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DEVELOPMENT OF MIRROR SYSTEMS FOR OPAQUE ACTIONS AND THE INFLUENCE OF EARLY MOTHER-INFANT INTERACTIONS

Thesis submitted for the degree of Doctor of Philosophy

School of Psychology and Clinical Language Sciences, University of Reading

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0.1 DECLARATION

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

....

Holly Rayson

0.2 DEDICATION

In memory of my grandfather, whose kindness and passion for life

I will always strive to mirror.

0.3 ACKNOWLEDGEMENTS

Writing this thesis has been a tremendously rewarding, but challenging endeavour, and would not have been possible without the involvement and support of so many people. It gives me great pleasure to acknowledge them here.

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0.4 DISSEMINATION OF WORK

PUBLICATIONS

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0.8 ABSTRACT

Mirror systems are widely thought to map perceptual representations of others’ actions onto the observer’s corresponding motor representations. This includes ‘opaque’ actions, which are unobservable when performed by the self (e.g. facial expressions and attention shifts). To date, few studies have looked at mirror systems for these actions in the infant brain, and even fewer have investigated how such systems might develop. Therefore, the main aims of the research presented in this thesis were to investigate potential mirror systems for opaque actions in very young participants, and how early social experience may influence the development of these systems. This was done using electroencephalography (EEG) to measure mu desynchronization, an index of mirror system activity, while infants and young children observed and executed various actions, and the manual coding of early mother-infant interaction videos. Two of the included studies, ***Chapters 2 and 4***, were designed to look at putative facial mirror system activity in 30-month-old children and 9-month-old infants, respectively. The ***Chapter 4*** study also considered the influence maternal mirroring of infant facial expressions at 2 months postpartum may have on mu desynchronization during observation of expressions at 9 months. The third study (***Chapter 5***) was designed to investigate potential involvement of a mirror system in the processing of others’ attention shifts at 6.5 and 9.5 months of age. Infants in this study had been recorded interacting with their mothers at 3.5 and 6.5 months postpartum, and the relationship between attention-related behaviours during early social exchanges and mu desynchronization in the EEG experiments was examined. Altogether, findings from this research suggest that mirror systems are involved in the processing of facial expressions and attention shifts from a very young age, and that early social interactions provide infants with the experience crucial for development of such systems.

1 INTRODUCTION

Traditionally, action and perception have been viewed as distinct entities, with the mind organized in a modular and hierarchical fashion. According to this perspective, each module is assigned a specific function, with sensory information coded in particular brain regions that permit abstract representations of the environment to be expanded upon. This information is then projected to other areas for response elaboration and execution of motor plans, and thus there is clear division between sensory and motor processes. However, in the early 1990s, a group of researchers from the University of Parma chanced upon a new class of visuomotor neuron in the macaque premotor cortex (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992), which challenged the idea that motor and perceptual functions are entirely separate phenomena. These 'mirror neurons' (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) have unique response properties, firing not only during the execution of an action, but also during the observation of other individuals performing a similar action. As such, the discovery of mirror neurons provided the first evidence for a neural mechanism directly mapping the visual representation of an action onto its cortical motor representation, suggesting that action and perception are in fact intimately linked (Casile, Caggiano, & Ferrari, 2011; Rizzolatti, Fogassi, & Gallese, 2001).

Though mirror neurons were first revealed in the macaque monkey, research now supports the existence of homologous mirror systems in the human brain (Molenberghs, Cunnington, & Mattingley, 2012), with the processing of many different types of action (e.g. manual actions, facial expressions, whole body movements, and attention shifts) thought to involve a mapping between own- and other-generated actions. A multitude of functional roles have been proposed for mirror systems, ranging from low-level action recognition, to involvement in empathy and theory of mind skills (Gallese, Eagle, & Migone, 2007). As well as in adults, there is now also considerable evidence for mirror system activity in the developing brain, both in macaque and human infants (e.g. Cannon et al., 2016; Ferrari et al., 2012; Marshall, Young, & Meltzoff, 2011; Vanderwert et al., 2015). The presence of a mirror system very soon after birth has been hypothesized to be critical for establishing an interpersonal link between infants and their caregivers (Rizzolatti et al., 2001), facilitating early social interactions. Subsequent development of more demanding types of social understanding, which presumably build on the capacity to map between observation and execution of actions (Marshall & Meltzoff, 2014), are also thought to involve a mirror system, including the ability to comprehend that other individuals also have goals, emotions, and intentions underlying their actions.

The overarching aim of the research presented in this thesis was to further investigate human mirror system activity in early childhood and infancy, including how early mother-infant interactions might influence the development of such systems. More specifically, the focus of these studies was on facial expressions and the directing of attention (via shifts in eye/head orientation), both of which represent actions that are relatively unexplored in the developmental mirror system literature, and differ from manual actions in that an individual cannot see themselves perform them: they are 'opaque' actions. In the remainder of this chapter, the potential importance of mirror systems in the processing of others' actions will be explored in more depth, as will the properties and proposed functions of these systems. This will be followed by a discussion of how mirror system activity has previously been explored in very young populations, and of theories concerning how mirror systems might develop in the infant brain. Finally, a brief overview will be given of the subsequent thesis chapters and the studies that comprise them.

1.1 SOCIAL INTERACTION, SOCIAL COGNITION, AND THE DISCOVERY OF 'MIRROR NEURONS'

Human beings are profoundly social animals, with the ability to manage complex social environments necessary for individual survival (Gallese, Keysers, & Rizzolatti, 2004). From birth, infants are thrust into this complicated social world, with which they must interact and swiftly learn from if they are to thrive. 'Social cognition' is the term used to describe the process through which we monitor, control, and predict the behaviour of others, which subserves our own responses during a social exchange (Adolphs, 1999). The process of social cognition is a multifaceted one, requiring many levels of comprehension. These range from the mere perceptual discrimination of feature characteristics, such as differences between people and objects, to the complex representation of intentions or beliefs as foundations of behaviour. Indeed, all cognitive processes involved in the perception and analysis of others' actions can be considered components of social cognition, which itself can be thought of to encompass any process related to the understanding of other individuals (Blakemore, Winston, & Frith, 2004).

Human social cognition seems to progress from a state in which infants can engage with other individuals via the coordination of behaviour, to one in which they are capable of comprehending that other people, as well as themselves, are independent beings. This end state is one in which the individual understands that others are endowed not only with objective, physical abilities, but also with subjective and internal psychological perspectives. At birth, infants seem prepared and motivated to engage with the social world, and even in the first days of life, demonstrate a fundamental sensitivity to social stimuli such as eye contact and faces (Farroni, Csibra, Simion, & Johnson, 2002; Valenza, Simion, Cassia, & Umiltà, 1996). From approximately 2months postpartum, infants start to play a much more active role during face-to-face interactions, deliberately seeking eye contact with their caregivers, and following looks to the adult with smiles, coos, and 'pre-speech' mouth movements with increasingly frequency (Beebe, 1982; Murray & Trevarthen, 1985; Stern, 1974, 1985; Trevarthen & Aitken, 2001). In fact, a shift in infant social cognition seems to occur around 2months of age, often described as the beginnings of 'primary intersubjectivity' (Trevarthen & Aitken, 2001). This term designates a period in which an infants' awareness of moving and feeling in relation to another individual grows, and furthermore, that this feeling is different from that experienced when they are alone. Through reciprocal interactions during the early months, such as the mutual give-and-take of facial expressions and vocalizations, infants are thought to develop a sense of shared experience with other people, which transforms over time into more complex social-cognitive skills. An example often used to demonstrate the transition that takes place around 2months, is that infants of this age become distressed and attempt to reengage with an adult who suddenly ceases to interact with them (Mesman, van IJzendoorn, & Bakermans-Kranenburg, 2009; Tronick, Als, Adamson, Wise, & Brazelton, 1978). This suggests that infants can already anticipate others' behaviour and detect disruptions to a social exchange, as well as have certain social expectations.

Another major shift in infant social cognition seems to occur around 9-10 months postpartum. This period of 'secondary intersubjectivity' (Trevarthen & Aitken, 2001; Trevarthen & Hubley, 1978) or the '9month revolution' (Tomasello, 1995) reflects an infant's growing awareness that others are affected by their actions, just as they are affected by the actions of others (Stern, 1985). Abilities often described as epitomizing this transition include 'joint attention', the process through which one coordinates their own direction of attention with that of someone else towards an object or event; and 'social referencing', whereby others' affective displays can be used to regulate one's own response towards an object, person, or situation (S Feinman, 1992; Striano & Reid, 2006). The emergence of these skills indicate that infants comprehend, at least in some basic sense, that others have feelings and intentions that they direct towards the external world. During the second year of life, infants also come to recognize that other people may experience mental states that are different to their own; for instance, that another individual cannot necessarily see an object that the infant can see themselves (Butler, Caron, & Brooks, 2000; Sodian, Thoermer, & Metz, 2007).

These developments in social cognition contribute to the rise in empathic and prosocial behaviour demonstrated by infants in the second year postpartum (Nichols, Svetlova, & Brownell, 2009, 2010; Zahn-Waxler, 1992), and serve as a foundation for the emergence of more complex capacities later on, such as theory of mind (Baron-Cohen, 1991; Charman et al., 2000).

The success of a social interaction relies heavily on the ability to analyse others' actions, as well as to infer the goals, emotions, and intentions behind those actions (Frith & Frith, 2007). As such, these capacities represent extremely important aspects of social cognition. Examples of others' actions that embody particularly rich sources of information, and hence are crucial to identify and interpret correctly during a social exchange, include the following: facial expressions, which can signal someone's emotional state or whether they intend to cooperate within an interaction; directing of attention, from which we can infer the focus of another's gaze and determine their social and environmental interest; and finally manual actions, which can indicate a person's intent aimed towards an object or provide non-linguistic communicative signals. The processing of such actions is vital throughout the lifespan, but obviously holds particular significance for infants and young children before they master verbal language (Leppänen & Nelson, 2009), with the social environment for infants comprised mostly of face-to-face interactions with their caregivers (Murray, 1992). These examples (i.e. facial expressions, directing of attention, and manual actions) are also good for illustrating that the perception and analysis of others' actions requires knowledge that extends beyond the purely physical. That is, comprehending others' actions also entails the ability to read others' emotions, intentions, desires, and in fact, all the phenomena that differentiate the social and inanimate worlds (Rochat & Striano, 2014). In accordance, although understanding the purely physical aspects of others' behaviour is essential (e.g. that people can move on their own and can't be in more than one place at a time), accessing the private mental realms of others is clearly necessary if we are to fully comprehend their actions.

With all primate behaviour embedded within a social environment, it is not surprising that a great deal of research has focused, and continues to focus, on elucidating the neuronal and cognitive mechanisms through which such processing might be achieved. Perhaps the most important point to keep in mind when thinking about this issue is that a shared element exists between the first and third-person experience of the social world (i.e. 'I do or I feel' with 'she does or he feels'), with both the observer and performer of actions possessing equivalent brain-body systems (Gallese et al., 2004). In other words, although the social world involves the observation of others' actions, it also involves the performance of those same actions by the observers themselves. As such, the capacity to match our own actions to those of others represents a significant component of processing another individual’s actions (Gallese et al., 2004; Rochat & Striano, 2014), with the ways in which we accomplish this a key area of investigation for cognitive neuroscience, as well as those interested in social-cognitive development. Indeed, many argue that an infant’s ability to detect that others are “like me” during observation of an adult performer is key for social learning, which gradually leads to the infant learning that they can act with intent and variety (Marshall & Meltzoff, 2011). Subsequent refinement in the ability to recognize and use this cross-modal equivalence between own and other actions is then suggested to serve as a foundation for understanding that others have internal mental states, and thus more mature social cognition (Marshall & Meltzoff, 2014).

The discovery of a new class of visuomotor neurons in the ventral premotor cortex (area F5) of the macaque monkey (di Pellegrino et al., 1992) yielded a potential insight into how the brain might match actions produced by self and other. These ‘mirror neurons’ were shown to fire not only when a monkey grasped an object themselves, but also when they observed another individual performing a similar action. This revelation provided the first evidence for a neural mechanism mapping the visual representation of an action onto its cortical motor representation, and suggests that perceptual and motor processes share a common neural code. The perceptual-motor coupling characteristic of mirror neurons has therefore been suggested to aid the brain in matching self- and other-generated actions via activation of corresponding neural processes in both the observer and performer (Gallese et al., 1996). Based on the discovery in macaques, it was hypothesized that a homologous mirror system may also be present in the human brain. This is now supported by a considerable body of research with human adults (Iacoboni & Dapretto, 2006; Molenberghs et al., 2012), and infant research indicates that mirror systems may be present from a very early stage in development (Vanderwert, Fox, & Ferrari, 2013).

The brain contains numerous mechanisms for automatically generating motor plans from behavioural goals, for translating those plans into movements, and for predicting the outcome of self-generated actions. Therefore, if the visual representation of someone else’s action can be mapped onto one’s own motor representations (motor repertoire), these same mechanisms could be used not only to predict or infer the outcomes and goals of others’ actions, but also to make inferences about the plans and intentions that underlie them. Accordingly, it has been suggested that the perceptual-motor coupling implemented by a mirror system could play an important role in the processing of others’ actions (Casile, 2013; Del Giudice, Manera, & Keysers, 2009; Fogassi et al., 2005; Gallese et al., 1996; Giese & Rizzolatti, 2015; Iacoboni & Dapretto, 2006; Rizzolatti &

Craighero, 2004; Rizzolatti et al., 2001; Vanderwert et al., 2013), and thus in social learning and skilled social interactions (Keysers & Gazzola, 2006). Nevertheless, although it is quite widely accepted that a mirror system could facilitate a mapping between actions produced by self and other, the precise functional role that this may serve is still hotly debated. A diverse set of functions has therefore been proposed, ranging from very low-level processes to highly complex skills. These include certain abilities that overlap in monkeys and humans (e.g. action recognition: Gallese et al., 1996, 2004; Rizzolatti & Craighero, 2004), but the contribution that such a system might make to many higher-level social-cognitive functions has only been attributed to human mirror systems (e.g. empathy, theory of mind: Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Gallese, 2001; Gallese & Goldman, 1998). This has led to the notion of an evolutionary progression of mirror systems and the wider systems that they are a part of (Oztop, Kawato, & Arbib, 2006). The underlying claim to most of the functional proposals is that the matching of self- and other-generated actions, which occurs via activation of the motor representation corresponding to an observed action, aids the observer in implicitly recognizing the actions of others. This results in a direct 'understanding' of an action, which is enriched by the first-person experience of performing it (Del Giudice et al., 2009; Vanderwert et al., 2013). Understanding in this limited sense could refer to the ability to differentiate an action from analogous ones, and to use this information to respond in appropriate ways (Casile, 2013), without any explicit, conscious, or meta-representation of the action. Theories that ascribe a role to mirror systems in more complex functions build upon this idea, suggesting that that they could also contribute to more advanced social cognition that likely involves a self-other mapping, at least at a low-level, such as empathy and the attribution of mental states (e.g. Carr et al., 2003; Gallese et al., 2004; Iacoboni, 2009; Rizzolatti & Craighero, 2004).

So far in this introductory chapter, the importance of processing others' actions for living in a profoundly social world has been highlighted, and the significance of mirror neuron discovery for ideas concerning how we might link actions performed by self and other discussed. In the next two sections, properties of monkey mirror neurons will be explored in more depth, as will the properties of comparable mirror systems in the human brain. This will be followed by a more detailed exploration of the various functional roles that have been hypothesized for mirror systems.

1.2 PROPERTIES AND FUNCTIONS OF MIRROR NEURONS

1.2.1 MIRROR NEURONS IN THE MONKEY

Following the original discovery by Pellegrino et al. (1992), research with macaque monkeys has more thoroughly explored the properties of mirror neurons. It should be noted that the method used to measure electrophysiological responses of individual neurons in the macaque involves the use of microelectrodes inserted into the brain to measure neurophysiological activity, and is referred to as single-cell recording. In the portion of premotor area F5 where mirror neurons were first revealed, approximately 17% of the neurons recorded from were found to demonstrate mirror properties (Gallese et al., 1996). That is, these neurons were shown to fire during both action execution and observation (Gallese et al., 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), with the additional finding of activity in both light and darkness confirming that during execution, activity cannot be explained by concurrent visual inputs (Rizzolatti et al., 1996). Along with the purely motor F5 neurons that control grasp execution, *two* functional types of neuron have in fact been identified which also have visual response properties (and are therefore termed ‘visuomotor’ neurons). The first of these are mirror neurons, which respond to the observation of actions performed by others, and the second, so-called ‘canonical’ neurons, which fire in response to three-dimensional object presentation (Rizzolatti & Fadiga, 1998; Rizzolatti & Luppino, 2001). Canonical neurons involved in controlling a certain type of grasp fire preferentially during observation of an object that affords that particular grasp type (e.g. they will fire during performance of a whole hand grasp of a sphere in the dark, but will also fire during observation of the same sphere alone without any actual grasping). Therefore, the key property of canonical neurons seems to be the matching of the size and shape of observed *objects* to the motor representations appropriate for grasping them. On the other hand, the key property of mirror neurons is that they match the observation of an *action* (the perceptual representation) with the motor representation used to execute a similar one (Rizzolatti & Fogassi, 2014).

All mirror neurons show some level of congruence between the visual actions they respond to and the motor responses they code. Around a third of the mirror neurons originally recorded from in F5 were found to respond in a strictly congruent manner (Gallese et al., 1996): that is, to observation and execution of the exact same action (e.g. to a precision grasp but not whole-hand grasp). Most of the other mirror neurons recorded from were found to be broadly congruent, responding to both observation and execution of actions that were slightly different, but had a clear relationship (Gallese et al., 1996). These broadly congruent mirror neurons can be divided into three categories: i) those that respond to the execution of a specific action (e.g. precision grip), but to observation of different forms of that action (e.g. both precision grips and whole hand grasping); ii) those that respond to the execution of a specific action, but to the observation of a related action (e.g. execution of an object grasp, but observation of manual object manipulation); and iii) those that respond to the execution of a specific action, but to the observation of different actions used to obtain a similar goal (e.g. grasping with the hand versus grasping with the mouth).

