in humans. There has been a lot of speculation about the functions of a possible human homologue of mirror neurons. In recent times, the mirror neuron system (MNS) has been proposed to play an important role in social cognition by providing a neural mechanism by which others' actions, intentions, and emotions can be directly understood. This MNS is thought to be the neurophysiological mechanism at the basis of the general capacity to bridge the gap between self and others, thus constituting the possible neural substrate for understanding others' actions and emotional states via a simulation mechanism. Indeed, it has been observed that seeing the actions or emotional expressions of others elicits neural activity in cells that are active even when the same actions or emotion expressions are performed or felt in first person (Leslie, Johnson-Frey & Grafton, 2004; Rizzolatti & Craighero, 2004). However, although intriguing, the involvement of the MNS in mediating important cognitive functions (e.g., action and emotion understanding, speech and music processing) in humans has been considered by some authors as unproved and hypothetical (Hickok, 2009; Turella, Pierno, Tubaldi & Castiello, 2009).

How our brain develops to sustain cognitive functions is a matter of study of a branch of science that is known as *developmental cognitive neuroscience*. This specific research field has emerged to answer one of the most essential questions that concern the human species, specifically, how the human brain and the cognitive processes that it supports develop from the prenatal period through adulthood (i.e., ontogeny). More precisely, it encompasses the empirical study of the neural mechanisms underlying the developmental trajectories of cognitive processes, ranging from the encoding of social and emotional signals (e.g., perception and understanding of others' actions and emotions) to the expression of complex forms of social behaviours.

As previously outlined, in adults a complex network of interconnected subcortical and cortical brain structures is believed to underlie social behaviour, cognition, and emotions. Although the functional properties of this network are well understood in adults, very little is known about its development and how it supports the progressive emergence of complex social skills. Those skills include such complex constructs as empathy, motivation, and theory of mind, which are difficult to map directly onto neural systems. For this reason, complex social processes are often broken down into more specific components. For example, the intricate and multifaceted construct of empathy can be decomposed in multiple subcomponents, including bottom-up elaboration of shared motor representations (i.e., affective sharing), which enable us to differentiate between our own perspective from those of others, and top-down executive processing that affects the degree of the empathic experience via our own motivation and intentions, helping us to regulate emotions (Decety & Meyer, 2008).

How studying development might be important for a full, or at least better, understanding of the neuroscience of cognitive processing? Assuming a developmental perspective can provide unique opportunities to explore how the components of complex systems, such as those pertaining the human brain and mind, interact in ways not possible in adults, where all the components are fully mature and operational. Furthermore, developmental studies allow the observation of the earliest periods of life, when infants are starting experiencing social stimuli, and the study of dissociation among skills that are not observable in adults, as different abilities emerge at different ages. A better understanding of the brain systems involved in cognitive skills, such as action and emotion understanding, and the role played by experience in shaping their development might be important not only for the understanding of normative development. Indeed, it may also provide a better understanding of the reason why certain abilities sometimes do not follow a typical developmental trajectory, as well as making available new tools for early disease detection and rehabilitation.

The research presented in the current dissertation investigates two of the most intriguing topics pertaining to the field of developmental cognitive neuroscience, namely, the development of the ability to understand others' actions and to comprehend others' emotions. Human actions and emotions are special as they can be experienced both from first or third person, and through experiencing the consequences of our own and others' actions and emotions, we become able to construct representations of ourselves and of our social environment. The human brain is equipped with structures (i.e., MNS) that are active both during first- and third-person experience of actions and emotions. In fact, when we perceive someone else's action or emotion expression we activate a network that is also active during action execution or expression of emotions. Therefore, the understanding of basic aspects of social cognition might depend on the understanding of neural mechanisms involved in our own personally experienced actions or emotions (Gallese, Keysers & Rizzolatti, 2004).

The studies described in the next chapters investigate the neural correlates of the emergence of the ability to perceive and understand others' actions and emotions. In fact, reading and understanding facial and communicative signals is important for young children, and even more for preverbal infants. Interactions with infants, without the aid of words, rely on the communication of emotions and intentions via the nonverbal means of the face, body, touch, and auditory cues (Feldman, 2007; Rochat, 2014). However, despite recent advances in the study of the development of action and emotion processing

(Gredeback & Daum, 2015; Leppanen & Nelson, 2009; Uithol & Paulus, 2014), the neuro-cognitive correlates of these abilities in infants and children are far from being fully understood. The present dissertation attempts to fill this gap by investigating the neural correlates of action and emotion perception and understanding in the first years of life.

Chapter 1 provides a review of existing models developed to tackle the developmental origins of mirroring mechanisms, and a discussion of the existing debate about the role of the motor system in action understanding. The studies reported in Chapter 2 and 3 focus on the neural correlates of 7-month-old infants' processing of human action sounds, as measured through event-related potentials (ERPs) (Chapter 2), and the neural mechanisms driving toddlers' ability to understand others' actions, as assessed by frequency oscillation through time-frequency analysis (Chapter 3).

As a second goal, this dissertation aims to deepen our knowledge about the development of the ability to understand others' emotions and the role played by the motor system in such an understanding across development. The ERP study presented in Chapter 4 investigates the neural correlates of 7-month-olds' ability to process static and dynamic facial emotional expressions, while the study presented in Chapter 5 utilizes surface electromyography (sEMG) to explore covert facial muscle reactions elicited by the observation of emotional expressions in 3-years-old children.

In Chapter 6 the results of the studies will be discussed in light of other existing evidence to provide an overall picture of the early stages of the development of action and emotion understanding. Within a neuroconstructivist framework, a developmental perspective will be proposed to address the existing theoretical debate about the role of the motor system in action and emotion understanding processes.

CHAPTER 1

THE DEVELOPMENT OF MIRRORING MECHANISMS: PERSPECTIVES ON ACTION AND EMOTION UNDERSTANDING[1]

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[1] Chapter based on: Quadrelli, E., & Turati, C. (2015): Origins and development of mirroring mechanisms: a neuroconstructivist framework. *British Journal of Developmental Psychology*, doi: 10.1111/bjdp.12110

ABSTRACT

The current chapter examines theoretical models developed to answer questions about the origins and early developmental processes determining the emergence of mirroring mechanisms. Strengths and points of criticism deriving from existing alternative positions are illustrated. Particular emphasis is put on the Neuroconstructivist framework with the aim of evaluating whether the hypotheses driven by this approach are in line with the available evidence. Specifically, within the Neuroconstructivist framework, it is proposed that mirroring mechanisms arise from gradual developmental processes as a result of a narrowing process driven by sensorimotor experience. Furthermore, it is suggested that a set of perceptual and motor constraints may shape the emergence of a specialized network for the processing of others' actions and emotions in our species, thus facilitating the development of a direct matching mechanism between executed and observed actions and emotions through experience. Finally, an overview about the existing debate on the role of the motor system in action and emotion understanding is provided.

1.1 Introduction

Action and emotion recognition are fundamental steps on which social behaviours depend. Perhaps one of the most complicated questions related to these abilities concerns how do we understand other people's behaviours and how do we assign goals, intentions, or affective states to others by simply perceiving their actions or expressions. We make these predictions on a regular basis, for example, when we help someone who cannot reach for the biscuits on the breakfast table or when we catch a ball someone throws to us. The ability to make these predictions and form expectations about what will happen next makes it possible for us to interact smoothly in our environment. As the observer of an action, we are by no means a passive spectator. We build in our own mind representations of the actions we see executed by other persons and we can internally take the emotional perspective of others. In that sense, the observer is not merely contemplating the action or expression of the observed agent, he is also attempting to understand others' emotional and mental states (Blair, 2005) or predict the outcome of the action (Jeannerod, 2006).

Motor theories of perception have a long history in psychology, dating back to motor interpretation of depth perception by Bishop Berkeley (1709), and have been proposed as explanations for a wide range of mental processes. Since the 1700s, Adam Smith (1759) also started noticing that people tend to imitate others' emotional expressions, thus suggesting that conscious empathy is linked to the instinctive motor mimicry of another person's expressions of affect (Lipps, 1903). Their least common denominator is that all these theories propose recruitment of the motor system or of motor competence during perception and posit that motor information is necessary for successful recognition of actions or emotions (Stasenko, Garcea & Mahon, 2013). Long ago, the notion that actions are intrinsically linked to perception was also supported by William James (1890), who stated that observing or mentally representing an action excites the motor program used to execute the same action. More recently, theories of embodied cognition have emphasized the role of the body and the environment in shaping cognition (Barsalou, 2008; Gallese & Sinigaglia, 2011). According to these accounts, in order to understand the actions and emotions of others, we rely on the motor plans and introspective states that we use when performing similar actions or expressing similar emotions. In other words, we understand others' through a simulation process incorporating our own plans and applying them to what we are perceiving.

Interest in this idea has grown recently, thanks to the discovery of mirror neurons (MNs), which has boosted a great deal of work in the neuroscientific investigation of the social aspects of cognitive development and has deepen our knowledge on the relations among action, perception and cognition. Originally found in area F5c of the monkey ventral premotor cortex (VPC), MNs have the peculiar feature of firing both when an individual performs a goal directed action (e.g., grasping) and when the same, or similar, action is perceived to be performed by another agent (di Pellegrino, Fadiga, Fogassi, Gallese & Rizzolatti, 1992; Fogassi et al., 2005). The activation of the monkey premotor cells during observation or listening of others' actions is considered to be evidence that MNs are actively involved in action understanding processes by representing and internally re-enacting -i.e., mirroring- perceived actions (Casile, Caggiano & Ferrari, 2011). Over the last twenty years, neurophysiological and brain imaging research on human adults demonstrated that observing another individual performing an action modulates the activity of the observer's motor cortex (e.g., Buccino et al., 2001; Molenberghs, Cunnington & Mattingley, 2012; Perry & Bentin, 2009), and highlighted the presence of mirror neurons in the human brain through single cell recordings (Mukamel, Ekstrom, Kaplan, Iacoboni & Fried, 2010; but see Keysers & Gazzola, 2010). Overall, evidence speaks in favour of a human mirror system, intended as a distributed cortical network, including the inferior frontal gyrus, dorsal and ventral premotor cortex, and inferior and superior parietal lobules, that reliably activates for both action observation and execution.

Since their discovery, mirror neurons have also been mentioned and connected to a wide range of human processes and capacities, among which action understanding (e.g., Gallese, Keysers & Rizzolatti, 2004), imitation (e.g., Iacoboni, 2009; Rizzolatti & Craighero, 2004), emotion processing (van der Gaag, Minderaa & Keysers, 2007; Wicker, Keysers, Plailly, Royet, Gallese & Rizzolatti, 2003), empathy (Gazzola, Aziz-Zadeh & Keysers, 2006; Pfeifer, Iacoboni, Mazziotta & Dapretto, 2007). Indeed, recent theoretical perspectives assign an additional role to mirroring mechanisms, through which we are allowed to embody other individual's intentions and to understand the meaning of the other's facial emotional expression (Enticott, Johnston, Herring, Hoy & Fitzgerald, 2008).

Focusing on the developmental processes that might drive the emergence of the human mirror system, three main theoretical frameworks have been proposed on the origins of mirroring mechanisms: the phylogenetic (Simpson, Murray, Paukner & Ferrari, 2014), the associative learning (Cook, Bird, Catmur, Press & Heyes, 2014) and the neuroconstructivist (Del Giudice, Manera & Keysers, 2009) accounts. Empirical evidence and limits for each of the aforementioned perspectives will be briefly outlined in the following paragraphs.

1.2 Phylogenetic account of mirroring mechanisms development

According to the boldest phylogenetic explanation, mirror mechanisms are a product of genetic evolution and are favoured by natural selection because of their crucial role in understanding and imitating others' actions (Rizzolatti & Arbib, 1998). In this vein, one fundamental prediction of this account is that perceptual-motor couplings should be present from birth, thus suggesting that sensorimotor matching mechanisms exist innately in monkey and human brains. Sensory and motor experiences only have a marginal facilitative role in the development of mirroring mechanisms (Bonini & Ferrari, 2011). Nonetheless, direct neurophysiological evidence of a mirror neuron system in humans at birth is far from being established. The available studies focus almost exclusively on neonatal imitation showing that newborns spontaneously reproduce tongue and lip protrusion and mouth opening movements up to 24 hours after presentation (Meltzoff & Moore, 1977, 1983, 1994; Kugiumutzakis, 1999). These findings have more recently been extended to other species, like chimpanzees (Myowa-Yamakoshi, Tomonaga, Tanaka & Matsuzawa, 2004) and macaques (Ferrari et al., 2006), thus suggesting the presence at birth of a common rudimentary mirror mechanism in humans and other primates.

Standing up for the nativist view, the *Active Intermodal Mapping* (AIM) model of newborn imitation, proposed by Meltzoff & Moore (1997), posits the existence of an innate mechanism allowing the "seen-but-unfelt" to be matched to the "felt-but-unseen". This model solves at its roots the so-called correspondence problem, consisting in translating perceptual information from a modelled action into a matching motor output. It hypothesizes that infants are equipped with an innate supramodal representational system encoding visual and proprioceptive representations of observed and executed actions that allows neonatal imitation. Electrophysiological evidence has also been provided in newborn monkeys using electroencephalography (EEG). Specifically, mu rhythm desynchronization over central electrode sites, which is considered a neural marker of sensorimotor cortical activity, was recorded during observation and imitation of facial gestures (Ferrari et al., 2012). Given that neonatal imitation involves cross-modal matching of perceptual and motor information, it was proposed that it might indicate a mirror neuron system that is innately functional soon after birth (Iacoboni & Dapretto, 2006; Lepage & Theoret, 2007; Meltzoff & Decety, 2003).

A longstanding debate surrounds neonatal imitation and its underlying mechanisms (e.g., Anisfeld, 1996; Jones, 2009; Jones, 2007; Ray & Heyes, 2011). Besides that, a criticism that might be levied to theories linking neonatal imitation to an innate mirror system is that even though newborns match movements they are exposed to, those actions are not goal-directed, a quality typically required to activate mirror neurons discovered in monkeys (Jones, 2009). Also, as the cortical regions involved in the mirror system are not fully developed at birth, it has been noticed that it is unlikely that neonatal imitation could be mediated by these areas, and thus, in turn, by mirror mechanisms (Oberman, Hubbard & McCleery, 2014). Over the years, the phylogenetic hypothesis gave way to an epigenetic turn, stating the importance not only of strictly genetic mechanisms - i.e., phylogenetic natural selection processes-, but also of the modality DNA can differently express proteins depending on the environmental influences (at cellular, tissue and organism levels) and the role of learning processes in explaining inter-individual variability of mirror responses (Evo-Devo perspective; Ferrari, Tramacere, Simpson & Iriki, 2013).

1.3 Associative learning account of mirroring mechanisms development

The associative learning explanation of action mirroring rejects the idea that mirror mechanisms are genetically inherited, holding that they are a product of sensorimotor experience (Cook, Bird, Catmur, Press & Heyes, 2014; Heyes, 2010). Specifically, mirror neurons are simple motor neurons activated during action execution. When the activation of motor and visual neurons is simultaneous (i.e., contiguous) and highly probable (i.e., contingent), the association between the motor and visual neurons is strengthened and transforms those motor neurons into mirror neurons (Ray & Heyes, 2011). This occurs, for example, when the perception of an action is frequently associated with the corresponding simultaneous and contingent motor command. The associative hypothesis implies that the perceptual-motor coupling properties of mirror mechanisms result from a domain-general associative learning process (Cook et al., 2014). In this view, evolution only provides humans and other primates with motor and visual neurons and the potential for them to be connected to each other (Heyes, 2010).

In terms of imitation, the associative model suggests that the correspondence problem is solved by exposing an individual to repeated experiences of contiguous and contingent observations and executions of the same actions (Ray & Heyes, 2011). Indeed, imitation occurs in a wide variety of species (Whiten, McGuigan, Marshall-Pescini & Hopper, 2004; Range, Viranyi & Huber, 2007), and seems limited to those actions with which animals accumulate sensorimotor experience (Catmur, Walsh & Heyes, 2009).

Studies exploring the role of sensorimotor experience in shaping mirror neuron system activity were carried out both in monkeys and human adults. In human adults, expert pianists and classical dancers display a greater mirror activation as compared to non-pianists or capoeira dancers in response to observation of fingers playing a piano or ballet movements respectively (Cross et al., 2006; Haslinger et al., 2005). Brief periods of sensorimotor experience are thus able to enhance (Press, Gillmeister & Heyes, 2007; Wiggett et al., 2012), inhibit (Cook, Dickinson & Heyes, 2012) and induce (Landmann, Landi, Grafton & Della Maggiore, 2011; Press et al., 2012) mirroring activity. Nonetheless, evidence that in adults sensorimotor experience modulates mirror mechanism activity cannot be directly translated into the idea that the emergence of mirror mechanisms in children is mainly derived from associative processes. Claims based on the study of fully formed adult brains may be inappropriate when applied to the study of the protracted period of development of the neocortex in infancy and childhood. Also, experience acquired in adulthood may determine temporary changes in cortical functioning, but might be insufficient to generate substantial brain circuit reorganizations, while early experiences, especially if taking place during sensitive periods of development, could trigger long-term rearrangements of the involved brain structures.

Despite growing evidence highlighting the role of active and observational experiences in moulding mirroring mechanisms (Cannon et al., 2015; Hunnius & Bekkering, 2014; Paulus, Hunnius, van Helk & Bekkering, 2012), only one study directly examined the effects of a visuomotor training on mirror activity in infancy. Pre-walking infants were trained to perform stepping movements on a treadmill while observing contingent (i.e., own movements in real time) or non-contingent (i.e., previously recorded movement) leg movements. Mu rhythm activity was measured before and after training. The results highlighted that the amount of post-training sensorimotor activation was predicted by the strength of visuomotor contingency during training (de Klerk et al., 2014). Nevertheless, no difference was found between pre- and post-training across conditions, thus the findings might be explained by the infants' previous experience with own leg movement observation and execution (e.g., kicking while they are lying on their back). For what concerns imitation, the associative model, instead of positing the existence of an innate mechanism computing similarities between observed and executed actions, suggests that the correspondence problem is solved by exposing an individual to repeated experiences of contiguous and contingent action observations and executions (Ray & Heyes, 2011).

Points of criticism are raised against the associative account. Since this position implies that all contingent sensorimotor experiences are learned equally well, some scholars argue that this approach cannot explain why some behaviours are learned more easily than others and why infants tend to imitate human rather than mechanical/non-human actions (Bertenthal, 2014). For example, 18-month-olds successfully imitate a human action, while failing to imitate the same action performed by a mechanical pincer (Meltzoff, 1995). In addition, given the cardinal importance of contingency and contiguity attributed to the associative learning model, some argue that the relatively low level of contingency in mother-infant interactions cannot allow the formation of learned associations (Ferrari et al., 2013). Thus, according to these opposing viewpoints, associative learning does not answer questions about how infants recognize similarities between own and others' actions.

1.4 Neuroconstructivist account of mirroring mechanisms development

A third alternative explanation of the development of mirror mechanisms is situated within the broader neuroconstructivist framework. Similarly to the Evo-Devo explanation proposed by Ferrari and colleagues (2013), it avoids the idea that a specific set of perceptual and motor neurons are genetically pre-programmed for coding specific actions, and also the hypothesis that trial-and-error learning mechanisms are solely responsible for the development of mirror system. However, differently from the Evo-Devo perspective, that tend to confine the role of experience to account for inter-individual differences (Ferrari et al., 2013), neuroconstructivism ascribes great value to experience-expectant processes, involving species-specific experiences that result in brain rewiring, which in turn leads to the development of specific neural systems (Greenhough, Black & Wallace, 1987). This way, higher cognitive functions become domain-specific as a result of the ontogenetic development (Karmiloff-Smith, 1998). Thus, unlike the Evo-Devo perspective, this view assigns a major emphasis to the gradual tuning of a cortical network to process specific information, evidenced by an increasingly selective cortical response during development – i.e. narrowing (de Haan, Humphreys & Johnson, 2002; Johnson, 2011).

Additionally, this model posits the existence of an early experiential canalization process that, by promoting the learning of perception-action couplings, is capable of ensuring the development of the mirror system (Del Giudice, Manera & Keysers, 2009). Mirror mechanism development is canalized by domain relevant predispositions of the perceptual-motor system that focus infants' attention toward actions performed by self and others, allowing the development of a specialized system devoted to their immediate understanding. Specifically, pre-specified early predispositions to attend to movements of specific body parts (i.e., hands and face) (Rochat, 1998; van der Meer, 1997; von Hofsten, 2004) are thought to facilitate the development of a direct matching between executed and observed actions through experience. These predispositions would protect the developing mirroring mechanisms from possible perturbations and to accelerate their developmental process.

In contrast to the associative learning explanation, Del Giudice and colleagues (2009) insist on the role of domain-relevant predispositions and experiential canalization. Nonetheless, in agreement with associative learning, these Authors consider Hebbian learning to be a fundamental learning mechanism at the basis of action mirroring. The Evo-Devo perspective acknowledges the concept of canalization also, although in this vein it is primarily described at the level of gene-expression modifications, and it is taken into account for explaining the variations observed in mirror neurons properties.

A neuroconstructivist explanation of action mirroring would be in line with recent models of human development (Karmiloff-Smith, 2006; Westermann et al., 2007). This perspective considers the developmental pathway not to be dependent on fixed genetic specifications or on simple and slow learning associations only, but to gradually emerge from the dynamic interaction between inborn domain-general properties of neural functioning and the structure of the input provided by the species-typical environment.

Below we present a set of predictions derived by the neuroconstructivist account of the development of action mirroring, and the corresponding supporting empirical data.

1.4.1 Hypothesis 1: Narrowing of mirroring mechanisms

Unlike the empiricist view, that considers experience gained in adulthood and infancy as equally important, neuroconstructivism acknowledges a key role to early inputs, that are responsible for tuning infants' abilities and lead to the progressive formation of domain-specific representations. Indeed, the neuroconstructivist approach to cognitive development considers brain specialization and domain-specificity for high level perceptual and cognitive functions to arise from gradual developmental processes, whose only biological constraints are the general properties of neural and body functioning (Westermann et al., 2007). This paragraph summarizes findings supporting a gradual specialization process of the mirror system.

Focusing on neurophysiological data, mu rhythm is an EEG oscillation recorded over sensorimotor scalp areas in the alpha frequency range (adults: 8-13 Hz; infants: 6-9 Hz) attenuating during action production and perception, consistent with the view that it may reflect motor system activation (Muthukumaraswamy & Johnson, 2004). Mu rhythm desynchronization magnitude during action execution and observation undergoes a gradual increase (Marshall & Meltzoff, 2011): 9- and 14-month-olds show a smaller decrease in mu power when observing (5% and 12% respectively) and performing (10% and 14% respectively) an action (Marshall, Young & Meltzoff 2011; Southgate, Johnson, Osborne & Csibra, 2009), compared to mu desynchronization magnitude levels recorded in 8-year-old children in response to observing (25%) and performing (60%) an action (Lepage & Theoret, 2006). This developmental increase might reflect an underlying intensification of the neural activity involved in perceptual motor coupling processes.

Crucially, while in adults mu rhythm desynchronization is reported to be specific to central sites (Babiloni et al., 1999), in infants this activity seems more widely distributed across the scalp (Saby et al., 2012; van Elk, van Schie, Hunnius, Vesper & Bekkering, 2008). This supports the notion that the regions involved in mirror mechanisms in adults are already active in early infancy, although a specific network becomes increasingly localized and tuned with development (Cohen-Kadosh & Johnson, 2007).

Additional evidence supporting a gradual specialization process comes from studies using surface electromyography (Natale et al., 2014; Turati et al., 2013). These studies demonstrate that motor resonance modulation elicited by the observation of a goal directed action is lacking at 3 months of age, is evident at 6 months of age during the observation of the latest phase of the action (i.e., during goal achievement), and precedes the action goal at 9 months, when the motor system is recruited during an earlier phase of the observed movement (i.e., before goal achievement), like in older children (Cattaneo et al., 2007). These findings point to a gradual process of specialization of mirror mechanisms during the first year of life.

Another line of research shows that motor resonance in adults occurs in response to the observation of actions within the observer's motor repertoire, while for actions like barking motor resonance is absent (Buccino et al., 2004; Buccino, Binkofski & Riggio, 2004). Further studies are needed to directly test the narrowing hypothesis, for example by examining infant action mirroring response to observation of actions performed by humans vs other species during the first year of life. Moreover, it will be important to extend the evidence gathered in the visual modality to other sensory modalities, for example by investigating infants' processing of human action sounds. Like other auditory social information (i.e., voices, Belin, Zatorre, Lafaille, Ahad & Pike, 2000), cortical specialization for human action sounds may be reflected in an increase in the tuning of the brain responses to human action vs non-human action sounds.

Combined with the ones reviewed above, these expected outcomes would support the hypothesis that action mirroring narrows throughout development, as highlighted for other perceptual domains (e.g., face recognition, language; Scott, Pascalis & Nelson, 2007). For example, for what concerns the face processing domain, evidence suggests that this system is initially broadly tuned and flexible and that a process of progressive narrowing takes place leading to responses specific to the geometry of the human face by 3 months of age (Macchi Cassia, Kuefner, Westerlund & Nelson, 2006). Indeed, early face preferences become increasingly tuned to the face exemplars populating the infant environment. A similar refinement process has recently been proposed to occur in the development of the emotion recognition mechanisms, with stabilization and pruning of synaptic connections being the neural counterpart of a narrowing process towards species-typical emotional expressions (Leppanen & Nelson, 2009). It could be hypothesized that active and observational experiences are responsible for shaping the gradual specialization of mirroring mechanisms (Cannon et al., 2015; Hunnius & Bekkering, 2014; Paulus et al., 2012; van Elk et al., 2008). Notably, infants' understanding of others’ actions does not depend on motor or passive experience only, since a variety of social cues such as gaze direction (Woodward, 2003), emotions (Phillips, Wellman & Spelke, 2002), hand gestures (Woodward & Guajardo, 2002), and motivation to interact with others (Paulus, 2014) are also important in developing the ability to encode action goals.

1.4.2 Hypothesis 2: Constraints on the development of mirroring mechanisms

According to Neuroconstructivism, a sequence of interactions between pre- and post-natal environment and multiple levels embedded in the human body (i.e., cells, tissues, and cortical circuits) is considered to drive the reorganizations of the cortical circuits (Johnson, 2011). The outcomes of developmental processes, rather than being inherently pre-specified, are probabilistic, because they are derived from a constellation of organismic and environmental constraints.

What constraints may interact so consistently to shape the emergence of common mechanisms for the specialized processing of others' actions in our species? A first set of constraints may be linked to the gradual development of an infant's own motor repertoire, which, as reviewed above, modulates the development of mirroring mechanisms. An infant's own proprioceptive and sensorimotor experience, as along with limitations in body movements, might constrain his/her perception of the surrounding environment, acting as a template that might match perceived actions. This idea is consistent with the associative learning explanation, as it posits that the kind of learning that produces mirror neurons occurs when there is correlated activation of sensory and motor neurons that are responsible for similar actions. Nevertheless, this process might also follow non-associative implicit and probabilistic learning mechanisms, such as statistical learning. This would explain why learning occurs in spite of the high variability of infant interactions with others, action scenes, action movements, and so on. Statistical learning is a way of acquiring structure within continuous sensory environments. Initially shown to be involved in word segmentation, it has been demonstrated to be a general mechanism that operates across domains and species (Krogh, Vlach & Johnson, 2013) and has recently been reported to operate in detecting regularities in action sequences (Monroy, Kaduk, Gerson, Hunnius & Reid, 2015). Some authors hypothesize that infants' ability to extract regularities from streams of actions might be one of the mechanisms that help them to predict how actions will be executed without necessarily being able to perform those actions (Hunnius & Bekkering, 2014).

On the perceptual side, a second set of constraints may rely on early visual preferences. The existence of an early attentional bias towards faces is well established in the face processing literature (Johnson & Morton, 1991; Valenza, Simion, Macchi Cassia, Umiltà, 1996). Newborns' preference for faces is interpreted as the cumulative effect of non-specific perceptual biases stemming from the general properties and intrinsic constraints of their visual system (Turati, 2004). It has been demonstrated that, rather than being affected by the specific face-like array of a visual pattern, newborns' visual behaviour is governed by general structural properties that faces share with other non-face visual stimuli, such as the presence of more patterning in the upper than in the lower part of the configuration (i.e., up-down asymmetry) (Macchi Cassia, Turati, & Simion, 2004). Nonspecific preferred structural properties may thus account for newborns' preferential response to face stimuli. Furthermore, in line with the crucial importance recently attributed to the role of organismic embodiment in structuring neural activity, recent studies have proposed that also prenatal learning and proprioceptive experience, together with the peculiar morphology of the newborn's sensory array, may inform the development of internal representations of facial structure (Wilkinson, Paikan, Gredeback, Rea & Metta, 2014).

A similar principle might be important as well for developing a mirror system (Meltzoff & Moore, 1997). Evidence is accumulating in support of the presence of a visual preferential response to other relevant body parts, in addition to faces. After birth, infants spend a great amount of their waking time looking at their own hands (White, Castle & Held, 1964). Newborns move their hands significantly more when they can watch them (van der Meer, 1997), and actively attempt to control arm movements to keep their hands visible (von Hofsten, 2004). Two-day-olds visually discriminate between a hand moving toward or away from the body, looking longer at the hand movement directed away from the body and toward the external world (Craighero, Leo, Umiltà & Simion, 2011). Additionally, neonates look longer at a biomechanically impossible hand closure compared to a possible one, suggesting that newborns are able to recognize the biomechanical properties of hand movements (Longhi et al., 2014).

These findings speak in favour of an early ability to recognize the hand as a salient body part and to process domain-relevant information related to hand actions. Notably, it is matter of debate whether such early preferences are due to an inborn sensitivity to the hand shape, or are driven by prenatal sensorimotor experience. During pregnancy, foetuses acquire substantial sensorimotor experience of their hands. The majority of the hand movements of foetuses are directed towards own body parts or the uterine environment (Jakobovits, 2009). Foetuses also show smaller velocity peaks for movements directed towards their eyes and mouth or their twin (Castiello et al., 2010; Zoia et al., 2007). Given the relevance of developmental processes during the prenatal period, disentangling the relative role of genetic predispositions and environmental factors in humans is almost impracticable.