Notably, F5 is not the only region of the macaque brain in which neurons respond to the observation of actions. The cortex of the superior temporal sulcus (STS), is a visual region where such neurons can be found, with actions that elicit a response including walking, head turns, arm movements, grasping (Perrett et al., 1989, 1990), and for a small subset, the observation of object-directed actions (Perrett et al., 1990). Unlike mirror neurons, STS neurons do not possess motor properties. That is, in contrast to F5 mirror neurons, they do not discharge during active movements in the dark when the monkey’s own hand is not visible. Another cortical area in which neurons respond to the observation of actions is area PF/PFG of the inferior parietal lobule (IPL) (Fogassi et al., 2005), which receives input from STS, and sends output to the ventral premotor cortex (including F5). Many neurons in IPL respond to sensory stimuli, but a significant portion also demonstrate motor properties during action execution, with about two thirds of these demonstrating mirror properties, i.e. respond both during action observation and execution (Fogassi et al., 2005). Therefore, the cortical mirror neuron circuit (see Figure 1.1) in macaques is usually described as comprising two main regions: portions of IPL (PF/PFG) and the ventral premotor cortex (F5). STS is not usually included as part of the circuit due to its lack of motor properties, however, it is thought to provide the primary visual input to the mirror neuron circuit via its projections to PF/PFG.

One interesting question is why the monkey does not automatically *produce* any movement they observe if mirror neurons are activated. Kraskov et al. (2009) investigated this issue by looking at corticospinal neuron activity located in F5. The authors first identified neurons that likely project to the spinal cord, then looked at the responses of these neurons during action execution and observation. Although many of these neurons responded when monkeys observed an experimenter grasp an object, about 25% of them demonstrated complete discharge suppression during grasp observation. Neurons that were suppressed during action observation still discharged strongly during grasp execution, and the suppression was specific to the preferred grasp type (e.g. if the neuron fires during execution of a precision grip, it would be suppressed by observation of a precision grip only) during execution. The authors suggest that this suppression might be involved in the inhibition, probably at the spinal cord level, of an observer's movement during action observation, which is why mirror neuron activation does not necessarily result in overt movement. The same research group (Vigneswaran, Philipp, Lemon, & Kraskov, 2013) have now also found neurons with mirror properties in the primary motor cortex of macaques, with many of these neurons demonstrating an increase in their discharge during observation of grasps, but also a considerable number showing a suppression in their discharge. Simultaneous recordings from grasping-related muscles confirmed the lack of detectable muscle activity during observation in this study. When compared to the firing of the same neuronal population during active grasping, the authors found that the neurons with increased discharge during observation were only half as active for action observation as for action execution. The neurons that demonstrated suppressed activity during observation showed the opposite pattern (i.e. were facilitated during grasp execution). As such, although many neurons in the primary motor cortex were active during action observation, direct input to the spinal cord seems to be either decreased or eliminated, and therefore is likely insufficient to produce overt muscle activity. It should be noted that it could be that mirror neurons exist in both primary motor and premotor (F5) cortex because they represent actions differently. For instance, primary motor cortex might represent more fine-grained motor movements that are part of an action (e.g. move this finger so much), whereas premotor cortex might representations might be more general (e.g. ‘grasp’).

So far, only mirror neurons associated with manual actions have been discussed, however, those responding to different actions have also been discovered. Early mirror neuron studies concerned the upper portion of F5, an area in which manual actions are primarily represented. Later on, neurons in lateral F5, an area in which mouth actions are represented, were investigated in rhesus macaques (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003). In this area, 25% of neurons recorded from demonstrated mirror properties, and although the majority responded most effectively during observation and execution of ingestive mouth movements, a subset was found to respond most strongly to communicative mouth gestures (e.g. lip smacking). Neurons with mirror properties, and associated with different types of action, have now also been found in other areas of the macaque brain. This includes the lateral intraparietal area (LIP), which is involved in the organization of eye movements. Mirror neurons in LIP were discovered by Shepard et al., (2009), and were shown to fire when a monkey gazed in the preferred direction of the neuron, but also during observation of a conspecific gazing in the same way. Although not classically a motor area, LIP is involved in gaze-related sensorimotor transformation, with activity in this area contributing to both overt and covert shifts of attention, as well as to the maintenance of attention at a fixation. LIP also projects to motor areas, and likely receives feedback connections from these areas as well. Findings such as these demonstrate that the motor (or motor-related) region in which mirror neurons are located is key to their visual properties (Rozzi, 2015).

1.2.2 HUMAN MIRROR SYSTEMS

As single-cell recordings cannot usually be obtained from humans, it is difficult to directly compare data from monkeys to that from human participants (though see one study by Mukamel et al., (2010) with epileptic patients that provides some evidence for mirror neurons in the human brain). Nevertheless, research using a variety of techniques (e.g. functional magnetic resonance imaging, fMRI; transcranial magnetic stimulation, TMS; electroencephalography, EEG) now strongly supports the existence of homologous ‘mirror systems’ in human adults. Mirror systems are defined as a *network of brain regions* activated when an individual performs an action, but also when they observe another individual performing the same or a similar action (Rizzolatti & Craighero, 2004).

fMRI is perhaps the most commonly used technique to investigate human mirror system activity. This is a functional neuroimaging technique that uses an MRI scanner (which contains a powerful electromagnet) to measure brain activity via detection of changes associated with blood flow. The key to MRI resides in the fact that the hydrogen nuclei signal varies in strength depending on the surroundings. This allows the discrimination of grey matter, white matter, and cerebral spinal fluid in structural images of the brain. fMRI relies on the idea that cerebral blood flow and neuronal activation are coupled. fMRI detects the magnetic signal from hydrogen nuclei in water (H_2O), with what is actually measured referred to as the blood oxygenation level dependent (BOLD) response. This results from differences in the MR signal of blood depending on the degree of oxygenation, which varies according to the level of neural activity. Many fMRI studies have now demonstrated overlapping activity in various brain regions during observation and execution of actions (including actions using the hand, foot, leg, mouth, and face), consistent with mirror system activation. Meta-analyses that have combined findings from these fMRI studies (Caspers, Zilles, Laird, & Eickhoff, 2010; Molenberghs et al., 2012) suggest that the cortical network that comprises a core human mirror system is made up of three regions: the posterior part of the inferior frontal gyrus (IFG), the premotor cortex (PM), and the inferior parietal lobe (IPL). As with the monkey mirror circuit, STS is thought to provide the primary visual input (Molenberghs et al., 2012). IFG, PM, and IPL are thought to be human homologues of the regions that make up the monkey mirror neuron circuit, and therefore the regions that comprise this human mirror system likely correspond to areas in which mirror neurons are found in the macaque (Rizzolatti & Craighero, 2004; Vanderwert et al., 2013). A comparison of mirror-related areas in the human and monkey brain can be found in Figure 1.1.

Therefore, even though definitive claims cannot be made about the presence of mirror neurons in the human brain, overlapping activation of regions during action execution and observation strongly suggests that visual-motor mapping is taking place, and that the human brain does contain a network of brain regions involved in 'action mirroring' at the very least. With this in mind, the term 'mirror neurons' will now be reserved for the discussion of monkey single-cell data or theoretical accounts of mirror neuron development, and 'mirror system' will be used when referring to activity in the human brain or comparisons between monkeys and humans.

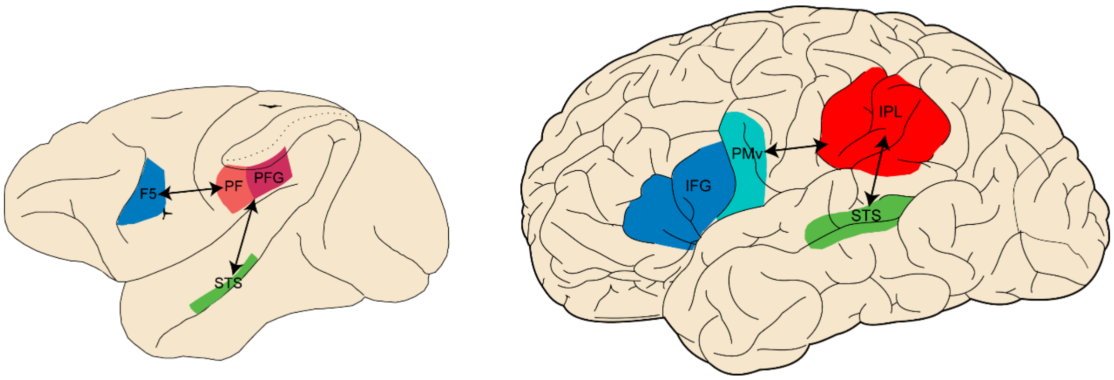

Figure 1.1: Mirror circuit in the macaque monkey (left) and the mirror system in humans (right). Single-cell recordings from macaques have shown that the mirror circuit is made up from portions of IPL (PF/PFG) and portions of the ventral premotor cortex (F5). Human fMRI studies have shown that during the observation and execution of actions, a cortical network formed by the inferior frontal gyrus (IFG), the premotor cortex (PM), and the inferior parietal lobe (IPL) is activated. These are thought to be the human homologues of the monkey regions included in the mirror neuron circuit. STS is thought to provide the primary visual input in both monkeys and humans.

As noted above, classic regions of a human mirror system consist of portions of the premotor cortex, IPL and IFG, with other regions often included as part of an 'extended' or additional mirror system. Many of these areas overlap with those in the monkey mirror neuron circuit, with posterior STS thought to provide the main visual input in both species. The exact functions of some of these areas are debated, therefore below, the anatomy of the mirror system will be discussed again with different functions these areas may serve in mind.

The posterior portion of the STS is thought to provide the primary visual input to the mirror system in both monkeys and humans (Keysers & Perret, 2004; Molenberghs et al., 2012). The STS is located in the temporal lobe, and different parts of it have been implicated in diverse aspects of social perception and cognition. These include the perception of biological motion and faces, linguistic processing, and basic perceptual and attentional functions such as the control of visual attention

(Deen, Koldewyn, Kanwisher, & Saxe, 2015). Neurons in STS do not have any motor properties, however they do respond selectively to biological movement observation (Frith & Frith, 1999; Grossman, Battelli, & Pascual-Leone, 2005; Oram & Perrett, 1994), with the activity of certain STS neurons being highly specific to the type of action observed (Perrett, Harries, et al., 1989). The STS projects to many other brain regions, including IPL and the amygdala (Rizzolatti & Fogassi, 2014; Pitcher, Japee, Rauth, & Ungerleider, 2016). Therefore, despite being a purely visual area, STS is posited to play an essential role in an observation/execution matching network because of its functional properties and connectivity, and potentially, in complex social behaviours such as emotion understanding that may also involve a mirror mechanism.

The IPL is a classic mirror system region, with mirror neurons found here in the monkey (Fogassi et al., 2005), and overlapping activity seen consistently during action observation and execution in humans (e.g. Montgomery & Haxby, 2008; Molenberghs et al., 2012). Additionally, cross-modal adaptation between human execution and observation of the same action has been found in this area, whereby activity is reduced during observation/execution if one has just executed/observed the same action ((Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008). This is thought to reflect the same population of neurons being activated during performance and visual perception, rather than a simple gross overlap in the region recruited. IPL is part of the dorsal visual stream, and has many subregions with diverse functional properties. Some of these encode spatial object features such as size, orientation, and location (Sakata et al., 1998), whereas others combine such features with information from the ventral visual stream (posterior STS) about body parts (e.g. movement of the hand or mouth). Parts of the IPL are thought to serve as an interface between perception and action, with different subregions specialized for different types of actions (e.g. reaches, Connolly, Andersen, & Goodale, 2003; saccades, Luna et al., 1998; Tunik, Frey, & Grafton, 2005). Many therefore claim that IPL could represent the spatial relationship between effectors and objects, providing the premotor cortex with the necessary inputs to recognize trajectories of these relationships as object-directed actions (Bonaiuto, Rosta, & Arbib, 2007; Oztop & Arbib, 2002).

The primary motor cortex projects directly to the spinal cord, and is thought to directly control movement by modulating muscle activity (Kakei, Hoffman, & Strick, 1999; Lemon, 2008; Todorov, 2000). This region is somatotopically organized (Lotze et al., 2000; Penfield & Rasmussen, 1950), whereby it is divided into specific representation areas for different body parts (e.g. hand, foot, mouth). Although not a classic mirror system area, mirror neurons have now been found in the primary motor cortex of macaques (Vigneswaran et al., 2013), with activation of this region in humans also having been found during action observation (e.g. Hari et al., 2014; Muthukumaraswamy & Johnson, 2004; Nishitani & Hari, 2000). Accordingly, many have suggested a role for the primary motor cortex as part of a frontal network involved in mental rehearsal or simulation of observed actions (Cisek & Kalaska, 2004; Vigneswaran et al., 2013). Work by Hari et al., (2014) suggests that human primary motor cortex contains different neuronal populations, one which is automatically activated during action observation, and one which is inhibited. The authors interpret this as being in line with evidence for mirror neurons that are both activated and suppressed in primary motor cortex (Vigneswaran et al., 2013), and could help explain why this area could be involved in simulation of observed actions without producing overt movement.

Directly anterior to primary motor cortex, and densely interconnected with it, is the premotor cortex. This region has some projections to the spinal cord, but mainly projects to the primary motor cortex itself (Kakei, Hoffman, & Strick, 2001). The premotor cortex is thought to be involved in planning manual actions (Batista et al., 2007; Cisek & Kalaska, 2002; Hoshi & Tanji, 2006; Nakayama, Yamagata, Tanji, & Hoshi, 2008; Tanji & Hoshi, 2000) and the spatial guidance of movements (Fogassi et al., 2001; Kakei et al., 2001; Kurata, 1993). Overlapping activity in human premotor cortex during action observation and execution has been found in a multitude of studies (see Molenberghs et al., 2012 for a meta-analysis), with the premotor cortex considered a core region of the classic mirror system. Furthermore, observation of actions involving the hand, foot and mouth seem to activate human premotor areas in a somatotopic fashion (Buccino et al., 2001). Motor representations are thought to be more abstract in the premotor compared to motor cortex (Rizzolatti & Luppino, 2001; Rizzolatti et al., 1988): for example, motor cortex might represent the movement of each individual finger, but premotor cortex might represent a particular type of grasp or coordinated movement of fingers to perform particular grasps. Therefore, as both motor and premotor cortices are often activated during observation of others’ actions, it could be that via a mirror system, both contribute to the simulation of an observed action, representing the observed action at the same level they do for execution (Kilner & Frith, 2008).

The IFG is often considered the human homologue of F5 in the monkey (Kilner, Neal, Weiskopf, Friston, & Frith, 2009), where mirror neurons for manual actions were first discovered, and mirror neurons for mouth actions found later on (Ferrari et al., 2003). Many fMRI studies have demonstrated overlapping activation during action observation and execution in the IFG (e.g. Jabbi & Keysers, 2008; Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2004; Newman-Norlund, van Schie, van Hoek, Cuijpers, & Bekkering, 2010), as well as cross-modal adaptation between action execution and observation (de la Rosa, Schillinger, Bülthoff, Schultz, & Uludag, 2016; Kilner et al., 2009). This is strong evidence for IFG constituting a core component of a human mirror system, but the specific function it may play is not clear. A number of suggestions have been made, including a role in goal inference where actions are object-directed (Newman-Norlund et al., 2010), linking action representations with other representations, such as emotions and semantics (Liakakis, Nikel & Seitz, 2011), and inhibiting automatic motor responses (Cai et al., 2011; Molnar-Szakacs et al., 2004). The IFG is composed of functionally distinct subregions: Brodmann areas 44, 45, and 47/12, which are interconnected (Greenlee et al., 2007), and therefore the IFG could play a role in all of these processes. Indeed, its connectivity with the insular (Catani et al., 2012), prefrontal (Catani et al., 2012), premotor (Catani et al., 2012) and primary motor cortices (Greenlee et al., 2004), as well as its overlap with ventral premotor cortex (Binkofski & Buccino, 2004) makes it a suitable region for linking cognitive representations such as semantics and goal-directed planning with high level motor representations in premotor cortex (Badre & D'Esposito, 2009).

As mentioned in the previous section, mirror neurons have been found in the LIP of the monkey (Shepard et al., 2009), an area involved in covert and overt eye movements, and thus could play an important role in a mirror system for attention orienting. Human research suggests that the equivalent region is also activated during observation of gaze shifts (Saito et al., 2010), with the frontal eye field (FEF), a premotor cortical region activated during covert shifts of attention and saccade preparation (e.g., Connolly, Goodale, Menon, & Munoz, 2002) also recruited during observation. LIP projects directly to FEF (as well as STS which could provide visual input to the system, Grosbras et al., 2005), suggesting that FEF may represent a premotor portion of a mirror system (Frischen et al., 2007).

Human studies have also revealed that regions not classically associated with a mirror system; i.e. areas not strictly related to motor functions; such as the somatosensory cortex, insula, and amygdala seem to have mirroring properties (e.g. Carr et al., 2003; Caspers et al., 2010; Keysers, Kaas, & Gazzola, 2010; Molenberghs et al., 2012; Wicker et al., 2003; Gazzola, Aziz-Zadeh, & Keysers, 2006; Keysers et al., 2004). This suggests that areas in addition to those comprising the core mirror system are involved in integrating other action features, for example, the affective components that accompany them (Keysers & Gazzola, 2009). Such activation could be viewed as being part of an extended version of the core mirror network, or it could be that separate, but overlapping, networks for different actions exist. Indeed, those such as Cattaneo and Rizzolatti

(2009) posit that brain-imaging studies have revealed two main networks of brain regions with mirror properties in the humans. The first of these is formed by the parietal lobe, premotor cortex, and caudal part of the inferior frontal gyrus (the 'parietofrontal mirror system'), and the second by the insula and the anterior mesial frontal cortex (the 'limbic mirror system'). The parietofrontal mirror system is suggested by these authors to be involved in the processing of voluntary behaviour, and the limbic mirror system in the processing of affective behaviour. The insula could link the parietofrontal mirror system with the limbic system, providing a mapping from an observed expression onto internal emotional representations (Dapretto et al., 2006; Rizzolatti, Cattaneo, Fabbri-Destro, & Rozzi, 2014). Similar proposals have been made by a number of other researchers (e.g. Keysers & Gazzola, 2009, 2014; Pineda, 2008; van der Gaag, Minderaa, & Keysers, 2007). For example, if one observes someone performing an emotional facial expression, activation of shared representations for action and emotion may take place, which requires a number of different anatomical and functional circuits. All the brain regions involved in this may not contain mirror neurons as such (i.e. neurons with visual and motor properties), but the type of representation they transform stimuli into (e.g. emotional or proprioceptive) may play a critical role in the mirroring process via elaboration of the information received (Pineda, 2008).

TMS research also provides compelling evidence that the activity of the human motor cortex is impacted by observation of others' actions, and thus supports the idea that a mirror system might facilitate a mapping between own and other action execution. TMS is a neurophysiological technique that involves inducing a current in a small area of the participant's brain. Specifically, a current is passed through a coil of copper wire, which is wound inside a plastic-insulated case and held over a participant's head. As the current passes through the coil it generates a magnetic field that can pass through the scalp and skull, and in turn, induces a current in the targeted brain region. The current induced by the magnetic field stimulates the neurons in the area beneath the coil, which briefly alters the typical function of those neurons. In many studies, TMS is used to stimulate the primary motor cortex (M1), sending action potentials (nerve impulses) along efferent nerves (those that carry impulses away from the central nervous system), and producing motor-evoked potentials (MEPs) in the muscle/muscles of interest. MEPs are recorded using electromyographic (EMG; a technique for recording the electrical activity produced by skeletal muscles, with EMG electrodes detecting the electrical potential generated by muscle cells) electrodes attached to the skin covering the muscles, with the amplitude of these MEPs indicating the level of excitability in the motor pathways. MEPs are most often recorded as participants observe different types of action, and the amplitude compared to MEPs stimulated during a baseline condition such as when participants are not observing any actions (e.g. Baldissera, Cavallari, Craighero, & Fadiga, 2001). As such, this type of change (increase or a decrease in amplitude) in MEPs during action observation is considered an indication of mirror system activity. That is, the mirror system (in this case, mainly the premotor cortex) projects to the primary motor cortex, and therefore during action observation, there is activity in mirror areas and an increase in excitability of the primary motor cortex. TMS can thus be used to measure this increase in excitability by comparing stimulation evoked MEPs during action observation with those evoked during the baseline condition. Mirror system activation is identified if MEPs induced during action observation are greater in amplitude than those in the baseline. In one of the first studies to utilize such an index, Fadiga et al. (1995) demonstrated that muscle activity in the hand and forearm was increased during observation of grasping actions that involved the same muscles, but not during observation of other stimuli such as three dimensional objects. Many TMS studies since have found similar modulation of the motor system during action observation (e.g. Enticott, Kennedy, Bradshaw, Rinehart, & Fitzgerald, 2011; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006), supporting a role for the motor system in action observation.

In addition to the fMRI and TMS research that has provided converging support for the existence of a mirror system in human adults, many studies have instead used EEG to investigate mirror system activity (Moore, Gorodnitsky, & Pineda, 2012; Muthukumaraswamy & Johnson, 2004; Pineda, 2005). Such research, along with the use of EEG to study mirror mechanisms in the developing brain, will be discussed later on in this chapter. For now however, the discussion will move on from mirror neuron properties in the monkey and mirror systems in the human brain to some potential functions that have been attributed to mirror systems.

1.2.3 THE FUNCTIONAL ROLE OF MIRROR SYSTEMS

Before mirror neurons were discovered in the macaque brain, processing others' actions was generally considered a strictly visual task, resulting from a chain of perceptual processes that compare previous experience with current visual input. This chain involves the hierarchical extraction of increasingly complex features, which are then compared to similar visual representations stored in the observer's memory (e.g. Marr & Vaina, 1982). This idea was supported by the work of Perrett and colleagues, who discovered neurons in the STS that respond to observation of biological movements (e.g. Perrett et al., 1985, 1989, 1990). However, although purely visual processes are no doubt important for the evaluation of others' actions, the discovery of mirror neurons suggests that there is a motor component to action observation. The visual responses of mirror neurons could encode others' actions with a representation that is directly connected to the observer's own motor experience, including motor and behavioural goals, as well as internal motivations and emotional states (Rizzolatti et al., 1996, 2001). It is important to note that most researchers advocating a role for a mirror system in action recognition and other more complex skills do not claim that this is the only way in which one can process others' actions. For example, visual mechanisms might allow the processing and evaluation of actions that are not part of an observer's own motor repertoire. However, when an observed action is one an individual has previously performed, it could be that mirror neurons serve to *enrich* the processing of that action (Del Giudice et al., 2009). This enriched knowledge includes the motor program used to execute that action (particularly how the action progresses over time), which could aid the observer in recognizing that action (Gallese et al., 1996) and predicting its outcome (Aglioti, Cesari, Romani, & Urgesi, 2008; Umiltà et al., 2001); or perhaps even to predict someone's future actions (Kilner, Friston, & Frith, 2007), plan one's own actions in response, or simulate the emotional and somatosensory feelings associated with another's action (Gazzola, Aziz-Zadeh, & Keysers, 2006; Keysers et al., 2004).

Those such as Marshall and Meltzoff (2014) have hypothesized that the development of mirror systems could be particularly important early on in life, with an infant's ability to map self-other similarities being crucial for social interaction, and consequently, for the emergence of many other important aspects of social-cognition. As outlined previously in this chapter, early on in development, infant social capacities undergo a number of transitions often referred to as different stages of 'intersubjectivity' (Trevarthen & Aitken, 2001); whereby at first, social interaction takes place in the form of reciprocal actions and turn-taking. These interactions could develop via imitative processes, facilitated by the self-other mapping of a mirror mechanism that allows infants to achieve an initial feeling that others are "like me" (Meltzoff, 2007), which serves as a foundation for intersubjectivity: e.g. my hand and your hand are similar, and I can imitate you action because I can identify the corresponding body parts to perform the same action myself (Marshall, Saby, & Meltzoff, 2013).

Before discussing the various functions that have been proposed, it is worth defining some terms that are often confused in the mirror system literature. Rizzolatti & Fogassi (2014) describe 'movement' as referring to simple joint displacement or orofacial twitches, and the term 'motor act' to a series of movements that are organized in such a way as to attain a specific *motor goal,* e.g. the shaping of one's hand in such a way as to grasp an object. Note, multiple motor acts could result in achievement of the same motor goal (e.g. precision pinches and whole hand grasps to achieve the same goal of grasping an object). The word ‘action’ is said to describe a sequence of fluently linked motor acts that, at its conclusion, determines the realization of a *behavioural goal*, e.g. the sequence of reaching, grasping and bringing a piece of food to the mouth (all motor acts with motor goals) for eating (the behavioural goal). Therefore, in the discussion below, ‘recognition’ could relate to the identification of specific movements, motor acts, or actions, which would involve activation of different mirror neurons or populations of mirror neurons. However, the term ‘action’ in this thesis is used generically so that the level (movement, motor act, action) does not have to be specified each time, and ‘goal’ is also used generically, so could refer to motor or behavioural goals. Although facial expressions are still referred to simply as actions here, it is important to note that they represent a class slightly different from manual actions, in that they are not necessarily under voluntary control or directed towards objects. Therefore, although they might not reflect any goals per se at their conclusion, they can still signal useful information to an observer, such as the internal emotional state of the performer.

So, how might different regions of a mirror system be involved in the processing of these various action levels, and how does this relate to the different functions that neural mirroring is suggested to serve? This will be discussed below, guided by examples given in Table 1.1. The focus is on manual actions, as most relevant research has focused on this type of behaviour, but then the applicability of this classification system to facial expressions will be considered. The rows in Table 1.1 distinguish between levels of action organization, from low-level movements, to motor acts which are comprised of multiple movements, and actions which consist of series of motor acts. The columns list possible functions of a mirror system at each level of organization, in which some (such as ‘Attribute mental states’) are only applicable to certain levels (such as ‘Motor acts’ or ‘Actions’).

Hierarchical theories of human motor control are prevalent and have a long history (Grafton & Hamilton, 2007; Hebb, 1949; Sherrington, 1906), with such models distinguishing between different levels of motor representation ranging from individual muscle movements, combinations of movements (motor acts), and finally to combinations of motor acts (actions); as defined in Rizzolatti & Fogassi (2014). These level distinctions are thought to reflect the fundamental organization of action in the central nervous system (Grafton & Hamilton, 2007), with certain brain regions representing actions at different levels of the motor hierarchy. While a great deal is known about the organization of lower levels of the motor hierarchy, such as movements and motor acts in the primary and premotor cortices (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995), the organization of the higher levels is not so clear. Nevertheless, an increasingly widespread idea is that human actions are often encoded in terms of higher level goals in certain brain regions (Grafton & Hamilton, 2007), and that observed actions provide important information about others' mental states (Frith & Frith, 2006). Therefore, it seems reasonable to assume that during observation, actions could be coded at different levels of the motor hierarchy in different regions, with each brain region coding the observed movement at the level it controls during movement execution (D'Ausilio, Bartoli, & Maffongelli, 2015; Kilner & Frith, 2008; Rizzolatti & Luppino, 2001; Rizzolatti et al., 1988).

The lowest level of action given in Table 1.1. is simple movements. Human studies demonstrate activation of primary motor cortex during execution and observation of manual actions (e.g. Cavallo, Bucchioni, Castiello, & Becchio, 2013; Fadiga, Craighero, & Olivier, 2005; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; McCabe, Villalta, Saunier, Grafton, & Della-Maggiore, 2015; Sartori, Bucchioni, & Castiello, 2012). This region is thought to represent very low-level movements (e.g. movement a particular finger), and thus could encode observed actions at the same level (Kilner & Frith, 2008; Rizzolatti & Luppino, 2001). In support of this claim, human TMS research has shown a strong congruence (e.g. the amplitude of MEPs induced by TMS in muscles involved in the observed movement are modulated by the amount of the observed aperture; MEPs become larger with increasing finger aperture and became smaller during the closure phase) between observed actions and evoked motor output (e.g. Fadiga et al., 1995; Gangitano, Mottaghy, & Pascual-Leone, 2004; Sartori et al., 2012); and MEG research has found a strong coherence between movement acceleration during object-directed manual actions and neural activation in sensorimotor cortex during action observation (Marty et al., 2015). However, although mirror neurons have been found in the macaque primary motor cortex (Vigneswaran et al., 2013), no one has recorded the kinematics of the observed action in monkey neurophysiology experiments, so whether or not primary motor cortex may represent simple movements in the monkey mirror circuit is not clear.

In the macaque, mirror neurons in the premotor cortex are thought to code motor acts rather than simple movements. During execution, F5 (premotor) canonical neurons are selective for grasp type and phase of the movement, while F1 neurons (primary motor) are selective for different phases of different grasps (Umilta, Brochier, Spinks, & Lemon, 2007). If mirror neurons in these regions code the same features during observation as during execution, this could mean that F5 neurons encode the combined movement of the fingers involved in the observed grasp, whereas an F1 neuron encodes the observed movement of an individual finger, and thus would be active during different grasps involving that finger. Furthermore, the firing of F5 mirror neurons increases during observation of grasping movements when the monkey knows there is an object to be grasped (visible or occluded) but not when the object is absent (Umilta et al., 2001), and certain neurons will fire not only during observation and execution, but also when a related sound to a behaviour is heard (Keysers et al., 2003; Kohler et al., 2002). In both of these cases, the motor act (grasping) is inferred, but the movements making up the motor act are unobservable. There is also evidence that activity in human premotor cortex can also reflect the encoding of motor acts rather than simple movements. For example, Gangitano et al. (2004) showed that MEP facilitation followed the time course suggested by an initial movement (rather than adjusting in real time) when observing a reach-to-grasp act that was suddenly modified by an unusual movement during completion. However, because TMS-evoked MEPs reflect cortical excitability in primary motor cortex, it is not clear whether or not this modulation of MEPs reflects primarily motor or premotor cortex properties and more research is therefore needed to determine the features of observed actions encoded in human premotor and motor cortices.

In humans, there is also evidence that IFG may represent actions, or sequences of motor acts to achieve a goal (note, IFG is actually considered by many to be the human homologue of macaque F5, and overlaps with ventral premotor cortex). During execution, IFG is involved in translating goals into actual action (Fincham, Carter, van Veen, Stenger, & Anderson, 2002; Tunik, Lo, & Adamovich, 2008). During observation, it seems to reflect mirroring of the action goal, whereby actions embedded in contexts (grasping actions to drink or clean up) yield the greatest activation (Iacoboni et al., 2005). It has been suggested (Fadiga, Craighero, & D'Ausilio, 2009) that IFG is involved in representation of abstract hierarchical structures, which would be important for constructing and traversing a hierarchy of action and motor act goals. This could also explain why this region appears to play a role language, which has its own hierarchical structure (Bornkessel, Zysset, Friederici, von Cramon, & Schlesewsky, 2005; Embick, Marantz, Miyashita, O'Neil, & Sakai, 2000; Tettamanti et al., 2002).

At each level of action organization, mirror systems have been proposed to play increasingly complex roles, from implicit action recognition and outcome prediction, to goal and mental state inference. In terms of recognition, this could simply be distinguishing one movement/motor act/action from another (e.g. for motor acts, a precision pinch from a power grasp) (Casile, 2013). Predicting outcomes could also be a function at all three levels (e.g. for movements, the finger will stop extending to 90 degrees rather than 80), however inferring goals only applies to motor acts and actions (e.g. the motor goal of a precision pinch is to have the forefinger and thumb around an object; or the behavioural goal of a reach-to-grasp-to-eat action is to eat the food). As previously noted, predicting outcomes and inferring goals may seem very similar, however there are cases where they could be different. For instance, the 'goal' of motor act may be to grasp an object, but perhaps the outcome is actually knocking the object over. In this case, even though the executer may have wanted to grasp the cup, the observer might predict that they will knock it over instead. Finally, for manual actions, the attribution of mental states might only apply to actions because they are sequences of motor acts intended to accomplish a desired state of the world, and as such, reflect the mental state leading to that desire.

Motor theories of social-cognitive development (i.e. those that assign a major role to the motor system in related processes) assert that through an individual's own motor experience, one can process the actions of others, as well as infer the goals and motivations underlying others' actions. The discovery of mirror neurons provided the first neural data in support of such theories, suggesting that when an action is part of an observer's own motor repertoire, the privileged knowledge this bestows can aid in its recognition when performed by someone else (e.g. Casile, 2013; Del Giudice et al., 2009; Rizzolatti et al., 2001). That is, because mirror neurons fire both during observation and execution of actions, and thus that the same cortical network involved in performing an action yourself is activated when observing another individual perform the same action, an observer can identify another's action because they 'know' what that action is when they perform it themselves (Vanderwert et al., 2013). Therefore at the lowest level, and constituting what might be the most basic function of a mirror mechanism, mirror system activation could result in the recognition that others are performing actions (Casile, 2013). Recognition can actually be further divided into implicit and explicit forms. Implicit recognition is 'data-driven' and unconscious, such as differences in neural responses and looking times, whereas explicit recognition involves conscious perception, such as verbal labelling. Early suggestions that the mirror system is involved in explicit recognition would predict that subjects would be unable to recognize an action after damage to motor areas, and while this has not always been found (Hickok, Houde, & Rong, 2011; Negri et al., 2007), some research does support this claim (Kalénine, Buxbaum, & Coslett, 2010; Michael et al., 2014; Serino, Annella, & Avenanti, 2009). Implicit recognition could involve the differentiation of one action from analogous ones (e.g. that one motor act represents a precision grip, but another represents a power grasp). It could be that mirror systems are more involved in implicitly recognizing actions in order to link them to representations in other regions, but this possibility requires further research investigating interactions between mirror system regions and other regions related to semantics.

There is evidence from human TMS and EEG studies (e.g. Aglioti, Cesari, Romani, & Urgesi, 2008; Denis, Rowe, Williams, & Milne, 2017; Stadler et al., 2012) that the motor system is involved in predicting the outcome of observed actions. Even if action processing can be achieved outside of the motor system, in some situations, speedier action recognition (and perhaps the inferring of goals or intentions) facilitated by a mirror system could result in more efficient prediction of others' actions; and hence may aid the planning of an observer's own actions in response. For example in the TMS study by Aglioti et al., basketball players (who had motor experience of the actions involved in the game) were shown to correctly predict the outcome of a basket throw after observing only the initial part of the action (before the ball left the hand), and were faster and more accurate at this than coaches who had similar levels of visual experience with these actions, but not as much motor experience. Additionally, the response of players, compared to that of the other groups, differed even before the ball was observed to leave the actor's hands. This implies that they were able to predict the outcome of the shot via the 'understanding' of the actor's body kinematics. Furthermore, players demonstrated time-specific motor activation during observation of basket throws, suggesting that athletes predicted the outcome of the throw by reading the body kinematics. Although the visual experts such as the coaches also demonstrated a specific increase of MEPs during observation, only the players demonstrated a time-sensitive motor response during observation of inaccurate shots. These findings therefore suggest that if an action is part of an individual's motor repertoire, a mirror system may aid the rapid prediction of the outcome of others' actions.