Overall, available evidence suggests that mirroring mechanisms, like other human specialized functions, should not be considered a phenomenon that can be studied by isolating the roles of motor and perceptual constraints and surrounding environment (Clark, 2007). Limitations in newborns' and infants' perceptual abilities and motor control restrict the potential complexity of environmental stimulation, but at the same time act as a filter on accessible experiences, thus favouring the development of increasingly complex representations, as a result of an environment that is perceived as increasingly complex

(Westermann et al., 2007). Within this view, infants pro-actively explore the environment instead of passively absorbing information (as in the empiricist explanation), selecting the experiences from which to learn and shaping their developmental pathways. Early sensitivities might guide their attention toward information relevant for action understanding, in turn bootstrapping the emerging mirror mechanisms.

1.4.3 Hypothesis 3: Mirroring mechanisms deriving from an experience-expectant process

Neuroconstructivist models of the development of highly specialized functions, such as language and face processing, posit that, rather than acting as independent mechanisms, genetic and environmental factors inextricably interact to produce developmental changes through experience-expectant processes (Maurer & Werker, 2014; Cohen-Kadosh, 2011). These processes underlie the development of those abilities that i) are common to all members of the human species, ii) depend on the exposure to certain experiences occurring over limited periods of time – i.e., sensitive periods, and iii) rely on initial sensitivities and constraints that prepare infants for learning about aspects of their world that have adaptive significance (Greenough & Black, 1992; Greenough et al., 1987).

Experience-expectant processes take advantage of cortical plasticity and allow the fine-tuning of aspects of development that cannot proceed to optimum outcomes as a result of genetic or experiential factors working alone. Experience-expectant processes differ from experience-dependent processes; the latter subserve expertise acquisition in adulthood, may contribute to explaining cultural and individual differences, and can occur at any time, so that the timing of the experience is not critical for typical development (as in the empiricist explanation). For what concerns processing of facial emotional expressions, it has been proposed that it is shaped by individual specific experiences, as demonstrated by studies investigating emotion recognition mechanisms in maltreated children. Indeed, children of abusive parents display a heightened sensitivity for angry expressions as compared to children reared in typical environments (Pollack, Cicchetti, Hornung & Reed 2000). Nonetheless, it is also suggested that the presence of facial emotional expressions common to all the members of our species might have led human brains to develop mechanisms that are biased for attending to emotionally salient stimuli from early infancy (Leppanen & Nelson, 2009).

Can we think of the development of mirror mechanisms as being mediated by experience-expectant processes? We can assume that it is adaptive for the human species to possess highly specialized abilities that allow them to immediately understand the actions of others. Although specific motor training in adults may modulate their activity, mirror mechanisms develop in all typically developing human beings, with characteristics specific to our own species compared to other primates (Rizzolatti & Craighero, 2004). Therefore, as for faces or language, it is likely that selection pressures have led to the genetic specification of neural tissue that has the potential to become specialized for mirror mechanisms, provided that appropriate and timely experience is available. In contrast to the view that the development of mirror mechanisms is an example of a general-purpose experience-dependent process, we propose that the timing of certain inputs during development is important for the typical development of the mirror system, and that alterations occurring during sensitive periods might divert the normal course of its development (Karmiloff-Smith, 1998).

Although evidence strongly suggests that both genetic and environmental factors play a role in the development of mirror mechanisms, literature still fails to specify what kind of experience is necessary, and when this experience needs to occur. In the face and language domains, deprivation or alteration of exposure to critical input in specific periods of development strongly affects the typical development of face and language processing

(Maurer & Werker, 2014). It might be hypothesized that a similar process might also occur in the development of mirror mechanisms. A vital issue for future consideration is that we know very little about the existence of different sensitive periods that affect the development of mirroring mechanisms in typical and atypical populations. Along this direction, recovery capacity from motor system impairments occurring early in life has been studied in children with congenital cerebral palsy (Buccino, 2014). Further research might explore the effects of impairments in early face recognition and hand gesture discrimination abilities on the typical development of mirror mechanisms. Indeed, Libertus & Needham (2014) recently highlighted the existence of a relationship between face preference and motor development in 3-month-old infants.

1.5 Action mirroring and action understanding

It is generally accepted that there is a relationship between the activation of the motor system during action perception and action understanding (e.g., Southgate, 2013). Also, consistent empirical findings suggest that action-mirroring processes are involved in understanding of others' actions (e.g., Cattaneo et al., 2011).

Developmental research indicates that the ability to detect and attribute goals to actions gradually emerges during the first year of life (Cannon, Woodward, Gredeback, von Hofsten & Turek, 2012; Csibra, 2008; Kamewari, Kato, Kanda, Ishiguro & Hiraki, 2005; Sommerville & Woodward, 2005). For instance, both 12-month-olds and adults visually anticipate the goal of a manual displacement action, while such ability is lacking in 6-month-olds, who track the observed action in a reactive manner (Falck-Ytter, Gredeback & von Hofsten, 2006).

It is well known, then, that infants from an early age are capable to interpret the movements of others as goal directed actions. However, the cognitive mechanisms underlying this ability and how the motor system is activated by simple observation of others' actions are still topics of hot debate, and different explanations have been offered so far. The direct-matching hypothesis (Rizzolatti, Fogassi & Gallese, 2001) posits that an action is directly understood when the observer's motor system resonates in response to the observed action, via an embodied simulation and "bottom-up" process. Accordingly, some propose that only actions for which infants have previously gathered sensorimotor experience will be interpreted as goal directed (e.g., Sommerville & Woodward, 2005). The teleological reasoning hypothesis (Csibra & Gergely, 2007) suggests that motor resonance is the result, rather than the cause, of action understanding. Specifically, the motor system is supposed to be activated by a "top-down" process in which the observed action is evaluated and reconstructed in terms of goals and sub-goals, and subsequently reproduced in the motor system through emulative processes (Csibra, 2007). Finally, within the recently revitalized ideomotor theories of cognition, it is proposed that repeated co-occurrence of an action and its effect would tie the activated motor program to the representation of the action effect, in a bidirectional association (Paulus, 2012).

Specifically, own action effect observation would allow the association between a motor code and an action effect. Subsequently, when another person performs a similar action, the perception automatically causes motor resonance as a consequence of the previously established action-effect association (Paulus, 2014). The activated effect representation modulates visual attention and facilitates the processing of corresponding information of a visual scene. Therefore, the role attributed to action mirroring in this model is only that of facilitating the processing of an action visual scene. A full understanding of an action requires higher level cognitive abilities, such as the processing of intentions as well as the social implications of the action (Paulus, 2012).

1.6 Emotion mirroring and the understanding of others' emotions

"*A bright and sparkling eye is as characteristic of a pleased or amused state of mind, as is the retraction of the corners of the mouth and upper lip with the wrinkles thus produced*". Already in 1872, Darwin made a link between emotions and motor activity, observing movements of specific facial muscles during expressions of emotions. In the last decades, researchers found out that our facial muscles are also active during the observation of emotions expressed by others (e.g., Dimberg & Thunberg, 1998). It is widely acknowledged that human beings are talented at imitating both voluntarily and spontaneously other people's behaviours, such as gestures or body postures (e.g., Chartrand & Bargh, 1999), tone of voice or pronunciation patterns (e.g., Neumann & Strack, 2000), and even breathing rates (e.g., McFarland, 2001).

Indeed, social psychological studies demonstrate that simple observation of others' behaviour tends to increase the likelihood of engaging in that specific behaviour (Bargh et al., 1996). This phenomenon, also known as *chameleon effect*, refers to the unconscious tendency to mimic specific behaviours of one's interaction partners (Dimberg, 1982). One of the most studied examples of unconscious imitative behaviour is linked to the observation of emotional expressions. This imitative behaviour, which takes the name of *facial mimicry*, refers to the muscular reactions, measurable using electromyography (EMG), and expressions of the observer generated by others' behaviours (Bourgeois & Hess, 2008).

One major question within this research field concerns how do we understand the emotional experiences of others and what is the exact role of the motor system in this process. In the previous paragraph, the existing debate about cognitive mechanisms underlying the development of action understanding abilities and the possible involvement of the motor system during observation of others' actions has been addressed. In what follows the debate about proposed models on the mental processing of emotional information and the role of the motor system in this process will be outlined.

In general, two main theories concerning the origination and underlying processes of emotion understanding have been put forward, both presuming a link between motor activation and the corresponding emotional state. The *embodied account* or mirroring route to emotion understanding posits the existence of a direct motor matching mechanism. The core idea of this account is that the observer selects a mental state for attribution and understands others' emotions after reproducing or re-enacting within himself the observed emotional state (Goldman & Sripada, 2005). When observing the emotional expressions of another person the contractions of the muscles involved in the expression are directly mapped and reproduced in the cortical motor centres of the observer leading to an internal simulation of the emotional expression and thereby to understanding of the corresponding emotions (Bastiaansen, Thioux & Keysers, 2009).

As some authors state, the motor matching mechanism could involve the MNS, which directly simulates the observed events. Indeed, relevant to the proposed role of the MNS in social cognition is evidence suggesting that, together with activation of the anterior insula and amygdala, the MNS might be involved in decoding the emotional states of others (Leslie et al., 2004). According to this perspective, the internal simulation of others' emotions is also thought to support our ability to empathize with others (Pfeifer, Iacoboni, Mazziotta & Dapretto, 2008). Along these lines, it has been suggested that infants have access to others' emotional states from very early in life via perceiving other persons' facial expressions. Moreover, findings related to infants' ability to produce edonic facial expressions, such as sadness and disgust (Tronick, 1989), together with perceptual discrimination of discrete facial expressions of emotion (Izard, 1982), suggest that subcomponents of full emotional expressions are present shortly after birth. Thus, infants engage with other people and with feelings expressed through both their own and others' bodies and faces. Some data suggest that automatic mimicry between self and others, which might provide information about the other's emotional state, might constitute the mechanism subserving emotion sharing between infant and caretakers which is present from the earliest months of life (Decety & Meyer, 2008).

The *emotional theory* or reconstructive route of emotion understanding is based on the assumption that facial mimicry is not the result of direct motor matching mechanisms. Instead, it is the outcome of an affective reaction and it is induced by an emotional state of the observer (Tamietto et al., 2009). According to this model, when a person is observed displaying a particular emotional expression, the observer utilizes perceptual information, coupled with factual reasoning capacities, to infer and attribute an emotional state to the observed person. Observing others' emotional expressions leads firstly to a cognitive evaluation and recognition of those emotions, occurring through integration of motivational, social, emotional, and personality factors, together with previously acquired information about observed expressions and their contexts, which than leads to activation of the brain motor structures. This view presupposes that the change in the affective state and the corresponding motor program put in place will not necessarily be congruent with the observed emotional expression, but more truly with the emotional interpretation of the observer (Hess & Blairy, 2001).

1.7 Conclusions

In the context of the hypotheses put forward by the neuroconstructivist account, it is important to explore whether domain-general principles like perceptual narrowing, experience-expectant processes and constraints on development, also apply to the perception and understanding of actions and emotions in the first years of life. For example, it is crucial to investigate whether processing action sounds goes through a process of perceptual narrowing and to test the hypothesis that exposure to human actions in the first months after birth leads to a perceptual narrowing for processing the related auditory information. The study presented in Chapter 2 was aimed to explore infants' ability to differentially process human action sounds from other sound categories will be presented. Seven-months-old infants were presented with randomly presented human action, human vocalization, environmental and mechanical sounds while their electrical brain activation was recorded using event-related potentials (ERPs). The purpose of this study is to lay the foundations for testing in the future the existence of an attunement mechanism towards the most experienced human actions sounds, as compared to other sound categories, occurring in the first year of life.

Additionally, the studies presented in the next chapters will also allow to deepen the existing debate between the aforementioned bottom-up and top-down perspectives about the cognitive mechanisms underlying action understanding and how the motor system is activated during others' action observation. Specifically, in a series of experiments comprised in Chapter 3, 14-month-old infants' somatotopic organization of mu rhythm desynchronization over the sensorimotor cortex will be recorded using EEG while observing a novel or a familiar action, after taking part in a training with different effectors. The aim of these experiments will be to assess how the observer's motor system is involved during action observation. Under a bottom-up view (Rizzolatti & Sinigaglia, 2010), it is predicted that the motor system will replicate the means used by the observed agent to arrive at a likely outcome (i.e., imitative mechanism), while under the top-down alternative (Csibra, 2007) a likely outcome will be first hypothesized and the motor system will internally simulate the end-state of the observed action that might be achieved by using one’s own means, not necessarily identical with those used in the observed action (i.e., emulative mechanism). Chapter 4 will be devoted to investigate the existence of attentional bias in processing facial expressions of emotions, by exploring the neural correlates of 7-month-old infants capability to process static and dynamic facial expressions of emotions. Finally, Chapter 5 will be dedicated to understanding the mechanisms underlying covert facial muscle reactions, as measured by means of surface electromyography (sEMG), elicited by the observation of emotional expressions in 3-years-old children. Finally, in Chapter 6, based on obtained results and on the previously stated hypotheses on action mirroring (i.e., narrowing, experience-expectant processes and constraints on development), an integrative model will be presented that combines the apparently competing approaches on action and emotion understanding within a Neuroconstructivist developmental perspective.

CHAPTER 2

THE EARLY PROCESSING OF HUMAN ACTION SOUNDS: AN ERP INVESTIGATION IN 7-MONTH-OLD INFANTS[2]

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[2] Results presented in this chapter have been previously published in Geangu, E., Quadrelli, E., Lewis, J. W., Cassia, V. M., & Turati, C. (2015): By the sound of it. An ERP investigation of human action sound processing in 7-month-old infants. *Developmental Cognitive Neuroscience*, 12, 134-144. doi:10.1016/j.dcn.2015.01.005

ABSTRACT

The MNS is often referred to as a trimodal system responding to motor, visual and auditory stimulations. However, most studies focus on the visual modality only, setting aside the auditory component of action coding. Only recently, evidence emerged to suggest that human adults perceive human action sounds as a distinct sound category, activating specific neural networks. Despite this new wave of evidence on adults, knowledge about the developmental process leading to such a specialization is limited. The study presented in this chapter investigates, using ERPs, the neural correlates of 7-month-olds' processing of human action sounds as compared to human vocalizations, environmental, and mechanical sounds. Results comparing human action sounds to the other categories revealed that the former produced a larger positive slow wave at left anterior temporal locations. Additionally, the comparison between human vocalizations and the other categories showed that the former generated increased negative amplitude at posterior temporal locations in both hemispheres. Moreover, human produced sounds revealed a different response profile as compared to non-human sounds at parietal and frontal locations in both hemispheres. The current study suggests that 7-month-olds process human action sounds as a distinct auditory category and provides novel evidence regarding the typical categorical processing of socially relevant sounds.

2.1 Introduction

Perception-action coupling mechanisms have been almost exclusively studied in the visual modality. However, mirroring mechanisms are not only triggered by visual stimuli. Indeed, a number of recent studies have extended the concept of mirror system also to the auditory domain: many neurons in the monkey premotor cortex also respond to the sound produced by the specific action they are selective for in the motor and visual domains (e.g., Kohler et al., 2002). Moreover, other studies suggest that human adults possess an auditory mirror neuron system (e.g., Bangert et al., 2006; Lahav et al., 2007), which resembles the one found in monkeys. Premotor and parietal cortices are active while adults listen to action related non-verbal sounds (Gazzola, Aziz-Zadeh & Keysers, 2006), sounds generated by tools (Lewis et al., 2005), and action-related sentences (Tettamanti et al., 2005), with the same areas being active during execution and sight of similar actions. Despite the increasing number of studies on the subject, the mechanisms underlying a possible action-listening network is far from being fully understood in adults and even further are the mechanisms determining its development in infancy. Nonetheless, supporting the idea that mirroring mechanisms can develop even in the absence of visual cues, results comparing blind from birth and sighted participants' brain activation during the auditory presentation of hand action sounds demonstrated that areas comprised in the mirror system network are activated by visual and auditory cues in the sighted group and that the same areas are engaged by action sounds in congenitally blind individuals (Ricciardi et al., 2009).

Even without having to get to consider the clinical circumstances under which sight modality is absent, for most individuals hearing is crucial to everyday social life, allowing communication through language and providing information about the dynamics of the social agents in our close environment. Action listening is something that happens almost automatically and takes part in many of our daily activities. We can often recognize the action of another individual even if we can only hear it. Consider, for example, listening to door knocking or finger snapping. It is quite easy for a human adult to recognize these sounds, and at the same time his brain might also internally simulate the conveyed action (Aziz-Zadeh et al., 2004).

Many studies, using different techniques, explored action sound processing in adults and converge to suggest that they are selectively processed by specific cortical areas (e.g., Galati et al., 2008; Giusti, Bozzacchi, Pizzamiglio & Di Russo, 2010). However, most developmental studies explored human action perception by using visual stimuli, focusing on infants' ability to extract intention-relevant units during the observation of complex human actions or demonstrating infants' early ability to anticipate and predict the goals of observed actions presented through videos or pictures (e.g., Geangu, Senna, Croci & Turati, 2015; Saylor, Baldwin, Baird & LaBounty, 2007). On the other hand, the great majority of studies using auditory stimuli in infancy are mainly interested in the examination of the development of cerebral specialization for the human voice. As a fact, it is known that perceiving fine changes in the pitch of someone's voice can tell us whether they are disappointed or happy (Grossmann et al., 2005). Moreover there is extensive evidence that human voices are perceived as a distinct category of natural sounds (Belin et al., 2004; Fecteau et al., 2004), processed in specialized brain regions located in the superior temporal sulcus (STS) (Grossmann, Oberecker, Koch & Friederici, 2010) and that specialization for vocal processing emerges very early in infancy (Blasi et al., 2011). However, much less is known about perceiving sounds associated with human actions (Lewis et al., 2005; Lewis et al., 2006; Lewis et al., 2011). It is acknowledged that in adults the rhythm and intensity of footstep sounds provide us with information about a social agent's speed of motion and emotional state (Sievers et al., 2013). Sound onset and offset also coincide with the occurrence of visual cues for motion, supporting the efficient segmentation of others' actions in meaningful units (Thomas & Shiffrar, 2010).

Importantly, we have little to no understanding of how this ability develops in the first years of life. At birth, infants can already orient their head towards sound sources, demonstrating to be able to execute a motor program initiated by auditory inputs (Morrongiello & Clifton, 1984). This early capacity is of paramount importance for leading to the development of subsequent object identification ability in the environment (Winkler et al., 2003). The origins of these abilities can be traced back to prenatal life, since foetuses identify low frequency sounds (250–500 Hz) by 19 weeks gestational age and gradually learn to detect high frequency sounds (1000–3000 Hz) after 35 weeks (Burnham & Mattock, 2010). The early maturation of the auditory system and in-utero access to social sounds (i.e., mother's voice, native language) are probably linked to newborns' ability to discriminate speech and non-speech vocalizations. For instance, newborns strongly prefer their mother's voice compared to a stranger's voice (Moon & Fifer, 1986) and the sound rhythm specific to their native language compared to that of other natural languages (Kuhl, 2010; Nazzi et al., 1998).

More recently, neurophysiological and neuroimaging studies have shown that processing speech and also non-speech human vocalizations elicits an increased activation of a specific cerebral network (Benavides-Varela et al., 2011; Blasi et al., 2011). Using functional near-infrared spectroscopy (fNIRS), Lloyd-Fox and colleagues (2011) showed an increase in oxygenated hemoglobin in the bilateral STS regions to non-speech vocalizations (i.e., crying, laughing, yawning, coughing) compared to non-human sounds (i.e., toys rattling, water running), supporting the emergence of cerebral specialization for human voice sounds over the first 6 months of life. Interestingly, the STS area has also been associated with observation of speech-like mouth movements in infants and adults, suggesting that this region of the temporal cortex is particularly sensitive to voice-associated cues (Belin et al., 2000; Lloyd-Fox, Blasi, Everdell, Elwell & Johnson, 2011).

Although there is a general consensus that voices play a prominent role in infants' early social and cognitive development, as previously mentioned, less attention has been devoted to the investigation of whether and how other types of human-produced sounds may affect infants' understanding of their social environment.

Actions, like language, are complex streams of information that does not come pre-segmented into meaningful units. However, there is evidence that infants are able to use acoustic cues, such as tones or mother's utterances, in order to segment action streams (Brand & Tapscott, 2007). Nonetheless, in everyday life, adults move in infants' proximity doing their daily duties, and while some of this motion is associated with vocalizations, it is almost always accompanied by the sounds generated by human actions. For adults, action sounds can be sufficient to discriminate between actions performed by another individual (Keysers et al., 2003) and even have an impact on the perception of visual information about actions. For example, the presence of action sounds like footsteps, but not other synchronous sounds, increases visual sensitivity in detecting point-light displays of coherent human gait (Arrighi, Marini, & Burr, 2009; Thomas & Shiffrar, 2010). Also, gender-ambiguous point-light walkers appear more female when paired with the sounds of female footsteps (Van der Zwan et al., 2009).

Like vocalizations, action sounds selectively activates specific cortical networks in the adult brain. A number of fMRI studies (Engel et al., 2009; Lewis et al., 2011) have shown that human action sounds preferentially activate those brain areas which have been functionally linked to processing others' actions as goal directed (i.e., left inferior frontal gyrus—IFG, inferior parietal lobule—IPL, and primary motor cortex—M1), together with areas typically associated with processing of biological motion cues from different sensory modalities (i.e., bilateral posterior superior temporal sulcus—pSTS and posterior middle temporal gyrus—pMTG). Moreover, similarly to what was found in monkeys (Kohler, Keysers, Umiltà, Fogassi, Gallese & Rizzolatti, 2002), listening to action-related sounds in humans generates a somatotopic pattern of activation in the left premotor cortex (Gazzola, Aziz-Zadeh & Keysers, 2006). Using transcranial magnetic stimulation (TMS), greater motor corticospinal excitability of hand muscles was measured in participants listening to sounds associated with bimanual actions as compared to leg or control sounds (Aziz-Zadeh, Iacoboni, Zaidel, Wilson & Mazziotta, 2004). At the level of the scalp, human action sounds trigger positive ERPs at left temporal and central locations associated with the activity of STS, while non-biological sounds elicit bilateral positive ERP activity at temporo-parietal and frontal locations associated with bilateral temporal activation (Pizzamiglio et al., 2005).

Despite the relevance that human action sounds have for adults' social understanding, no study to now has investigated infants' ability to process human action sounds in the earliest stages of postnatal life. To the best of our knowledge, only one recent study demonstrated that infants' auditory perception of a rattle's sound activates the associated motor program involved in the production of that sound (i.e., hand action) and that it is capable to create an action-effect binding by using auditory information (Paulus, Hunnius, van Elk, & Bekkering, 2012). Specifically, it was proven that 9-month-old infants undergoing a training in which they learned to actively produce a rattle sound, showed a stronger suppression of the mu frequency band over central sites when subsequently presented with the rattle sound as compared to two novel sounds.

The aim of the current study is to investigate the neural correlates of infants' processing of sounds produced by human actions in comparison to human non-speech vocalizations and non-biological sounds. This study will be of fundamental importance in assessing whether human action sounds are specifically processed already in infancy, and will contribute in laying the foundation to future studies exploring the putative involvement of mirroring mechanisms in the processing of this sound category in the first years of life.

In light of earlier demonstration that 7-month-olds show auditory cerebral specialization for speech and non-speech human vocalizations (Blasi et al., 2011; Grossmann et al., 2010; Lloyd-Fox et al., 2011), we tested infants of this age using ERPs. EEG has high temporal accuracy and has been successfully used to investigate infants' processing of visual and auditory social information (de Haan, 2007 & Trainor, 2010). For example, it has been investigated the development of infants' ability to detect changes in auditory features important for processing socially relevant sounds (Kushnerenko et al., 2002). These and many other findings render ERPs a promising method for investigating whether human action sounds are processed distinctly from non-biological sounds and whether human action sounds and human non-speech vocalizations represent distinct sub-categories of human produced sounds.

Infants were presented with four sound categories: human action sounds (HA), human non-speech vocalizations with neutral emotional prosody (HV), sounds produced by automated mechanical devices (MEC), and sounds produced by nature (ENV). Matter of investigation were putative electrophysiological differences in activation between HA and other types of sounds (HV, MEC, and ENV); between human produced sounds (HA and HV) and non-human produced sounds (MEC and ENV); and between HV and the other sound categories (HA, MEC, ENV).

Based on existing evidence from adult and infant studies using similar stimuli and paradigm, we hypothesized that infants' enhanced processing of HA would reveal itself in a larger amplitude of the ERP late slow wave (LSW) component at temporal sites

(Grossmann et al., 2005; Grossmann & Johnson, 2007). In order to determine whether HA and HV are processed as instances of the global category of human produced sounds, we analysed ERP responses recorded at frontal and parietal locations. A larger LSW for both HA and HV compared to MEC and ENV sounds was expected to be recorded at frontal electrodes (Guillem et al., 2001; Quinn et al., 2006), while an increased negativity in ERP responses to human (HA, HV) compared to non-human action sounds (MEC, ENV) was expected at parietal locations (Hirai & Hiraki, 2005; Marshall & Shipley, 2009). Finally, although no previous study investigated infant ERP responses to neutral non-speech human vocalizations compared to non-vocalization sounds, extant evidence on infant ERP correlates of voice processing suggests specific activation at fronto-central and temporal locations within both hemispheres (Cheng et al., 2012; Grossmann et al., 2005).

2.2 Methods

2.2.1 Participants

Fifteen 7-month-old infants (6 females, M = 214 days, SD = 8 days) were included in the final analyses. All infants were born full-term (37–42 weeks gestation), had a normal birth weight (>2500 g), did not suffer of any neurological or other medical conditions, and were observed to have normal vision for their age. Eight additional infants were tested but not included in the final sample due to fussiness (n = 3), excessive artifacts (n = 4), or technical problems with data collection (n = 1). The procedure followed the ethical standards (the Declaration of Helsinki, BMJ 1991; 302:1194) and was approved by the University ethical committee. Parents gave written informed consent for their infants' participation.

2.2.2 Stimuli

Participants were presented with audio recordings of HA (i.e., footsteps, clapping, zippering), HV (i.e., yawning, sighing, coughing) depicting relatively non-communicative and emotionally neutral vocal expressions, ENV (i.e., wind, rain, water flowing), and MEC (i.e., engine start, micro-wave oven, washing machine) sounds. Each category included 9 different exemplars. The auditory stimuli were extracted from or modified based upon an existing database of category specific sounds (Engel et al., 2009). They were screened by 6 adult listeners and edited to 1000 ms duration. All of the sound stimuli were assessed for various “bottom-up” spectro-temporal signal attributes that may correlate with their “top-down” conceptual boundaries or anticipated ERP response differences. Sounds were initially balanced psychophysically for perceived overall loudness. The intensity of the sounds was then assessed quantitatively for total Root Mean Square (RMS) power using Adobe Audition 3 (Adobe Systems Inc.) and balanced to roughly –28 dB RMS power across all four categories. A pitch analysis was performed for each sound based on an autocorrelation method using Praat software (http://www.fon.hum.uva.nl/praat/), with standard default settings (75 Hz pitch floor and 600 Hz ceiling). Using methods described earlier (Lewis et al., 2005; Lewis et al., 2009; Lewis et al., 2012), we derived a Harmonics-to-Noise Ratio (HNR) mean value, a measure of spectro-temporal dynamics based on entropy (Wiener entropy) in the acoustic signal (Tchernichovski et al., 2001), plus a measure of spectral structure variance (SSV) of the sounds. The SSV is a measure of changes in signal entropy over time that has been shown to have utility in categorizing natural sound signals (Reddy et al., 2009).

2.2.3 Procedure

ERPs were recorded while infants sat on their parent's lap at a distance of approximately 60 cm from a 24-inch monitor in a dimly lit, audiometric and electrically shielded cabin. The auditory stimuli were randomly presented using E-Prime software v2.0 (Psychology Software Tools Inc., Pittsburgh, PA) over two speakers placed to the left and right of the monitor. No more than two sounds from the same category were presented consecutively. A trial consisted of 1000-ms stimulus presentation followed by a silent interstimulus which varied randomly in duration between 900 and 1100 ms. A black fixation cross on a grey background was displayed on the monitor during the entire stimulus presentation. The procedure continued until maximum 288 trials were presented (72/category) or until the infant became bored. In order to minimize infants' movements and maintain their interest, an experimenter was present to quietly blow soap bubbles throughout the entire procedure. Both the parent and the experimenter avoided visual contact and any attempt for social interaction with the participant. Stimulus presentation lasted approximately 12 min.

2.2.4 EEG acquisition and pre-processing

EEG was recorded continuously using a 128-electrode HydroCel Geodesic Sensor Net (Electrical Geodesic Inc., Eugene, OR) and amplified using an EGI NetAmps 300 amplifier. The signal was referenced online to the vertex electrode (Cz), a bandpass filter of .1–100 Hz was applied, and the data were sampled at 500 Hz. Impedances were checked prior to the beginning of recording and considered acceptable if lower than 50 kΩ. EEG data were further processed offline using NetStation v4.6.4 (Eugene, OR). The signal was band-pass filtered (0.3–30 Hz), and the ERP trials were segmented with a 100 ms baseline and 1000 ms following stimulus onset. Data were corrected to the average voltage during baseline and re-referenced to the algebraic mean of all channels. To eliminate artifacts, segmented data were automatically rejected whenever the signal exceeded ± 200 µV at any electrode. Data were further checked through visual inspection for eye-movements, eye-blinks and other body movement artifacts not detected by the automated algorithm. Trials were excluded if more than eighteen bad channels were detected. Of the remaining trials, individual bad channels were replaced using spherical spline interpolation. Individual subject averages were computed separately for each channel across all trials within each condition and then re-referenced to the average reference. Across participants, the mean number of trials contributing to the average ERP was 34.35 (HA: 35, SD = 11.5; HV: 34.6, SD = 10.8; ENV: 34, SD = 11.1; MEC: 33.8, SD = 10.2). A similar number of trials contributed to the final analysis for each condition, F(3,42) = .203 p > .80. Because this was the first study investigating infant electrophysiological response to human action sounds and emotionally neutral non-verbal vocalization using random stimulus presentation, we were unable to formulate predictions regarding the specific timing and polarity of all ERP components. Accordingly, like in other infant ERP studies (e.g., Quinn et al., 2006), our analyses were based on visual inspection of the waveforms, which revealed several time windows and scalp regions of interest (ROI). In line with previous studies (Grossmann et al., 2005), a difference in the amplitude of the late slow wave (LSW) was observed between 300 and 800 ms from stimulus onset at anterior temporal locations, giving rise to an anterior positive slow wave—PSW (Figure 1), and a difference in the amplitude of the NSW was observed at posterior temporal ROI between 470 and 570 ms (Figure 3). A positive component (Pc) was observed in the frontal ROI, with maximum amplitude between 300 and 500 ms as previously described (Friederici et al., 2007; Parise et al., 2010). A PSW with maximum differentiation between conditions within 550 and 750 ms from stimulus onset was evident at the frontal ROI (Figure 2) and within 550–730 ms at the central ROI. Similar to previous studies on biological motion (Hirai & Hiraki, 2005; Marshall & Shipley, 2009), a NSW was observed at parietal ROI (550–650 ms), which differentiated between human and non-human produced sounds (Figure 2). All ERP components included in the analysis were analyzed as average amplitudes, averaging all datapoints within the given time window. The same procedure was also used for the Pc component. Due to the fact that at least one condition did not show a clear peak voltage, the average amplitude for the entire window rather than the peak voltage was included in the analysis.