There is also evidence that mirror systems could be involved, not in predicting the outcome of an observed action, but inferring the goal. Human parietal regions, for example, are sensitive to the goal of a manual action but not the trajectory taken by the observed hand (Hamilton & Grafton, 2006). Some mirror neurons in macaque IPL appear selective for the next motor act that comes in an action (e.g. after reaching, grasping to eat or to place a piece of food; Fogassi et al., 2005; Rozzi, Ferrari, Bonini, Rizzolatti, & Fogassi, 2008). Because these IPL mirror neurons fire during observation of the grasp differentially, depending on the following movement (to place or to eat), this response could reflect a prediction being made about the final goal of an action. In accordance, IPL mirror neurons could perhaps encode the inferred intentions of an observed action by combining bottom-up information from the action itself, and top-down information about the context (Fogassi et al., 2005). However, it is not clear from this study whether IPL is encoding the inferred goal of the action overall or reflecting prediction of the next motor act since actions involving only two motor acts were used. Predicting the next motor act and inferring the action goal may seem very similar, but it could be, for example, that predicting the next motor act in an action is based simply on statistical regularities in observed sequences rather than mirroring. Nevertheless, even if statistical inference was used in some situations, it would probably be more accurate and rapid if one could infer the action goal. Some properties of F5 mirror neurons suggest that some of them may encode the goal or outcome of a motor act or action (Vanderwert et al., 2013). For example, a subset of F5 mirror neurons fire when an action is performed using different effectors (Ferrari et al., 2003), when only the sound of an action is provided (Keysers et al., 2003; Kohler et al., 2002), and when the end of an action is occluded so that the goal has to be inferred (Umiltà et al., 2001).

The study by Umilta et al. (2001) is frequently used to support the proposal that mirror neurons are involved in the inference of goals during action observation, as the neurons in F5 fire when the monkey observes an experimenter reach behind a barrier to grasp an object whether an object is present or not. For successful actions, the outcome and the goal are the same. However, for unsuccessful actions, or those with unintended consequences, the goal can be quite different from the actual outcome. In Umilta et al.'s study the experimenter knew whether or not there was an object behind the barrier, and therefore whether the monkey mirror neuron activation reflected the inference of goals or prediction of the action outcome is unclear. To address this, a condition would have to be included which dissociates the goal from the outcome, in which the observed person does not know that the object is not behind the screen (but the observer does), and see if mirror system activity is modulated. If the same mirror neuron fires when the experimenter reaches behind the screen and there is no object (but the experimenter thinks that there is), this neuron could be encoding the inferred goal of the motor act (to grasp the object). If however, the neuron does not fire, this could be because the outcome of the motor act (no grasp) is predicted. This is an example of a false-belief task, which great apes have recently been shown to pass (Krupenye, Kano, Hirata, Call, & Tomasello, 2016), but whether this is the case in macaques, and whether a mirror system is involved, is unknown.

Table 1.1: In this table, examples are given of different movements, motor acts, and actions, and how these may relate to different functions have been attributed to mirror systems. This list is not exhaustive and is just intended to provide examples of possible outcomes, goals, and mental states associated with various movements, motor acts, and actions.

	Recognition	Predict outcome	Infer goals	Attribute mental states

Movements	Bending a finger	Finger will be at 90 degrees		
	Extending the elbow	Elbow will be extended		
	Mouth twitch	Corner of mouth will be pulled back		
Motor acts	Reaching	Hand will be at object	Bring hand to object	
	Precision Pinch	Forefinger and thumb will be around object	Grasp object	
	Power grasp	All fingers and thumb will be around object	Grasp object	
	Involuntary smile	Corners of mouth up, cheeks up, eyes squinted		Happy
	Voluntary smile	Corners of mouth up, cheeks up	Communicate approval	
Actions	Reach, grasp, and bring food to mouth	Food will be in the mouth	Eat the food	Hungry

The proposals outlined above have led to the suggestion that a mirror system may be implicated in far more complex social-cognitive skills (which are thought to involve a mapping between self- and other-generated actions), such as imitation, empathy, and even theory of mind skills (e.g. Carr et al., 2003; Gallese et al., 2004; Iacoboni, 2009; Rizzolatti & Craighero, 2004). While a mirror system may be useful in attributing mental states to other people, it is generally agreed that the attribution of mental states does not involve a mirror system alone. Many theorize that such 'theory of mind' (ToM) capabilities derive from an integration of mirror and mentalizing systems (Keysers & Gazzola, 2007), which processes others' intention in a more abstract sense, including in the absence of any observable biological motion (Van Overwalle & Baetens, 2009). A recent meta-analysis found that ToM components that rely on more affective, visual, or implicit stimuli engage mirror system regions more strongly, whereas higher-level cognitive, verbal, or explicit stimuli relied much more on metalizing areas such as the dorsal mPFC and TPJ (Molenberghs, Johnson, Henry, & Mattingley, 2016). However, some research has shown that disrupting the neural activity of mirror-related frontal areas impairs mentalizing abilities (Herbet, Lafargue, Moritz-Gasser, Bonnetblanc, & Duffau, 2015). The Mental State Inference (MSI, Oztop, Kawato, & Arbib, 2006, 2013; Oztop, Wolpert, & Kawato, 2005) model shows how the mirror system could interact with some other systems such as the mentalizing system for inferring mental states from observed actions. Oztop et al. argue that the anatomical location of mirror neurons in the monkey (such as the premotor cortex) and their response during grasping suggest that the main function of mirror neurons is based in grasp control, but that they could serve higher cognitive functions if augmented with additional neural circuits.

From the evidence presented here, it clear then that action observation is much more complicated than it may first appear (it may occur at a number of levels, which may involve different regions of the brain), and that the involvement of different areas could have different implications for what is mirrored and its function. A view is emerging that a mirror system mediates a cascade of visuomotor processes at different levels of description, from exact movements to abstract action goals achieved (Lestou, Pollick, & Kourtzi, 2008), and that an alternative to the apparent discrepancy between those who argue mirror activity reflects kinematic or goal-related information, is that both goal and kinematics modulate different parts of the observer's motor system and that this is dependent on the context (McCabe et al., 2015). For instance, McCabe et al., found that there was only an influence of a goal on motor system activity during action observation if the identity of the object to be grasped was known before movement onset. Movement kinematics, however, modulated activity whether or not information about the goal was provided, suggesting that depending on the information available, both goal and kinematics may drive motor facilitation during action observation. Others suggest that the final goal of an action modulates the excitability of the motor system at movement start, but the kinematics features take over as the action unfolds (Cavallo et al., 2013). Indeed, such results do not seem surprising as one can understand and reproduce others' actions at different levels, and thus presumably they would be analysed at different levels as well. If someone waves, for example, an observer could reproduce the goal of the wave by saying hello, the motor act by waving one of their own arms, or the movement by waving their same arm in exactly the same way. Perhaps implicit recognition of movements and/or low-level goals in mirror regions could be used by other regions to infer higher-level goals and mental states but the primary functionality of the manual mirror system is likely to capitalize on the observer's motor expertise in order to quickly and accurately predict the outcome of observed actions in order to rapidly formulate and make an appropriate response.

More recently, F5 mirror neurons have been found to also integrate several other features of observed actions, such as the distance (Bonini, Maranesi, Livi, Fogassi, & Rizzolatti, 2014; Caggiano, Fogassi, Rizzolatti, Thier, & Casile, 2009) or point of view from which a manual action is presented (Caggiano et al., 2011), including from an observer's own point of view (Caggiano et al., 2011; Maranesi, Livi, & Bonini, 2015), suggesting that they may play a role in planning responses to observed actions. A benefit of integrating this extra information could be that it allows mirror neurons to represent others' actions in terms of relevant features for analysis of subsequent actions and the planning of one's own actions (Casile, 2013; Casile et al., 2011), e.g. whether or not to interact with or approach the observed other. These characteristics therefore suggest that mirror neurons could play an important role in successful social interaction. Until such research was conducted, the response characteristics of mirror neurons to the observation of self-performed actions had not been explored. Interestingly, it has been proposed that at some point in phylogenetic history, a mirror system may have served to provide feedback signals for visually directed grasping (e.g. Bonaiuto & Arbib, 2010). According to this theory, the same system might later have been exapted through a generalization process, enabling the interpretation of others' actions related to social interactive and communicative functions. Those such as Ferrari et al., (2013) posit that the process of mirror neuron function being exapted to serve additional functions to the ones they evolved for, such as to recognize and 'understand' others' actions and emotional states, is especially likely in humans.

It has been suggested that a mirror system could have played a role in the evolution of a 'language ready brain' (Rizzolatti and Arbib, 1998; Arbib, 2002, 2016). This theory posits that language evolved from a basic mechanism not originally related to communication; a mirror mechanism for grasping. It is suggested that early in evolutionary history, a manual mirror system allowed observed actions to be linked to semantic representations, laying the ground for a gestural communication system which could then be expanded upon for vocal communication (Arbib, 2002, 2016). This account is supported by the intriguing fact that mirror neurons for manual and facial actions are interspersed in the macaque ventral premotor cortex (Ferrari et al., 2003), as well as that the human IFG, Broca's area, which is traditionally viewed as a language area, overlaps with ventral premotor cortex (Binkofksi & Buccino, 2006) and demonstrates manual mirror properties as well (Binkofski et al., 2000; Kilner et al., 2009). An earlier, but related theory called the 'motor theory of speech perception' (Galantucci, Fowler, & Turvey, 2006; Liberman & Mattingly, 1985) is supported by studies showing that when one hears or sees someone speak, the corresponding motor representations used to make those sounds are activated, which in turn, are linked to sematic representations (e.g. Bell-Berti, Raphael, Pisoni, & Sawusch, 1979; Fadiga, Craighero, Buccino, & Rizzolatti, 2002; Kerzel & Bekkering, 2000; M. Sato, Buccino, Gentilucci, & Cattaneo, 2010; Skipper, van Wassenhove, Nusbaum, & Small, 2007). Although many studies have shown recruitment of the motor system during speech perception, this theory has been criticised on the grounds that infants show even greater phonetic discrimination abilities than adults (Kuhl, 2004; Trehub & E., 1979), and that emphasis should therefore not be on the motor rather than auditory cortex (Diehl, Lotto, & Holt, 2004). However, recent evidence suggests that there is greater activation of corresponding motor representations during speech perception in difficult conditions, i.e. noisy environment, foreign accent (Adank, Nuttall, & Kennedy-Higgins, 2016; Du, Buchsbaum, Grady, & Alain, 2016; Nuttall, Kennedy-Higgins, Devlin, & Adank, 2017; Nuttall, Kennedy-Higgins, Hogan, Devlin, & Adank, 2016). Therefore, an alternative idea is that a mirror system could be useful in situations where another's speech is more difficult to comprehend.

Finally, how might the possible divisions outlined in Table 1.1. relate to facial expressions rather than manual actions? Because facial expressions are intransitive (i.e. not directed at a particular object), and can be both voluntary (e.g. a smile to communicate approval during a social interaction) or involuntary (e.g. a spontaneous smile when hearing a funny joke), it is more difficult to categorise them according to the motor hierarchy outlined for manual actions. However, some possible examples of how this might be achieved are given in Table 1.1, and research strongly supports mirror system involvement in the processing of observed facial gestures. In the monkey, along with hand mirror neurons, mouth mirror neurons (ingestive and communicative) have been found in F5 (Ferrari et al., 2003), and a lot of human research demonstrates overlapping neural activation during the observation and execution of facial expressions (e.g. Carr et al., 2003; Leslie et al., 2004; Hennenlotter et al., 2005; van der Gaag et al., 2007; Kircher et al. 2012; Moore et al., 2012); as well when one experiences an emotion and sees the associated facial expression (Wicker et al., 2003). Viewing an emotional facial expression also interferes with performance of simple facial motor tasks, resulting in an increase of activity in the ventral premotor cortex/IFG that is correlated with emotion intensity (Lee, Dolan, & Critchley, 2008; Wild, Erb, Eyb, Bartels, & Grodd, 2003). Certain facial actions such as biting are object directed, and therefore could be represented more similarly to manual actions (e.g. biting an apple), but facial *expressions* (e.g. emotional such as smiling, or non-emotional such as mouth openings) are not directed at objects, and so are unlikely to involve the processing of object spatial relationships. This means that brain regions involved in a facial mirror system may overlap with those involved in a manual mirror system, but are likely to recruit separate neural populations. In Table 1.1., a mouth twitch was given as example of a simple facial movement, as this involves the movement of an individual muscle. Execution of such movements may be coded in primary motor cortex, including low-level movements involved in mastication, swallowing, speech and nonverbal communication (Morecraft, Stilwell-Morecraft, & Rossing, 2004; Yao et al., 2002). In the macaque, the primary motor cortex projects to the contralateral facial nucleus, which innervates the lower facial muscles (Jenny & Saper, 1987), and stimulation of the face representation in primary motor cortex causes discrete movements of the tongue and individual facial muscles (G. M. Murray & Sessle, 1992). These properties are similar to those of the arm and hand areas of primary motor cortex, and as mirror neurons that respond during observation of grasps are found in this region (Vigneswaran et al., 2013), observation of facial movements might also recruit the corresponding face representations in primary motor cortex, but this remains untested.

Facial expressions were included in the 'motor act' row of Table 1.1 as they comprise a number, or series, of facial movements. Monkey research supports the idea that premotor cortex is involved in the execution of facial 'motor acts', with lateral ventral areas projecting more bilaterally to the facial nucleus than primary motor cortex (Morecraft et al., 2004); prolonged stimulation of precentral and premotor cortex resulting in coordinated movements of the face to stereotyped postures (Graziano, Taylor, & Moore, 2002); and neurons in the ventral premotor region being active during execution of complex movements such as sucking, lip smacking and chewing (Ferrari et al., 2003). The premotor cortex is also involved in encoding such acts during observation (e.g. Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Hennenlotter et al., 2005; Leslie, Johnson-Frey, & Grafton, 2004; Maringer, Krumhuber, Fischer, & Niedenthal, 2011; Oberman, Winkielman, & Ramachandran, 2007; Rychlowska et al., 2014; Stel & van Knippenberg, 2008; van der Gaag, Minderaa, & Keysers, 2007), and observation of motor acts, including those performed with the mouth, activate human premotor areas somatotopically (Buccino et al., 2001). It is difficult to include an equivalent example for facial expressions in the action row of Table 1.1. if one defines an action as a sequence of facial expressions to achieve a motor or behavioural goal. This is likely because, aside from speech, facial actions such as facial expressions are organized less hierarchically than manual actions since manual actions can cause direct changes to the physical environment, and thus build upon the results of previous actions in a sequence (facial expressions are more likely to occur in isolation than in a sequence).

So, at each level of action organization, what role might a facial mirror system play? One possibility is that it is simply involved in the recognition of different expressions (e.g. distinguishing one from another). Explicit and implicit recognition of facial expressions are thought to be distinct processes (Mathersul et al., 2009), involving separate but overlapping networks of brain regions (Ralph Adolphs, 2002; Habel et al., 2007). Explicit recognition is the volitional mapping of an observed facial expression onto a discrete category with an associated label, such as 'happiness' or 'sadness'. On the other hand, implicit recognition involves the automatic activation of representations associated with a facial expression, including emotional and motor components (e.g. the 'feeling' of happiness and the motor commands used to smile). TMS research shows that premotor cortex seems to be involved in implicit recognition of emotional expressions (Balconi, Canavesio, & Finocchiaro, 2014). The IFG has also been associated with the semantic aspects of facial processing (Ishai, Ungerleider, & Haxby, 2000), and shows persistent activation during emotion perception and has extensive interconnections with other nodes of the face processing network (Foley, Rippon, Thai, Longe, & Senior, 2012). Research also suggests that individual differences in the ability to recognize facial expressions are associated with differences in the structure of the right IFG specifically (Uono et al., 2016). It has been suggested that the simulation triggered in premotor cortex by facial expression observation results in simulated activity in the somatosensory cortex, aiding in implicit recognition by linking the simulated motor representations to corresponding emotional representations (Adolphs et al., 2000). Indeed, a number of studies show activation of somatosensory cortex during observation of expressions (e.g. Wicker et al., 2003; Hennelotter et al., 2005; Gazzola et al., 2006), and lesions of the right somatosensory cortex impair successful retrieval of implicit conceptual knowledge about the emotions signalled by facial expressions (Adolphs et al., 2000).

Predicting outcomes could be a function of the facial mirror system at both the level of movement and motor acts. Though this hasn't been explicitly tested, this could be imagined to facilitate smooth social interactions by allowing the observer to predict the performance of a smile and respond accordingly after observing only the initial part of the motor act. Indeed, participants report feeling that interactions are smoother when facial mimicry occurs (Stel & Vonk, 2010), and computational models have shown that prediction can be used to recognized observed expressions (Cohn & Schmidt, 2004). However, as facial expressions occur very quickly (Schmidt, Bhattacharya, & Denlinger, 2009), much quicker than manual actions, it is also possible that prediction is not a main function of a facial mirror system.

Many facial expressions involve both motor and emotional components, and can be produced both voluntarily and involuntarily (such as smiling) to a certain degree. Although such expressions are not directed toward an object, voluntary facial expressions could be viewed as goal-directed in the sense that they can influence other people (van der Gaag et al., 2007). Indeed, generating intentional expressions is a very complex, socially learned form of communication (Niedenthal & Brauer, 2012) and is functionally and neurally distinct from spontaneous expression of emotion. For example, damage to primary motor cortex or its descending projections is associated with impaired voluntary execution of facial expressions but preserved involuntary emotional encounters, whereas damage to the midline cortex and insula are associated with difficulties in involuntary smiling while maintaining complete voluntary control of the same muscles involved (Laplane, Talairach, Meininger, Bancaud, & Orgogozo, 1977; Morecraft, Louie, Herrick, & Stilwell-Morecraft, 2001; Morecraft et al., 2004). However, it is also probable that a functional overlap in emotional (involuntary) and voluntary circuitry exists at the cortical level, as well as subcortically (Morecraft et al., 2004). While involuntary facial expressions automatically signal an emotional state, voluntary expressions can still convey emotional meaning, but can also hide underlying intentions and feelings during a social interaction (e.g. deception, deliberate empathizing). It has been suggested that the motor and emotional aspects of facial expressions are processed by separate, but linked, mirror systems which work together to contribute to facial expression recognition (Van der Gaag et al., 2007), with emotional facial expressions eliciting more activation in regions such as the amygdala, insula, and IFG (Carr et al., 2003; Kircher et al., 2013; Van der Gaag et al., 2007; Wicker et al., 2003). It has been proposed that the insula links the frontal components of the mirror system, such as the IFG, with the limbic system, providing a mapping from an observed expression onto internal emotional representations (Dapretto et al., 2006; Rizzolatti et al., 2014).