ERP mean amplitudes within each region of interest were analysed using 4 (category: HA, HV, ENV, MEC) by 2 (hemisphere: left and right) repeated measures ANOVAs. All statistical tests were conducted at .05 level of significance (two-tailed), and paired-sample t-tests were corrected for multiple comparisons using the Holm-Bonferroni stepwise procedure.

2.3 Results

2.3.1 Human actions vs. other sound categories

Anterior temporal electrodes

Anterior temporal electrodes recorded a PSW occurring within a 300–800 ms window, suggesting a differentiation between the HA sounds and the other types of sounds. A 4 × 2 repeated measures ANOVA on the mean amplitude of this PSW showed a significant effect of condition, $F(3,42) = 4.650$, $p = .022$, $\eta^2 = .248$, which was qualified by a significant Condition × Hemisphere interaction, $F(3,42) = 4.979$, $p = .001$, $\eta^2 = .248$. Post-hoc pairwise comparisons showed that at left temporal locations HA sounds elicited increased mean positive amplitude (M = 3.563 µV, SD = 3.735) compared to HV (M = −2.626 µV, SD = 5.766), t(14) = 5.805, p < .001, MEC (M = −3.459 µV, SD = 3.998), t(14) = 5.573, p < .001, and ENV (M = −3.370 µV, SD = 3.749), t(14) = 5.805, p < .001, sounds (Figure 1). HA also elicited a higher amplitude of the PSW in the left (M = 3.564 µV, SD = 3.735) compared to the right (M = −.689 µV, SD = 3.249) hemisphere, t(14) = 3.336, p = .035. All other differences were not significant (p > .258).

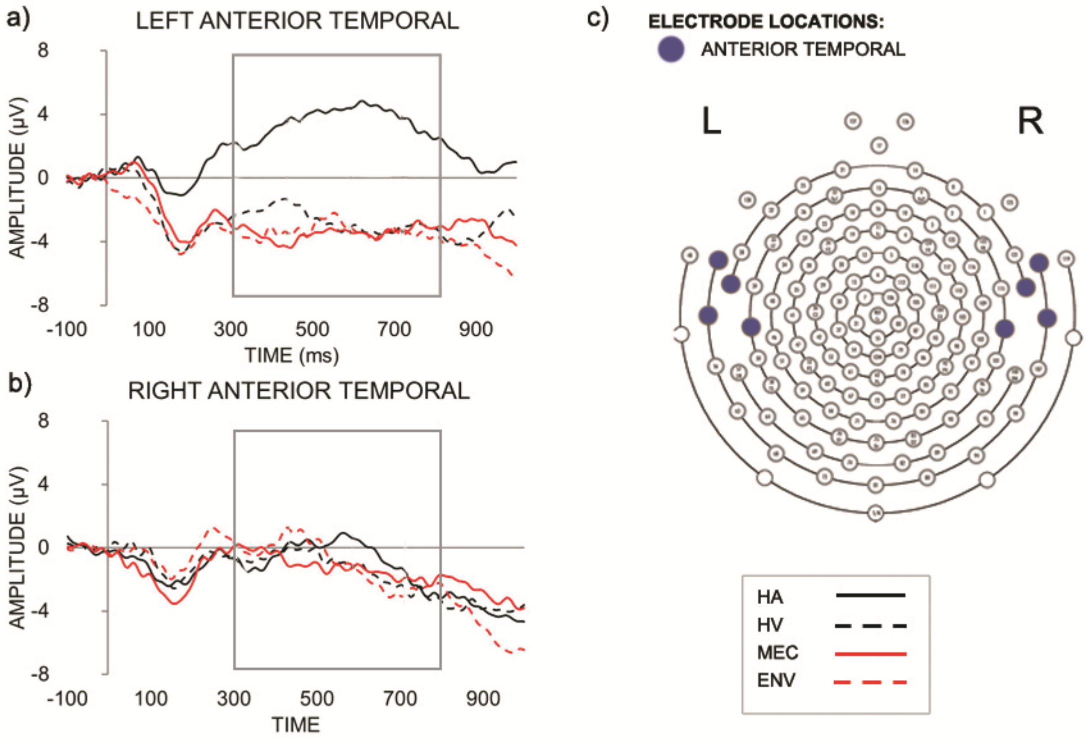

Figure 1. Waveform plots depicting grand-average ERPs in response to HA (solid black line), HV (dash black line), MEC (solid red line), ENV (dash red line) over the right (A) and left (B) anterior temporal areas. C) Electrode groupings for the anterior temporal areas consisting of channels 108 (T4), 113, 114, 120 on the right and 45 (T3), 43, 44, 49 on the left. Please note that the positive is plotted upwards.

2.3.2 Human produced vs. non-human produced sounds

The average amplitudes recorded at both parietal and frontal electrodes within different time windows suggested a differentiation between human (HA, HV) and non-human (MEC, ENV) produced sounds.

Parietal electrodes

A 4 × 2 repeated measures ANOVA on mean amplitude of the NSW recorded within the 550–650 ms window in the parietal ROI showed a significant effect of condition, $F(3,42) = 3.402$, $p = .026$, $\eta^2 = .196$. Pairwise comparisons suggested that HA sounds elicited bilaterally a larger negativity (M = –3.068 µV, SD = .971) compared to MEC (M = .158 µV, SD = 1.091, p = .032) and ENV (M = –.970 µV, SD = .746, p = .035) sounds but not to HV sounds (M = –1.795 µV, SD = 1.099, p = .232) (Figure 2). All other comparisons were non-significant (p > .09).

Frontal electrodes

The 4 × 2 repeated measures ANOVA on average amplitude of the frontal Pc (300–500 ms) revealed a main effect of condition, $F(1,42) = 4.059$, $p = .013$, $\eta^2 = .225$. Pairwise comparisons revealed that HV elicit a significantly higher amplitude (M = 5.271 µV, SD = .873) compared to MEC sounds (M = 2.433 µV, SD = .782), p = .025. However, the condition main effect was qualified by a significant Condition × Hemisphere interaction, $F(1,42) = 3.396$, $p = .026$, $\eta^2 = .195$. In order to disentangle this interaction, post-hoc paired t-tests were performed, with the significance threshold corrected for multiple comparisons: HA sounds elicited a larger Pc amplitude on the left (M = 6.126 µV, SD = 4.962) compared to the right (M = 1.93 µV, SD = 2.832) hemisphere, $t(14) = 3.517$, $p = .048$. Although HA and HV tended to elicit a larger Pc on the left hemisphere compared to the ENV and MEC sounds, these differences did not reach the corrected significance threshold (p > .09). No other post-hoc comparisons were significant. A 4 × 2 repeated measures ANOVA on the average amplitude of the frontal PSW (550–750 ms) showed a significant effect of condition, $F(3,42) = 5.788$, $p = .001$, $\eta^2 = .327$. Pairwise comparisons revealed that HA sounds elicited bilaterally a larger Pc amplitude (M = 4.475 µV, SD =

.930) compared to MEC (M = .501 µV, SD = 1.167, p = .005) and ENV (M = –.685 µV, SD = 1.042, p = .001) sounds but not to HV (M = 4.475 µV, SD = .930, p = .071) sounds. HV also seemed to trigger a Pc of larger amplitude (M = 2.310 µV, SD = 1.172) compared to MEC sounds (M = –.970 µV, SD = .746, p = .055), but this fell short of significance. All other comparisons were non-significant (p > .118) (Figure 2).

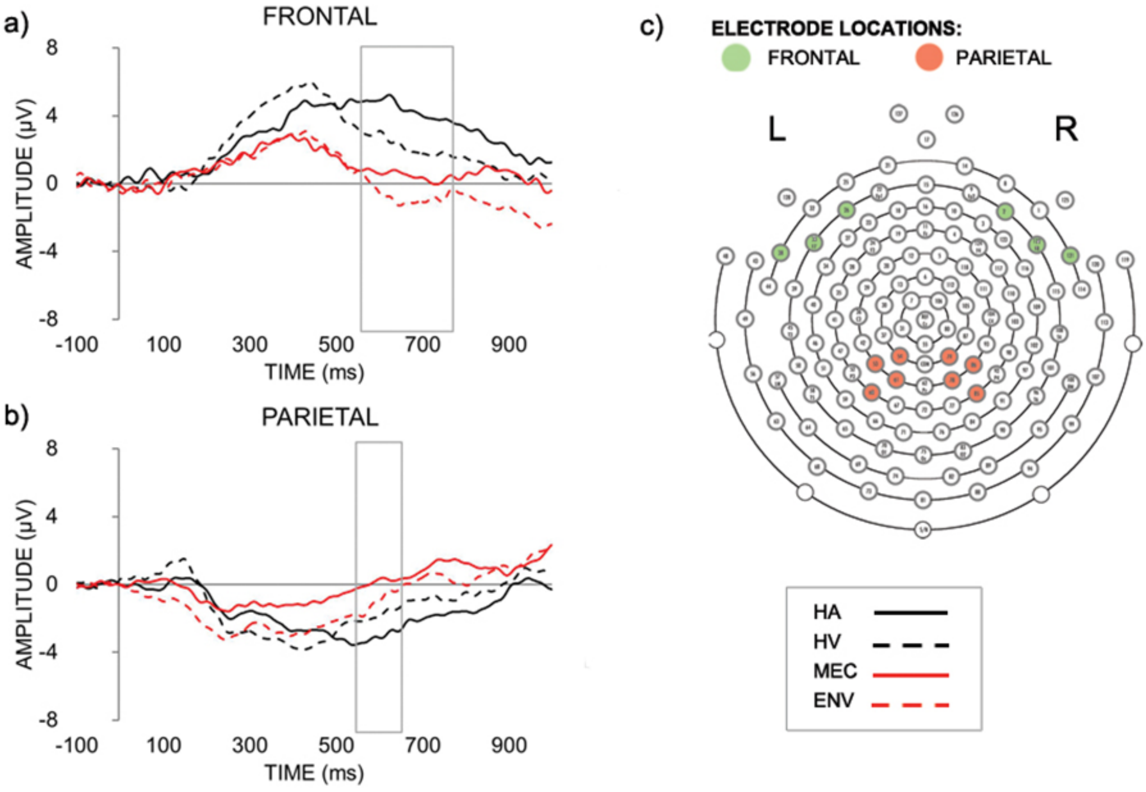

Figura 2. Waveform plots depicting grand-average ERPs in response to HA (solid black line), HV (dash black line), MEC (solid red line), ENV (dash red line) over the frontal (A) and parietal (B) areas. C) Electrode groupings for the frontal area (green) consisting of channels 26, 33 (F7), 38, 2, 121, 122 (F8) and for the parietal area (red) consisting of channels 53, 54, 60, 61, 78, 79, 85, 86. Please note that the positive is plotted upwards.

2.3.3 Human vocalizations vs. other sound categories

A differentiation between human vocalization (HV) and the other types of sounds was suggested by the average amplitudes recorded at parietal and central electrodes within different time windows.

Posterior temporal electrodes

A 4 × 2 repeated measures ANOVA on the NSW mean amplitude (470–570 ms) recorded at posterior temporal locations showed significant main effects of condition, F(3,42) = 5.221, p = .004, η^2 = .272, and hemisphere, F(3,42) = 6.834, p = .020, η^2 = .328. Post-hoc pairwise comparisons showed that the negative component was larger in the left (M = –2.461, SD = 1.011) compared to the right (M = –.610 µV, SD = .551) hemisphere (p = .020). Moreover, on average, the amplitude of the component across the two hemispheres was larger for HV (M = –3.764 µV, SD = 1.014) compared to HA (M = –.878 µV, SD = .952, p = .016), MEC (M = –.837 µV, SD = .814, p = .001), and ENV (M = –.663 µV, SD = .908, p = .004) sounds (Figure 3). All other comparisons were non-significant (p > .828).

Central electrodes

The ANOVA on the average amplitude of the PSW (550–730 ms) recorded at central locations revealed a main effect of condition, F(3, 42) = 3.428, p = .026, η^2 = .197. On average, infants showed a bilateral increased positivity for HV (M = 6.705 µV, SD = .804) compared to HA (M = 4.016 µV, SD = .783, p = .006), MEC (M = 4.523 µV, SD = .682, p = .029), and ENV (M = 4.043 µV, SD = 1.297, p = .026) sounds (Figure 3). All other comparisons were non-significant (p > .490).

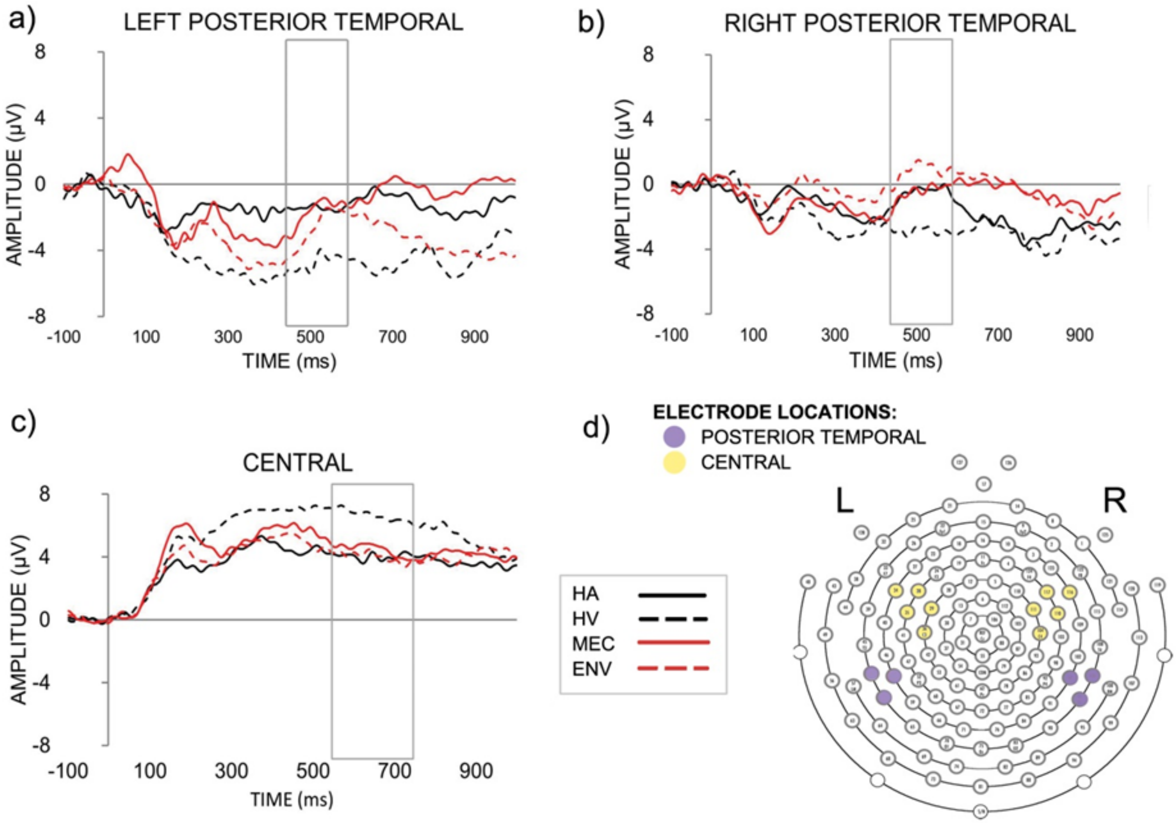

Figure 3. Waveform plots depicting grand-average ERPs in response to HA (solid black line), HV (dash black line), MEC (solid red line), ENV (dash red line) over the right (A) and left (B) posterior temporal areas and over the central area (C). D) Electrode groupings for the central area (yellow) consisting of channels 28, 29, 34, 35, 36 (C3), 111, 117, 104 (C4), 110, 116 and for the posterior temporal area (violet) consisting of channels 96 (T6), 97, 101 on the right and 50, 51, 58 (T5) on the left. Please note that the positive is plotted upwards.

2.4 Discussion

The aim of the present study was to explore whether human action sounds are processed distinctly from other social and non-social sounds that infants typically encounter in their natural environment, and whether action sounds and non-speech vocalizations represent distinct sub-categories of human produced sounds. In order to do so, 7-month-old infants' electrophysiological responses elicited by living (i.e., HA & HV) versus non-living (ENV & MEC) categories of sounds were compared. Results speak in favour of an early sensitivity to human action sounds, as demonstrated by the specific ERP modulation identified at anterior left temporal electrode sites. Also, human vocalizations generated a specific activation at posterior temporal scalp locations across both hemispheres, which was absent for human action sounds, thus suggesting that human action sounds and human vocalizations are differentially processed in the brain at a certain level. Moreover, the undifferentiated activation elicited by the two subcategories of human sounds at frontal and parietal scalp locations indicate that they might be treated as exemplars of a broader category of human produced sounds.

Human action sounds produced greater activation at anterior left temporal locations compared to the other sound categories. The LSW amplitude is considered to reflect more diffuse activation of neural systems and to be related to an enhancement in sensory processing (de Haan & Nelson, 1997; Grossmann et al., 2005), thus suggesting that human action sounds elicit a heightened sensorial processing in comparison to other sound categories at 7-months of age. Brain activation recorded at temporal locations have also been found to be sensitive to adult processing of human action sounds and to be linked to the STS and the premotor cortex activation (Pizzamiglio et al., 2005).

Interestingly, these brain areas are part of the network specialized for processing auditory information related to human actions (Engel et al., 2009; Lewis et al., 2011). Although the technique used to record infants' brain activity does not have high spatial resolution, and does not provide evidence for the neural network underlying the anterior temporal PSW, our results uphold a specific perceptual processing of human action sounds at 7-months of age. In fact, it is important to note that results obtained for this sound category over the anterior temporal sites did not extend to human vocalizations, which, instead, induced a selective modulation at posterior temporal scalp locations. It is well established that auditory perception might be better and predominate over vision in specific circumstances (Shams et al., 2000).

Given that each animal or human action produces a characteristic sound that may permit its unequivocal recognition, the importance of the hearing sense is striking from both an evolutionary and an ontogenetic perspective. Particularly in ancient times when it was pitch dark at night, the detection of potential danger (e.g., the footsteps of enemies) and the consequential implementation of fight-or-flight behaviour mainly relied on audition. Nowadays, hearing the footsteps of an individual may provide precise (e.g., specific identity) as well as general (e.g., sex or mood) information about an individual. Similarly, hearing hands clapping may allow an individual to draw several inferences about a given event.

For what concerns human vocalizations, our results parallel previous evidence by showing larger NSW amplitude across both hemispheres in response to emotionally neutral non-speech vocalizations compared to non-voice sounds. Indeed, they suggest that 7-month-old infants manifest increased sensory processing of emotionally neutral non-speech vocalizations compared to non-voice sounds, which could potentially rely on a voice specific brain network. While it is not possible to provide an incontrovertible interpretation of the cortical sources of the effects observed in our study, it is possible that the differences in polarity and scalp location between non-speech vocalizations and speech associated with emotional prosody are due to differences in the subserving areas involved in processing these types of stimuli. Indeed, imaging methods providing higher spatial resolution (Blasi et al., 2011; Grossmann et al., 2010) have shown that emotional voice stimuli modulate the activation of several brain areas in addition to the temporal cortex (e.g., insula, orbitofrontal cortex and inferior frontal cortex).

Although human actions and human non-speech vocalizations in the current study elicited distinct patterns of temporal ERP responses, results show that the two sound categories also tend to overlap over the frontal and parietal electrode sites. This is possibly due to the fact that they share important features related to the biological source of the sounds.

Human action sounds were found to elicit a larger NSW bilaterally at parietal scalp locations compared to the non-living sounds, suggesting that in order to process the auditory information associated with human actions, infants use mechanisms involved in the wider processing of information about biological agents. In general, this is consistent with human lesion and neuropsychological studies showing that semantic knowledge relating to different categories of objects, including the distinction between “living” and “non-living things” (Hillis & Caramazza, 1991; Silveri et al., 1997; Warrington & Shallice, 1984), is represented along partially segregated systems in the brain (Grossmann et al., 2002; Glushko et al., 2008; Moore & Price, 1999). The parietal NSW has been shown to manifest sensitivity to visual information about biological human motion in 5- and 8-month-old infants, and adults (Hirai et al., 2003; Hirai & Hiraki, 2005; Marshall & Shipley, 2009). Similar to the infant ERP responses to point light displays depicting different types of canonical human motion (Marshall & Shipley, 2009), in our study, the auditory features of different human actions elicited an extended NSW, distributed across small clusters of parietal electrodes in both hemispheres. This pattern of responses might reflect the extensive processing required by the presentation of multiple exemplars of human action sounds (Hirai & Hiraki, 2005; Marshall & Shipley, 2009).

Moreover, we recorded greater amplitude of the frontal PSW in response to human action compared to non-living sounds for both hemispheres. Frontal PSW is acknowledged to be a neural correlate of global-level category formation in 6-month-old infants (Quinn et al., 2006). It has also been associated in adults with the integration of stimuli features into distinctive representations, updating these representations with newly acquired information, and its subsequent retrieval (Guillem et al., 2001; Kusak et al., 2000; Wilding et al., 1995). Thus, the effects we observed might reflect the processing and integration of human action sound features into distinctive representations, which may relate to a mechanism toward attaining a sense of meaningfulness to the listener. Compared to non-human sounds, the auditory information related to human actions comprises many correlated features, which are in part highly salient to the infant (e.g., features related to animacy, meaningful action events, associated visual information) (Rakison, 2010; Rakison & Poulin-Dubois, 2001). Integrating all these characteristics across multiple exemplars into a coherent representation, as well as updating previous representations with the information provided by new exemplars, could lead to the larger frontal PSW. The results concerning human non-speech vocalizations supported only partially this interpretation. Although human vocalizations elicited a frontal PSW similar to that elicited by other human-produced sounds, it was only marginally different from that recorded for non-human sounds. Future studies, which specifically manipulate the degree of familiarity for human produced sounds, are needed in order to disentangle whether auditory stimuli elicited increased allocation of attention due to their novelty or social saliency (de Haan & Nelson, 1997; Quinn et al., 2006; Kooijman et al., 2005).

The present study provides the first evidence that category-specific conceptual processing observed in adults may already be present at an emerging state already at 7-months of age. The sound stimuli we used were carefully matched for acoustic features, therefore psychophysical properties cannot account for the obtained results. Nevertheless, it will be particularly interesting for future research to show which, if any, of these properties may be driving the responses to biological events, thereby revealing fundamental organizational principles during neurodevelopment.

Auditory cues about action and motion are critical for our ability to detect others in our environment and to understand the meaning of their actions (Thomas & Shiffrar, 2010). In adults, an extended brain network has been functionally linked to the processing of auditory information about human actions, which partially overlaps with the one associated with processing related visual information (Calvert et al., 2000; Engel et al., 2009; Kable et al., 2005; Lewis et al., 2011). Moreover, evidence exists in adults supporting the notion of a link between action audition and execution, specifically involving fronto-parieto-temporal networks that are considered part of the MNS (Aglioti & Pazzaglia, 2010). Our study contributes to this line of research by providing the first evidence for a specific pattern of electrophysiological brain responses to human action sounds in 7-month-old infants. These responses might reflect the activity of an extended brain network that specializes for processing information related to human actions. The increased tuning of a particular cortical network for processing specific social information might be reflected in an increasingly selective neural and behavioural response pattern. Specifically, at an early stage of development, a certain behavioural response or pattern of brain activation can be unselectively recorded in response to closely related stimuli. However, during development it is expected that these responses become more fine-tuned to specific social stimuli (de Haan et al., 2002; Johnson, 2010).

Current results converge with a large body of literature showing significant developments in the ability to process action-related information after the age of 6-months (e.g., Daum et al., 2008; Woodward, 2013), as well as increasing cortical specialization for processing different types of social information around the same age (e.g., Blasi et al., 2011; de Haan et al., 2003; Pascalis et al., 2002). Seven-month-old infants seem to have already reached a level of development that allows them to discriminate between HA sounds compared to other human and non-human sounds, however the ontogeny of such ability is still to be defined. Specifically, at which age selective neural and behavioural responses to HA sounds compared to other human and non-human sounds can be first observed and whether any developmental change occurs beyond the age of 7-months are important questions that still need to be addressed. Precisely, it will be particularly interesting to investigate whether the observed anterior temporal dissociation between HA sounds and the other sound categories is present even at an earlier age and whether the parietal and frontal differentiation between 'living' versus 'non-living' sounds becomes more strong and distinct in older infants. Likewise, it will be important to test the hypothesis that early exposure to human actions in the first months after birth leads to a perceptual narrowing towards the most experienced auditory information.

In order to test the hypothesis put forward by the aforementioned neuroconstructivist model that the neural correlates of action sound processing tune to own species sounds, future studies might explore whether older infants maintain the ability to discriminate between sounds associated with actions produced by humans as compared to non-human agents (i.e., animals) and non-action sounds. Of particular importance would also be to verify whether the pattern of ERP responses we report is restricted to human action sounds. A large body of literature shows that processing social stimuli like faces and voices goes through a process of perceptual narrowing (see Maurer & Werker, 2014 for a review). Thus, it will be important to investigate whether processing action sounds is specific to human actions. All these potential lines of work will provide both confirmation of our current results and new knowledge. Moreover, future research should aim at understanding the role of human action sounds in the development of infants' abilities to understand others' actions.

In this sense, it will be interesting to establish whether infants' premotor cortex, as part of the human action sounds processing network, is responsive to human action sounds. A growing number of studies report a somatotopic distribution of mu desynchronization recorded in infants in response to visually observing actions performed using different effectors (e.g., feet and hands) (de Klerk, Johnson & Southgate, 2015; Saby, Meltzoff & Marshall, 2013). Future studies should test the hypothesis that human action sounds elicit in infants a similar somatotopic mu desynchronization, for example presenting infants with HA sounds generated by hands (i.e., clapping) and feet (i.e., walking) and performing time-frequency analysis to reveal whether the mu frequency records selective suppression in response to HA compared to non-human sounds.

CHAPTER 3

YOUR WAY OR MY WAY? EMULATIVE MOTOR ACTIVATION DURING ACTION OBSERVATION IN 14-MONTH-OLDS[3]

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[3] This study was carried out under the supervision of Dr. Victoria Southgate at the Centre for Brain and Cognitive Development (CBCD), Birkbeck College, University of London. Data collection and analysis were conducted in collaboration with Katarina Begus, PhD candidate at CBCD. A manuscript based on the results reported in this chapter is in preparation. Quadrelli, E., Begus, K., & Southgate, V. (in preparation). Action prediction in infancy is supported by motor emulation.

ABSTRACT

Much evidence is consistent with the idea that an observer's own motor system plays a role in the prediction of others' actions. Under one view, the role of the motor system in action observation is to emulate a way in which a goal will be achieved. This hypothesis was tested by providing 14-month-old infants with different means (i.e., foot or mouth) of achieving the same novel end, after which they observed an agent using a different means, which was outside or within infants' capabilities, to achieve the same outcome. The known somatotopic pattern of mu rhythm desynchronization was used to investigate whether, when infants observed an experimenter interacting with the object, they exhibited motor activation that matched the effector with which they had been trained. A somatotopic mu rhythm desynchronization was observed related to the effector used by the infant to achieve the goal during training, rather than to the effector used by the actor during testing. Differently, infants undergoing a passive observational training generated a prediction about the agent's action by using imitative mechanisms. Taken together, these findings support the hypothesis that the observer's motor system plays an emulative role in action prediction and that infants' emulative motor activation is linked to active experience with the action.

3.1 Introduction

Action prediction is a fundamental component of our interactions with the world, including interactions with other people. For example, when we view someone else reach for an object, we anticipate what is going to happen by moving our gaze to the object before the arrival of the other person’s hand. Therefore, making quick and accurate predictions about how others will act is arguably one of the greatest challenges faced by any social species. While it has been known for many years that an observer’s own motor system is recruited when they observe others’ actions, there is now considerable data to suggest that observation-induced motor activity plays a crucial role in action prediction. For example, both adults and infants recruit their motor systems predictively when the context allows them to generate action predictions (Kilner, Vargas, Duval, Blakemore & Sirigu, 2004; Southgate et al., 2009; Southgate & Begus, 2013; Southgate & Vernetti, 2014; Natale et al., 2014; Turati et al., 2013).

Perhaps the most compelling demonstration of the causal involvement of the motor system in action prediction comes from studies investigating the effects of repetitive transcranial magnetic stimulation (rTMS), or concurrent motor load, on participants' ability to generate action predictions. For example, Cardellicchio, Sinigaglia & Costantini (2012) and Stadler and colleagues (2012) showed that rTMS over premotor cortex impairs participants’ action predictions. Furthermore, Stadler and colleagues (2011) demonstrated that an individual's ability to make accurate predictions about an observed action is impaired when the participant is simultaneously required to perform a different action. Given recent data demonstrating that monkey mirror neurons are also largely predictive (Maranesi, Livi, Fogassi, Rizzolatti & Bonini, 2014), the weight of the evidence now points in favour of a predictive role for the motor system in action perception.

The mechanism through which an observer's motor system contributes to action prediction is widely thought to involve so-called 'forward models', in which a copy of the predicted sensory effects which accompany motor commands, and which are used to monitor our own on-going actions, are also exploited in order to make predictions about the future course of another's motor acts (Miall, 2003; Wilson & Knoblich, 2005). Specifically, given that the observer can infer the goal of an observed action, they could use their own motor experience to predict the associated motor commands and the subsequently associated kinematics, and form a prediction about how the observed action will unfold. Under some of these models, prediction and understanding are achieved through a process of motor simulation, whereby the observer reproduces the exact goal and precise kinematics of the observed movement without necessarily requiring explicit reflective mediation (i.e., imitative prediction), as if they themselves were aiming to achieve that outcome (Csibra, 2007; Rizzolatti & Craighero, 2004). This process is essentially a process of motor imagery whereby the observer imagines himself performing a particular action, but in action prediction this simulated action course is used to generate predictions about how someone else's action might unfold. Notably, according to Flanagan & Johansson (2003), action prediction and action understanding occur simultaneously. That is, low-level sensory information from performing an action directly taps into the motor system, which then in turn outputs the estimated goal (i.e., direct-matching hypothesis) (Rizzolatti et al., 2001). From this perspective, action prediction reflects the direct activation of a motor program, which includes – in addition to understanding the goal of the action – task specific internal simulation of the observed action (Flanagan & Johansson, 2003).

As previously highlighted in Chapter 1, this view of action prediction as exploiting representations contained within our own motor system has been interpreted in different ways. On the one hand, it seems clear that motor expertise with the observed action plays a facilitative role in action understanding and prediction. Thus, being able to capitalize on motor representations closely matching the observed action should be expected to result in better predictions (e.g., Sommerville, Woodward & Needham, 2005). This has been demonstrated in the case of professional basketball players who are better at predicting the success of another player's basketball shot than those with equivalent visual expertise (e.g. coaches), suggesting that corresponding motor representations, gained through motor experience, are exploited for predicting others' actions (Aglioti, Cesari, Romani & Urgesi, 2008). Likewise, ballet dancers and piano players being experts with ballet sequences or piano pieces are better able to predict how the sequences unfold (Cross et al., 2006; Haslinger et al., 2005). In a similar vein, Knoblich & Flach (2001) demonstrated that observers are better at predicting the course of observed actions when they, rather than someone else, produced those actions. Consistent with this evidence are demonstrations that when human adults and infants use the initial kinematics of an action to generate predictions, these predictions are modulated by the extent to which the observer can access a corresponding motor representation (Ambrosini, Reddy, de Looper, Costantini, Lopez & Sinigaglia, 2013). In fact, infant research has shown that only those infants who can competently perform a particular action are able to anticipate that action's goal when it is performed by someone else (Cannon & Woodward, 2012; Gredeback & Kochukhova, 2010; Kanakogi & Itakura, 2011). These findings are expected if we indeed make use of our own kinematic model to generate predictions about others' actions, and speak in favour of the hypothesis that our motor system internally simulates observed actions.

Nevertheless, the relationship between action production and action prediction does not appear to be deterministic. We can still generate predictions, albeit less accurate, about the course of actions for which we do not have available any corresponding motor representation. For example, Stadler and colleagues (2012) found that although participants could predict with less accuracy the reappearance of a point light walker displaying an artificial compared to a human velocity profile, their predictions were above chance for both types of motion. While some have suggested that the prediction of actions that we cannot perform likely depends on processes instantiated in non-motor brain regions (Buccino et al., 2004; Rizzolatti & Sinigaglia, 2010), according to the *action reconstruction hypothesis* (Csibra & Gergely, 2013; Southgate, 2013), motor activation and action prediction follow action understanding. Specifically, this view posits that goal encoding precedes motor simulation, thus suggesting that motor activation reflects the observer's re-enactment of achieving the goal without necessarily reproducing the exact kinematics of the observed movement (i.e., emulative prediction). In line with this view, there are data that implicates the motor system in the prediction of non-executable actions and events. For example, Southgate & Begus (2013) demonstrated the involvement of the motor system whenever the context permitted 9-month-old infants to generate a prediction, and this was the case irrespective of whether or not infants could themselves execute the observed action. Similarly, Cross and colleagues (2012) have shown not only that regions of the motor system are recruited during the prediction of non-human actions, but also that they were recruited to an even greater extent by non-human than by human actions. The apparent involvement of the motor system during the prediction of non-executable actions is consistent with the hypothesis that the motor system functions as an emulator, allowing observers to access their own kinematic models to form predictions about how someone else's action will unfold. This view predicts that, when the observer knows the intended goal of the actor but lacks an equivalent kinematic model to that used by the actor, they would still attempt to generate a prediction using an alternative kinematic model.

While there is increasing evidence supporting this view, there are no studies that have directly tested this hypothesis by using neurophysiological techniques. One useful measure for exploring the neural correlates of action perception is desynchronization of the mu rhythm, or sensorimotor alpha suppression, which is typically recorded from central electrode sites over the sensorimotor cortex. In adults, the mu rhythm occurs in the alpha frequency range (8-13 Hz) and is desynchronized during both action execution and observation. Several studies demonstrated that performed or imagined hand actions resulted in augmented mu desynchronization at C3 and C4 overlying the lateral hand representation areas, while performed or imagined foot actions resulted in more suppression at Cz overlying the more medial foot representation areas (e.g., Pfurtscheller et al., 2000). Furthermore, recent findings in adults support the notion that sensorimotor alpha suppression reflects the modulation of the sensorimotor cortex by mirror neuron areas in the parietal and frontal cortex, and suggest that mu-rhythm desynchronization can be used as a valid indirect marker of MNS activity (Arnstein et al., 2011; Muthukumaraswamy & Johnson, 2004).

There is currently a great deal of interest within the infant research community in uncovering a possible infant somatotopically organized mu rhythm (de Klerk, Johnson & Southgate, 2015; Saby, Marshall & Meltzoff, 2012). In Saby and colleagues' study, 14-month-old infants observed a live model performing a button-pressing action with either the foot or the hand. Results showed that infants who observed the hand action exhibited more sensorimotor alpha suppression over the hand areas (C3 & C4), while infants who observed the foot action showed more mu desynchronization over the foot areas (Cz).

In the present study we exploited the demonstrated possibility to record somatotopically organized motor activation (de Klerk et al., 2015; Saby et al., 2012) to investigate whether, during action prediction, human infants would recruit a motor representation different from the one used by the observed actor. In Experiment 1, we created a proxy for the situation of observing someone else in pursuit of a goal using a motor plan with which infants have no experience. Fourteen-month-old infants gained experience manipulating a novel object with a specific effector (foot or mouth), and subsequently observed an actor manipulating the same object using a different effector (elbow), which produces an action that 14-month-olds are unable to reproduce (Jones, 2009). It was predicted that, if the way in which the motor system generates predictions for others' actions is by a process of motor emulation, the recruited motor representation should involve the effector with which the infant has gained experience manipulating the object. We had two groups of infants who gained experience manipulating the novel object with different effectors (foot or mouth), so that any difference between their somatotopic pattern of activation during observation of the very same elbow action would result from their training differences. Two additional experiments were performed to rule out possible alternative interpretations of the obtained results, as further detailed below.

3.2 Experiment 1

3.2.1 Methods

3.2.1.1 Participants

A total of 36 infants (21 females; Mean age = 59.6 weeks; SD = 2.04) were randomly assigned to one of two training conditions (foot, n = 18; mouth, n=18). A further 21 infants were tested but excluded from the analysis (11 from foot condition; 10 from mouth condition) because they (a) didn't meet the minimum training criterion (see Procedure for further details, n=11), (b) used their hands to turn on the light (see

Procedure; n=5), (c) had too few artifact-free test trials (n = 3) and (d) fussed out during test (n=2).

3.2.1.2 Procedure

The experiment comprised two phases: a training phase (where infants gained experience manipulating a novel object with a particular effector) and a subsequent testing phase (where infants observed an experimenter manipulating the same object with a different effector).

Training Phase: Prior to testing, infants took part in a training phase in which, depending on condition, they were repeatedly shown how to turn on a commercially-available push lamp using either their foot or their mouth, depending on the group to which they were assigned. An experimenter ostensively demonstrated the action by turning the lamp on and off again 3 times, either with her foot or her mouth (Figure 4a). The experimenter then invited the infant to turn on the lamp. To be included in the study, infants were required to imitate the experimenter's action at least 4 times. If they did not approach the lamp, the experimenter continued to provide demonstrations, and encouraged the infant to try, until the infant had turned the lamp on or off with the specific effector at least 4 times. Due to infants varying willingness to attempt the novel action, different infants received differing numbers of demonstrations, and infants in the mouth condition typically required more persuasion to turn on the light compared to infants in the foot condition (mouth: range = 18-53; foot: range = 7-44). To avoid infants to form a motor association between the lamp and their hands, parents were requested to hold their infants' hands to prevent them from using their hands; infants who managed to turn on the light with their hands were excluded from the sample. The light box was placed on the floor during foot action demonstrations, and mounted on the side of a cupboard during mouth action demonstrations. Infants in the mouth training group often found it difficult to stand and simultaneously turn on the lamp with their mouth; if they did not approach the lamp while it was mounted, the experimenter removed the lamp from the cupboard and held it horizontally in front of the infant instead.

Testing Phase: Infants were seated in front of a puppet stage with the curtains closed. A camera was positioned underneath the stage to record the infant and another camera was positioned behind and above the infant to record the sequence of events on the puppet stage. This scene video was synchronized with the EEG recording and used afterwards to retrospectively mark the opening of the curtain on the EEG recording. The curtains were closed for roughly 2 seconds between trials and once the curtains were opened, the agent waited roughly 1 second to begin his action on the lamp and then returned to a resting position upon which the curtains were closed (Figure 4a). As the study was live, the length and timing of each trial varied slightly. However, as the point at which the curtains were fully opened was marked as the principal event around which the segmentation occurred, the onset of the Anticipatory Period (AP) was the same for all infants. Trials were repeated until the infant became disinterested, or until they had completed roughly 40 trials. A minimum of 10 artefact-free test trials was required for infants to be included in the sample. Infants included in the final sample contributed a mean of 21 (range: 10-38) valid trials to the analysis in the foot-training condition and 20 trials (range: 12-34) in the mouth training condition.

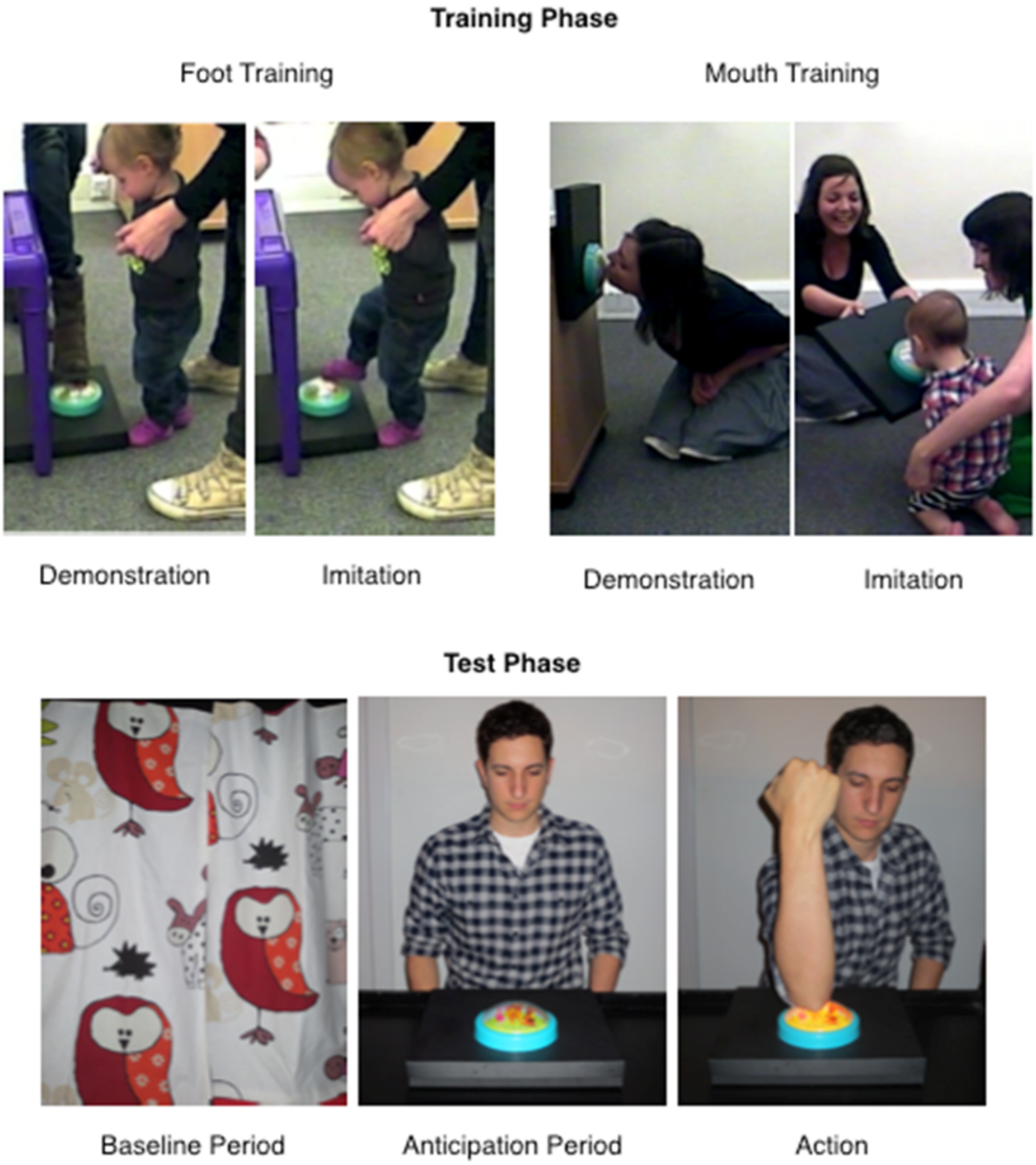

Figure 4. Experiment 1 a) infants received training to use either their foot or their mouth to illuminate a push lamp and b) all infants then took part in the same Test Phase in which curtains opened to reveal an agent who first paused for ~1000 ms (Anticipatory Period), and then turned on the lamp with his elbow.

3.2.1.3 EEG acquisition and processing

EEG was recorded using a 128-electrode Geodesic Sensor Net (EGI Inc., Eugene, Oregon). EEG was sampled at 500 Hz, recorded with respect to the vertex electrode and re-referenced to the average prior to analysis. Time-frequency analyses were performed on each artefact-free trial using a continuous wavelet transform with Morlet wavelets at 1

Hz intervals in the range comprised between 5 and 20 Hz. To eliminate distortion created by the wavelet transform, the first and last 500 ms of each trial were removed and a 400 ms baseline period was chosen. Average wavelet coefficients within infants were calculated by taking the mean across trials. As in previous studies (de Klerk et al., 2015; Saby et al., 2012), activity over a cluster of four left-hemisphere sensorimotor electrodes (30, 36, 37, and 42), four right-hemisphere sensorimotor electrodes (87, 93, 104, and 105) and six sensorimotor electrodes over the midline (7, 31, 55, 80, 106 and Cz) were analysed. The scalp locations of these left lateral, medial, and right lateral electrode clusters correspond to the locations of C3, Cz, and C4 in the international 10–20 system of electrode placement. The medial cluster is thus located over the leg representation area of the sensorimotor cortex, while the left and right electrode clusters are located over the bilateral arm representation areas. EEG data was recorded and pre-processed using Netstation and analysed using WTools (developed by E. Parise, L. Filippin, & G. Csibra, available upon request)

3.2.1.4 Data coding and analysis

Following recording, EEG was segmented into 4000 ms segments, beginning 2500 ms before, and ending 1500 ms after, the point at which curtains became fully open to reveal the seated agent. The point at which the curtains became fully open was marked on the EEG from the synchronously recorded video. A 500 ms period, beginning 1500 ms before the reappearance of the agent, was selected as a baseline. This was a period when the curtains were closed between trials. Averaged activity in the baseline period was subtracted from a 400 ms window, beginning 100 ms before the curtains were fully open, but in which the agent was already fully visible. This Anticipatory Period constituted a period in which the agent was stationary, looking down towards the lamp (see Figure 4b).

Average wavelet coefficients within participants were calculated by taking the mean across trials. Any segments in which infants made limb movements, or were not looking at the stage during either the baseline or AP, were excluded from analysis. From the retained segments, amplitude in the 6-9 Hz frequency range was averaged over a 500-ms baseline during which the curtains were still closed, and compared with a 400-ms AP beginning 100 ms before the curtains were fully open (where the agent was already fully visible).

Our primary analysis focused on a cluster of 6 channels corresponding to Cz in the international 10-20 system of electrode placement that, in previous work (e.g., de Klerk et al., 2015), showed a significantly greater suppression in sensorimotor alpha activity during observation of foot rather than hand actions. We focused on these channels because we had a strong hypothesis that, if the motor system is recruited to emulate expected outcomes, the foot region would be differentially activated during action prediction depending on training condition (foot vs. mouth). Specifically, we hypothesized that infants trained to use their foot to turn on the light would show activation of their foot region in AP in expectation of the agent using her elbow to turn on the light, whereas infants trained to use their mouth would not. Like previous works (e.g., Southgate & Begus, 2013), motor activation was defined as a significant decrease in sensorimotor alpha, averaged over the 6-9Hz frequency range, from baseline to AP. Given that we had no specific hypotheses about the involvement of the hand region, and no previous data to indicate which channels might reflect activation of the mouth region, activation of the bilateral hand regions (i.e., C3 and C4) in AP was only explored in follow-up analyses.

3.2.2 Results

A repeated-measures ANOVA performed on the foot electrode cluster, with time (500-ms baseline vs. 400-ms AP) as a within-subjects factor, and training (foot vs. mouth) as a between-subjects factor revealed a significant Time x Training interaction, F (1,34) = 5.95, p = .020, η_p^2 = .15. To follow-up this interaction, separate paired-sample t-tests were carried out on data from each training condition. Infants in the foot training condition showed a significant decrease in alpha amplitude from baseline to AP, t (17) = 2.14, p = .047, indicating activation of the motor foot region when they expected the experimenter to act on the lamp, Infants in the mouth training condition did not show any change in activation of the foot region, t (17) = -1.23, p = .236. Thus, infants who were trained to use their foot to turn on the lamp recruited their own foot region just before the agent could be expected to begin approaching the lamp, whereas no activation of this very same region was apparent during the same anticipatory period in infants who were trained to use their mouths.

We performed a second ANOVA on the bilateral hand electrode clusters to test whether infants in either training group recruited their motor hand area, an area that has been previously reported to be involved in the prediction of both hand (Marshall & Meltzoff, 2011) and non-executable actions (Southgate & Begus, 2013), with a predominant left lateralization (Saby et al., 2013). The ANOVA including time (baseline vs. AP), location (left vs. right hand cluster) and condition (foot vs. mouth) revealed no significant main effects or interactions (*p*s > .088), including a marginal effect of time, F (1,34) = 3.10, p = .088, η_p^2 = .083, indicating a non-significant trend towards more activation over the hand area in AP than baseline in both the foot and mouth training groups.

Overall, results showed that, while there was clear activation of the foot area in AP for infants trained to use their foot to turn on the lamp, there was no corresponding activation of the hand area in either training group.

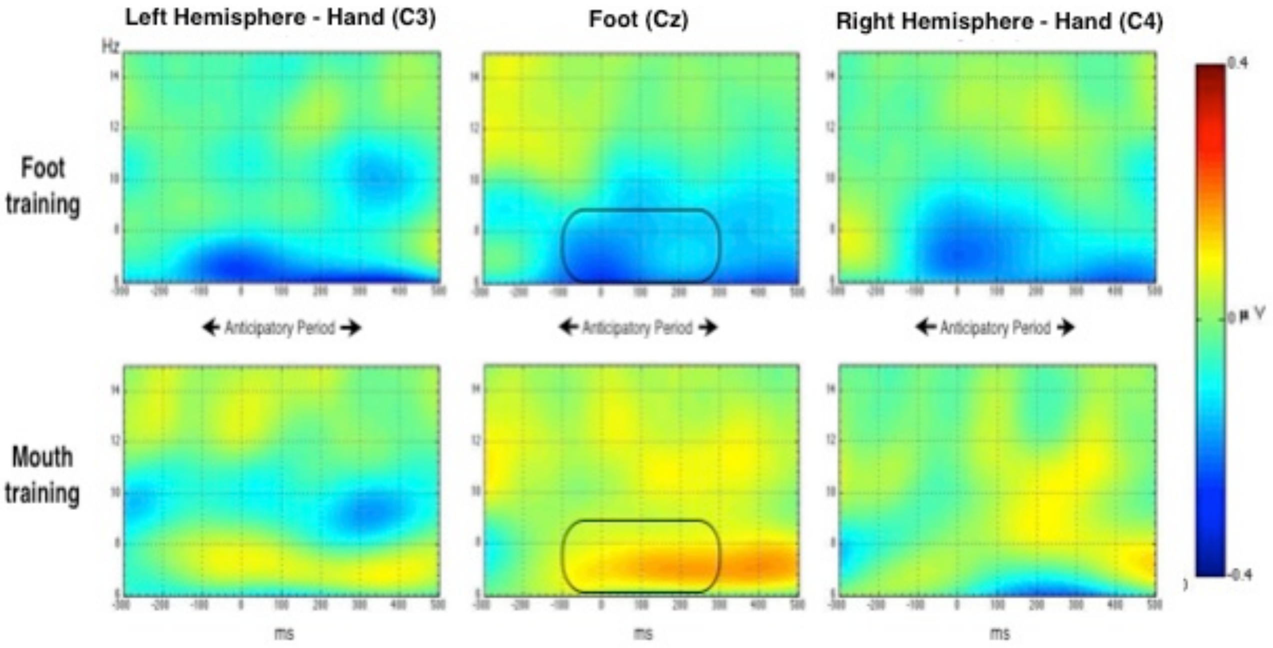

Figure 5. Time-Frequency plots showing the Anticipatory Period (AP) for each electrode cluster of interest for the two training groups. Blue colours indicate stronger desynchronization.

3.3 Experiment 2

Experiment 2 was aimed to replicate and extend the results of Experiment 1 by testing for the generalizability of the observed effects and by adding further controls to the experimental conditions tested in the previous experiment.

Specifically, the first aim of Experiment 2 was to test whether the results of Experiment 1, showing that infants emulate others' action outcomes using their own means, are confined to cases where infants lack the means used by the agent, as was the case for the elbow-action used in Experiment 1. The alternative hypothesis would be that infants draw upon their own action experience even when they could potentially use another motor programme. Infants included in Experiment 1 were only those who performed the action using the demonstrated effector (foot or mouth), but at least 5 infants were excluded because they used their hands, proving that 14-month-old infants are well capable to turn on the light using hands as the default effector. Therefore, to disambiguate between the two hypotheses outlined above, in Experiment 2 EEG recordings were performed on an additional group of infants, trained to turn on the light with their feet, while they observed the agent turning on the lamp with his hands (rather than with his elbow).

The second goal of Experiment 2 was to control for the possible confounding generated in Experiment 1 by the simultaneous appearance of the lamp and the agent. In Experiment 1 we interpreted motor activation upon agent appearance as reflecting infants' expectation about the agent's forthcoming action. However, an alternative possibility is that the appearance of the lamp, which coincided with the appearance of the agent, triggered an associated motor response in the infant (i.e., the motor representation that infants had formed during their training with the lamp). Previous work has shown that infants readily form action-effect associations, and the observation of an effect (e.g., the lamp) might be sufficient to trigger associated motor experience (Paulus, Hunnius, Vissers & Bekkering, 2011a; 2011b; Paulus et al., 2012). To control for the possible confounding arising from the lamp appearance, in Experiment 2 the setting was adjusted so that the lamp was always visible to the infant, and the curtains opened to reveal the agent alone. This way, the lamp appearance was not anymore tied to the appearance of the agent and thus could not affect infants' motor activation responses during AP.

Eighteen infants who had received training with their foot participated in Experiment 2. One infant was excluded from the sample due to fussiness so that the final sample included 17 infants (9 females; Mean age = 60.43 weeks; SD = 2.20 weeks). All aspects of the Methods were identical to Experiment 1, with the only exception being the effector used by the agent to turn on the lamp (the hand rather than the elbow) and the timing of the lamp appearance (it was always visible to the infant rather than appearing at the same time as the agent). Infants contributed a mean of 21 trials (range: 13-37).

3.3.1 Results

Like in Experiment 1, our primary question was whether the infant's motor foot region was at all activated during AP. However, as infants in Experiment 2 observed hand actions during test, we explored the involvement of both the foot and hand motor regions with a 2 (time: baseline vs. AP) x 3 (location: left (C3), centre (Cz), right (C4)) repeated-measures ANOVA. These analyses revealed a marginal Time x Location interaction, $F(2,16) = 2.90$, $p = .085$. As our primary hypothesis was that foot training would lead to involvement of the motor foot region during AP, we followed up this interaction through separate paired-samples t-tests for each location. These tests confirmed that there was a significant decrease in sensorimotor alpha, indicating motor activation, over the foot channels (Cz) from baseline to AP, $t(17) = 2.23$, $p = .040$, but not over either the left, $t(17) = .370$, $p = .716$, or right, $t(17) = .354$, $p = .727$, electrode clusters.

Thus, infants who had been trained to use their own foot to turn on the lamp recruited their motor foot region during AP, even when they were observing the agent using effectors that they themselves were able to use to perform the same action. The absence of a significant decrease from baseline to AP over either C3 or C4 suggests that infants did not activate their motor hand region when they could predict the action of an agent who was using his hands. These data suggest that infants prioritize their own action experience and recruit the motor representations formed during this experience when generating predictions about how others' actions will unfold towards the same outcome.

3.4 Experiment 3

Data from Experiment 2 replicated and extended those of Experiment 1 by showing that infants predict others' action outcomes by using emulative mechanisms. In fact, results obtained in Experiment 2 demonstrate that infants refer to their own action experience (i.e., foot training) even when they could potentially use another motor programme (i.e., hand action), thus rejecting the hypothesis that they emulate only when lacking the means used by the agent, as was the case in Experiment 1 (i.e., elbow action). Additionally, results from Experiment 2 suggest that observed effects are not due to action-effect associations since the lamp appearance was not tied to the appearance of the agent and thus could not affect infants' motor activation responses during AP.

Nevertheless, data from Experiment 1 and 2 do not allow teasing apart whether it was really the sensorimotor experience of producing the outcome with their foot that led to the recruitment of their motor foot region during action prediction, or rather the visual experience of watching the demonstrator turning on the lamp with her foot, which may have been sufficient to create a motor representation of the action. Indeed, one could imagine that the ostensive demonstration of turning on the lamp with the foot conveyed normative information to the infant that this specific lamp should be turned on with one’s foot, and that first-person sensorimotor experience using one’s foot is superfluous.

To investigate the role of first-person motor experience in the recruitment of the motor-foot region during action prediction observed in Experiments 1 and 2, we ran a third experiment (Experiment 3) in which the procedure was adjusted so that, during the training phase, infants received the same observational experience of the demonstrator turning on the lamp with her foot as infants in Experiment 1 and 2, but they did not have the opportunity to themselves produce the action. A new group of 21 infants (9 females; Mean age = 59.12 weeks; SD = 1.6 weeks) took part in the experiment. All aspects of the Methods were identical to Experiment 2, with the only exception of the possibility for he infants to perform the demonstrated action during the training phase. The number of demonstrations each infant received was matched with those received by each specific infant in Experiment 2, and during the test phase infants observed the agent turning on the lamp with his hand. Thus, any difference in the recruitment of the foot region between infants tested in Experiment 2 and Experiment 3 would have been due to the infants' first-person experience using his/her foot, as visual experience observing the demonstrator was equated across the experiments. The infants included in the sample contributed a mean of 20 valid trials (range: 11-40).

3.4.1 Results

As in Experiment 2, a repeated-measures ANOVA was performed with time and location as repeated-measures factors. The time x location interaction approached significance, F(2,16) = 3.58, p = .052, and so we followed it up through separate paired-samples t-tests on each location. Unlike Experiment 1 and 2, there was no significant decrease in sensorimotor alpha from baseline to AP over the motor foot region, t (17) = .916, p = .373. There was, however, a significant decrease in sensorimotor alpha from baseline to AP over the left C3 cluster of electrodes, t (17) = 2.95, p = .009, indicating activation of the left motor hand region during the anticipation period. No decrease in sensorimotor alpha was apparent over the right motor hand region, t (17) = .317, p = .755.

These results confirm the hypothesis that experience observing the demonstrator turning on the lamp with her foot is insufficient to generate a motor representation that infants can exploit for action prediction. However, the recruitment of the left motor hand region during the anticipatory period suggests that infants did generate a prediction about the agent's action on the lamp, despite having no prior experience of interacting with the lamp themselves, and this prediction is based on a motor representation that encompass the effector that is most commonly use by infants to act on object. However, results do not clarify whether infants recruited the hand region because they emulated the expected effect with their hand, or because this region serves as a default region for action prediction in the absence of specific experience performing the observed action.

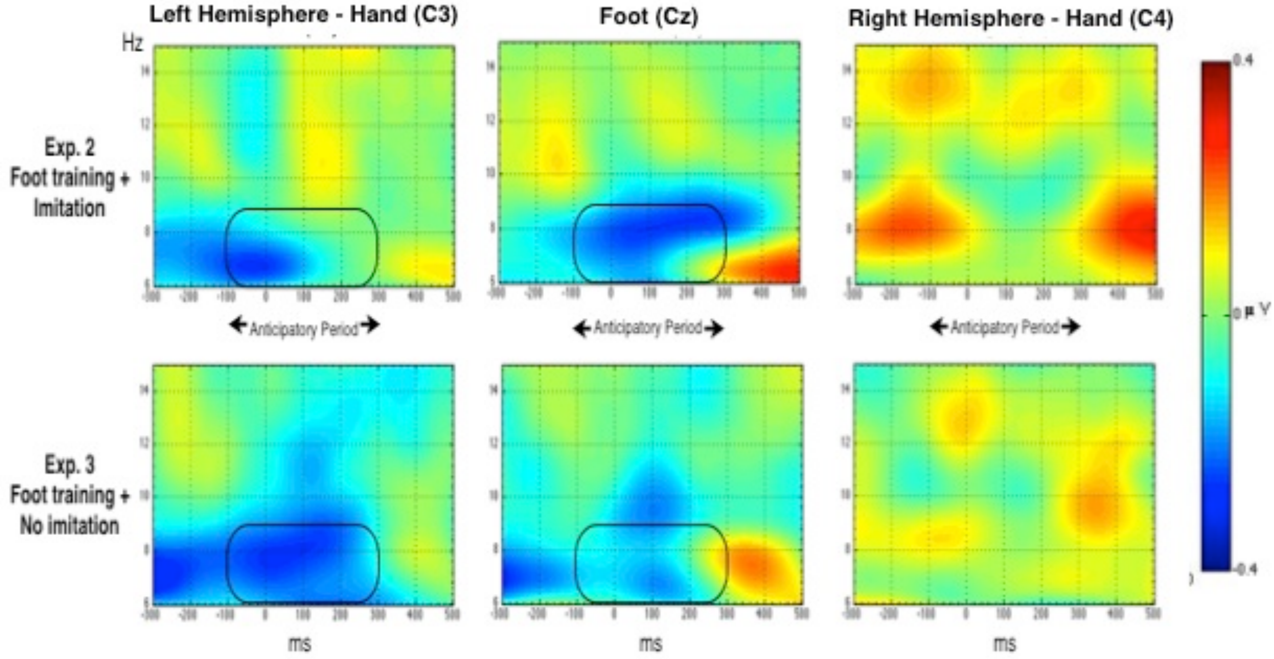

Figure 6. Time-Frequency plots showing the Anticipatory Period for each electrode cluster of interest, for infants in Experiments 2 and 3. Blue colours indicate stronger desynchronization.