Perhaps then areas such as IFG, along with other regions that can be considered part of an ‘extended’ mirror system for faces, could be involved in the attribution of mental states. Indeed, activity in the IFG during the perception of expressions of basic emotions correlates with participant scores on the empathy quotient (EQ) scale (Chakrabarti, Bullmore, & Baron-Cohen, 2006), reduced IFG activity in psychopathic (who have very low levels of empathy is related to decreased IFG activity (Decety, Skelly, Yoder, & Kiehl, 2014), and patients with lesions in the IFG lesions are impaired in emotional empathy and emotion recognition (Shamay-Tsoory, Aharon-Peretz, & Perry, 2009).

1.3 ELECTROENCEPHALOGRAPHY AND MU RHYTHM MODULATION AS AN INDEX OF MIRROR SYSTEM ACTIVITY

As noted early on in this chapter, one of the principal techniques that has been used to investigate mirror system activity in humans is electroencephalography (EEG). EEG is a non-invasive neuroimaging technique, suitable for use with more difficult populations such as those with autism spectrum disorders and very young children. As such, this has been the main method employed by researchers to explore mirror systems in the developing brain. The experimental chapters included in this thesis utilized EEG in a number of studies to record putative mirror activity in very young participants. Therefore, the next sections of this chapter will provide a more detailed account of what EEG is, what neural signals it records, and why it is considered appropriate for use in mirror system research. This will be followed by a review of the studies that have utilized EEG to investigate mirror system activity in both adults and young children/infants.

1.3.1 WHAT IS ELECTROENCEPHALOGRAPHY?

EEG is the recording of electrical brain activity (fluctuations in the excitability of neural populations) from electrodes placed on the scalp. Primarily, the waveforms recorded using EEG reflect activity of the cerebral cortex, but are also influenced to some extent by electrical activity of underlying brain structures. EEG is measured in microvolts (µV), with the key frequencies of interest including those up to around 150 Hertz (Hz), and different frequencies of oscillations associated with different neural processes. The electrical signals detected by scalp EEG are relatively weak, and thus need to be amplified during recording. The use of EEG has a number of advantages over other techniques: for example, it is a non-invasive and relatively cheap method to record large-scale brain activity, although the spatial resolution is quite poor compared to fMRI, the temporal resolution is far superior, and EEG is less sensitive to movement.

Electrical activity associated with neuronal firing arises in two ways: action potentials and postsynaptic potentials. Action potentials are electrochemical changes that run from the start of an axon at the cell body to the axon terminals where they cause the release of neurotransmitters into the synaptic cleft (see Figure 1.2). Postsynaptic potentials occur when neurotransmitters bind to receptors on the membrane of the postsynaptic cell, causing ion channels to open or close, and resulting in a graded change in electrical potential across the cell membrane which, if strong enough, may cause an action potential to be generated in that cell (see Figure 1.2). Scalp EEG most likely reflects the summation of postsynaptic potentials triggered by presynaptic neurotransmitter release, rather than action potentials themselves. This is due to both the timing of action potentials and the physical arrangement of axons. Action potentials are very brief, making it more difficult for a large number of them to be active simultaneously, and thus to sum up to a measurable signal at larger distance. The duration of postsynaptic potentials (typically tens to hundreds of milliseconds) is much longer than action potentials (around 1 millisecond). These factors permit postsynaptic potentials to summate rather than cancel each other out, which produces voltage changes with greater amplitudes that can be recorded using EEG.

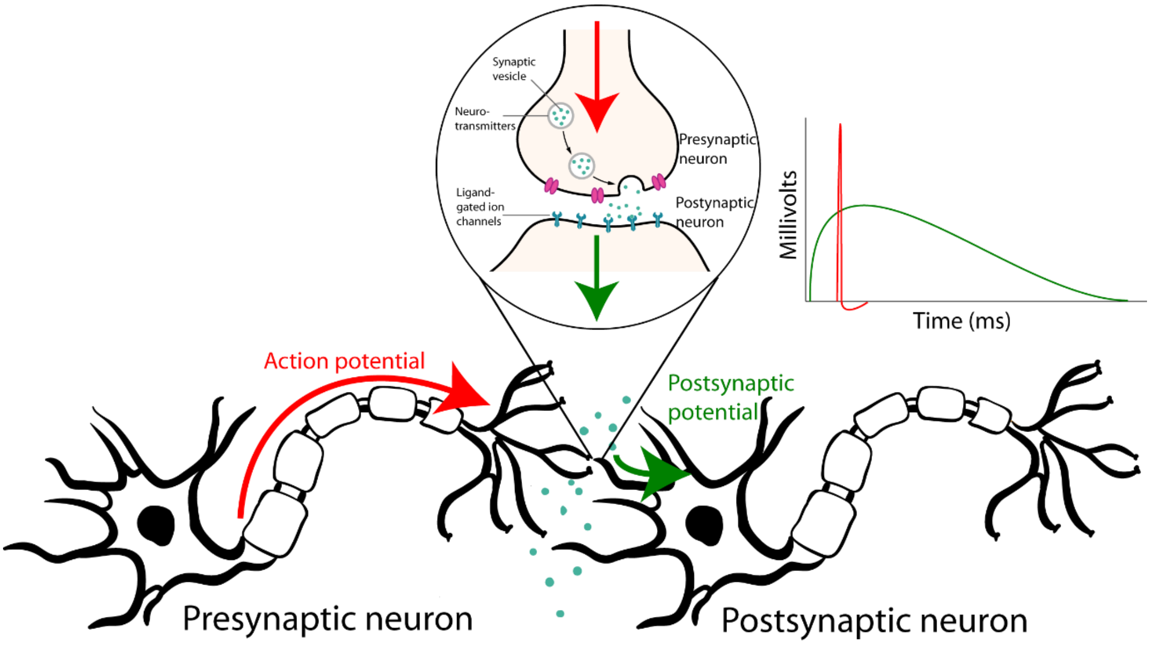

Figure 1.2: Action potentials (left; a brief electrical charge that travels down a neuron's axon) and postsynaptic potentials (right; changes in the membrane potential of the postsynaptic terminal of a chemical synapse. If the postsynaptic cell is sufficiently depolarized, an action potential will occur).

The activity generated by postsynaptic potentials in a single neuron is very small, but the synchronous activity of many neurons is of course much greater. As such, electrical activity recorded using EEG is reflective of large populations of active neurons. The tissue between the neurons and the scalp functions as a volume conductor, which allows the activity of these neuronal populations to be recorded. To enable EEG recording from the scalp, each neuron must generate an electrical field that is oriented in a way that ensures the cumulation of effects. To achieve this, the neurons must be organised in an open rather closed field, whereby the neurons' dendrites must all be positioned on one side of the structure, and all the neurons' axons must depart from the opposite side (Figure 1.3). Such open fields occur where neurons are arranged in layers, which is how they are organized in the majority of the cortex. This open field structure gives rise to many small 'dipoles', which are separated pairs of positive and negative charges. The current flow along postsynaptic dendrites creates a small dipole, with synchronous activity of many neighbouring dipoles summing to produce a detectable dipolar signal at the scalp. This dipole can be interpreted as an active area of the cortex, and describes the strength and direction of current flow within this area (Figure 1.3).

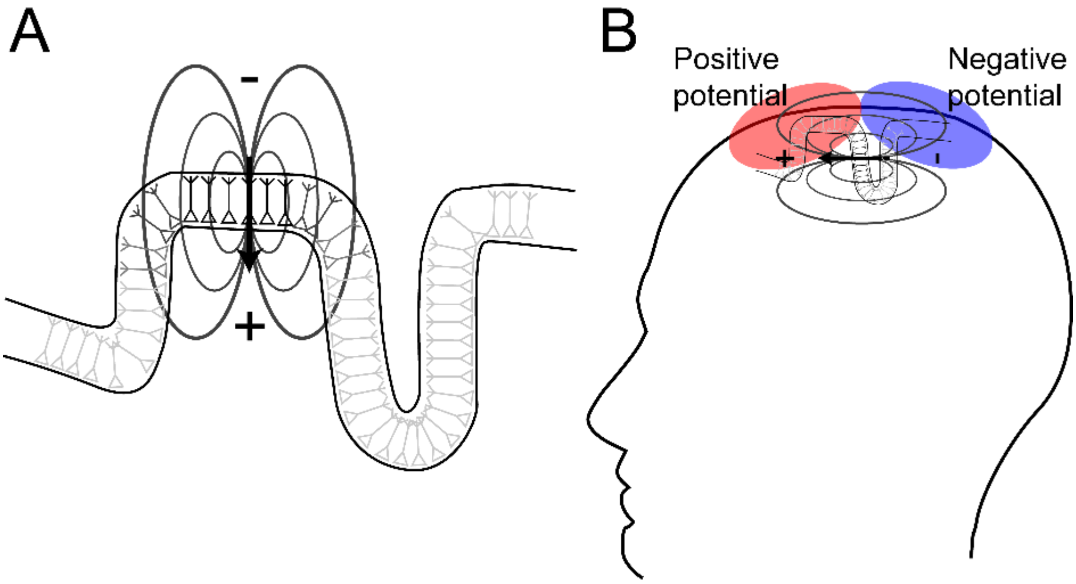

Figure 1.3: A) Open fields of neurons in the cortex. B) Measured dipole signals at the scalp.

Today, EEG tends to be recorded from 32, 64, or 128+ electrodes, which are typically mounted in a stretch-lycra cap. These caps make the electrodes easier to position on the head and allow electrodes to be placed all over the scalp. The position of electrodes corresponds approximately to different areas of the cerebral cortex (frontal, central, temporal, parietal, and occipital), which is usually based on the 10-20 system (Jasper, 1958; see Figure 1.4). According to this system, the first letter of an electrode name relates to the brain region over which it is positioned (e.g. C for central region). The letter is followed by a number, such as F3, or another letter such as Z. Even numbers indicate sites on the right side of the head, odd numbers the left side. The numbers increase as the distance from the centre of the head increases. Z is used as a label for the midline, which extends from the front to the back of the head.

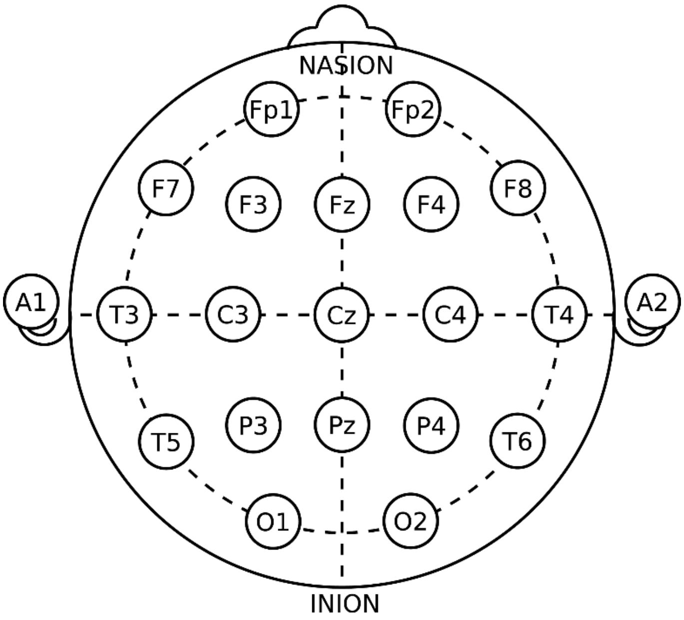

Figure 1.4: EEG electrode layout according to the 10-20 system.

As noted above, EEG data contain rhythmic activity which reflects neural oscillations. Certain oscillations are affected by task events, while others do not change. Oscillations are designated by three pieces of information (Figure 1.5 and Figure 1.6); frequency, which refers to the oscillation speed and has units of hertz (Hz) (number of cycles per second); power, which refers to the quantity of energy in a frequency band (the squared amplitude of the oscillation); and phase, which refers to the position along the sine wave at any given time point (measured in radians or degrees). Power and phase are independent, which means that neural dynamics measured via power are different from those measured via phase.

The rhythmic activity arising from the brain is comprised of a number of superimposed frequencies, but these can be separated using signal processing methods. Different cognitive processes and neural functions use different frequency ranges, or indeed, a combination of frequency ranges. The frequency bands most often associated with cognitive processes range from 2 to 150 Hz, which in an adult human corresponds to delta (2 – 4 Hz), theta (4 – 8 Hz), alpha (8 – 13 Hz), beta (13 – 30 Hz), lower gamma (30 – 80 Hz), and upper gamma (80 – 150 Hz) bands, though there are no exact boundaries defining these. Examples of associated cognitive functions include memory for the theta band, and attention and feature binding for the gamma bands.

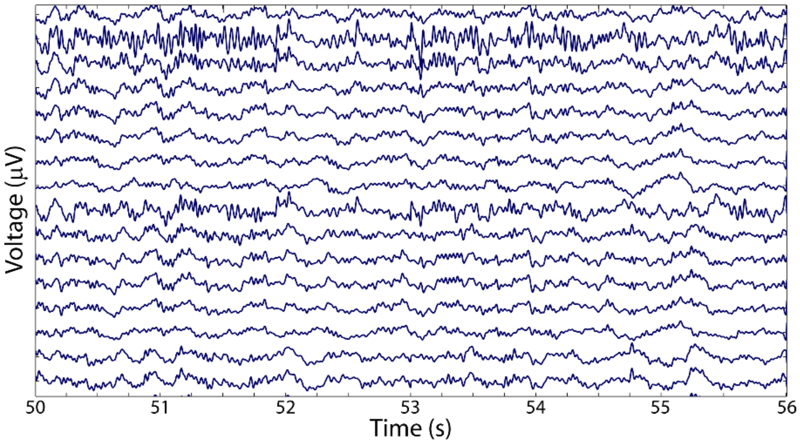

Figure 1.5: Raw EEG data (after 0.1-Hz high-pass filtering) showing oscillations at different speeds and for various lengths of time. Each line corresponds to a different electrode.

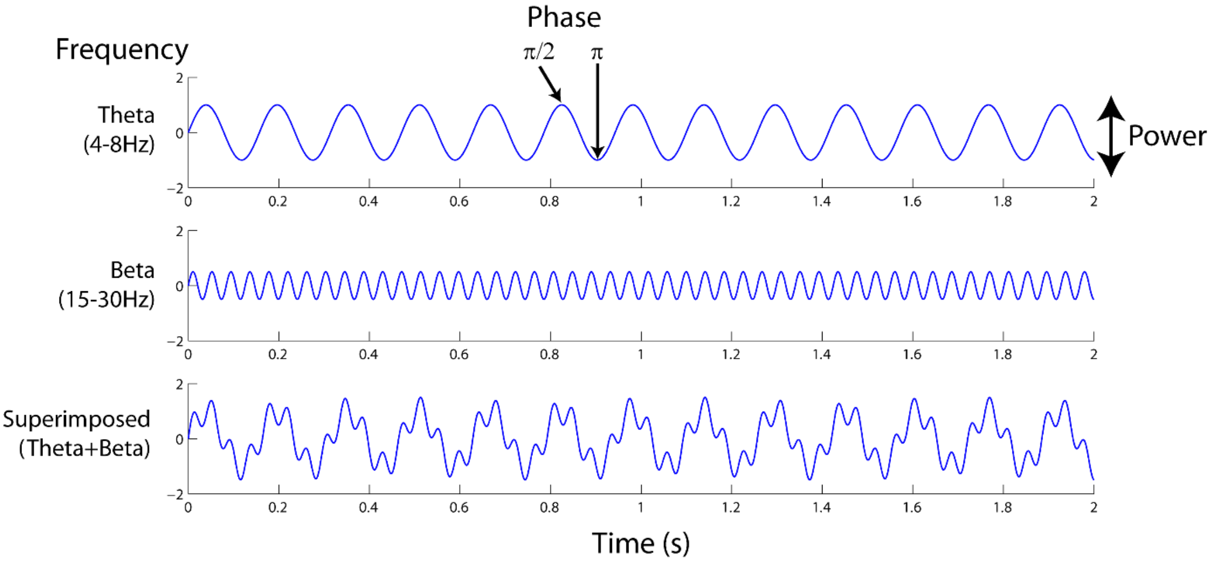

Figure 1.6: The three dimensions that define oscillations: frequency, power, and phase.

1.3.2 MODULATION OF THE MU RHYTHM AS AN INDEX OF MIRROR SYSTEM ACTIVITY

A considerable body of research has now utilized EEG to investigate human mirror systems, with modulation of the 'mu' frequency band, or 'mu rhythm', proposed as an indirect index of its activity (Cuevas, Cannon, Yoo, & Fox, 2014; Fox et al., 2016; Marshall & Meltzoff, 2011; Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy, Johnson, & McNair, 2004; Pineda, 2005, 2008). The frequency in which mu occurs lies within the alpha band (8-13 Hz in adults), and tends to be strongest over central regions (sensorimotor areas around C3 and C4 according to the 10-20 system). The amplitude of this rhythm decreases during action execution, which is thought to result from desynchronization in the firing of neuronal populations (which fire in synchrony at rest), and is associated with the cortical processing of movement-related information (Pfurtscheller & Lopes da Silva, 1999). There is also a posterior alpha rhythm that occurs in the same frequency band as mu, but this tends to be strongest over occipital regions (visual areas around electrodes O1 and O2 according to the 10-20 system), and becomes more synchronized (i.e. the amplitude is increased) by a reduction in light or when an individual closes their eyes. The mu rhythm, in contrast, is largely unaffected by light/eyes opening and closing, and instead is modulated by movement execution (e.g. manual actions) and somatosensory stimulation (e.g. touch) (Kuhlman, 1978). For these reasons, the central mu rhythm is considered a functionally and topographically distinct oscillation from the posterior alpha rhythm (Niedermeyer, 1997).