3.5 Discussion

As outlined in Chapter 1, a large body of evidence suggests that observing others' body movements activates motor representations in the observer's brain (e.g., Aglioti et al., 2008; Avenanti et al., 2007; Fadiga et al., 1995), thus suggesting that perception and prediction of others' actions involves the activation of the observer's motor system (Costantini et al., 2013; Elsner et al., 2013). While the involvement of an observers' motor system during action perception is clear, there still remains little consensus on what role this motor involvement plays. It would seem from studies reported in the literature that activation of motor representations is imitative in nature. Apparently, the motor system simulates in a strictly congruent fashion action stimuli being observed. The representations of the muscles involved are the same as those used in the observed action and their activation is temporally and strictly coupled with the dynamics of the observed movement (Fadiga et al., 2005). However, the automatic tendency to mirror is clearly not always the best response in real-life situations. Indeed, according to an alternative view (i.e., action reconstruction hypothesis) (Csibra & Gergely, 2013; Southgate, 2013), action prediction follows action understanding. This view argues that goal encoding must precede motor simulation. Thus, this theory proposes that motor activation reflects the observer's re-enactment of achieving the goal, as though the observer had executed the action.

The present study investigated whether 14-month-old infants exhibit an emulative or imitative somatotopic pattern of activation over the sensorimotor cortex during action observation. To this aim, infants went through a training in which they had to observe and imitate an action consisting in turning on a lamp by using different effectors. EEG was then recorded to measure mu rhythm desynchronization during the observation of another experimenter performing the same goal-directed action (i.e., turning on the lamp) by using a different effector. Infants draw upon a motor representation formed through their own sensorimotor experience achieving an outcome during the prediction of others' actions towards the same outcome (Experiment 1 and 3) even when that action does not match this motor representation, that is, even when the agent perform the action using an effector different from the one the infants have been trained to use (Experiment 2).

Overall, the obtained results support the hypothesis that motor system activation during action prediction reflects an emulative process (i.e., activation of the motor program most strongly associated with the expected outcome). In the current study, it is assumed that this emulative process draws upon associations between actions and effects, formed during the training phase. Available evidence suggests that bi-directional action-effect associations can be recruited to anticipate the behaviour of an agent whose goal is known. For example, infants readily form bi-directional action-effect associations (Elsner, 2007) and, following action-effect training, activate their motor system in response to the presentation of the effect presented in isolation (Paulus et al., 2012). In adults too, the observation of a familiar goal performed with an unusual effector (e.g., pressing a foot pedal with the hand) elicits muscle activation in the effector more traditionally associated with that action (e.g., the foot) (Senna et al., 2013). In the current study however, rather than being recorded during the observed action, this activation was elicited during an anticipatory period, when the infant could expect a forthcoming action.

In Experiment 1 it was hypothesized that if the way in which the motor system generates predictions for others' actions is by a process of motor emulation, anticipation of the action goal should involve the specific effector with which the infant has gained experience manipulating the object. Indeed, infants who were trained to use their foot to turn on the lamp recruited their own foot region upon agent appearance and right before the agent began approaching the lamp. Moreover, both infants who were trained to use their mouths or feet to turn on the lamp recruited to a lesser extent their hand region in this same anticipatory period during the observation of the elbow action. This marginally significant effect obtained for the hand area might be interpreted as reflecting activation of the motor program related to the effector that infants most commonly use to act on objects (i.e., hand) (de Klerk et al., 2015; Southgate & Begus, 2013). Thus, results of Experiment 1 are consistent with the hypothesis that infants have reproduced the outcome of the observed action using their own means (i.e., emulation) (de Klerk, Johnson & Southgate, 2015). In fact, under the emulation hypothesis, when an observer do not have available the motor program that is being used by the actor, they could use an alternative motor program through which to achieve the goal of the observed action (Csibra, 2007; Southgate, 2013).

However, given that the appearance of the lamp coincided with the appearance of the agent, results obtained in Experiment 1 might also be explained as reflecting sensorimotor activation deriving from an action-effect association generated by the motor representation that infants shaped during the active training with the lamp. Indeed, previous work has shown that infants are already capable to form action-effect associations, and that the observation of an effect (e.g., the lamp) is sufficient to trigger associated motor experience (Paulus, Hunnius, Vissers & Bekkering, 2011a; 2011b; Paulus et al., 2012). According to this perspective, when actions are predicted on the basis of observed action-effect associations, the observer implicitly relies on the assumption that an action is directed towards the same goal state that has been produced by earlier, similar actions, and that the effect will be achieved by an actor in a similar way, as it was achieved before (Elsner & Aschersleben, 2003; Uithol & Paulus, 2014).

Experiment 2 rules out the possibility that the sensorimotor alpha suppression recorded during the anticipatory period reflects activation of the sensorimotor representation that infants had associated with the lamp, rather than a sensorimotor representation involved in action prediction. Indeed, the setting was adjusted so that the lamp was always visible to the infant, and the curtains opened to reveal only the experimenter. This way, the activation of an associated motor response triggered by the appearance of the lamp could not contribute to any difference from baseline in mu rhythm desynchronization during the anticipatory period. Nevertheless, one might contest that the activation of the associated foot movement still does not imply that infants were drawing upon this representation in order to predict the others' action. Perhaps the agent's reappearance just triggered in infants the expectation that the lamp would become illuminated, and just thinking about this effect activated – through acquired action-effect associations – the representation of the action that infants trained to use their foot have associated with this effect. This of course calls into question the issue of whether the observed motor activation is causally involved in action prediction, or whether it is simply correlated with action prediction. Indeed, while the presence of motor activation tells us that infants must have made a prediction about the agent's action, it is not possible to know whether motor activation in itself is causally involved in making this prediction, or whether it reflects another process.

The second aim of Experiment 2 was to understand whether infants' predict others' action outcomes by using emulative mechanisms (i.e., using their own means) only when the observed actions are implemented with means that are not part of their motor repertoire (i.e., elbow action), or whether infants rely on their own action experience even when they might use another familiar motor programme (i.e., hand action). Results showed that infants prioritize their own action experience and rely on the motor representations formed during the active training when generating predictions about how others' actions will unfold towards the same outcome. Indeed, infants who underwent the training in which they had to exercise using their own foot to turn on the lamp, recruited their motor foot region right before the agent began approaching the lamp, even when they were observing the agent using a means which was within their motor capabilities (i.e., hand action). Furthermore, the absence of significant sensorimotor mu suppression over either the right or left hand electrode sites suggests that infants did not activate their motor hand region when they could predict the action of an agent who was using his hand.

The possibility that the emulative activation of infants' motor region observed in Experiment 1 and 2 was due to active experience of producing the outcome during the training rather than visual experience of watching the demonstrator turning on the lamp with her foot, was assessed in Experiment 3. Specifically, it was tested whether passive experience obtained from other-produced actions might provide a similar learning opportunity than that obtained from active experience obtained from self-produced actions

(Yu & Smith, 2012). Results showed a lack of mu rhythm desynchronization over the sensorimotor foot area and a concurrent sensorimotor alpha decrease over the hand area, suggesting that passive experience acquired during training is not sufficient for generating a motor representation that can be exploited for action prediction.. However, despite having no prior active experience of interacting with the lamp, infants did generate a prediction about the agent's action, and this prediction is based on a motor representation that encompasses the effector that is most commonly used by infants to act on object.

Results from Experiment 3 are partially similar to those obtained by Saby and colleagues (2013) in which 14-month-old infants were not provided with any experience with the object before observing the actor performing the hand or foot actions. These authors observed greater desynchronization over hand areas for the infants observing hand actions carried out on the lamp, however they also observed greater suppression over the foot area for the infants observing foot actions. Moreover, the lack of activation of the foot area observed in Experiment 3 as compared to Experiment 1 & 2 might be attributed to the different trainings – active vs passive experience. From a theoretical perspective, this finding might be consistent with the direct matching hypothesis of action understanding. Indeed, if action understanding requires access to a motor representation of the action, active experience more than that acquired through action observation alone would be fundamental (Cannon et al., 2015; Sommerville, Hildebrand & Crane, 2008). However, it is also possible that information acquired through active experience might be better comprehended as compared to information learned through observation alone. Indeed, self-produced effects might be particularly arousing for infants or it is also known that human beings tend to learn more easily from information they helped producing (Kang et al., 2009; Lewis, Sullivan & Brooks-Gunn, 1985; Southgate, 2013). Moreover, given that infants of this age would, by default, attempt to interact with the object with their hands

(Gergely et al., 2002), it is likely that, in the absence of an action-effect association deriving from active experience, infants activated the left hand region during the anticipatory period because they understood that the effect could be brought about by using their hands. However, activation of the left motor hand region is not selective for hand regions, as earlier evidence showed that it is recruited for the prediction of non-executable actions (e.g., self-propelled objects and claw-actions) as well (Southgate & Begus, 2014). Thus, it remains open to debate whether infants recruited the hand region because they emulated the expected effect with their hand, or because this region serves as a default region for action prediction in the absence of specific experience performing the observed action.

Taken together, results suggest that 14-month-old infants are capable to predict observed actions even in the absence of the ability to perform that action and of the corresponding motor representation. The activation of the sensorimotor cortex during action observation may depend on infants' understanding of the action goal and their expectations about how this goal will be achieved. Moreover, these findings seem to support the hypothesis that the observer's motor system plays an emulative, rather than imitative, role in action prediction and that infants' emulative motor activation is linked to active experience with the action. In conclusion, the current data provide support for the emulative view of motor activation during action prediction. Indeed, in most cases, where the agent and the observer share the same biomechanical constraints, and the same perception of object affordances, the motor program recruited will overlap. However, the training paradigm employed in the current study and the absence of pre-existing motor associations in infants, reveals a plausible mechanism through which recruitment of the motor system supports action prediction. Nonetheless, whichever might be the role of the motor system in action prediction and understanding, the fact that it is involved in facilitating the prediction of observed actions both within and outside of the infants’ limited motor skills provides infants with a powerful tool to predict others’ actions.

CHAPTER 4

EMOTION IN MOTION: PROCESSING OF EMOTIONAL FACIAL EXPRESSIONS IN 7-MONTH-OLD INFANTS[4]

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[4] Data collection and analysis were conducted in collaboration with Stefania Conte, PhD candidate at the University of Milano-Bicocca (UNIMIB). Results from this study will be presented at the International Conference on Infant Studies (ICIS) to be held on May 26-28 2016 in New Orleans. Quadrelli, E., Conte, S., Macchi Cassia, V., Turati, C. Temperamental traits affect emotional expression processing of static and dynamic faces: an ERP study with 7-month-old infants

ABSTRACT

The ability to decode facial expressions is an important component of social interaction and functioning, and it is even more fundamental early in life, prior to the development of verbal communication. An important neural correlate of emotion processing in infancy is the negative central (Nc) component, indicating attentional orienting to salient stimuli. Several studies demonstrated that 7-month-olds allocate more attention to fearful as compared to happy faces. Other studies found that 7-month-olds showed heightened sensitivity to happy as compared to angry faces, while 12-month-olds showed the opposite pattern of neural response. The current study aims to investigate how variations in infants' temperamental traits affect the neural responses elicited by static and dynamic happy, angry and neutral facial expressions in 7-month-old infants. Obtained results suggest that static happy faces generate faster attentional responses as compared to angry and neutral faces. Furthermore, dynamic faces do not seem to facilitate the processing of emotional expressions, apparently making it more difficult to deploy attentional resources to an expression over the others. Finally, this study highlights the role of individual differences related to temperamental traits, and specifically to the surgency dimension, in modulating attentional responses towards emotional expressions.

4.1 Introduction

Social communication is a dynamic process in which rapidly changing visual inputs need to be quickly evaluated. In the context of social interactions, human faces provide an extraordinarily important source of information, especially for infants. For instance, lip movements support speech comprehension (Lewkowicz & Flom, 2014), gaze direction informs about spatial attention (Okumura, Kanakogi, Kanda, Ishiguro & Itakura, 2013), and facial expressions communicate the emotional state of others (Fridlund, 2014). Moreover, research using point-light or biological motion displays, schematic and computer-animated faces suggests that movement enhances the accuracy of attribution of facial affect (e.g., Nusseck, Cunningham, Wallraven & Bulthoff, 2008). Thus, it seems that we are equipped to quickly recognize subtle changes in the facial composure of conspecifics. Although some studies have shown a particular sensitivity for dynamic facial movements, for example, in learning faces (Pilz, Thornton & Bulthoff, 2006), identifying persons (O'Toole, Roark & Abdi, 2002), recognizing emotional expressions (Ambadar et al., 2005; Biele & Grabowska, 2006; Kamachi, Bruce, Mukaida, Gyoba, Yoshikawa & Akamatsu, 2001;), most studies on emotional facial expression rely on static stimuli (e.g., Adolphs, 2002).

Studies in healthy adults have demonstrated that several cortical and subcortical brain regions are involved in the perception and evaluation of facial expressions of emotions (Haxby, Hoffman & Gobbini, 2002; Adolphs, 2002). The fusiform gyrus and superior temporal sulcus are critically involved in face processing and in extracting emotional cues from faces, and amygdala is known to be specifically activated in the processing of fearful stimuli (Pessoa, McKenna, Gutierrez & Ungerleider, 2002). Moreover, several studies demonstrated the crucial role of prefrontal areas in emotional processing (e.g., Esslen, Pascual-Marqui, Hell, Kochi & Lehmann, 2004) and the existence of reciprocal connections with limbic structures, which allow interpreting the current situation in light of past emotional experience.

More recently, evidence has accumulated suggesting a more distributed activation pattern of these networks in response to dynamic faces, which has been proposed to reflect augmented attentional orientation towards dynamic emotional expressions (Fichtenholtz, Hopfinger, Graham, Detwiler & LaBar, 2007). Moreover, an enhanced activation in visual areas to dynamic as compared to static facial expressions has been found in adults (Recio, Sommer & Schacht, 2011), thus suggesting that facial motion might improve the perception of emotional expressions (Ambadar, Schooler & Cohn, 2005). Therefore, progress has been made in understanding the effect of motion on the neural mechanisms underlying emotional information processing in adults. However, little is known about how movement information affects the development of these mechanisms and when the developing brain starts to respond differentially to emotional versus neutral faces.

Even though infants do not possess all the mechanisms for identification of an emotion such as the verbal label for expressing the conceptual knowledge linked to the emotion conveyed by the expression, they are still able to respond to emotional signals and have some understanding of the delivered emotional message. For example, infants tend to regulate their own behaviour based on emotional signals and they can respond to facial expressions with vocalizations or emotional expressions of their own (Soken & Pick, 1999), possibly reflecting the initiation of a pathway for the understanding of social meaning.

At birth, infants' visual acuity is poor (Banks & Salapatek, 1983), making it unlikely for newborns to discern subtle differences from facially communicated emotional signals. However, infants show a very early interest in looking at faces (Goren, Sarty, & Wu, 1975), which is driven by an innate preference for face-like stimuli (Johnson, 2005; Turati, 2004). Despite the existence of an early predisposition to attend to faces, there is no clear evidence of facial expression discrimination in few-day-old infants (i.e., longer looking to changes in facial expression) (Farroni, Menon, Rigato & Johnson, 2007). The extensive experience with observing others' faces that infants accumulate during the first months of life gradually leads to a more finely tuned representation of faces and the different information they convey (e.g., identity, expression, and direction of others' attention; Johnson, 2005; Nelson, 2001). Three-month-old infants are able to discriminate between different expressions of emotion (Schwartz, Izard & Ansul, 1985): after habituation to a smiling or a frowning face, infants at this age looked longer at a novel identity displaying a novel expression than at the same identity displaying the familiar one (Barrera & Maurer, 1981).

By 5-7 months the infants' visual system is sufficiently developed to support discrimination of most facial expressions (Bornstein & Arterberry, 2003), however 5-month-old infants prefer to look at happy faces over angry and neutral faces (Grossmann, Striano & Friederici, 2007). Furthermore, evidence for the ability to recognize expressions of emotions other than happiness, such as fear and anger, is less consistent and the habituation order of the expression categories appears to be critical for the recognition effects to occur (Nelson, Morse & Leavitt, 1979; Caron, Caron & Myers, 1985). This early discrimination and visual preference for positive emotional expressions is taken as evidence for an early *positivity bias*, that would result from the predominant exposure of infants to positive interactions with adults in the first months of life (Vaish, Grossmann, & Woodward, 2008). Later on, by 7 months of age, infants preferentially attend to a fearful over happy faces (Kotsoni, de Haan, & Johnson, 2001; Nelson & Dolgin, 1985) demonstrating an attentional *negativity bias,* which might result from an increased experience with perceiving fearful expressions. Indeed, improvements in infants' motor abilities and the consequent increased risk of incurring in dangerous situations augment the probability to be exposed to caregivers' negative facial expressions (Campos et al., 2000). The preference for fearful faces might also reflect a difficulty in disengaging attention from fearful facial expressions. Indeed, 7-month-old infants are less likely to disengage their attention, as assessed recording their eye movements, from a face to a peripheral stimulus if the face displays a fearful as compared to a happy or neutral expression (Leppanen et al., 2010). Further developmental changes in emotional face processing occur between 7 and 12 months. By 12-month-old infants show a preference for angry compared to happy faces (Grossmann, Striano & Friederici, 2007), suggesting that anger might be processed distinctly from other negative emotions (Vaish, Grossmann & Woodward, 2008).

From a developmental perspective, these changes in attentional responses to different emotions may be experience-based, with early disproportioned experience with positive facial expressions that subsequently shapes the enhanced attentional responses to negative, and more novel, expressions together with species-specific predisposition to code negative expressions as signalling aversive situations.

To date, numerous studies have consistently identified three key event-related EEG components in infants that are sensitive to face stimuli and that may also have emotion-sensitive properties: the N290, the P400, precursors to the adult face-sensitive N170, and the negative central (Nc) components. However, previous studies indicate that the N290 and P400 components are more strongly connected to general face processing than to emotion processing (de Haan, Pascalis & Johnson, 2002). By contrast, the most studied neural correlate of emotion processing in infancy is the Nc, a negative deflection typically recorded over fronto-central electrode sites and occurring between 300 and 800 ms after stimulus presentation. This component is thought to reflect allocation of attentional processing resources linked to the appraisal of the motivational significance of emotional expressions (de Haan, 2007) and to originate in the anterior cingulate cortex (Reynolds & Richards, 2005), known to be part of the so-called anterior executive attention network (Posner, 1995). It is believed to gradually emerge in development, being present in few days old newborns with a peak latency ranging between 1000 and 1200 ms (Nelson, 2001), decreasing to about 600 ms in 6-month-olds (Ackles & Cook, 1998) and 400-500 ms in 1- to 3-year old children (Parker & Nelson, 2005).

Consistent with the aforementioned behavioural studies, 7-month-old infants' preference for fearful expressions is manifested not only in terms of overt visual preference but also in brain activity, since greater amplitudes of ERPs related to sensitivity to negative, as compared to positive facial expressions have been observed (de Haan & Nelson, 1999; Leppanen, Moulson, Vogel-Farley & Nelson, 2007; Nelson & de Haan, 1996). More specifically, the Nc component has been found to be larger to fearful faces as compared to happy faces (Nelson & de Haan, 1996), while data comparing activation elicited by fearful and angry expressions are mixed (Nelson & de Haan, 1996; Kobiella, Grossmann, Reid & Striano, 2008). According to one view, the larger Nc to fearful compared to happy faces reflects the emerging interactions between the amygdala and the anterior cingulate cortex (Peltola, Leppanen, Maki & Hietanen, 2009). ERPs cannot directly measure the activity of subcortical structures, such as the amygdala, but they can do so indirectly, via their effects on cortical activity. Other studies found that Nc discriminates between happy and angry faces, with 7-month-old infants showing a larger Nc to happy as compared to angry faces and 12-month-olds showing the opposite pattern (i.e., angry faces eliciting greater amplitudes as compared to happy faces) (Grossmann, Striano & Friederici, 2007). In addition, paralleling behavioural evidence, ERP studies showed no evidence of an attentional bias toward fearful faces in 3- to 5-month-old infants (Hoehl & Striano, 2010).

In the bulk of the research conducted to date, infants' data were pooled and examined at the group level, with little attention paid to individual differences. Thus, in the current study we sought to add an individual difference dimension, by examining whether differences in infants' temperament might be associated with differences in infants' electrophysiological responses to dynamic and static emotional faces. Few investigations started addressing this topic and have found that infant temperament is associated with individual differences in the neural correlates of attention allocation to emotional faces.

Indeed, an ERP study with 7-month-old infants reported that being higher on fearfulness is related to a larger Nc to fearful faces over right frontal electrode sites (de Haan, Belsky, Reid, Volein & Johnson, 2004). However, Martinos, Matheson and de Haan (2012) found that 3- to 13-month-old infants with higher scores on the Negative Affect scale, measuring the degree to which infants show distress and soothability difficulties (see Methods for further details), allocated greater attention to happy than fearful faces. This discrepancy in results has been explained as deriving from differences in participants' age between the studies and from greater variability in the participants' age range in the latter compared to the former investigation. Other studies have shown that 7-month-old infants scoring lower on soothability (i.e., subscale of the Negative Affect temperament dimension) manifest larger Nc amplitudes to fearful faces (Taylor-Colls & Fearon, 2015). In line with these results, a recent study exploring brain metabolism using functional near-infrared spectroscopy (fNIRS), showed that oxyhemoglobin (oxyHb) responses to smiling faces over the left prefrontal cortex were negatively correlated with the Negative Affect temperament factor (Ravicz, Perdue, Westerlund, Vanderwert & Nelson, 2015).

Another interesting issue that received little to no attention concerns the role of motion in the processing of emotional facial expressions in infancy. Existing studies on adults' processing of emotional facial expressions converge to suggest that natural moving faces might provide a more valid stimulus basis for the examination of the neural correlates of facial expression perception (e.g., Kilts, Egan, Gideon, Ely & Hoffman, 2003; Trautmann, Fehr & Hermann, 2009). Relying on this set of evidence, in the present study we aimed to compare activation patterns elicited in 7-month-old infants by static compared to dynamic stimuli, and to check whether dynamic stimuli might influence the emergence of early attentional biases to negative emotional expressions. Moreover, in light of recent studies demonstrating the role of infants' temperamental dimensions in moulding their attention to emotional stimuli (e.g., Grossmann, Johnson, Vaish, Hughes, Quinque, Stoneking & Friederici, 2011), we analysed individual differences in infants' neural responses to happy, angry and neutral faces. We used happy expressions since, as previously outlined, a happy face is likely the first emotional expression that an infant sees in the world, and the emotional expression most commonly experienced from a very early age, and to examine angry faces since much less work has investigated the Nc in relation to this facial expression.

4.2 Methods

4.2.1 Participants

Twenty-seven 7-month-old infants (11 male infants, M = 206 days, SD = 8 days, range = 194-225 days) were included in the final sample, 15 in the Static group and 12 in the Dynamic group (data collection is still in progress). An additional 23 infants were tested but could not be included in the final sample because of fussiness (n = 13), excessive artifacts (n = 7), or technical problems with data collection (n = 3). All infants were born full-term (37-42 weeks' gestation) and with normal birth weight (> 2500 g). This attrition rate is in line with other infant ERP studies (de Haan et al., 2004). Infants needed to have at least 10 artifact-free trials per emotional expression condition to qualify for further data analysis. The protocol was carried out in accordance with the ethical standards of the Declaration of Helsinki (BMJ 1991; 302: 1194) and approved by the ethical committee of the University of Milano-Bicocca. Participants were recruited via a written invitation that was sent to parents based on birth record provided by neighbouring cities. The study was explained to the parents and their written consent was obtained.

4.2.2 Temperament assessment

Infant temperament was measured using the Infant Behaviour Questionnaire-Revised (IBQ-R; Gartstein & Rothbart, 2003) in its very short form, a parent-report measure that was completed by the mother or primary caregiver of each subject within a week of the visit to the lab when ERPs were recorded. This tool is validated for 3- to 12-month-old infants and has shown good inter-rater reliability between mothers and fathers and adequate internal consistency (Putnam, Helbig, Garstein, Rothbart & Leerkes, 2013). Each response is recorded on a seven-point scale ranging from 1 (Never) to 7 (Always). The IBQ-R very short form assesses the frequency of specific temperamental behaviours in three main temperamental dimensions: Negative Affect (NA), analogous to the personality trait of Neuroticism, and defined by high positive loadings on sadness, distress to limitations and fear and negative loadings on falling reactivity; Surgency (SU), analogous to the personality trait of Extraversion and defined by high scores approach, vocal reactivity, smiling and laughter and activity level. Ten of the 23 infants who did not provide usable EEG data provided a completed IBQ-R questionnaire. Infants who were excluded did not significantly differ from those included in terms of temperament traits (lowest *p* = .126).

4.2.3 Stimuli

Stimuli used in the dynamic condition consisted of 6 female Caucasian actresses posing a happy (HA) or angry (AN) face extracted from an existing and validated database (Yin, Sun, Worm & Reale, 2008). Dynamic neutral (NE) expressions were created by recording in the lab 3 videos of female actresses displaying a neutral expression while moving their mouth as for speaking. Thus, on the whole, 3 identities contributed to each facial expression. In the static condition, the same female Caucasian actresses posed in neutral or fully emotional – happy or angry - displays extracted from videos used in the dynamic condition (Figure 7). All videos and photographs were edited to 1.0 s duration, shown against a grey background and oval-cropped so that no hair or other features could be seen. When viewed from approximately 60 cm, all faces subtended 15.3° of visual angle vertically and 10.5° of visual angle horizontally. All stimuli were screened and selected by 7 adult raters for their emotional valence before editing and cropping them in Photoshop CS4.

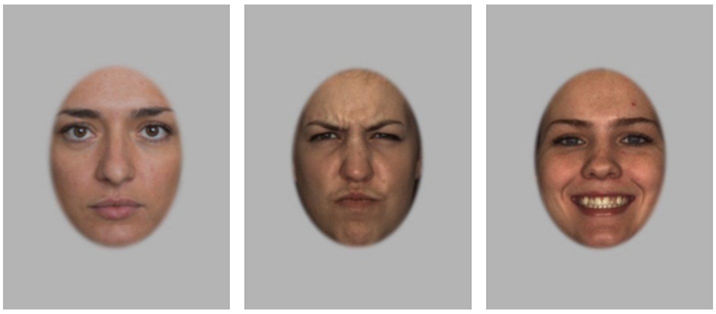

Figure 7. Examples of the neutral (left), angry (central) and happy (right) facial expressions used as stimuli in the static condition.

4.2.4 Procedure

The experiment took place in a dimly lit, audiometric and electrically shielded cabin, where participants were seated on their mother's lap, at approximately 60 cm from a 24-inch monitor, in a behavioural state of quiet alertness. Stimuli were presented using E-Prime software v2.0 (Psychology Software Tools Inc., Pittsburgh, PA). Mothers were instructed to remain as still as possible and to keep silence during the experimental session in order to avoid any acoustic interference. The whole experiment was recorded through an infrared videocamera, hidden over the monitor, which fed into the data acquisition computer, located outside the testing cabin. The data acquisition computer displayed the live image of the infants' face and body to allow the experimenter to pause or terminate the session when the infant became too fussy. The experimental session was terminated when infants attended to the maximum number of trials (n = 270) or got tired of the experiment. Stimuli were presented randomly to each infant, with the only constraint that facial expressions from the same category could not occur more than three times consecutively. The interstimulus interval varied randomly between 900 and 1100 ms. The duration of the recording for the present paradigm was around 10 minutes.

4.2.5 EEG recording and processing

The electroencephalogram (EEG) was recorded with a 128-electrode HydroCel Geodesic Sensor Net (Electrical Geodesic Inc., Eugene, OR). EEG was recorded continuously and referenced to the vertex electrode (Cz). The signals were amplified using an EGI NetAmps 300 amplifier with a sampling rate of 500 Hz. Impedances were checked online prior to the beginning of the session and considered acceptable if lower than 50 KΩ. EEG data were processed offline using NetStation v4.6.4 (Eugene, OR). The signals were band-pass filtered with 0.3-30 Hz, baseline corrected to the average voltage during the 100 ms before stimulus onset and re-referenced to the algebraic mean of all the channels. For eliminating artifacts, segmented data were automatically rejected whenever the signal exceeded ± 200 μV at any electrode and then hand-edited for eye and body movement artifacts. Specifically, trials in which eye-blinks, eye-movements or in which substantial drifts were clearly visible in the ERP data were excluded from further analysis. Data from individual electrodes were also manually rejected if there were artifacts resulting from poor contact or movement. Entire trials were excluded if more than 18 sensors had been rejected. Of the remaining trials, individually excluded channels were replaced using spherical spline interpolation. Across participants, the mean number of trials contributing to the average ERP and statistical analyses was 19.9 (HA: 20.2; AN: 19.8; NE: 19.8) per emotion in the dynamic condition, and 17.8 (HA: 19.5; AN: 17.1; NE: 16.8) per emotion in the static condition. A similar number of trials contributed to the final analysis for each condition, $F(3,63) = 2.016$; $p > .12$. Inspection of the grand-averaged waveforms revealed a well-defined Nc component over fronto-central electrode sites (Taylor-Colls & Fearon, 2015), subsequently analysed within a time window of 330-530 ms. The individual electrodes that were selected covered one channel grouping for each hemisphere; left: 35, 36, 41, 42, 47; right: 93, 98, 103, 104, 110 (see Figure 8).

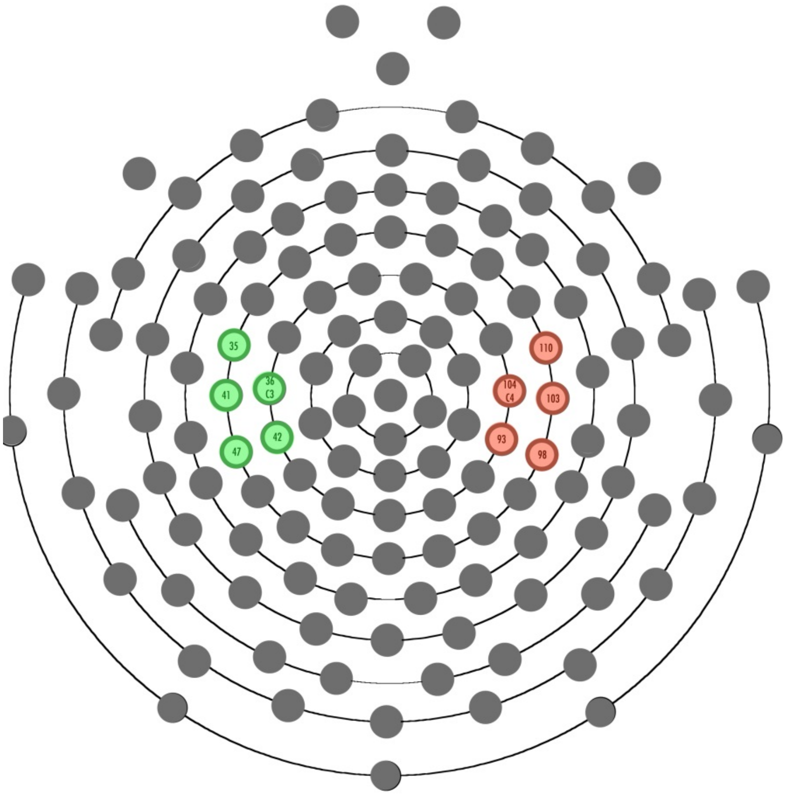

Figure 8. Electrode clusters selected for the Nc component. The left electrode cluster is highlighted in green, the right one is in red.

4.2.6 Data Analysis

The analysis performed on the mean amplitude and peak latency of the Nc were conducted using IBM SPSS 22.0 (IBM Corporation, Armonk, NY, USA) and involved the use of a 2 x 3 x 2 repeated measures ANCOVA. The analysis included one between-subjects factor (Condition: Dynamic and Static) and two within-subjects factors: Emotion (AN, HA, NE) and Hemisphere (left and right). Additionally, Surgency and Negative Affect temperamental traits were entered as continuous covariates. Similarly to Taylor-Colls & Fearon (2015), temperament effects were followed up by correlational analyses between temperament and difference scores based on a subtraction of average amplitudes or latencies for neutral faces from emotional faces[5] (i.e., AN-NE; HA-NE). All statistical tests

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[5] Note that for latency values a positive/higher differential score indexes a slower (relative) attention allocation to emotional expressions, whereas a negative score indexes a faster (relative) attention allocation to emotional expressions.

were conducted on a .05 level of significance (two-tailed), and paired-sample *t*-tests were corrected for multiple comparisons using the Holm-Bonferroni stepwise procedure.

4.3 Results

4.3.1 Amplitude

Results obtained for amplitude values revealed that, irrespectively of the experimental condition (i.e., Static or Dynamic stimuli), the Nc was more negative over the left (M = -10.18 μV) than the right (M = -9.44 μV) hemisphere, as highlighted by the main effect of Hemisphere, F(1,22) = 4.564, $p < .05$. This effect was qualified by a marginally significant Hemisphere x Surgency interaction, F(1,22) = 3.734, $p = .066$, that was followed up by non-significant correlations (all *p*s > .24). All other effects were not significant ($p > .11$).

4.3.2 Latency

Analysis of the peak latency of the Nc showed a significant Emotion x Hemisphere x Condition interaction, F (2,44) = 3.487, $p < .05$. To follow-up this interaction we analyzed emotion effects over the two hemispheres for the static and dynamic conditions separately. For the static condition (Figure 10a), a marginally significant main effect of emotion, F (2,28) = 2.662, $p = .087$, was observed, reflecting quicker Nc latencies elicited by happy (M = 397 ms) compared to both neutral faces (M = 410 ms), t(14) = -2.11, $p = .05$, and a trend towards faster response to happy compared to angry faces (M = 412 ms), t(14) = 1.94, $p = .073$ (Figure 9). All other effects were not significant ($p > .30$).

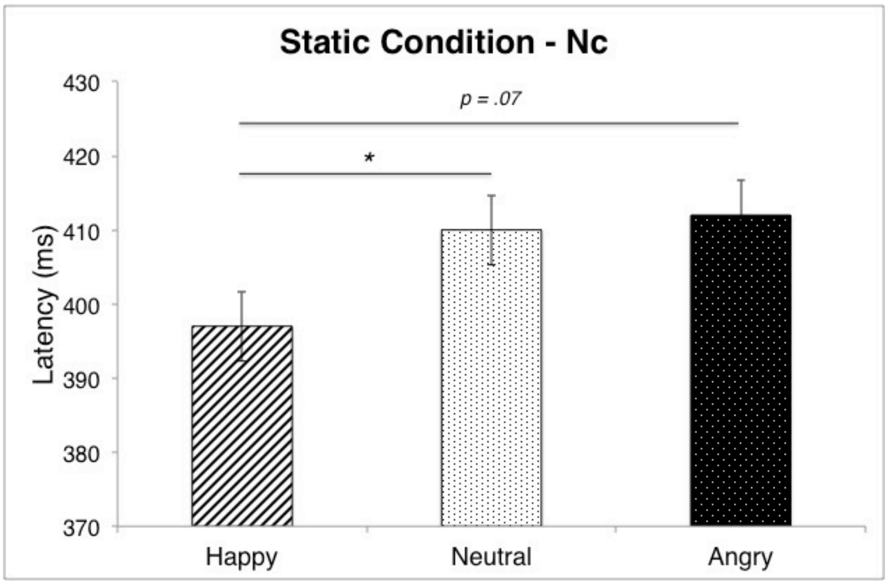
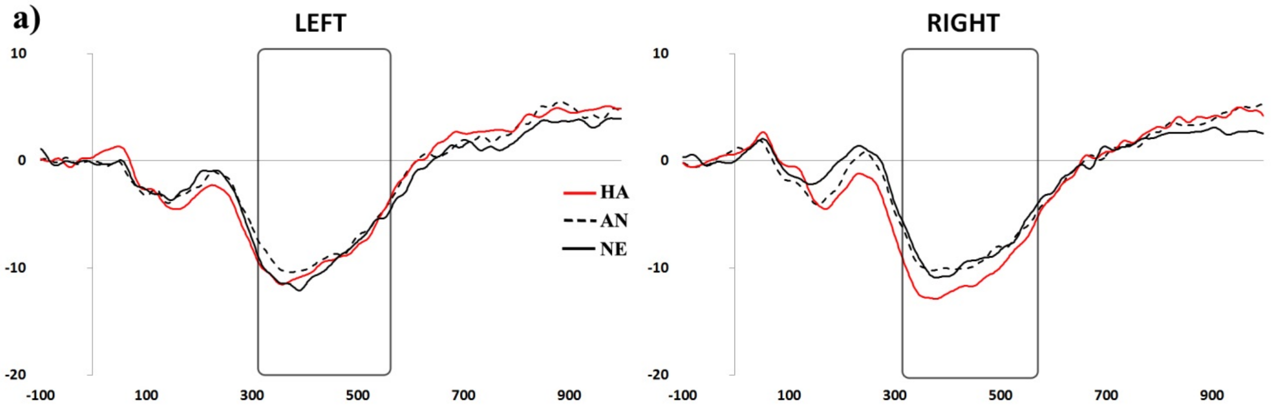


Figura 9. Mean peak latency values (ms) recorded in response to happy, neutral and angry static facial expressions within the 330-530 Nc time window.

For the dynamic condition (Figure 10b), only a marginally significant main effect of hemisphere, F(1,11) = 4.428, *p* = .059, was observed, with Nc latency peaking more quickly over the left (M = 434 ms) as compared to the right (M = 457 ms) hemisphere. Results also showed a a main effect of Hemisphere,



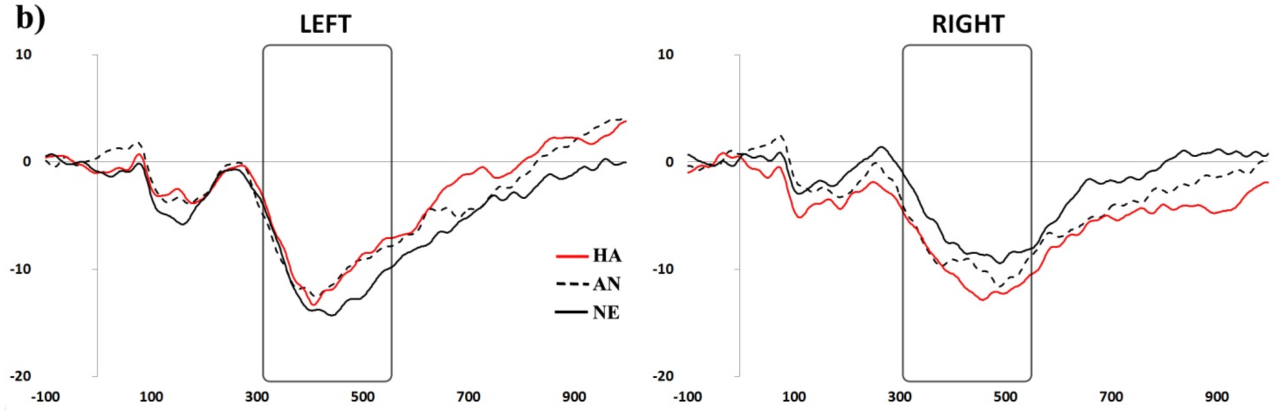


Figure 10. Grand average event-related potential waveforms for happy (solid red), angry (dashed black) and neutral (solid black) faces over the left (C3) and right (C4) frontocentral regions for 7-month-old infants tested in the static (a) and dynamic (b) conditions.

F(1,22) = 5.037, *p* < .05, with a quicker peak reached over the left (M = 419 ms) than the right (M = 430 ms) hemisphere. This effect was qualified by a marginally significant Hemisphere x Negative Affect interaction, F(1,22) = 4.102, *p* = .055, that was followed-up by non-significant correlations (all *p*s > .35). Finally, there was a significant Emotion x Hemisphere x Surgency interaction, F(2,44) = 5.788, *p* < .01. Correlations between Surgency and the Nc difference scores over the left and the right hemispheres were examined, and a marginally significant correlation for the relative Nc latency for happy faces over the left hemisphere (*r* = -.38, *p* = .058), and a significant correlation for the relative Nc latency for angry faces over the left hemisphere (*r* = -.48, *p* < .05) were found. The direction of the two correlations implies that infants with higher Surgency ratings had faster (more negative scores) Nc latency responses to happy and angry faces, relative to neutral faces. Two scatterplots showing these associations are presented in Figure 11.

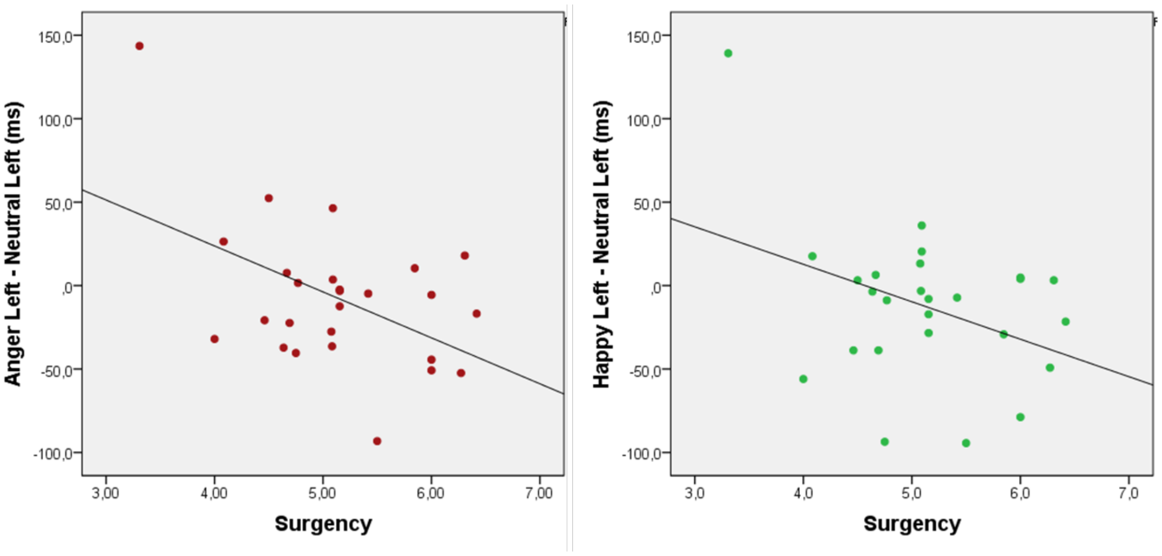


Figure 11. Scatterplots of angry minus neutral (left) and happy minus neutral (right) Nc peak latency as a function of the Surgency temperament scale

4.4 Discussion

The aim of the present study was two-fold. The first was to compare the electrophysiological correlates elicited by dynamic and static faces displaying positive (i.e., happy), negative (i.e., angry), and neutral facial expressions in 7-month-old infants. This was done in order to assess whether the attentional activation pattern to static facial expressions as obtained in previous research would extend also to dynamic emotional expressions or if dynamic facial expressions facilitate or impair performance by augmenting or diminishing attention capture towards angry expressions. The second aim of the experiment was to investigate whether temperamental differences may affect attentional response patterns to expressions of emotions.

As for the first aim, a difference in the latency of the attentional response between the static and dynamic conditions was highlighted. Consistent with existing findings obtained on amplitude values of the Nc (e.g., Grossmann et al., 2007), results showed that static happy faces elicited a faster Nc as compared to angry and neutral facial expressions. Under the assumption that an earlier Nc reflects faster allocation of attentional resources to the considered stimulus (Reynolds & Richards, 2005), these results indicate that 7-month-old infants' attention was triggered more quickly by happy facial expressions than by neutral and angry expressions. In line with Grossmann and colleagues' claims (2007), these results might be due to the fact that the emergence of the attentional bias toward angry faces occurs at a different pace as compared to that for fearful faces. Looking time measures reveal that both 7- and 12-month-old infants look longer at happy than at angry facial expressions; on the other hand, 7-month-olds' ERPs reflect a larger Nc to happy than to angry faces, whereas 12-month-olds' ERPs show an adult-like enhanced posterior negativity to angry faces (Grossmann et al., 2007; Schupp et al., 2004). This pattern of electrophysiological findings suggests that by 7 months infants may not detect the threat conveyed by an angry face, thus allocating more attentional resources to the preferred happy than to angry faces. However, by 12 months of age, the adultlike pattern of brain responses suggests that infants detect an angry face as a threatening signal, as demonstrated by behavioral and electrophysiological experiments, where they look less and show an enhanced attention allocation to angry faces (Adams & Kleck, 2005; Vaish, Grossmann & Woodward, 2008). It is possible that only when infants begin independent locomotion (at the end of the first year of life) mothers begin to use prohibitions and to express negative emotions such as anger and fear toward their infants as they are now mobile enough to face real dangers (Bertenthal & Campos, 1990; Campos et al., 2000). The early predominance of positive expressions might positively skew infants' psychological reference point so that later on, the novelty of negative emotions causes a negativity bias (see also Baldwin & Moses, 1996; Mumme, 1993), with fearful faces starting to attract more attention earlier than angry expressions (Vaish et al., 2008).

Differently from adult findings in which dynamic, especially happy, facial expressions tend to enhance neural activity (Recio et al., 2011), as demonstrated by a greater activation in structures normally associated with emotion processing, results obtained in the current study in the dynamic group suggest that motion does not seem to facilitate the processing of emotional stimuli. Indeed, no effect of emotion and no difference between anger, happiness or neutral expression was found in the dynamic condition for the Nc component. However it is important to note that presented data are only preliminary and that data collection is still on-going. It is thus possible that the lack of significant emotion effects might be due to the smaller number of infants in the dynamic condition. Nonetheless, it is also possible that the neural structures responsible for the attentional processing of moving and static emotional face stimuli mature throughout development and may start to show signs of adult-like responses towards the end of the first year of life. This result is in line with observations that neural responses elicited by faces become more adult-like across development (de Haan et al, 2003; Halit et al, 2003). An interesting possibility is that infants are more skilled at processing emotions from static than dynamic faces because of the different rates of maturation of the visual pathways involved in processing form (i.e., “ventral/what stream”) and motion (i.e., “dorsal/where stream”). Indeed, research suggests that the dorsal visual stream, involved in spatial transformation and movement processing, undergoes a longer developmental time course than the ventral visual stream, which is involved in processing shapes and textures (Hickey, 1977), with both visual streams developing well beyond infancy. One possible alternative explanation for results obtained in the dynamic condition is that, although videos provide more ecological stimuli, it is difficult to control for differences in the level of expression portrayed and the temporal aspects of the emotional expression.

Even though no difference in attentional processing of emotional expressions was found, one possible limitation of the dynamic stimuli is that the neutral face chosen for the start of the stimulus may determine when the emotional expression is first perceived.

Indeed, there is debate as to whether neutral faces can really be considered emotion-less (Iidaka et al., 2005; Somerville et al., 2004), and the choice of using a neutral face as a starting point for the emotional expression may influence the time point at which the emotional expression is perceived. For example, if the neutral face was perceived as more positive than negative in nature, the point at which a negative emotion, like anger, could be perceived first might be different from the time point at which happiness is perceived. Additionally, the fact that in the current study dynamic stimuli generated a faster attentional response over the left as compared to the right hemisphere suggests that the connections between the left amygdala and the prefrontal cortex may be more influential in emotion processing at an early stage, with the right subcortical-cortical pathway becoming more active with development. Indeed, previous studies have revealed a pattern of left-lateralised amygdala and prefrontal activation in adolescents when viewing overtly presented affective stimuli (Killgore & Yurgelun-Todd, 2004). Thus, it is possible that the neural networks involving the amygdala go through a period of cerebral organisation (Hasan et al, 2007; Shaw et al, 2008), neuronal specialization (Rabinowicz et al, 2009), and volume changes in (Yurgelun-Todd, Killgore, & Cintron, 2003). Additionally, previous electrophysiological studies show that connections between the amygdala and the prefrontal cortex may become more right lateralised with maturation towards adulthood.

For what concerns the second aim of the study, it was investigated whether specific temperamental traits might affect the attentional processing of emotions. Indeed, it is possible that the development of attentional biases towards emotional facial expressions might be related to individual differences in the maturation and development of cortical networks in the brain (Leppanen & Nelson, 2009). With respect to the two traits of infant temperament considered, obtained results suggest that infants with a stronger tendency to approach novelty (i.e., higher surgency scores) had faster attentional responses to both happy and angry faces, relative to neutral faces. These results further add to existing evidence and demonstrate that interesting individual differences can be found when investigating the attentional processes that generally occur in 7-month-old infants. Indeed, results reveal that infant temperament is related to differences in the neural processing of emotional facial expressions, thus demonstrating that it critically shapes the way in which infants' brains respond to emotional information.

The finding that infants who scored high on the Surgency scale showed faster Nc response to happy and angry expressions over the left hemisphere, indexes a faster allocation of attention to happy and angry facial expressions than infants who scored low on the same scale. This result shows that high levels of engagement with the environment, rather than lowering infants' neural response to happy and angry facial expressions, appears to heighten infants' attentional responsiveness to emotional stimuli. Unlike earlier studies, we did not find significant associations between negative affect temperamental trait and attentional response elicited by negative emotional expressions (e.g., Taylor-Colls & Fearon, 2015; Rajhans, Missana, Krol & Grossmann, 2015). This difference between the current and previous studies might depend on the fact that previous studies used fearful faces rather than angry expressions. Moreover, methodological differences related to stimulus material could also have played a role. In fact, previous studies employed only static facial expressions while in the current experiment analysis were carried out by comparing activation elicited by static and dynamic stimuli.

It is important to note that presented results are only preliminary and that data collection is still on-going. It is thus possible that the lack of a clear emotion specificity emerged from the analysis on the effects of temperamental differences in the processing of emotional expressions might be due to the small samples size. Thus, it will be important to increase the sample size in order to provide more robust findings and to perform further studies to corroborate the obtained results. Moreover, the correlation between neural response and attention to facial features (e.g., eye and mouth regions) could be assessed in future studies by recording infants' eye movements through an eye tracking apparatus whilst ERPs are recorded. Specifically, tracking infants' eye movements would provide information that are critical in order to assess whether there is a bias in attention towards the eye or mouth regions while emotions are unfolding in the dynamic condition and whether this bias differs with age.

Future studies should also investigate the effects of motion on the face-sensitive N290 and P400, as the possible integration of these components to the adult N170 may result in motion influencing the perceptual processing of presented emotional expressions. Finally, as temperamental individual differences seem to affect attentional patterns to emotional stimuli, future research might also explore additional sources of individual differences from multiple levels of observation, ranging from gene polymorphism expression (Grossmann et al., 2011) to the quality of mother-infant relationship.

CHAPTER 5

THREE-YEAR-OLDS' RAPID FACIAL EMG RESPONSES TO EMOTIONS EXPRESSED BY FACES AND BODIES[6]

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[6] Results reported in this chapter were previously published in: Geangu, E., Quadrelli, E., Conte, S., Croci, E., Turati, C. (2016): Three-year-olds' rapid facial EMG responses to emotional facial expressions and body postures. *Journal of Experimental Child Psychology,*144, 1-14

ABSTRACT

Affect sharing or the ability to feel the emotion another person experiences is the defining component of empathy. One proposed potential mechanism responsible for affect sharing is emotional mimicry. Evidence has emerged to suggest that spontaneous facial mimicry is recorded in school age children in response to images of adults displaying basic facial emotional expressions. However, there is little to no evidence to suggest the existence of mimicry of others’ emotional expressions from infancy to preschool age. The facial muscle activity when observing emotional expressions can be measured using facial electromyography (EMG) in adults and older children. This study investigates whether facial muscle activity of 3-year-old children in response to emotional expressions is driven by mirroring or reconstructive mechanisms. We recorded EMG activation from the zygomaticus major and frontalis medialis muscles to presentation of happy, angry, fearful and neutral facial and bodily expressions. Results highlighted no specific EMG activation in response to bodily expressions. However, observing happy faces generated an increased activation of the zygomaticus major and decreased activation of the frontalis medialis. On the contrary, observing angry faces elicited the opposite pattern of activation. In sum, the study suggests that preschool children muscle activity results from the possible interplay of both reconstructive and mirroring mechanisms.

5.1 Introduction

Imitation and emotion understanding have long been studied by developmental and social psychologists and the neural circuits that underpin these phenomena are accumulating great interest in recent times, fostered by discoveries in cognitive neuroscience. Human infants are the most imitative creatures in the world. Even though sporadic imitation has been documented in other species, humans imitate a larger range of behaviours than other species, they do it spontaneously and without any specific training (Decety & Meltzoff, 2011).

Emotions play a key role in our lives and understanding the emotions of other people is essential for adequate social functioning. Although people's more subtle emotions can remain puzzling, we are more often capable to catch what is going on in other individuals. However, how our brain associates feelings to the facial expressions of other people's emotions remains poorly understood. Mere observation of emotional expressions of the people we interact with tends to elicit covert mimicry of the observed facial expressions. For example, people tend to spontaneously smile when they observe another person smile, because seeing and making a smile is frequently paired in our social environment. Our responses can vary from being overt, observable with the naked eye, to being covert and only detectable by using specific electrophysiological measurements (i.e., electromyography – EMG) of the muscles involved in generating these expressions. Additionally, covert responses can vary from being extended to long periods of activity to being very rapid and subtle, also called rapid facial responses (RFRs).

Forms of emotional expression congruency can be recorded in humans from the first months of infancy (e.g., Haviland & Lelwica, 1987), throughout childhood (e.g., Beall et al., 2008; Deschamps et al., 2013; de Wied et al., 2006; Oberman, Winkielman, &

Ramachandran, 2009) and adulthood (e.g., Bavelas et al., 1986; Hess & Blairy, 2001; Magnee et al., 2007), and the tendency to automatically mimic and synchronize facial expressions, vocalizations, postures, and movements with those of another person has largely been documented (Hatfield & Cacioppo, 1994). Importantly, these expressivity-matching responses have been attributed essential socio-emotional functions, with relevance for emotional contagion (Hatfield & Cacioppo, 1994), empathy (Decety & Jackson, 2004; de Vignemont & Singer, 2006), social communication (Hess & Burgeois, 2010), as well as social coordination through affiliation (Lakin & Chartrand, 2003), to name just a few. Despite a large body of research investigating the mechanisms underlying the variety of these abilities and their functions in adults, we still have limited knowledge about their development (Beall et al., 2008; Jones, 2007).

As previously discussed in Chapter 1, two main theoretical assumptions have been put forward regarding the underlying processes of emotion understanding. On one hand side, several researchers regard the unconscious and spontaneous muscular activation, or rapid facial responses (RFRs), as deriving from motor responses, triggered by observing others' emotional expression, without any direct affective underpinnings, usually coined as mimicry (Bavelas et al., 1986; Chartrand & Bargh, 1999; Hoffman, 1984; Meltzoff & Moore, 1977). Relying on the facial feedback hypothesis, according to which one appraises one's own emotions by perceiving their bodily concomitants, Sonnby-Borstrom (2002) proposed that muscle activation enables one to automatically share and understand another's emotions. Mimicking others' emotional displays is presumed to rely on mirroring mechanisms, whereby perceiving the pattern of motor behaviour specific for expressing different emotions activates in the observer the same motor response (Hatfield & Cacioppo, 1994; Meltzoff, 2007; de Waal, 2009). When observing the facial expressions of another person, the muscle contractions involved in the given expression are directly reproduced within the premotor cortices of the observer (Bastiaansen, Thioux & Keysers, 2009).

At the neural level, the matching between observed facial expressions and spontaneous mimic response might be based on the involvement of the mirror neuron system (Carr et al., 2003). A similar neural mechanism underlying action understanding has been proposed to mediate our understanding of the emotions of others. Specifically, when we see someone experiencing an emotion, we automatically internally represent the state associated with that emotion and activate the same neural structures that are involved in the production of emotion expressions (Gallese, Keysers & Rizzolatti, 2004; Pfeifer et al., 2008; Lee et al., 2006, 2008). The insula, which is thought to represent a neural correlate of emotional contagion, together with areas such as the primary somatosensory or motor cortices, are equally active during observation of emotional expressions and when the same emotion expression is experienced (Jabbi & Keysers, 2008; Carr et al., 2003). According to this theoretical account, once elicited, the RFRs can lead to a change in the affective state of the observer through associations with previously experienced emotions, generating emotional contagion. Indeed, scholars supporting this view state that given that our brain has a lifelong experience with the correlation between our own facial configuration and our personal internal affective states, the simulation of other people's facial configuration could trigger matching affective states (Cappella, 1993; Hoffman, 1984; Laird et al., 1994; Lipps, 1907).

In support of this view, it has been shown that adults' vocal (Hatfield et al., 1995), facial (Davis et al., 2010; Manstead, 1988; Matsumoto, 1987), and postural (Duclos et al., 1989; Stepper & Strack, 1993) cues are capable to elicit or bias experienced emotions. Intriguingly, there is also some evidence that posing or blocking emotional displays can influence experienced emotional state as well as their evaluation of the emotional stimuli (Strack et al., 1988; Niedenthal et al., 2001).

However, even though on first sight evidence for the motor theory of RFRs seems to be highly convincing, recent research cast doubts on the assumption that mimicry represents some sort of automatic motor resonance with another person's affective display. A reconstructive explanation of RFRs suggests that these responses might be considered as affective reactions, possibly being the result of more complex mechanisms involving a combination of motor, affective, and cognitive processes (Beall et al., 2008; Burgeois & Hess, 2008; Hess et al., 1998; Jones, 2007; Moody & McIntosh, 2006, 2011; Moody et al., 2007). Several investigations demonstrate the influence of top-down processes on mimicry, such as those associated with the relationship between empathizer and target (Lakin & Chartrand, 2003), the affective state of the observer (Moody et al., 2007), or the perspective from which pain in others is witnessed (Lamm et al., 2008).

Indeed, the change in the affective state is not mandatory in all social situations and emotional mimicry has also been proposed to serve communicative functions and to be guided by cultural norms (Hess & Burgeois, 2010; Lakin et al., 2003;). Smiling in response to others' smiles can signal acknowledgement of affiliative intentions as well as the desire to affiliate, and may not necessarily lead to a change in the observers' affective state (Hess & Blairy, 2001; Hess & Burgeois, 2010; Hess et al., 2000; Knutson, 1996). The emotions of other people are usually highly salient for us, conveying important information for our social success and survival. Processing such emotional information can elicit a change in our affective states as observers, which is further expressed through face, body posture, and prosody.

According to this view, the change in affective state and the corresponding RFRs will not necessarily be congruent with the observed facial expression, but rather congruent with the emotional interpretation and the affective state of the observer. Moreover, any emotional expression modality and any emotional information can elicit such responses. Conversely to the above-mentioned studies on detection of facial expressions and supporting the reconstructive account of RFRs, Hess & Blairy (2001) could not demonstrate a direct link between the degree of facial mimicry and accuracy of emotional recognition. Moreover, studies in clinical populations with participants affected by disorders of facial expressivity (e.g., facial paralysis or Möbius syndrome) did not highlight any clear emotion recognition impairment (Calder et al., 2000; Keillor et al., 2002). Additionally, research investigating RFRs elicited by expressions of anger seems to favour this latter perspective. Indeed, angry expressions, similarly to what happens when perceiving fearful expressions, elicit an augmented allocation of attention and a fast activation of the limbic system, possibly because they are perceived by children and adults as threat signals (Kret et al., 2011; Monk et al., 2008; Nelson & Nugent, 1990; Pichon et al., 2009). From an evolutionary perspective, feeling fear in response to others' anger might have an adaptive value, since it can facilitate removal from dangerous situations (LeDoux, 2000; Moody et al., 2007). It has been shown that adults in a high state of fear respond very fast to observing pictures of angry faces, with an increased activation of the facial muscles involved in expressing fear (Moody et al., 2007). This suggests that the RFRs are more related to the observer's internal emotional state rather than with the observed expression.