While the primary motor cortex is not part of the classic mirror system, it does receive projections from the premotor cortex, and also sends efferent copies of its output to the somatosensory cortex. As such, activity in the sensorimotor cortex (primary motor and primary somatosensory cortex, see Figure 1.7) is likely to reflect activation of premotor areas. The fact that the mu rhythm is most prominent over central electrodes overlaying the sensorimotor cortex, suggests that it is a marker of activity in this region. Of course, due to its poor spatial resolution, EEG activity recorded from particular electrodes does not guarantee that this is coming from neural populations directly below that location. However, as mu does appear distinct from the occipital alpha rhythm (Pineda, 2005), and as the cortical source locations from which mu is generated appear clustered mainly around the central sulcus (some also around parietal regions) in sensorimotor regions (Babiloni et al., 2016; Hari, Salmelin, Mäkelä, Salenius, & Helle, 1997; Salmelin, Hämäläinen, Kajola, & Hari, 1995), the claim that mu rhythm modulation reflects sensorimotor activity is convincing.

As well as the fact that mu modulation seems to reflect sensorimotor cortex activity , the finding that mu power is not only reduced during movement *execution*, but also during *observation* of other individuals performing similar actions (e.g. Lepage & Théoret, 2006; Muthukumaraswamy & Johnson, 2004; Perry & Bentin, 2009; Streltsova, Berchio, Gallese, & Umiltà, 2010), supports a decrease in mu power constituting a useful proxy measure of mirror system activity (Marshall & Meltzoff, 2011; Muthukumaraswamy & Johnson, 2004; Pineda, 2008). Further backing for this comes from research showing that mu rhythm activity co-varies with BOLD activity in mirror system regions (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011) during simultaneous EEG and fMRI acquisition; e.g. IPL and dorsal premotor area. These areas have strong cortico-cortico connections with the primary sensorimotor cortex (Hari et al., 1997). Mirror neurons have also recently been found in the macaque primary motor cortex (Vigneswaran et al., 2013), and some have argued that the sensorimotor cortex is actually a critical component of an ‘extended’ mirror system (Pineda, 2008).

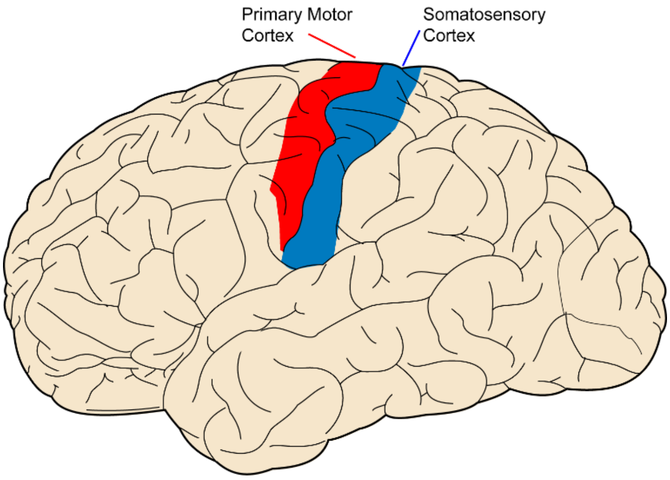

Figure 1.7: Sensorimotor cortex: area of the brain made up of the primary motor and somatosensory cortex, associated with coordinating muscle motion and the perception of own muscle and joint motion (i.e. voluntary movement), and where mu is thought to arise from.

One possible objection to the idea that mu power reduction is an index of mirror system activity is that it could simply reflect movement planning, which might be measurable as very small muscle contractions. However, early magnetoencephalography (MEG; a functional neuroimaging technique, similar to EEG, for mapping brain activity by recording magnetic fields produced by electrical currents that arise naturally in the brain) research has shown that the motor cortex can be activated during action observation without simultaneous muscle contraction (Hari et al., 1998). Thus sensorimotor activation during observation is unlikely to be explained by covert imitation (i.e. movement of muscles involved in the observed action).

There have now been many studies with adult human participants that have utilized EEG to investigate putative mirror system involvement in the processing of actions, including object grasping (Muthukumaraswamy & Johnson, 2004), facial expressions (Moore et al., 2012), and whole body movements (Orgs, Dombrowski, Heil, & Jansen-Osmann, 2008). Indeed, the mu rhythm also appears to respond to much of the same stimuli as have been tested in monkey studies, including, in addition to the mapping between visual and motor representations of manual actions, the mapping between auditory and motor representations of actions (Lepage et al., 2010), and observation and execution of oral/ingestive communicative gestures (Muthukumaraswamy, Johnson, Gaetz, & Cheyne, 2006). As with any technique, some obstacles arise when comparing various EEG studies, due to factors such as the conditions and tasks included, or variations in the baseline used to calculate changes in mu amplitude (if, indeed, one is utilized at all) (Tangwiriyasakul et al., 2013; Hobson & Bishop, 2016). Nevertheless, a recent meta-analysis (Fox et al., 2016) revealed that EEG mu desynchronization is shown consistently during action observation and execution. This was found to be true despite the numerous methodologies employed, and was found for several types of actions (e.g. both object- and non-object-directed). This meta-analysis also demonstrated topographic mu specificity for the central scalp locations during execution (i.e. greater decrease in mu amplitude for central compared to frontal and occipital regions). Although this was not found for observation, not many studies have reported activity from more than one scalp location during observation (but see de Klerk, Johnson, & Southgate, 2015; and Marshall et al., 2013 for evidence of somatotopic organization during observation of actions in infants). The results from this analysis, alongside all the other supporting evidence, strongly indicate that the use of EEG and modulation of the mu rhythm is a valid technique for exploration of mirror system activity.

1.3.2.1 Investigating neural mirror systems in infancy using EEG

There appears to be a rhythm analogous to mu at a very early stage in human development. Therefore, along with its suitability for use with more difficult populations, EEG has become the preferred method for exploring potential mirror system activity in infancy and childhood. In these younger populations, the mu frequency range is lower than it is in adults (Stroganova, Orekhova, & Posikera, 1999), and gradually increases with age (Marshall, Bar-Haim, & Fox, 2002). More precisely, the 6-9Hz frequency band has been identified as functionally equivalent to the adult 8-13Hz band during early development (Stroganova & Orekhova, 2007; Stroganova et al., 1999). For example, Stroganova et al. (Stroganova et al., 1999) showed that unlike occipital alpha, the amplitude of the 6-9Hz central rhythm in infants aged 7-12-months did not change while in darkness, which is the same lack of response found in adulthood. The frequency of mu actually seems to peak around 5-6Hz in 5-month-old infants, and based on investigation of changes in peak mu band frequency over time, the 6-9Hz band seems most appropriate for investigating mu rhythm activity from around 10 months postpartum, up to around 4 years of age (Marshall, Bar-Haim, & Fox, 2002). This is similar to the peak frequencies revealed in a more recent study by Berchicci et al. (2011) at these ages, with a peak of around 7-8Hz found at 9 months postpartum, with the most extreme changes in mu peak frequency occurring during the first year of life and then very slowly up until 5 years of age (though still not reaching the adult peak). There are a number of possible reasons for this dramatic increase in peak frequency early on in life, including rapid structural/functional development of cortical neural network foundations, changes in the skull, general neuronal maturation, density of neuronal assemblies, synaptogenesis, and development of myelination across the cortex (Berchicci et al., 2011; Marshall et al., 2002).

As well as a gradual rise in the peak frequency during development, the magnitude of mu power reduction over central regions has been shown to increase with age. Children around 8 years old demonstrate around a 60% decrease in mu power during the execution of grasping actions (Lepage & Théoret, 2006), which is comparable to that adulthood (Muthukumaraswamy et al., 2004). This is also the case during the observation of grasping actions, with a decrease in mu power of around 25% seen in both children of this age and adults (Lepage & Théoret, 2006; Muthukumaraswamy et al., 2004). In infants, these reductions in mu power during both observation and execution of manual actions are much smaller. For example, in Southgate et al. (2009) and Marshall et al. (2011) where infants were aged 9-14 months, a 10-12% decrease in mu power was found for action execution, and 5-14% decrease for action observation. Methodological differences make comparison of such studies difficult (e.g. socially interactive/turn-taking vs. blocked observation and execution conditions, time windows of interest), as do individual differences. Despite this, the increase in mu power reduction during observation and execution over time does indicate developmental changes to a neural mechanism that facilitates mapping between own and other actions (Marshall & Meltzoff, 2011).

The majority of EEG research that has investigated putative mirror system activity in infants has involved reaching/grasping actions, with a reduction in mu power during the observation of manual actions found in infants as young as 6-8 months of age (Nyström, Ljunghammar, Rosander, & von Hofsten, 2011; Southgate & Vernetti, 2014). Although this does suggest involvement of the sensorimotor cortex in action observation, as an execution condition was not included in either of these studies, limited claims can be made in terms of mirror system activity. However, other researchers have found similar results during both observation and execution of actions in slightly older infants (Cannon et al., 2016; Marshall et al., 2011; Southgate, Johnson, El Karoui, & Csibra, 2010; Southgate et al., 2009). More recent research has shown that modulation of the mu rhythm during observation and execution of actions may be somatotopically organized by at least 14 months of age (de Klerk et al., 2015; Marshall et al., 2013). That is, greater decreases in mu power are found in the hand area of the sensorimotor cortex compared to the leg area when observing hand actions, and vice versa when observing leg actions. Similarly, distinct cortical regions of premotor and posterior parietal cortices are activated by observation/execution of mouth, foot, and hand actions (Buccino et al., 2001).

Though the exact developmental pathway of the mu rhythm remains unclear, the modifications that take place over the course of development could reflect a number of processes occurring in the child's brain (see earlier in this section also), including refinement of the sensorimotor system (Vanderwert et al., 2013) based on experience. In the previous discussion of potential mirror system functions, it was stated that those who posit a role for a mirror system in action observation claim that this system responds to others' actions only when the observer has previously performed a similar action themselves; i.e. only if the motor representations of such actions already exist in the observer's motor repertoire. In line with this hypothesis, fMRI studies have demonstrated increased activation of mirror system areas during observation of a movement that has been performed extensively, such as in dance moves observed by trained dancers (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006). Apparent activation of a mirror system also seems to improve a basketball player's ability to predict the outcome of actions related to their sport more quickly and more accurately than that of non-players (Abreu et al., 2012; Aglioti et al., 2008). In adult EEG research, greater reductions in mu rhythm power have also been found in dancers versus non-dancers during observation of dance steps, with dancers of course more familiar with such movements (Orgs et al., 2008). This evidence suggests that experience modulates mirror system activity during action observation. Interestingly, motor experience seems to be the determining factor in this modulation (Cannon et al., 2014; Gerson et al., 2015). In the fMRI study by Calvo-Merino et al. (2006), male and female ballet dancers observed dance moves specific to both their genders. Greater activation in mirror regions was found during observation of moves performed by their own gender (which were part of their motor repertoire), even though as dance partners, they had more visual experience with the moves of the opposite gender. Similarly, basketball players were better at predicting action outcomes and showed greater mirror system activation than coaches, who had just as much visual, but less motor experience of the observed actions (Aglioti et al., 2008). Thus, the differences between players/coaches and dancers/dance partners shows that, crucially, it is motor experience rather than visual experience that influences mirror system activity.

Behavioural research suggests that, like adults, an infants' ability to process others' actions is influenced by their prior motor experience. In one EEG study with 14–16-month-olds (van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008), infants' sensorimotor activity was recorded as they observed other infants either walking or crawling. Greater mu power decreases were demonstrated during observation of crawling compared to walking, with the degree of this decrease significantly correlated with infant’ previous crawling experience. As infants of this age have much more experience with crawling than walking themselves, this shows that modulation of the mu rhythm during observation is sensitive to the level of motor experience an infant has had with the observed action. In another study by Paulus et al. (2012), 8-month-old infants were allowed ‘training time’ to gain experience with rattle that made a unique sound. EEG was then used to record infant neural activity as they listened to both novel and familiar sounds, and the sound of the rattle. Reduction in mu power was found to be greatest when infants heard the sound associated with the rattle action. The degree of mu power reduction recorded over sensorimotor areas during action observation also correlates with 9-month-old infant’s action execution ability, with infants who are more competent at reaching and grasping demonstrating greater mu modulation during an observation condition (Cannon et al., 2016). One study has even found that in 12-month-old infants, the modulation of mu during observation of another individual lifting an object was related to the observer’s grip strength (Upshaw, Bernier, & Sommerville, 2016), with infants with a higher grip strength demonstrating a greater decrease in mu rhythm power during observation. Furthermore, the relationship between grip strength and mu power modulation was found to increase with the object weight. This could reflect an infant’s ability to recognize the effort associated with lifting objects of varying weights, as a consequence of their own grip strength. These results imply the early emergence of a neural mechanism that integrates own and other actions, which seems to be based on infants’ prior motor experience, and is reflected in modulations of the mu rhythm.

Research therefore suggests that the mu rhythm is present and is modulated during observation and execution of manual actions by at least 9 months postpartum; however, it is not clear exactly when this mirror system might emerge. As mentioned above, a reduction in mu power has been demonstrated during the observation of manual actions around 6-8 months (Nyström et al., 2011; Southgate & Vernetti, 2014), although no execution conditions were included in these studies. As mirror system activity seems dependent on prior motor experience, it would not be surprising if evidence for a manual mirror system was not found in very young infants, as successful grasping only begins to occur around 4 to 5 months (Murray, 2014; von Hofsten, 2004; von Hofsten & Rönnqvist, 1988). Further research is now required to determine whether the modulation of a mu-like rhythm in human infants younger than this indicates that a mirror system linking own- and other-generated actions is present at even earlier stage in development.

1.4 DEVELOPMENT OF MIRROR SYSTEMS

Considering the attention that has been paid to elucidating the properties and functions of primate mirror systems, surprisingly little is currently known about their ontogeny. As such, furthering knowledge on how mirror systems might emerge is now of great importance, especially given the significant roles that mirror systems are suggested to play in various aspects of social-cognition and its development (Gallese et al., 2004; Marshall & Meltzoff, 2011). In the following sections, theories attempting to explain how mirror neurons might develop will be presented, as well as evidence in support of these different accounts. The special case of mirror systems related to actions that one cannot see themselves perform will then be discussed, as this type of action is the focus of subsequent experimental chapters included in this thesis.

1.4.1 GENETIC VERSUS LEARNING ACCOUNTS

In the most basic sense, ideas concerning the development of mirror neurons can be divided into two camps: (i) that which emphasizes the evolutionarily adaptive value of mirror neurons, positing that they acquire their properties via genetic pre-programming; and (ii) that which rejects any genetic foundation for mirror neurons, emphasizing instead the role of sensorimotor experience and the notion that these neurons acquire their properties via simple and generalized learning processes. This division of theories is one typically portrayed by those championing the latter position (Brass & Heyes, 2005; Cook, Bird, Catmur, Press, & Heyes, 2014; Heyes, 2001, 2010), who refer to the two opposing accounts as the 'adaptive hypothesis' and the 'associative hypothesis' respectively. However, this dichotomy of theories is rather crude, and fails to accurately portray the position adopted by those who assign a genetic role to the development of mirror neurons. In fact, most contemporary theories of mirror neuron development ascribe an important role to *both* genetics and sensorimotor experience, which will be demonstrated later on in this chapter. In the rest of this section, evidence will be presented in support of the adaptive and associative hypotheses, as they are described by Heyes and colleagues.

1.4.1.1 The adaptive hypothesis

Proponents of the associative account (Heyes and colleagues) describe the adaptive hypothesis as asserting that mirror neuron development is the result of genetic evolution, favoured by natural selection because of the vital contribution they make to action recognition and understanding (Rizzolatti & Arbib, 1998). According to this interpretation of theories with a genetic component, mirror neurons that encode the observation and execution of particular actions should be present at birth, and their development should not rely on postnatal experience.

Although no single-cell recordings have been obtained thus far, EEG research with newborn macaques suggests that a mirror system could present very soon after birth (Ferrari et al., 2012; Vanderwert et al., 2015), and therefore could be used in support of the adaptive hypothesis. These studies found that power in the mu band is decreased in the infant monkey over central electrodes during observation and execution of facial gestures such as lip smacking, which is consistent with sensorimotor cortex activation, and thus with activation of a mirror system in the first days of life. Comparable studies have not yet been conducted with human infants, however evidence that human neonates can imitate adult facial expressions could suggest the presence of an innate mirror system. In the seminal work by Meltzoff and Moore (1977, 1983, 1994), newborn infants were shown to spontaneously produce particular facial gestures after presentation by an experimenter, even 24 hours after the event. The original neonatal imitation experiment (Meltzoff & Moore, 1977) involved presenting infants aged around 2 to 3 weeks with movements such as tongue protrusion and mouth opening. In the period immediately following presentation, the rate of infant execution of that movement was reported to increase compared to the frequency of the other movements. This was later shown for infants aged a mere 72 hours (Meltzoff & Moore, 1983). An intriguing finding is that neonatal facial imitation appears to start decreasing around 2 months postpartum, and seems to stop by 6months of age (Abravanel & Sigafoos, 1984; Fontaine, 1984). This could be for a number of reasons, such as that older infants have different abilities, expectations, and motivations during their social interactions (Simpson, Murray, Paukner & Ferrari, 2014), with spontaneous and overt imitation of any facial expression obviously not a very useful form of communication in adulthood. The reason that this is proposed to reflect mirror system activity, is that imitation of adult facial expressions implies the cross-modal matching of visual and motor information, which occurs despite the very limited opportunities available for the type of sensorimotor learning that could build up associations between the perceptual and motor representations of that facial expression (Lepage & Théoret, 2007; Meltzoff & Decety, 2003b). Note, neonatal imitation of certain facial gestures is also demonstrated in macaques (Ferrari et al., 2012; Vanderwert et al., 2015).