The RFRs relying on emotion-specific programs can also be to a certain degree automated. When adults are presented with masked emotional faces and body postures, which they are not able to consciously see, they nevertheless show RFRs consistent with the emotional valence of the stimuli (Tamietto & de Gelder, 2008). The modulation of the RFRs by early cognitive processes may explain the dissociation in the chain of processes elicited by perceiving others' emotions, activating either mirroring mechanisms or top-down processes. Neuroimaging studies show that both the emotion related circuitries and cortical networks typically associated with mirroring mechanisms are activated during imitation and passive viewing of facial expressions of emotions. However, due to the poor temporal resolution of the method they cannot disambiguate which mechanism determines the other (Carr et al., 2003; Lee et al., 2006, 2008; Pfeifer et al., 2008).

It is widely agreed that at least beginning with the age of 20 months children systematically reproduce in a spontaneous manner various non-emotional motor gestures observed in adults (Flynn & Whiten, 2008; Hopper et al., 2010; Jones, 2007), and evidence exists from Meltzoff's seminal studies that newborns less than 1 hour old can mimic human actions (e.g., tongue protrusion) (Meltzoff & Moore, 1977). However, a less clear picture emerged so far with regards to their facial responses to others' expressions of emotions. Human infants seem to be biologically predisposed to affectively resonate with basic affective – positive and negative – states of others. Emotional contagion occurs when the vocal, facial and gestural cues of one individual generate a similar state in the perceiver (see Eisenberg, 2000, for a recent review). Newborns' contagious crying in response to others' cries has generated much theoretical debate in developmental psychology (Martin & Clark, 1987; Geangu et al., 2010). Moreover, by 10 weeks of age, infants respond differently to three maternal affect expressions when the presentation is simultaneously facial and vocal – joy, anger, and sadness, and can mirror joy and anger expressions (Haviland & Lelwica, 1987). Therefore, infants might be equipped with early predispositions subserving basic and vital functions, which might subsequently be shaped to allow them in the first few months of life to engage in face-to-face interactions with caregivers, essential for mutual regulation of emotional engagement (Trevarthen, 1979). Additionally, evidence suggests that by middle childhood children respond to others' affect, more easily negative affect, with congruent emotional states and understand how and when to regulate the display of emotion depending on social experiences and relying on the cognitive prediction of how they will be perceived by others (Decety & Svetlova, 2012; Gnepp & Hess, 1986).

However, only few studies specifically investigated children's RFRs to others' emotional displays by using EMG recordings of the facial muscles. Children between the ages of 6- and 12-years show selective and congruent activation in their facial muscles in response to observing a variety of adult and child emotional facial expressions (i.e., happiness, anger, sadness, fear, and disgust) presented in either a static or dynamic way (Beall et al., 2008; Deschamps et al., 2014; de Wied et al., 2006; Oberman, Winkielman, & Ramachandran, 2009), leading scholars to assume that RFRs are the result of mirroring mechanisms (Deschamps et al., 2014; de Wied et al., 2006; Oberman, Winkielman, & Ramachandran, 2009). Moreover, endorsing this view, one study using fMRI with children, demonstrated that passively observing facial expressions leads to an increased activation of the cortical areas known to be part of the MNS (Pfeifer et al., 2008). Some studies, however, suggest that children's RFRs may also involve affective processes. Specifically, using EMG Beall et al. (2008) recorded facial muscular activation in response to static adult facial displays of happiness, anger, and fear from 7- to 12-year-old children. Similarly to the other studies, an increased activity in the zygomaticus major (i.e., smiling muscle) was recorded when children looked at happy faces. Unlike in the other developmental studies, but similarly to some adult investigations (Moody et al., 2007; Magnée, de Gelder, Van Engeland, & Kemner, 2007), seeing angry faces elicited a selective increased activation of the medial frontalis muscle (i.e., muscle involved in fear expression) (Darwin, 2002; Ekman, 1979). Therefore, school-aged children seem to display a facial expression that matches their affective state, in this case fear, in response to anger as a potential threat (Monk et al., 2008; Nelson & Nugent, 1990).

Discrepant results might be due to the fact that most of the studies in which children react with RFRs matching the perceived expression use active tasks in which participants are asked to specifically pay attention to the emotional expression and to verbally label it (Oberman et al., 2009; de Wied et al., 2006). This increased attention to the emotional expressions may have influenced subsequent processing, activating those mechanisms involved in mimicry (Achaibou et al., 2008). Indeed, when individuals focus their attention on mimicking a facial expression, MNS cortical areas are more active than during passive viewing (Pfeifer et al., 2008).

Given that most research on emotional RFRs focused on children over 6-years of age, the aim of the current study is to reduce this gap by investigating 3-years-old children's RFRs using EMG measurements of facial muscles activity. In order to help disambiguate the mechanisms involved in children's RFRs they will be presented with emotional stimuli containing cues about the motor acts required for mimicking the associated expression (i.e., faces) and emotional stimuli in which such information is absent (e.g., emotional body postures). Indeed, if RFRs are equally present in response to both stimuli categories, one might deduce that affect processes are responsible for the observed muscular activation (de Gelder et al., 2004; Magnée et al., 2007; Tamietto & de Gelder, 2008). By doing this, the current study will sought to test whether the pattern of RFRs in preschool-aged children is consistent with a mirroring interpretation or could also be regarded as a result of a reconstructive mechanism.

Taking into account that by the age of 3 years, children recognize and correctly label both bodily and facial expressions of emotions (Nelson & Russell, 2011), we present 3-year-old children with static images of faces and body postures displaying happy, anger, fear, and neutral emotional expressions. Recording the selective activation of the facial muscle representative for a certain emotional expression (i.e., zygomaticus major for happiness, corrugator supercilii for anger; frontalis medialis for fear) in response to both faces and body postures would be more consistent with an emotional processing interpretation (Magnee et al., 2007b; Tamietto & de Gelder, 2008). This idea would find further support in the finding that observing displays of anger elicits the selective activation of the frontalis medialis, the facial muscle specific for expressing fear (Beall et al., 2008)

5.2 Methods

5.2.1 Participants

A total of 22 healthy 3-year-old children (10 females; mean age = 40.42 months, age range = 36.50 – 47.57 months) were included in the final analysis. Nineteen additional children were tested, but then discharged from the final sample because they refused to watch the stimuli (n = 7), moved too much during trial presentation (n = 8) and did not complete the minimum number of trials required for data analysis (n = 4). The protocol was carried out in accordance with the ethical standards of the Declaration of Helsinki (BMJ 1991; 302:1194) and approved by the Ethical Committee of the University. Parents gave written informed consent for their children to participate in the study.

5.2.2 Stimuli and Procedure

Participants were presented with color photographs of human female faces and bodies displaying happy (HA), angry (AN), fear (FE) and neutral (NE) expressions on a 24” LCD monitor at a distance of approximately 80 cm. Face stimuli were selected from the Radboud Faces Database (RaFD; Langner et al., 2010), while body stimuli were extracted from the Bodily Expressive Action Stimulus Test database (BEAST; de Gelder & Van den Stock, 2011). Both face and body stimuli were screened and selected by 3 adult raters for their emotional valence. In order to ensure that the processing of the emotional information expressed through body postures is not influenced by the facial expression, all faces on the body stimuli were masked with an opaque patch (Figure 12). Each stimulus was presented at the center of the screen on a grey background for 500 ms and was preceded by an inter-stimulus interval of 2000 ms consisting of a grey screen with a central fixation cross, similar to previous studies using this paradigm (Oberman et al., 2009). In a completely within-subjects design, face and body stimuli were presented in alternating blocks. Each block consisted of 20 randomly presented stimuli (5 for each emotional expression), with the only constraint that the stimuli displaying the same emotion could not occur more than twice consecutively. The order of presentation was counterbalanced across participants, so that half of them started the experiment with the body and the other half with the face condition.

Figure 12. Examples of the face (a) and body (b) emotion expressions used as stimuli in the study.

Upon completing informed consent procedures, participants' faces were cleaned and scrubbed with NuPrep Gel to ensure good quality signal recording from the EMG electrodes. Children sat on a chair in a dimly lit, audiometric and electrically shielded cabin. An experimenter was present throughout the entire procedure so that participants' movements were minimized and their interest and attention were maintained. Children were instructed to relax, to not move or talk, and to watch the pictures on the screen. No other instruction was given to the participants. In order for the children to familiarize with the procedure and to ensure that they understood the instructions, each session started with 8 practice trials in which an equal number of faces and bodies were displayed. Total duration of the task was approximately 15 minutes and at the end of the session, participants received a small reward.

5.2.3 sEMG Recordings and Data reduction

EMG was used to record the levels of muscle activation for the zygomaticus major (raises the cheek), the medial frontalis (raises the brow), and the corrugator supercilii (knits brow). These muscles were chosen based on previous studies showing that their activation is a reliable marker for facial expressions of happiness (zygomaticus major), anger (corrugator supercilii), and fear (frontalis medialis) (Cacioppo et al., 1986; Ekman & Friesen, 1976; Frois-Wittman, 1930). A D360 Digitimer electromyograph was used to continuously record the EMG signal from the selected muscles using bipolar montages, following previously established guidelines (Tassinary & Cacioppo, 2000). Ambu Neuroline 700 surface adhesive 4 mm Ag-AgCl electrodes for pediatric use were placed on the child's face at locations corresponding to each muscle. The electrodes were positioned longitudinal to the muscle, with an inter-electrode distance of 10 mm between their centers. Electrodes were positioned on the left side of the face to obtain maximal reactions (Fridlund & Cacioppo, 1986). The reference electrode was positioned just below the hairline, ~3 cm above the nasion. Impedance was kept between 5 and 10 kΩ using a conductive EMG gel (Viasys Electrolyte Gel). The EMG signal was amplified online by a factor of 1000 and recorded at a sampling rate of 1 kHz with a 10-1000 Hz bandpass filter. The EMG signal was filtered offline (150 Hz; high-pass: 30 Hz), and further rectified for analysis using Spike2 software (Cambridge Electronic Design Ltd., Cambridge, UK). Because of difficulties and excessive noise recorded from the corrugator supercilii muscle, data acquired from this electrode site were excluded from further analysis. One consequence of the lack of data from this muscle is that it will make it difficult to draw conclusions regarding the presence of RFRs specific to anger. Nevertheless, considering our prediction of fear RFRs to the emotional stimuli expressing anger, intact recordings of the frontalis medialis will allow us meaningful interpretations of the results in this respect (Beall et al., 2008).

Children's looking time toward the stimuli was coded offline and trials in which they looked at the stimuli for less than 70% of its duration or were moving, were discarded. In order to avoid any spurious effect produced by participants' movements while watching the stimuli, trials were also discarded whenever signal noise and motion artifacts contaminated the EMG recordings. Only children with at least 4 trials per emotion/condition were included in the statistical analyses. Across participants, the mean number of trials contributing to the statistical analyses was 13.02 (HA: 13.09; AN: 12.77; FE: 13.59; NE: 12.64) per emotion in the face condition, and 12.98 (HA: 13.41; AN: 12.82; FE: 13.23; NE: 12.45) per emotion in the body condition. A similar number of trials contributed to the final analysis for each condition, $F(3,63) = 2.016$; $p > .12$

Average amplitude values were calculated for each 100 ms interval from 500 ms pre-stimulus onset to 1500 ms post-stimulus. In order to reduce the impact of extreme values and standardize the observed activation, we transformed raw data in Z scores within participants and muscle sites. Next, each 100 ms interval post-stimulus onset was baseline corrected by subtracting the average amplitude of the 500 ms pre-stimulus interval from the average amplitude of each 100 ms post-stimulus onset interval. Finally, trials of the same emotion and condition were averaged to obtain one value for each 100 ms interval of every trial type. Previous studies with children using a similar paradigm have shown that the facial muscles usually begin to show differentiated activation in response to facial expressions of emotions after 500 ms from stimulus onset, reaching the peak around 1000 ms in the case of longer stimulus presentations (Beall et al., 2008; Oberman et al., 2009), which is also consistent with adult studies (Dimberg, 1982; Dimberg & Petterson, 2000; Moody et al., 2007). Visual inspection of the data in the current study suggested a similar pattern, with the recorded muscles showing differentiated activation between 800 - 1300 ms post stimulus onset. The mean amplitude values for this time window were further analyzed using a 2 (Condition: bodies and faces) x 4 (Emotion: HA, AN, FE, NE) x 2 (Muscle: zygomaticus major and medial frontalis) repeated measures ANOVA. All statistical tests were conducted at .05 level of significance (two-tailed), and paired sample t-tests were corrected for multiple comparisons using the Holm-Bonferroni stepwise procedure. Furthermore, in order to confirm that the EMG activity of a specific muscle changed in response to a certain emotional stimulus, each significant Emotion x Muscle interaction was followed-up by a comparison of the non-baseline corrected EMG data of each condition during the 800-1300 ms post stimulus onset with that recorded during the pre-stimulus 500 ms baseline when a fixation cross was displayed. For this purpose, we used paired t-tests at .05 level of significance (two-tailed).

5.3 Results

Table 1 shows the mean activation (with SDs) for the zygomaticus and frontalis muscles across conditions. The results of the 2 (Condition: face stimuli, body stimuli) x 4

(Emotional expression: happy, anger, fear, neutral) x 2 (Muscle: Zygomaticus Major, Frontalis Medialis) repeated measures ANOVA show a significant interaction between condition, emotion, and muscle, F(3,60) = 6.008, p = .001, η2 = .231. No other significant main effects or interactions were found (p > .291). In order to unpack this interaction 4 (Emotion: happy, anger, fear, neutral) x 2 (Muscle: Zygomaticus Major, Frontalis Medialis) repeated measures ANOVAs were performed separately for each condition.

Table 1. Mean (M) and standard deviation (SD) values of the electromyography activation recorded from the zygomaticus and frontalis muscles in response to facial and bodily expressions of emotion in the 800-1300 ms time window.

		Zygomaticus (Z scores)	Frontalis (Z scores)
		M (SD)	*M (SD)*
Anger	Face	-.075 (.147)	.060 (.122)
	Body	.059 (.208)	-.073 (.219)
Happiness	Face	.090 (.160)	-.057 (.112)
	Body	.013 (.106)	.045 (.123)
Fear	Face	-.038 (.158)	-.024 (.141)
	Body	-.022 (.196)	-.006 (.172)
Neutral	Face	.024 (.163)	.038 (.144)
	Body	-.023 (.234)	.022 (.128)

5.3.1 Facial expressions

A significant interaction between emotional expression and muscle emerged, F(3,60) = 5.310, p = .003, η2 = .210, suggesting a selective activation of the recorded muscles for specific emotional expressions. Post-hoc pairwise comparisons revealed that observing facial expressions of happiness elicits increased activation of the zygomaticus major (M = .090; SD = .160) compared to observing angry faces (M = -.075; SD = .147), t(21) = 3.452, p = .026. In contrast, observing facial expressions of anger led to an increased activation of the frontalis (M = .060, SD = .122) compared to observing happy faces (M = -.056, SD = .112), t(21) = 3.396, p = .036 (Figure 13). The use of standardized Z scores also allowed us to compare the level of activation between muscles. The analysis of the difference in activation for both zygomaticus and frontalis within emotion expression, further supports the results of selective activation by showing that observing facial expressions of happiness leads to activation of the muscle responsible for smiling (zygomaticus major, M = .090; SD = .160) and deactivation of the muscle which raises the eye-brows (frontalis medialis, M = -.056, SD = .112), t(21) = 3.696, p = .014, while observing angry faces leads to activation of the frontalis (M = .060, SD = .122) and deactivation of the zygomaticus (M = -.075; SD = .147), t(21) = 3.387, p = .036. When compared to the baseline, observing happy facial expressions elicited an increased activation of the zygomaticus major (t(21) = 2.392, p = .026), while the angry faces led to a decrease in the activation of the same muscle (t(21) = -2.501, p = .021). In contrast, observing happy faces led to a decrease in the activity of the frontalis muscle from the baseline levels (t(21) = -2.688, p = .014), while the same muscle tended to show an increased activation in response to angry faces when compared to the baseline, although it was marginally significant (t(21) = 1.947, p = .066). No other significant differences emerged.

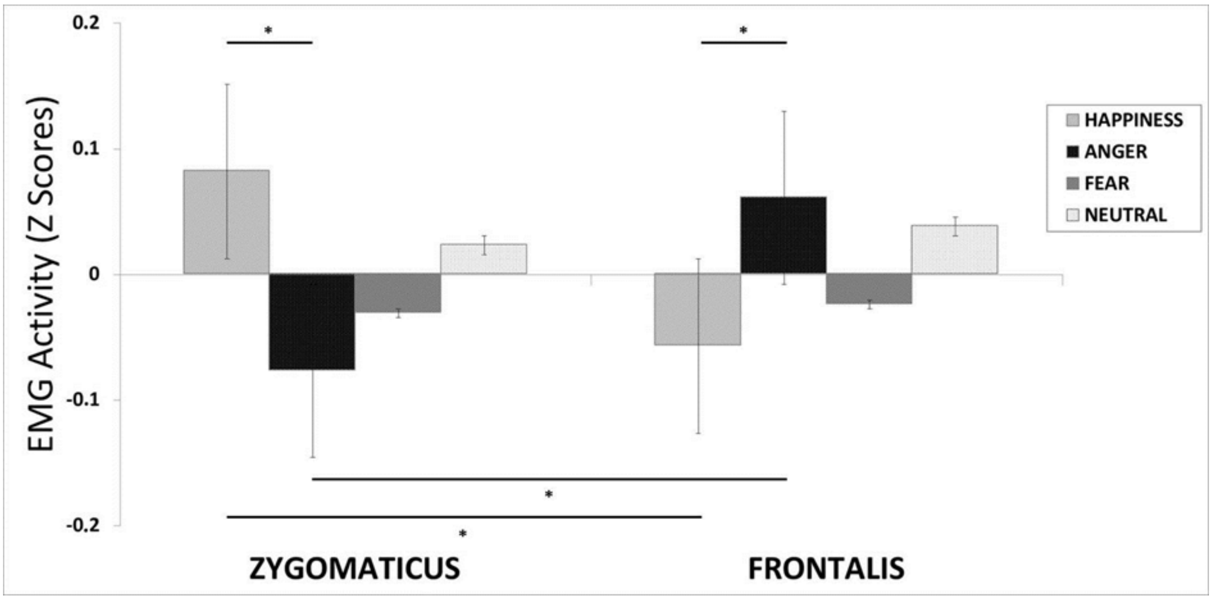

Figure 13. Electromyographic activation recorded from the zygomaticus (left) and frontalis (right) muscles in response to facial expressions of emotion in the 800-1300 ms time window. The error bars represent the standard errors

5.3.2 Bodily expressions

The analysis of the average muscle activation recorded in response to observing body postures did not show a significant interaction between the emotional expression and the type of muscle, Emotion x Muscle, F(3,60) = 2.355, p = .100, η2 = .105 (Figure 14). Similar levels of activation of both zygomaticus major and frontalis medialis were recorded in response to all types of body postures, p > .960.

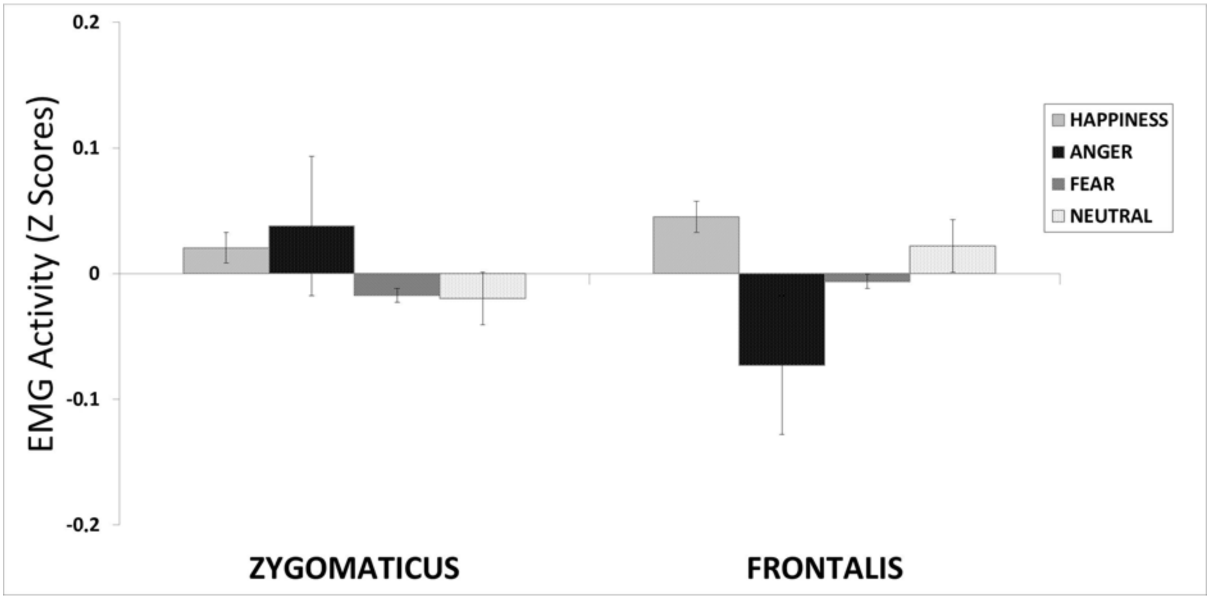

Figure 14. Electromyographic activation recorded from the zygomaticus (left) and frontalis (right) muscles in response to body expressions of emotion in the 800-1300 ms time window. The error bars represent the standard errors.

5.4 Discussion

The aim of the current study was to investigate whether 3-year-olds show RFRs to others' expressions of emotions, and to explore the mechanisms underlying these responses. For what concern bodily expressions of emotions, unlike previous adult studies (e.g., Magnée et al., 2007) current results suggest that observing human bodies with happy, angry, fearful, and neutral postures did not generate selective RFRs. The lack of this specificity effect for bodies in 3-year-old children could apparently speak in favour of the mirroring explanation of RFRs, since at a first glance our results could be interpreted as an outcome of a direct motor reaction in the absence of emotional processes (Bavelas et al., 1986; Chartrand & Bargh, 1999; Hoffman, 1984; Meltzoff & Moore, 1977). In adults, emotion specific facial muscle activity has been recorded in response to both faces and bodies expressing happiness and fear (Magnee et al., 2007; Tamietto & deGelder, 2008). Although only few studies have investigated the development of processing emotional information expressed in body postures, they converge in showing that already by the age of 6-8 months after birth, infants visually discriminate and display different neural processing abilities between positive and negative emotional body postures (Missana, Atkinson, & Grossmann, 2014 Zieber et al., 2014). It is thus less likely that the lack of emotion specific RFRs in 3-year-old children is due to an inability to tell apart between different emotional body postures. Also, 3-years-old children correctly label emotional expressions both for bodies and faces (Nelson & Russell, 2011), suggesting that this ability might not necessarily account for the RFRs to body postures. It is possible that the ability to interpret emotional information conveyed through bodies may develop at a different pace than faces, potentially explaining the lack of emotionally specific RFRs to emotionally body postures in 3-year-old children. In the current study we did not include any measure of affect knowledge to assess whether 3-year-old children discriminate, label, and understand the meaning of different means of emotional expressivity.

Contrarily to the mirroring explanation, RFRs elicited by emotional facial expressions did not fully follow the pattern of muscle activation expected in case of direct matching mechanisms (i.e., zygomaticus major for happiness, frontalis medialis for fear), this explanation is less likely to be the case. Indeed, in line with previous studies with older children (Beall et al., 2008) and adults (Moody et al., 2007), we have shown that 3-years-old children manifest selective RFRs to static facial expressions of happiness and anger. More specifically, it was possible to highlight an increased activation of the zygomaticus major and a decreased activation of the frontalis medialis in response to passive observation of happy faces. On the contrary, observing angry faces elicited an opposite pattern of activation. These findings were supported by the analysis of the EMG responses both when conditions were directly compared one with the other and when each condition was compared to the baseline.

Based on the responses to happy facial expressions alone, both theoretical accounts on the mechanisms subserving RFRs might be supported. In fact, seeing someone smiling could be processed as a cue for pleasant social interaction leading to a happy response in the observer, usually expressed through smile. Likewise, mimicking the observed smile in order to acknowledge others' affiliative intentions would lead to this response (Hess & Blairy, 2001; Hess & Burgeois, 2010; Hess et al., 2000; Knutson, 1996). However, results obtained on muscular activation in response to angry facial expressions suggest that reconstructive processes may also be involved and thus do not solely rely on mirroring mechanisms (Beall et al., 2008; Burgeois & Hess, 2008; Hess et al., 1998; Jones, 2007; Moody & McIntosh, 2006, 2011; Moody et al., 2007). Precisely, angry faces led to a change in RFRs that is more typically involved in the facial expression of fear (Beall et al., 2008; Moody et al., 2007). An angry face with the eye gaze directed at the perceiver is usually regarded as threatening and potentially elicits fear (Öhmann, 2005). From an evolutionary perspective, fear may facilitate removal from the threatening situation and would therefore be more adaptive in more threatening situations (Moody et al., 2007).

However, the lack of information about the response of the corrugator muscle to static angry faces may be regarded as limiting our conclusions. Despite this limitation, the activation of the frontalis, even in the absence of activity from the corrugator, is specific for expressing fear, not anger (Boxtel, 2010; Eckman & Friesen, 1978). Further investigations in which measures of emotional arousal (e.g., heart rate, pupil dilation, galvanic skin response) are recorded simultaneously with facial EMG from all three muscles, could help elucidate whether the 3-year-olds' RFRs to others' emotional facial expressions are associated with a change in the affective state, thus further supporting the reconstructive interpretation. The observed response pattern elicited by angry faces may also depend on children individual differences in their level of arousal as well as the regulatory efficiency to respond to emotions, since the temperamental characteristics recorded during the first years of life are known to affect attentional biases (see Chapter 4), emotion understanding and empathy development (van der Mark, van IJzendoorn, & Bakermans-Kranenburg, 2002; Young, Fox, Zahn-Waxler, 1999).

Neither the emotionally neutral nor the fearful faces elicited selective activation of the recorded facial muscles. The fact that in our study static fearful faces did not elicit selective RFRs in 3-year-old children is in line with Beall et al. (2008) findings for 7- to 12-year-old children and Moody et al. (2007) findings for adults, yet, in contrast to those of Deschamp et al. (2014) and Oberman et al. (2009). Facial expressions of fear are typically regarded as cues for threat (Adams, Gordon, Baird, Ambady, & Kleck, 2003; Pessoa, Japee, & Ungerleider, 2005), which capture attention and elicit fear (Öhmann, 2005; Vuilleumier, 2002). However, a fearful face with direct eye gaze, like in the current study, may be very ambiguous with respect to its significance for the observer. Indeed, fearful faces with eye-gaze directed towards a specific aspect of the environment more clearly points to the specific source of threat and are more meaningful than a fearful face with the eye-gaze oriented towards the observer (Magnée et al., 2007; Tamietto & de Gelder, 2008). Amygdala activation in adults is enhanced in a social learning context in which a fearful face directs attention toward a referent in the environment compared to the emotional expression in isolation (Hooker, Germine, Knight & D'Esposito, 2006). This further indicates that these responses are less likely to be the result of mirroring mechanisms since the corresponding motor model is not present (Moody & McIntosh, 2006; Tamietto et al., 2009) being more likely interpreted as evidence supporting reconstructive mechanisms.

Alternatively, the lack of selective RFRs in our study could be due to the fact that 3-year-old children's abilities to process fearful facial expressions are not sufficiently mature. As outlined in Chapter 4, infants' ability to discriminate fearful from other emotionally positive and negative facial expressions has been extensively reported at both behavioural and at neural levels in infants as young as 5 to 7 months (Schwartz, Izard, & Ansul, 1985; Hoehl & Striano, 2008). However, scholars converge to suggest that it takes many years before children reach the adults' level of accuracy and speed in recognizing facial expressions. Specifically, children's emotion recognition emerges gradually over time, with happiness recognised earliest and with the greatest accuracy, followed by sad or angry expressions, then by expressions of surprise or fear (Herba & Phillips, 2004; Gao & Maurer, 2009, 2010). In a similar way, children have difficulties in recognising neutral facial expressions (Gross & Ballif, 1991). Moreover, it is possible that 3-year-old children experience less negative than positive emotional expressions, and in particular they may encounter fewer instance during everyday life of other people manifesting fearful than happy and even angry facial expressions (Gao & Maurer, 2010; Grossman, Striano, Federici, 2007). Our findings that the frontalis muscle tends to show less change from baseline in response to angry faces than the response of zygomaticus in response to happy faces could be regarded as indirectly supporting the idea that a differential amount of experience with certain emotional expression may have an impact on children's RFRs. The most experienced emotional expressions could trigger more easily RFRs than the less experienced ones.

The discrepant results in RFRs to fear may also be due to differences in saliency of the fearful expressions as cues for threat used in the current and previous studies. For example, Oberman et al. (2009) asked children to verbally label and categorize the observed emotional expressions, while Deschamp et al. (2014) presented dynamic stimuli.

Unlike Deschamp et al. (2014), we asked children to watch static facial expressions of fear with gaze directed towards the observer, without any further instructions. These procedural aspects may have modulated children's processing of emotional expressions. Indeed, it is possible that in passive tasks using static stimuli (i.e., providing depleted emotional information), the interpretation of fearful expressions as cues for threat is more dependent on specific features of the face (e.g., eye-gaze) (Hoehl & Striano, 2010). In real-life encounters, facial expressions are often ambiguous, sometimes a mix of several emotions, often very slight and always dynamic, moving from neutral or from another emotion to the current emotional or neutral display (Mühlberger et al., 2011). Yet much of the research on facial mimicry used photographic images of idealized emotional expressions. For example, Rymarczyk et al. (2011) compared muscular responses to static and dynamic (neutral to emotional) happy and angry expressions of the same actors within participants. Happy dynamic expressions produced faster and stronger mimicry than static ones, while dynamic angry faces elicited faster corrugator activation. Compared to still images, dynamic expressions might draw attention to the change occurring, which is also a further cue, in combination with direct gaze, that the facial expression is directed towards the participant. It is possible that in passive tasks using static stimuli that provide impoverished emotional information, the interpretation of fearful facial expressions as cues for threat is more dependent on certain features of the face or of the environment pointing to the source of threat, like the eye-gaze (Fox et al., 2007; Hoehl & Straino, 2008; Hoehl & Straino, 2010; Neath et al., 2013). It is thus possible that the static fearful stimuli used in our study and in Beall et al. (2008) were not sufficiently informative with respect to the potential threat. Future studies in which the orientation of the eye-gaze in fearful and angry faces is specifically manipulated, as well as the use of both static and dynamic stimuli, could greatly contribute to understanding the underlying mechanisms of RFRs to emotional faces in children. Moreover, of capital importance will be to explore whether other emotional expression modalities than those included in this study are used (i.e., emotional prosody) together with measures of affect knowledge for understanding if the lack of selective RFRs for emotional expressions other than faces reflect the presence of mirroring mechanisms, reconstructive processes or a combination of both.