As such, neonatal imitation indicates that there might be, at least in some rudimentary form, a mirror system present at birth which facilitates a mapping between the infant's visual representations of others' facial features and the corresponding motor representations. However, the existence of neonatal imitation has itself been questioned by some researchers, e.g. whether it might merely reflect an arousal mechanism, rather than imitation (Anisfeld, 1996; Jones, 2009), with proponents of the associative hypothesis using such arguments to reject this phenomenon as evidence for a mirror system in the newborn. These criticisms have in turn been countered. For instance, it has been suggested that methodological differences between studies and low statistical power may have resulted in null findings, and that individual differences in imitation ability may account for inconsistent findings in the literature (see Simpson, Murray, Paukner, Ferrari, 2014 for an in depth rebuttal of neonatal imitation critics). Nevertheless, it is true that without neural data in support, neonatal imitation alone does not allow one to make very strong conclusions about the presence of a mirror system at birth, therefore such investigations with human infants are now required. It does seem reasonable to assume that if a mirror system is involved in an ability as crucial as action recognition, it might be 'innate' to some extent during phylogenetic history, though the key issue of how exactly mirror neurons could be pre-programmed to map visual and motor representations for very specific actions from birth still needs to be clarified in both monkeys and humans (Del Giudice et al., 2009).

1.4.1.2 The associative hypothesis

Those in the associative camp state that there is no reason to assume that mirror neurons are genetically pre-programmed, and that development is purely the result of sensorimotor experience; that is, that development of mirror neurons occurs due to learned associations between sensory and motor representations of an action, which are built via concurrent self-observation and execution of actions (Cook et al., 2014; Heyes, 2010). Accordingly, the associative hypothesis also postulates that mirror neurons do not represent any kind of social adaptation, as domain-general learning mechanisms are sufficient to explain their emergence (Cook et al., 2014).

The associative hypothesis posits that mirror neurons start off as strictly motor neurons involved in the execution of actions, but receive many weak connections from sensory (e.g. visual) neurons. However, when these 'pre-mirror' neurons fire immediately after sensory neurons (i.e. firing is contiguous), and this firing is highly probable (i.e. firing is contingent, meaning there is a predictive relationship/correlation between motor and sensory activation), an association between the sensory and motor neuron is strengthened (see Figure 1.8). This strengthening is what ultimately transforms the original motor neuron into a mirror neuron (Ray & Heyes, 2011), or in other words, is what bestows the original motor neurons with visuomotor properties. If the sensory neuron happens to fire during observation of an action, self-observation while performing that action will cause the activated motor neuron to develop mirror properties. For example, if the visual perception of a particular grasp is regularly associated with the simultaneous and contingent motor command used to perform that grasp, the association between the visual neurons and motor neurons activated will be strengthened. This will result in the motor neurons used to execute an action eventually acquiring visual responses to the same action as well, thus forming mirror neurons.

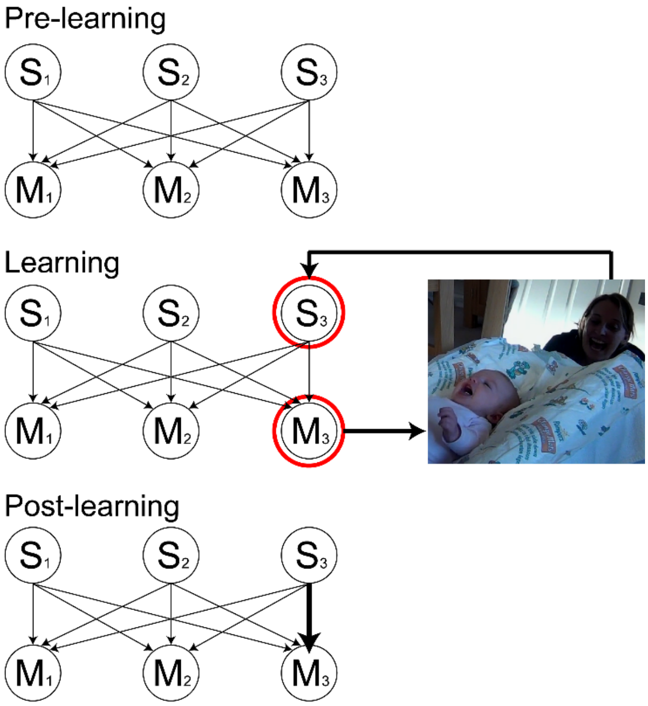

Figure 1.8: Associative hypothesis: figure modified from Heyes (2010).

Research that could be used in support of the associative hypothesis has investigated the influence of sensorimotor experience on mirror system activity in adults. Studies presented earlier in this chapter demonstrated how sensorimotor experience seems to influence mirror system activity (e.g. of male and female dancers, dancers and basketball players and their coaches) during the observation of actions (Aglioti et al., 2008; Calvo-Merino et al., 2006; Orgs et al., 2008). It also appears that mirror activity can be generated (Press et al., 2012), inhibited (Cook, Dickinson, & Heyes, 2012), and increased (Press, Gillmeister, & Heyes, 2007) by short periods of sensorimotor training, which could indicate that mirror systems are not fixed by genetic pre-determination, but are dependent on experience for their emergent responses. Some research with macaques also shows that after months of sensorimotor training with a tool, some neurons in the premotor cortex demonstrate mirror properties specific for that tool (Ferrari, Rozzi, & Fogassi, 2005; Umiltà et al., 2008), indicating that mirror systems are somewhat plastic in regards to individual experience.

Behavioural studies provide further evidence for the importance of sensorimotor experience, indicating that motor competence influences perception. For example, grasp recognition appears to improve greatly between 6 and 9 months (Woodward, 2003, 2005; Woodward, Sommerville, & Guajardo, 2001), which coincides with the developmental timeline of infant grasping skills. Even for pre-grasping infants aged only 3 months, grasping execution has been suggested to have a causal effect on recognition; i.e. infants who were given grasping training before being presented with such actions performed by others perceived actions as goal directed more often than infants who had not received training (Sommerville, Woodward, & Needham, 2005). Interestingly in this last study, the opposite case was not found: infants who had observed many examples of other people executing grasping actions did not then perform better during grasp execution themselves. This suggests that execution and recognition of grasps are unidirectionally linked, which is in accord with the idea that mirror system development requires repeated self-observation of executed grasps. One EEG study has looked at how visuomotor training might modulate the mu rhythm in human infants (de Klerk et al., 2015). In this study, infants who had not yet learned to walk were trained to execute some stepping movements while viewing contingent or non-contingent leg movements, with neural activity recorded before and after training. The degree of mu desynchronization post-training was predicted by the amount of visuomotor contingency during the training period. These results could therefore be interpreted in terms of the associative learning account, with results potentially reflecting the infants’ amount of prior sensorimotor experience (i.e. with execution and observation of their own leg movements such as kicking).

The research presented in the previous paragraphs does indicate that mirror system activity is modulated by sensorimotor experience, however, it seems wrong to base speculations concerning the protracted neural development in infancy on the adult brain, with experience in adulthood (e.g. in the studies involving sensorimotor training) perhaps resulting in temporary changes to cortical activity rather than permanent changes to neural functioning. Indeed, very early experiences in infancy and childhood, particularly during sensitive developmental periods, could result in enduring re-organization of neural structures (Quadrelli & Turati, 2016), and thus have more permanent or fundamental effects on mirror systems. Additionally, the associative camp does not take into account the facts that species-typical development of various genetically-based adaptations (e.g. vision, human language) are context-dependent, highly plastic, and influenced considerably by experience (Ferrari et al., 2013). For example, the fact that human language ability is heavily influenced by experience does not mean that there is no genetic component. Such findings therefore do not discount the possibility of an innate, rudimentary, mirror system being present at birth, at least for certain actions (i.e. this may be the case for facial expressions but not manual actions: see Section 1.4.3), which might then be influenced by an infant's sensorimotor experience and become gradually refined via learning processes (Gallese, 2009). This could take the form of coarse-grained projections between visual and motor areas, resulting in a crude mirror system whose connections could then be selectively pruned by experience (Bonaiuto, 2014). Similar ideas to this will be discussed in the following section.

1.4.2 HYBRID APPROACHES TO DEVELOPMENT

The literature presented thus far illustrates two opposing views on mirror neuron development: one relying solely on genetic pre-programming, and one on learning processes and sensorimotor experience. In reality, this separation is far too simplistic. In fact, the majority of theories concerning the development of mirror neurons assign a role to *both* genes and sensorimotor experience, which contradicts the black and white 'genetic versus learning' dichotomy often presented by proponents of the associative account. Such a hybrid account indeed seems more plausible than a theory attributing development to either genetic or learning processes, being far more consistent with current understanding of evolutionary biology and how interactions between genes and the environment contribute to development (Del Giudice et al., 2009).

Without acknowledging a role for genetics in pre-wiring the mirror system, the purely associative explanation seems to assume that that all neurons in the brain are directly or indirectly connected to one another, and therefore would necessitate incredibly frequent occurrences of appropriate action observation and execution to associate a sensory stimulus with the correct motor representation (Bonaiuto, 2014). In fact, the associative perspective makes a 'wealth of the stimulus' argument, meaning that the early environment contains sufficient sources of the correlated sensorimotor experience required to develop mirror neurons both quickly and efficiently (e.g. self-observation of manual action execution; Cook et al., 2014; Ray & Heyes, 2011), and thus does not necessitate any genetic foundation/social adaptation. However, considering the huge range of possible representations in sensory and motor domains, how can a purely associative process be computationally manageable in the developing brain? Indeed it would appear this is not feasible, with nearly all computational models of mirror neuron development (e.g. Bonaiuto, Rosta, & Arbib, 2007; Metta, Sandini, Natale, Craighero, & Fadiga, 2006; Oztop & Arbib, 2002) suggesting that some kind of crude connectivity must already be in place between the appropriate brain regions to form useful associations, and that constrained, relevant input representations are also necessary to make the range of potential associations tractable; i.e. to make useful associations between visual and motor neurons. This lends itself to theories of mirror system development involving both learning processes and certain intrinsic features to constrain development. For example, infants seem to demonstrate an inherent motivation to look at their own hands (van der Meer, 1997; von Hofsten, 2004; White, Castle, & Held, 1964), and thus could represent an example of a domain-specific behaviour that would serve to channel development of a mirror system for manual actions, via provision of the appropriate visual input for association with infants' corresponding hand movements.

Of course, one major difference from the associative hypothesis that is adopted by some theories attributing a role to genetics in mirror neuron development, is that mirror neurons represent some kind of social adaptation. Conversely, proponents of the associative account would say that domain-general processes alone can explain the emergence of such neurons (Cook et al., 2014), and that therefore they would not have been selective for by evolution for their adaptive social value. At the very least however, and presumably even according to the associative account, evolution presumably served to provide infants with sensory and motor neurons, as well as the possibility of linking the two together. In fact, although the associative camp may portray theories as being either based on genetic predetermination or learning processes alone, many argue that current theories concerning development of mirror neurons represent largely compatible endeavours to elucidate how experience might shape an extremely complicated phenomenon (Del Giudice et al., 2009), but do so using various levels of description. That is not to say there are no differences between the various accounts, which can be seen in the below discussion of a few of the existing theories.

1.4.2.1 The Hebbian account

One theory that incorporates both a learning and genetic component, and which has been outlined quite thoroughly in previous literature, is the Hebbian account of mirror neuron development (Keysers & Perrett, 2004; e.g. Keysers, Perrett, & Gazzola, 2014). Although the Hebbian account suggests that mirror neurons emerge without genetic pre-determination *per se*, it embraces the idea that genetic pre-wiring at a coarse scale and/or genetic pre-dispositions do contribute to their ontogenesis in certain ways (e.g. a bias towards looking at one's own hands: Keysers & Perrett, 2004). There are three key assumptions to this theory: (i) anatomical connections are present between the temporal, parietal, and premotor areas (areas that are part of a mature mirror system) at birth; (ii) these connections are realized by synapses whose strengths are modulated by Hebbian learning; and (iii) that infants observe themselves executing actions. Based on these assumptions, Hebbian proponents posit that the activation of a particular population of premotor neurons in the infant causes them to execute a specific action (e.g. precision grasp), with the infant also being able to observe themselves perform that action. This observation activates a particular group of neurons in the STS that respond preferentially to the observation of that specific action, with this sensory signal then projected to the premotor neurons that originally implicated the action execution (neurons with congruent action coding), as well as to some other neurons responsible for different (incongruent) actions. When this sensory signal reaches the premotor neurons responsible for the original action, which are still active, the synchrony results in Hebbian potentiation of the synapses involved. When the signal reaches premotor neurons that are not responsible for the original action, which are not currently active, this leads instead to Hebbian depression of the synapses involved. After many of these execution-observation loops, the statistical properties of pre- and post-synaptic activity will reduce the incongruent action-perception connections and potentiate the congruent ones. Thereafter, if an infant sees the original action performed by another individual, the population of neurons in the infant's STS which respond to the sight of the same self-generated action are activated, and through the potentiated congruent synapses, this activates premotor neurons responsible for performing that action in the infants' brain (which have of course acquired mirror properties) (Keysers & Gazzola, 2014; Keysers & Perrett, 2004).

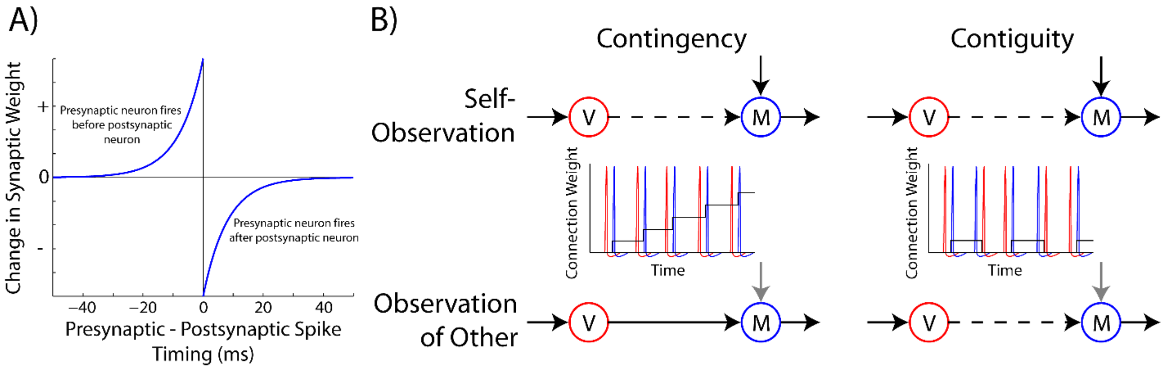

Figure 1.9: Hebbian learning hypothesis: A) Connection strengths between neurons are modified based on the relative timing of a neuron's output and input spikes. B) If a postsynaptic neuron tends to spike immediately after a presynaptic neuron, the synapse between them is potentiated and can gradually become stronger. C) If strengthening of neuronal connections is based on congruity alone, a temporal jitter could lead to the potentiation and depression of synapses cancelling each other out.

The learning component of the Hebbian account is clearly similar to that of the associative hypothesis, and therefore before discussing the differences between the two further, it is useful to mention a confusion that seems to exist within the literature regarding the difference between associative and Hebbian learning accounts of mirror neuron development. Supporters of the associative hypothesis (Cook et al., 2014; Cooper, Cook, Dickinson, & Heyes, 2013) claim that according to the Hebbian account, contiguity (i.e. sensory and motor neurons firing close together in time) alone is sufficient for development of mirror neurons, and neglects the role of contingency (i.e. the predictive relationship between the firing of sensory and motor neurons). Without contingency, these authors claim that mirror neurons would not necessarily map an observed action to a motor representation that was logically related, and thus mappings would end up corresponding to a huge, partially-random collection of executable actions. For instance, say every now and again one sees their own hand move, but by coincidence, also see a flashing light. With contiguity and not contingency, this would result in the gradual build-up of a link between performance of the hand action and the flashing light. Proponents of the associative hypothesis claim that contingency would solve this problem by detecting that the individual’s hand action was not predictive of the light; i.e. that sometimes you might see the light without performing the hand action, and that other times, you might execute the hand action without seeing the light. Therefore in this case, no mapping would be built up between the hand action and the flashing light.

However, the Hebbian learning account of mirror neuron development is actually based on modern knowledge concerning ‘spike time dependent plasticity’ (STDP), which does in fact take both contiguity and contingency into account (Keysers & Gazzola, 2014; Keysers et al., 2014). STDP is a process that modifies connection strengths between neurons, and is based on the relative timing of a particular neuron's output and input spikes (Caporale & Dan, 2008). That is, if a neuron tends to spike immediately after a presynaptic neuron spikes, it means that the connection from that particular presynaptic neuron is made a little stronger. On the other hand, if a spike tends to happen immediately before a presynaptic neuron spikes, the connection from that particular presynaptic neuron is made a little weaker. Accordingly, inputs that might contribute to the postsynaptic neuron's spiking activity are made stronger, and inputs that do not contribute to the postsynaptic neuron’s spiking are made weaker. Eventually, only a subset of the original connections remains, while the impact of the other connections is reduced to nearly zero. If two neurons simply fire together without a consistent ordering, as the associative proponents describe, the expected ‘temporal jitter’ would make the presynaptic neuron sometimes fire just before and sometimes just after the postsynaptic neuron, and potentiation and depression would cancel each other over time; and thus would lead to no net change in connection strength. Therefore it seems that the claim made by associative learning proponents that the Hebbian account would inevitably result in ‘junk’ or ‘superstitious’ associations (Cooper et al., 2013), is unfounded. Indeed, proponents of the associative learning account seem to have misinterpreted or omitted some important elements of the Hebbian account when critiquing it, but in doing so, actually end up assuming a comparable position (Keysers et al., 2014).

Returning then to the discussion of genetic and learning processes, it was noted that although the Hebbian and associative accounts share similarities, there are still a number of differences between the two. To recap, the Hebbian hypothesis states that learning processes work together with certain genetic factors to produce mirror neurons; that is, sensorimotor experience is thought to be vital for strengthening the sensory-motor couplings characteristic of a mirror system; however, a certain degree of pre-wiring and adaptive predisposition also serve to guide development (e.g. coarse connections between appropriate brain regions and infant preferences for attending to particular stimuli). In other words, because of pre-existing anatomical connections in the brain, and because infants typically demonstrate certain behaviours like looking at their own hands, some neurons are able to acquire mirror properties via 'Hebbian synaptic potentiation': i.e. the linking of visual neurons that respond to observation of an action with motor neurons involved in producing that action, which results in the motor neurons acquiring visuomotor/mirror response properties (Del Giudice et al., 2009). It is clear then that the main point of divergence between the Hebbian and associative hypotheses is that the former acknowledges an important role both for genes and sensorimotor experience.