In sum, the current findings provide valuable insight into 3-year-old children's facial responses to others' emotions, particularly when displayed in static images, and show that EMG recordings can be a used as a useful tool to investigate RFRs at this age. Taken together, reported results speak in favour of RFRs as the result of complex mechanisms in which reconstructive processes may play an important role. However, it is important to emphasize that this type of processes do not necessarily exclude the existence of mirroring mechanisms operating in parallel as a function of the experience acquired with the observation and enactment of emotional expressions across development. It will be particularly interesting to explore whether RFRs to others' emotions are related to children's abilities to share the emotional experiences of people around them or whether they contribute to how well children understand their own and others' emotions. Further, combining EMG with fMRI measurement can help discover the pathways of facial mimicry (Likowski et al., 2012). Given the rapid progress in *f*MRI technology, this seems a particularly promising avenue for future research (Heller et al., 2014). If one assumes that there is a fast route to "mirror" facial expressions, the question at what stage of information processing this route is modulated becomes inevitable. In light of recent research showing that EMG is a valid tool to be used even with infants (Natale et al., 2014; Turati et al., 2013), the current findings add to a growing body of research on the development of complex social and emotional abilities like empathy (Decety & Svetlova, 2012; Decety, 2015; Geangu, 2015; Geangu et al., 2011) and social understanding (Meltzoff, 2007;

Carpendale & Lewis, 2006) and open an important possibility for addressing long standing questions about infants' facial responses to others' emotional expressions (Field et al., 1983; Geangu et al., 2011; Kaitz et al., 1988; Haviland & Lelwicka, 1987; Ray & Heyes, 2011).

GENERAL DISCUSSION

TOWARD A NEUROCONSTRUCTIVIST MODEL OF ACTION/EMOTION MIRRORING AND ACTION/EMOTION UNDERSTANDING[7]

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[7] Chapter based on: Quadrelli, E., & Turati, C. (2015): Origins and development of mirroring mechanisms: a neuroconstructivist framework. *British Journal of Developmental Psychology*, doi: 10.1111/bjdp.12110

The comprehension of other people's behaviour is a simple as much as a complex process. We daily meet people and interact with them effortlessly, usually understanding their actions, intentions, emotions and thoughts. Humans naturally live in a social environment and the human brain is highly specialized to process social stimuli and to drive appropriate responses. Notwithstanding the apparent simplicity of these processes, they are indeed very complex. To understand what a conspecific is doing or feeling requires the processing of his movements, to observe whether he is interacting with an individual or approaching an object, to detect where his gaze is directed to, to perceive subtle signs of the body language and to integrate what we see with the information we already have about this person and with our general knowledge on the world facts.

As extensively explained throughout this thesis, the MNS has been invoked to explicate many different aspects of social cognition, ranging from imitation (e.g., Rizzolatti et al., 2001) to action understanding (e.g., Rizzolatti, Fadiga, Gallese & Fogassi, 2006), empathy and emotion understanding (e.g., Gallese, 2003; Sommerville & Decety, 2006), and even language (e.g., Gallese & Lakoff, 2005). However, despite two decades of research on the MNS, the development of mirroring mechanisms in the brain has remained relatively unknown. Developmental cognitive neuroscience encompasses the empirical study of the neural mechanisms underlying the emergence of cognitive and social processes. One issue this branch of research is particularly interested in is elucidating the neural mechanisms underlying the comprehension of human actions and emotions. As it has already been described in the Introduction, much progress has recently been made within this field by combining distinct approaches and employing sophisticated neuroimaging techniques. Indeed, a basic assumption of this branch of research is that a full understanding of the development of cognitive and social competencies requires a multilevel analysis, wherein both biological and social levels of analysis, as well as their relations, are considered. Importantly, by studying early development, it is possible to understand what types of experiences are necessary to learn from and relate to others, including predicting and interpreting others' behaviours and emotions. Thus, although many social cognitive milestones have been established, we need now to understand the mechanisms of developmental change and how these mechanisms account for brain and behavioural functioning at different ages. Understanding the mechanisms of development is an interdisciplinary problem that demands the study of infancy and the integration of fields such as neuroscience, social psychology and anthropology. Moreover, it is only through the use of multiple methods that new insights into the development of the developing mind will be found.

The present doctoral project was dedicated to partially address the existing gap in research about the development of how we perceive and understand human actions and emotions. In particular, Chapter 1 provides a review of existing models developed to tackle the developmental origins of mirroring mechanisms, and a discussion on the existing debate about the role of the motor system in action and emotion understanding. Furthermore, experiments described in the Chapter 2 and 3 focused on the neural correlates of 7-month-old infants' processing of human action sounds, as measured through ERPs, and the neural mechanisms driving toddlers' ability to understand others' actions, as assessed by exploring mu rhythm desynchronization during observation of others' actions. Results described in Chapter 2 provide the first evidence of an early sensitivity to human action sounds, similar to the one already demonstrated for the human voice, as we showed that 7-month-old infants are already capable to process human action sounds as a specific sound category. These results further underline the critical role of auditory cues in humans' ability to detect and understand the meaning of others' actions (Thomas & Shiffrar, 2010), and extend evidence obtained in adults, by suggesting that a brain network devoted to the processing of human action sounds begins to emerge already in the first year of life. Results obtained in Chapter 3 show that 14-month-old infants rely on their own action experience, thus using emulative (i.e., top-down) mechanisms, when predicting the outcomes of observed actions implemented both with novel or familiar means. However, they also suggest that active experience, more than that acquired through action observation alone, is fundamental for generating a better comprehension of the action. In fact, 14-month-old infants exposed to an active training tended to activate the motor schema they have been trained to when observing and predicting the same action carried out with different effectors. On the contrary, infants undergoing a passive observational training generated a prediction about the agent's action by using mirroring (i.e., bottom-up) mechanisms.

The experiments described in Chapter 4 and 5 investigated the development of the ability to recognize the emotions expressed by others and the role played by the motor system in this process. The study presented in Chapter 4 investigated the neural correlates of 7-month-old infants' sensitivity to static and dynamic facial expressions of emotions. Results showed that infants in the static condition allocate more attentional resources to happy as compared to angry and neutral expressions, and that infants' attentional responses to emotional expressions were not enhanced by dynamic stimuli, but rather hindered by naturally moving faces. Additionally, results of this study highlight the role of individual differences related to temperamental traits in shaping the attentional patterns towards emotional expressions. The study described in Chapter 5 investigated the mechanisms underlying covert facial muscle reactions by measuring sEMG activity elicited by the observation of emotional expressions in 3-years-old children. Findings from this study suggest that facial muscle responses derive from complex mechanisms in which reconstructive processes might interact with mirroring processes. Bodily expressions did not generate specific sEMG activation. On the other hand, observing happy facial expressions elicited the muscular activation pattern predicted by both the mirroring and the reconstructive accounts, while observing angry expressions elicited activation of muscles involved in expression of fear, in line with the reconstructive account.

As already mentioned in Chapter 1 and extensively described within the subsequent chapters, an intense debate exists about the role of the motor system in the humans' abilities to understand others' actions and emotions, and two main theories have been proposed to account for the development of these abilities. In what follows, based on the hypotheses on action and emotion mirroring outlined in Chapter 1 (i.e., narrowing, experience-expectant processes and constraints on development), and on results of the studies presented in the current dissertation, an integrative model that combines the apparently competing approaches on action and emotion understanding within a neuroconstructivist developmental perspective will be presented.

The two main theories concerning the development of action and emotion understanding abilities, known as the *direct-matching* (Rizzolatti & Craighero, 2004) and the *teleological reasoning* (Csibra, 2007) hypotheses, assume a different role for the motor system as they argue for a different involvement of "bottom-up" and "top-down" processes.

However, given the inherent complexity of our environment, it is possible to hypothesize that a powerful cognitive system should take advantage of both "top-down" and "bottom-up" processes for the processing of others' actions and emotions (Baldwin, 2005). Recent models about adult cognitive functioning state the inadequacy of the top-down versus bottom-up dichotomy and propose integrative frameworks that emphasize not only the role of stimulus- and cognitive-driven activation, but also of the effects of previously acquired experience/knowledge (Awh, Belopolsky & Theeuwes, 2012). Accordingly, many researchers have suggested that, in human adults, action observation flexibly engages different neural systems, which play different but potentially complementary roles during the observation of others' actions (Cross et al., 2011; Jeannerod, 2006; Keysers & Gazzola, 2007). Moreover, existing research on emotion understanding suggests that this process as well is not mediated by a single mechanism, either top-down or bottom-up and scholars do not reject one theory or the other (Magnée et al., 2007; Tamietto et al., 2009).

In this light, the neuroconstructivist explanation overcomes the existing top-down versus bottom-up dichotomy and offers an interesting middle-ground view for interpreting and possibly guiding research on the development of mirroring mechanisms. In fact, the emergence of motor resonance mechanisms that allows the immediate understanding of others' actions and emotions may be considered to be the result an experience-expectant narrowing process, which is driven by a number of motor and perceptual constraints.

Early predispositions to attend to movements of specific body parts (i.e., hands and faces), together with social motivation to interact with significant other people, may help infants to comprehend the complexity they have to deal with after birth, selecting and constraining the relevant stimuli to which it is worth focus attention. Results obtained in Chapter 2 provide first evidence of an early sensitivity to process human-produced sounds, possibly reflecting a preparedness to deal with these auditory stimuli. This predisposition probably involves, as in the case of other social stimuli like faces, a coarsely specified but slightly biased neural network that requires exposure to species-typical sounds in order to be refined and develop towards a more mature form. This developmental process might entail the conservation of some initially existing connections and pruning of others, in order to result in a better-refined neural connectivity and to lead to a narrowing of the range of sounds to which the network is responsive. In light of results achieved in Chapter 2, showing that 7-month-old infants can selectively process human action sounds, it will be important to explore the existence of any developmental change in the processing of this sound category beyond the age of 7 months. Indeed, future research in this direction will be particularly relevant for testing the hypothesis of perceptual narrowing put forward by the neuroconstructivist model mentioned in Chapter 1.

Additionally, infants' understanding of the goals of others appears highly affected and constrained by the gradual emergence of their own perceptual and motor abilities and this might as well be the case for the ability to understand others' emotional expressions. Indeed, evidence from studies exploring both typical and atypical development suggests that early perceptual experience, possibly interacting with innate predispositions, is capable to shape emotion recognition mechanisms later in development. The universal nature of some facial expressions and their presence throughout the human phylogenesis, raise the possibility that humans have come to expect the occurrence of facial expressions at a particular time in development (Leppanen & Nelson, 2009). However, despite the relevance of experience-expectant mechanisms, it is not excluded that the representations of emotional expressions are also moulded by individual-specific experiences. For example, children of abusive parents, who are exposed to high levels of parental expressions of negative emotions and with a history of being physically abused, exhibit a heightened sensitivity and a response bias for signals of anger (e.g., Pollak & Kistler, 2002), as inferred by the amplitude of attention-sensitive ERPs to angry facial expressions (Pollak & Tolley-Schell, 2003). Moreover, it was also shown that sensitive parenting, involving the sharing of positive emotions, together with temperamental traits, are able to modulate infants' attentional responses to facial expressions of emotions (see Chapter 4; Taylor-Colls & Fearon, 2015).

For what concerns the action understanding domain, it was demonstrated that 6-month-olds who viewed actions that were more common in their own experience (i.e., feeding actions) visually anticipated the goal of the observed action (Kochukhova & Gredeback, 2010). If 3-month-olds practiced picking up toys by using sticky mittens, they became able to attribute a goal when observing a grasping action (Sommerville, Woodward & Needham, 2005). Similarly, anticipatory looking behaviour of 6-month-olds in response to grasping actions was found to be related to their skills at reaching for objects (Kanakogi & Itakura, 2011; Daum & Gredeback, 2011; Ambrosini et al., 2013).

Yet, it is likely that infants first need to process the multiple dimensions of observed movements to construe the meaning of the action they are observing. Observed actions have to be reconstructed based on multiple features, such as familiarity (Gredeback & Kochukhova, 2010), motivation (Paulus, 2014), efficiency (Southgate & Csibra, 2009), visual (Grossmann, Cross, Ticini & Daum, 2013), auditory (Paulus et al., 2012), emotional (Phillips, Wellman & Spelke, 2002) and social cues (Fawcett & Gredeback, 2013), as well as featural, configural and temporal information sources (Loucks & Sommerville, 2012b). These features drive action representations distributed widely over cortical and subcortical areas.

Nonetheless, visuo-motor experience acquired during development together with attunement processes, are proposed to shape infant perceptual-motor couplings, so that the processing of specific actions becomes direct and automatized. As a result of a narrowing process, the understanding of highly experienced actions and emotions may occur bypassing “top-down” and distributed activation through the generation of a quicker and direct motor resonance response to perceived stimuli, made possible by mirror mechanisms (Figure 15).

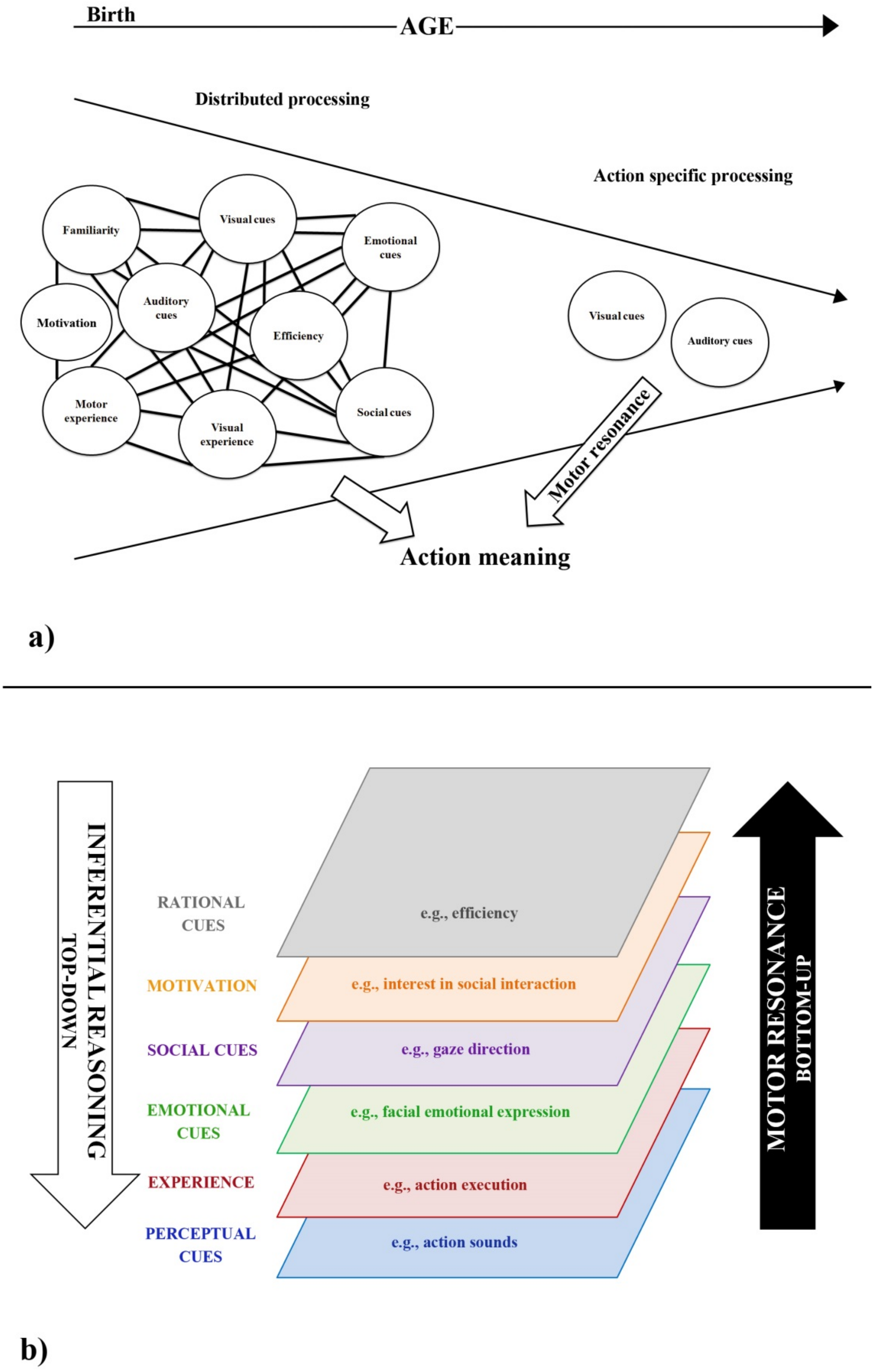

Figure 15. Schematic representation of the proposed integrative model displaying *(a)* the gradual attunement process (oblique arrows) that shapes mirroring mechanisms during development. Early in life action understanding requires an inferential and distributed processing. Acquired experience and narrowing processes gradually generate a direct motor resonance response. *(b)* The model posits the existence of a multilayer structure involved in action understanding, which considers the existence of an interplay between higher-level inferential and direct mirroring paths (from Quadrelli & Turati, 2015).

As recognized by Rizzolatti and Sinigaglia (2010), and by Gallese and colleagues (2004) for the emotion domain, there is no doubt that, in some cases, understanding the motor behaviour of others might requires mechanisms different from mirroring. Action and emotion understanding are multi-layer processes involving different levels of representation, from the goal that drives a given chain of motor acts, to the attitudes (e.g., beliefs, desires) that explain the observed behaviour in terms of its plausible psychological reasons.

Differently from Rizzolatti and Sinigaglia (2010), a developmental perspective would posit that direct-matching mechanisms gradually emerge from a narrowing process occurring during ontogenetic development. Indeed, narrowing is understood as a domain-general process acting upon several knowledge domains (Scott et al., 2007): as described in Chapter 1, it can be hypothesized that a similar process occurs within the action and emotion perception domains too. Specifically, it could be hypothesized that top-down processes are relevant mechanisms driving infants' understanding of others' actions and emotional states and that observed actions or emotional expressions have to be reconstructed based on identified goals, situational meanings, and/or other significant features early in life. At a later stage, bottom-up mechanisms might start operating in response to those actions or expressions that have become familiar as a result of active and observational experiences responsible for the narrowing process.

Indeed, similar to action mirroring, the evidence highlights a gradual process of specialization and tuning of action understanding abilities. While 5-month-olds were shown to attribute goals to non-human agents (Luo & Baillargeon, 2005), 9-month-olds simulated the actions performed by mechanical claws to a lesser extent than those performed by human agents (Boyer, Pan & Bertenthal, 2011). Fifteen- and 18-month-olds reproduced the outcomes of actions demonstrated by human actors (Meltzoff, 1995) and by human-like agents (Johnson, Booth & O'Hearn, 2001; Johnson, 2003), but not by mechanical pincers. This developmental trajectory in the processing of actions performed by mechanical devices seems to indicate a progressive tuning toward human actions compared to the actions performed by both human and non-human agents.

A gradual narrowing process was also observed by researchers investigating the sources of information attended to when discriminating between visual actions. Specifically, 4-month-olds discriminated between changes in actions at the featural, configural and temporal information levels, while 10-month-olds and adults differentiated between changes at the featural level only. These findings indicate that younger infants are better able to discriminate between a wider range of action properties than older infants and even adults (Loucks & Sommerville, 2012a; 2012b).

The neural counterpart of this process, which has yet to be thoroughly studied, is possibly reflected by the fact that, while younger infants activate a widespread and non-specific network in response to action observation, later in development specific and localized regions are selectively activated. In this direction, increased activation of the right inferior frontal-premotor region was observed using functional near-infrared spectroscopy in 4-month-olds regardless of the familiarity of the agents (i.e., robot or human) performing an unfamiliar action (Grossmann et al., 2013). Also, as recently outlined, infants' action experience affects early cortical specialization, as the degree of cortical activation, within the posterior superior temporal sulcus, to the perception of manual actions in 4- to 6-month-old infants correlates with their own level of fine motor skills (Lloyd-Fox, Wu, Richards, Eldwell & Johnson, 2015).

Direct activation of mirroring mechanisms does not exclude the involvement of higher cognitive functions at a different level of analysis, because inferential and direct-matching mechanisms should not be considered as mutually exclusive, as also suggested by the results of the studies presented in Chapter 3 and 5. Indeed, for what concerns the action understanding domain, it was shown that the two mechanisms could be flexibly recruited according to the specific circumstances. In particular, infants undergoing an active training were able to use the newly acquired experience to predict the on-going action, thus relying on top-down, inferential, processes. On the contrary, infants who did not take advantage of an active imitative experience appeared to predict the unfolding action by counting on mirroring mechanisms, thus activating the motor schema implemented by the observed agent. Similarly, results obtained in Chapter 5, pointed out that emotion understanding derives from complex mechanisms in which reconstructive and mirroring processes might interact with each other. Precisely, it was shown that both the mirroring and the reconstructive accounts could hold when considering muscular activation elicited by the highly familiar happy facial expressions. However, observing the less familiar and possibly threatening angry expressions elicited activation of muscles involved in expression of fear. This suggests that in response to the perception of a threat it might be adaptive to flee, not to simulate the threatening agent's observed movements. In line with current views that distributed neural representations underlie domain-specific knowledge (Barsalou, Simmons, Barbey, & Wilson, 2003) and that in adults action or emotional expression observation may flexibly engage different and complementary neural systems (Cross et al., 2011; Jeannerod, 2006; Goldman & Sripada, 2005; Keysers & Gazzola, 2007), the presented model states that an action scene might not correspond to a unique representation in our brain, but to a distributed representation of multiple dimensions in different layers, possibly involving the whole organism (Hutto, 2013). In a similar vein, the processing of emotional expressions might not solely require a single mechanism, either top-down or bottom-up, but it might demand the integration or the flexible use of both (Tamietto et al., 2009).

Understanding the actions and emotions of others may operate at multiple levels in a distributed and dynamic fashion. Thus, it is plausible that “top-down” inferential processes and “bottom-up” direct-matching processes interact, exchanging information to understand a given situation. Finally, within a multi-level model, action and emotion understanding might take advantage of different and non-competitive processes so that the direct mirroring and higher-level inferential paths can be adaptively activated according to situational cues, for instance to face highly familiar or never experienced actions, respectively.

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APPENDIX

Questionario sul comportamento infantile – Revisione 2000

IBQ-R - Very Short Form

Codice _______________ Data di nascita del bambino _____ ______ _____

giorno mese anno

Data odierna _______________ Età del bambino _____ ________

mesi settimane

Sesso del bambino _______________

ISTRUZIONI:

Si prega di leggere attentamente prima di cominciare

Dopo aver letto ciascuna delle sottostanti descrizioni del comportamento del bambino, indichi la frequenza con cui quel comportamento si è verificato DURANTE LA SCORSA SETTIMANA (gli ultimi sette giorni) cerchiando uno dei numeri nella colonna di sinistra. Questi numeri indicano la frequenza con cui si è verificato il comportamento descritto nel corso dell'ultima settimana.

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(X)
Mai	Molto raramente	Meno della metà del tempo	Circa la metà del tempo	Più della metà del tempo	Quasi sempre	Sempre	Non applicabile

Utilizzi la colonna "Non Applicabile" (X) nel caso in cui, nel corso dell'ultima settimana, non abbia osservato il bambino nella situazione descritta. Per esempio, se la situazione menziona il bambino che deve attendere per ricevere cibo o bevande, e nell'ultima settimana non ci sono state occasioni in cui il bambino ha dovuto attendere, faccia un cerchio sulla colonna (X).

"Non Applicabile" è diverso da "Mai" (1). Utilizzi l'opzione "Mai" quando nel corso dell'ultima settimana ha osservato il bambino nella situazione, ma il bambino non ha mai

intrapreso il comportamento descritto. Per esempio, se il bambino ha dovuto attendere per ricevere cibo o bevande almeno una volta ma non ha mai pianto in maniera forte durante l'attesa, faccia un cerchio sulla colonna (1).
Si assicuri di aver cerchiato un numero per ciascuna domanda.

1. Durante l'ultima settimana quando veniva vestito o svestito con quale frequenza il bambino si è dimenato e/o ha tentato di divincolarsi?
   1 2 3 4 5 6 7 X

2. Quando il bambino veniva fatto dondolare vigorosamente per gioco, con quale frequenza ha riso?
   1 2 3 4 5 6 7 X

3. Quando il suo bambino era stanco, con quale frequenza ha mostrato disagio?
   1 2 3 4 5 6 7 X

4. Quando al bambino veniva presentata una persona a lui sconosciuta, con quale frequenza si è aggrappato ad un genitore?
   1 2 3 4 5 6 7 X

5. Durante l'ultima settimana, con quale frequenza il bambino è stato contento di sentir leggere?
   1 2 3 4 5 6 7 X

6. Durante l'ultima settimana, con quale frequenza il bambino ha giocato con un gioco o un oggetto per 5-10 minuti?
   1 2 3 4 5 6 7 X

7. Con quale frequenza durante la scorsa settimana il bambino si è diretto velocemente verso nuovi oggetti?
   1 2 3 4 5 6 7 X

8. Quando lo si metteva in acqua per il bagnetto, con quale frequenza il bambino ha riso?

1 2 3 4 5 6 7 X

9. Quando arrivava l'ora di andare a letto o del riposino e il suo bambino non voleva andare, con quale frequenza ha piagnucolato o singhiozzato?

   1 2 3 4 5 6 7 X

10. Dopo aver dormito, con quale frequenza il bambino ha pianto se non arrivava nessuno entro pochi minuti?

    1 2 3 4 5 6 7 X

11. Nell'ultima settimana, mentre lo nutriva tenendolo sulle gambe, con quale frequenza il bambino è sembrato desiderare di stare per conto proprio appena finito di mangiare?

    1 2 3 4 5 6 7 X

12. Quando cantava o parlava con il suo bambino, con quale frequenza lui si è calmato immediatamente?

    1 2 3 4 5 6 7 X

13. Se messo supino, con quale frequenza il bambino si è dimenato e/o ha ruotato il corpo?

    1 2 3 4 5 6 7 X

14. Durante il gioco del cucù, con quale frequeza il bambino ha riso?

    1 2 3 4 5 6 7 X

15. Quando giocava, con quale frequenza il bambino ha distolto lo sguardo quando il telefono suonava?

    1 2 3 4 5 6 7 X

16. Con quale frequenza il bambino si è arrabbiato (ha pianto o si è agitato) se lasciato nella culla?

    1 2 3 4 5 6 7 X

17. Con quale frequenza durante la scorsa settimana il bambino ha sobbalzato per movimenti improvvisi (ad es. quando veniva mosso improvvisamente)?

1 2 3 4 5 6 7 X

18. Durante l'ultima settimana, con quale frequenza il bambino è stato contento di ascoltare il suono delle parole, come nelle filastrocche?

1 2 3 4 5 6 7 X

19. Durante l'ultima settimana, con quale frequenza il bambino ha guardato le figure su libri e/o riviste per 5 minuti o più?

1 2 3 4 5 6 7 X

20. Quando il bambino si trovava in un posto nuovo, con quale frequenza si è mostrato eccitato nell'esplorare il posto nuovo?

1 2 3 4 5 6 7 X

21. Durante l'ultima settimana, con quale frequenza il bambino ha sorriso o riso quando gli veniva dato un gioco?

1 2 3 4 5 6 7 X

22. Dopo una giornata in cui era agitato, con quale frequenza il suo bambino si è messo a piangere?

1 2 3 4 5 6 7 X

23. Con quale frequenza durante la scorsa settimana il bambino ha protestato se messo in uno spazio delimitato (seggiolino, box, seggiolino della macchina, ecc.)?

1 2 3 4 5 6 7 X

24. Quando veniva tenuto in braccio, con quale frequenza nell'ultima settimana, il bambino è sembrato contento?

1 2 3 4 5 6 7 X

25. Quando mostrava al bambino qualcosa da guardare, con quale frequenza lui si è calmato immediatamente?

1 2 3 4 5 6 7 X

26. Quando gli si lavavano i capelli, con quale frequenza il bambino ha vocalizzato?

1 2 3 4 5 6 7 X

27. Con quale frequenza il suo bambino ha notato il rumore di un aereo che l'ha sorvolato?

1 2 3 4 5 6 7 X

28. Quando al bambino veniva presentata una persona a lui sconosciuta, con quale frequenza si è rifiutato di andare con la persona sconosciuta?

1 2 3 4 5 6 7 X

29. Quando lei era occupata con altre faccende e il suo bambino non riusciva ad ottenere la sua attenzione, con quale frequenza ha pianto?

1 2 3 4 5 6 7 X

30. Durante l'ultima settimana, con quale frequenza il bambino è stato contento di essere coinvolto in attività ritmiche delicate, come dondolare o oscillare?

1 2 3 4 5 6 7 X

31. Durante l'ultima settimana, con quale frequenza il bambino ha fissato un giocattolo appeso nella culla, il paracolpi della culla o i quadri sulle pareti per 5 minuti o più?

1 2 3 4 5 6 7 X

32. Quando il bambino voleva qualcosa, con quale frequenza è sembrato frustrato quando non riusciva ad ottenerla?

1 2 3 4 5 6 7 X

33. Quando il bambino si trovava con più persone a lui sconosciute, con quale frequenza ha continuato ad essere a disagio per 10 minuti o più?

1 2 3 4 5 6 7 X

34. Durante l’ultima settimana quando veniva cullato o abbracciato, con quale frequenza il suo bambino è sembrato contento?

    1 2 3 4 5 6 7 X

35. Quando si dava un colpetto affettuoso o massaggiava alcune parti del corpo del bambino, con quale frequenza lui si è calmato immediatamente?

    1 2 3 4 5 6 7 X

36. Con quale frequenza il suo bambino ha vocalizzato quando era in macchina?

    1 2 3 4 5 6 7 X

37. Se messo in un seggiolino o in un seggiolino per auto, con quale frequenza il bambino si è dimenato e ha ruotato il corpo?

    1 2 3 4 5 6 7 X

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