More specifically, according to the Hebbian account, mirror neurons are thought to develop through 'experiential canalization' of learning processes, guided by genetic predispositions (Del Giudice et al., 2009). Canalization in this sense refers to the protection of a developmental process against disturbance (Waddington, 1942), meaning that critical features of an organism can develop reliably and species-typically, resilient to individual variations in the environment and their genotypic makeup (e.g. Flatt, 2005). Interactions between genes and environment result in development, both acting as potential sources of invariance and stability, with canalization the result of predictable interactions between genetic mechanisms and dependable environmental features (West-Eberhard, 2003). Thus, an organism's sensory experience plays a vital role in directing ontogeny, and it is this that results in experiential canalization. This idea does not negate the importance of genetics, but emphasizes that there is a need to identify how genes, environment, and experience interact to shape development. For example, in the case of infant manual actions, genetics may impact brain development by influencing both anatomy and physiology, by affecting the tendency to produce certain movements, and by predisposing the related systems to learn from manual actions at the most appropriate time (Del Giudice et al., 2009; Keysers & Gazzola, 2014).

The idea of experiential canalization in this account, combined with that of learning processes, suggests that individuals are not endowed with innate representations of others' actions at birth. Rather, natural selection achieved this indirectly via modifications to the parameters of infant behaviour, which serves to ensure that ideal conditions for Hebbian training of visuomotor neural associations come about. These ideal conditions could therefore guide development of mirror neurons, at least for some basic actions such as grasping. In terms of manual actions, Del Giudice et al. (2009) posit that evolution has biased infants towards attending to their own hands and has optimized the parameters of self-executed motor patterns, which results in maximized Hebbian learning at the synaptic level. Note then, according to this explanation, visuomotor learning itself is not fully aimed towards mirror system development, but is necessary for skilful performance of the actions themselves. Therefore, the canalization of Hebbian learning that may facilitate development of a mirror system would be stabilized by evolutionary pressures for development of a well-coordinated visuomotor system (Del Giudice et al., 2009; Keysers & Gazzola, 2014).

Visual preferences towards looking at the hands, a bias presumably subserved by genetic predisposition, is a good candidate for a behaviour that might lead to canalization of the learning processes necessary for development of manual mirror system. Indeed, infants tend to look at their hands for a great deal of waking time very soon after birth (White et al., 1964), with newborns moving their hands more when they can see them (van der Meer, 1997), and trying to control arm movements to keep their hands in view (von Hofsten, 2004). In Craighero et al. (2011), 2-day-old infants were shown to orient more frequently, as well as gaze longer, at a hand shape for whole hand prehension when the movement was directed away from the body and toward an object. The authors argue that this finding may support the presence of some basic sensory-motor couplings very soon after birth, however, no other study has looked at this, and no neural data have been provided in support. Newborns also tend to preferentially look towards biometrically impossible compared to possible hand movements (Longhi et al., 2015), implying they are drawn to the novelty of such actions, and thus already have some expectations as to how hands ought to move. Interestingly, this finding did not hold true for static images of the hands, highlighting the importance of motion for the perception of bodies in infancy, which appears to provide additional information about the biological plausibility of the hand gesture. Looking times were additionally no different during the static and movement conditions, therefore results could not be explained as a mere increase of the overall salience of the movement condition (and attracting more attention). Such evidence suggest that infants can identify the hands as salient body parts from very early on, and that they process domain-specific information regarding manual actions.

1.4.2.2 The Neuroconstructivist account

Recently, another account of how mirror systems may emerge was proposed by Quadrelli and Turarti (2016), which falls within a wider neuroconstructivist framework. Like most other theories, this account attributes a role for both genetic predisposition and sensorimotor experience to mirror neuron development. As such, Quadrelli and Turarti reject the idea that visual and motor neurons are genetically pre-programmed to code specific actions at birth, but agree that simple learning processes alone are likely insufficient. In this way, the neuroconstructivist account seems similar to the Hebbian account, though, more like the associative hypothesis, it is expressed at a higher, more cognitive-level of description. Neuroconstructivism in general has been described as constituting a unifying framework for the study of cognitive neuroscience (Karmiloff-Smith, 2009; Westermann et al., 2007), representing an attempt to define how the brain might gradually sculpt itself and become more and more specialized over time. More specifically, this is suggested to occur via a number of phylogenetic (e.g. gene-gene interaction or gene-environment interaction) and ontogenetic (e.g. prenatal and postnatal) processes, with neural system development greatly constrained by various interacting factors (innate and extrinsic) (Westermann et al., 2007). Neuroconstructivists assign a significant role to experience-expectant processes, which are thought to require species-specific experiences to determine neural connectivity and refinement. This is proposed to result in the development of specific neural systems (Greenough, Black, & Wallace, 1987), with more advanced cognitive functions becoming domain-specific as a consequence of ontogenetic development (Karmiloff-Smith, 2009). In other words, this refers to the idea that the development of capacities common to all members of the species rely on exposure to specific experiences within a sensitive period, and that they depend on early sensitivities and constraints that prime infants for learning about particular features of their environment with adaptive importance (Greenough et al., 1987). Experience-expectant processes allow infant cortical plasticity to be taken advantage of, which enables the refinement of developmental features that may not lead to the most advantageous outcomes if reliant on genetic factors or experience alone. Note, this differs from *experience-dependent* processes, which refers more to the acquisition of skills during adulthood that can take place at any time, and might contribute to things like cultural and individual differences (where timing of the experience is not crucial for typical development). Indeed, an essential component of neuroconstructivism is that brain plasticity early in life is different from that in adulthood, with a special role given to the evolving social environment of infants, which results in long-lasting neural changes (Westermann, Thomas, & Karmiloff-Smith, 2010).

According to a neuroconstructivist framework, the development of mirror neurons is therefore not dependent on genetic predetermination or on very simple associative learning processes. Instead, a mirror system is suggested to progressively emerge from the dynamic interaction between intrinsic domain-general properties of neural functioning and the structure of the input provided by a species typical environment (Quadrelli & Turati, 2016). Like the Hebbian learning account, the neuroconstructivist approach suggests that mirror system development is canalized by the visuomotor system's tendency to direct infant attention towards certain actions, which enables a specialized system dedicated to their recognition (and perhaps more advanced action understanding) to emerge. Specific actions which infant predispositions may focus attention to include the movement of certain body parts such as their own hands (von Hofsten, 2004), which is suggested to strengthen the mapping between motor and visual representations of actions involving those body parts. Such predispositions are proposed to shield developing mirror systems from any potential disturbances, as well as to fast-track their development. Such predispositions are of course incompatible with the (purely) associative hypothesis of mirror neuron development, implying that genetics shape at least certain aspects of their emergence.

The neuroconstructivist account also suggests that the consequences of developmental processes are probabilistic, rather than innately specified, due to their origination from a number of physiological and environmental constraints. Such constraints could interact to reliably shape the formation of common mechanisms for the specialized processing of others' actions, including an infants' own motor development. As previously discussed, the motor repertoire available to infants has been found to influence mirror activity (e.g Cannon et al., 2016; van Elk et al., 2008), which supports this idea that an infant's own motor development might restrict the development of a mirror system. This implies that an infant's own sensorimotor experience could constrain perception of others' actions, representing a template that may be used to match observed actions to (Quadrelli & Turati, 2016). On one hand, this concept seems to support the learning accounts of mirror system development, acknowledging that the type of learning that results in mirror neurons occurs when sensory and motor neuron activity is contiguous and contingent. On the other hand, such a constraining process could rely on probabilistic learning mechanisms, such as statistical learning, which could elucidate why learning might arise in the face of highly variable infant-other interactions. Statistical learning allows for extracting structure from continuous sensory environments, which has been shown to be a general mechanism in operation across domains and different species (Krogh, Vlach, & Johnson, 2012). It has been proposed that the ability to draw regularities from action series may be a mechanism that aids infants in prediction of how actions will be executed, without needing the ability to perform those actions themselves (Hunnius & Bekkering, 2014). However, it could also be hypothesized that for certain actions, for which infants do regularly receive contiguous and contingent sensory and motor experience, a mirror system might develop to aid the rapid recognition of those actions early on in life.

In summary, the neuroconstructivist approach argues that the restricted perceptual ability and motor control of infants limits the stimulation available at various developmental stages, but because of this, infants benefit from the resultant filtering of those experiences that are available (Quadrelli & Turati, 2016). From this perspective, a progressive increase in action representation complexity is thus favoured, which is a consequence of the environment being perceived as progressively complex (Westermann et al., 2007, 2010). This means that early sensitivities could direct infant attention towards relevant inputs for mirror system development, which in turn might help shape the emergence of any functional properties such as action recognition. Therefore according to this account, both genetic and learning processes would contribute to the development of mirror systems.

1.4.2.3 The Epigenetic account

The epigenetic theory of mirror neuron development, proposed by Ferrari et al. (2013), strongly stresses a genetic basis of mirror neurons, but still posits that experience is very important in facilitating learning processes and modulating the expression of particular genes. The field of epigenetics focuses on the changes in gene expression that occur in response to various environmental factors (both prenatal and postnatal). An ‘epigenetic mechanism’ then, refers to a process through which experience can increase or decrease the production of specific proteins by regulating the expression of the genes that code for them. This can occur at cellular or tissue level, or even at the level of the whole organism. Gene expression can be switched on and off by various epigenetic mechanisms, which can impact neural function and connectivity in order to produce and stabilize functional brain architecture. For example, early postnatal experience interacting with other individuals could produce modifications in gene expression through epigenetic marks, such as DNA methylation, which could alter the pattern of neuronal wiring in particular brain networks, including perhaps a mirror system (Ferrari et al., 2013; Simpson, Fox, Tramacere, & Ferrari, 2014; Tramacere, Ferrari, & Iriki, 2015).

More specifically in terms of mirror neuron development, epigenetic events are proposed, over the course of phylogeny, to have both aided and stabilized mirror neurons (i.e. a sensorimotor mechanism involved in the processing of others' actions), with the markers of this gene expression consistently emerging in future generations if exposed to particular and predictable conditions (e.g. vision of their own hands). This results in pervasive modifications to the phenotype, with experience influencing the mirror system, which is 'experience-expectant', due to the deliberate seeking out of specific environmental inputs (Ferrari et al., 2013; Tramacere et al., 2015). This would mean that if any disturbance occurred in the 'expected' environment, alternative strategies may need to be found to re-wire neural networks. The epigenetic account states that maintenance and facilitation of mirror system expression was favoured by natural selection, because of the advantages new emergent neuronal responses provided, e.g. more rapid or accurate recognition of others' actions. Although there is no experimental evidence for this as of yet, research concerning epigenetic mechanisms and their stabilization in populations shows that epigenetic processes may have resulted in the development and evolution of various cognitive and emotional processes, e.g. such as stress responsiveness, and learning or memory skills (Fischer, Sananbenesi, Wang, Dobbin, & Tsai, 2007; Meaney, 2001).

It is important to note, that unlike the adaptive theory as portrayed by associative account proponents, the epigenetic hypothesis does not simply state that mirror neurons are 'present from birth'; i.e. that they are entirely based on genetic predetermination. Indeed, like in the Hebbian and neuroconstructivist accounts, though at the level of genes, an epigenetic approach also considers the process of canalization of the learning processes and conditions required to strengthen the visuomotor couplings characteristic of mirror neurons (Ferrari et al., 2013). This is suggested to be facilitated in the prenatal environment, although exactly how the cellular and molecular modifications necessary to canalize mirror systems and their developmental trajectories would occur are not known currently. Such facilitation in the perinatal period is suggested to account for the neonatal ability to imitate certain adult facial gestures at birth (Simpson, Fox, Tramacere, & Ferrari, 2014). Additionally, and as mentioned in an earlier section, the epigenetic account suggests that, especially for humans, the functions mirror neurons may serve now (e.g. recognizing others' actions, imitation learning) may not be the original function (e.g. monitoring of own grasps) for which mirror neurons evolved (Bonaiuto & Arbib, 2010; Ferrari et al., 2013; Tramacere et al., 2015). Thus, proponents of this account would agree with the associative camp that it is wrong to say that natural selection selects certain 'good' genes, but instead acts on phenotypes, which are the consequence of complex interactions, including environmental influence on gene expression (Simpson et al., 2014). It would perhaps then be better to explore epigenetic regulatory factors that might result in the emergence of predictable developmental trajectories, rather than trying to discover genes that produce specific phenotypes. For instance, in infant macaques, research is starting to demonstrate that epigenetic mechanisms can explain how early social environmental difficulties increase the likelihood of disease and disorder (e.g. Provençal et al., 2012; Provençal, Massart, Nemoda, & Suomi, 2016).

Finally, this account draws attention to the capacity of mirror neurons to link between the perception of own- and other-generated actions, which is fundamental in bestowing mirror neurons with a social function. The epigenetic account proposes that at some point during mirror neuron evolution, visual inputs (i.e. specific biological stimuli) concerning others' actions attained the capacity to trigger activity in a particular visuomotor population of neurons. This sensitivity could then be modulated in these neurons by epigenetic mechanisms that modify gene expression at a very early stage in brain development. These modifications may not have been heritable at first, but could have had an impact at both a behavioural and cognitive level. It is of course very beneficial for the brain to be plastic early in development, which would allow refinement of connections between sensory and motor neurons into configurations that are appropriate for a particular environment (Ferrari et al., 2013).

So to conclude, although the specific epigenetic mechanisms that could underlie mirror neuron development are not known as of yet, it seems a promising area of investigation for future research. This account provides another example of how most theories of mirror neuron development do, in fact, assign an important role to both genes and experience, and suggests that even if some features are established at birth, mirror neurons are likely to undergo functional refinement via individual experience and environmental interaction. Furthermore, even if mirror neurons were the result of evolution, perhaps to be most suitable for sensorimotor transformation, they could have been exapted to perform additional functions. It is important to keep in mind that selection pressures do not only operate on the final phenotype, but on the interactions between genes and the environment, and between molecular factors and the environment (Simpson, Fox, Tramacere, & Ferrari, 2014). Therefore, mirror neurons could have evolved to support the learning of basic functions (e.g. sensorimotor recognition of others’ behaviour, which may be essential, even though not specifically an adaptation, for more complex functions such as sensorimotor learning; Bonini & Ferrari, 2011). It is obvious that the interaction of genes and experience via learning can only take place if the fundamental neural circuitry is already there to support such learning, hence mirror neurons could serve to scaffold these interactions soon after birth, having themselves been altered by epigenetic processes across evolution (Ferrari et al., 2013; Simpson, Fox, Tramacere, & Ferrari, 2014; Tramacere et al., 2015).

1.4.3 HOW COULD A MIRROR SYSTEM DEVELOP FOR ACTIONS AN INFANT CANNOT SEE THEMSELVES PERFORM?

The majority of theories presented above stress that although certain genetic factors are no doubt important, sensorimotor experience (i.e. the observation of oneself performing actions) is also critical for the development of mirror neurons. Indeed, much of the evidence currently available supports this claim, even if there is a rudimentary mirror system present at birth. If this is the case, however, how could a mapping between the visual and motor representations of an action one cannot see oneself perform emerge? For example, facial expressions represent a type of action that is unobservable when performed by the self (i.e. is an ‘opaque’ action), but research with both monkeys and adult humans suggests that a mirror system is involved in the processing of facial expressions (Casile et al., 2011; Vanderwert et al., 2013). Indeed, F5 mirror neurons have been found in the macaque for both ingestive and communicative mouth gestures using single-cell recordings (Ferrari et al., 2003). In human adults, studies using a variety of techniques (fMRI, TMS, EEG) have also demonstrated an overlap in the activation of mirror-related brain regions during observation, execution, and imitation of facial expressions (e.g. Carr et al., 2003; Leslie, Johnson-Frey, & Grafton, 2004; Moore et al., 2012; van der Gaag et al., 2007). This includes activation of core areas of the mirror system during facial expression observation, such as the premotor cortex (which is implicated in the execution of expressions), but also other areas including parts of the limbic system (which are involved in experiencing the emotion that corresponds to an observed facial expression). Such findings imply that a mirror system could map the visual perception of others’ facial expressions to particular motor programs and/or emotional representations in the observer, and as such, may facilitate the implicit recognition of the observed facial expression. Some researchers go even further, claiming that this mapping could be involved in facial mimicry and empathic processes (Braadbaart et al., 2014; Gros, Panasiti, & Chakrabarti, 2015).

Despite the sizeable amount of evidence for a facial mirror system activity in adults and monkeys, no study has looked at how a mirror system for facial expressions could develop in humans, or even whether such a system is present from early on in life. The basic mechanisms for primate sensorimotor coordination develop in the womb (Kurjak et al., 2004), with the foetus acquiring substantial sensorimotor experience of their hands in the womb. However, the nervous system is still immature at birth, with most neuronal circuitry involved in perception and action greatly refined over the first months in a hierarchical manner (Guillery, 2005). The first systems to be functionally refined are those related to eye and mouth movements. Some of these movements are likely to represent mere neonatal reflexes, whereas others might represent more complicated and coordinated motor acts, even though they are not smoothly controlled at that point (Casile et al., 2011).

Some researchers have argued that the early refinement of systems relating to the face is consistent with evidence that neonates (both monkey and human) can imitate adult facial expressions (Ferrari et al., 2006; Marshall & Meltzoff, 2011). As neonatal imitation implies cross-modal matching, i.e. the mapping between the observed expression of another individual with the infant’s own motor commands used to execute that expression, it has been proposed that such a phenomenon could be facilitated by a mirror system, which is suggested to be innate at least in some form (Ferrari et al., 2006, 2012; Marshall & Meltzoff, 2011). EEG studies with newborn macaques have provided evidence for sensorimotor cortex involvement during observation and execution of facial expressions very soon after birth, which is consistent with mirror system activity (Ferrari et al., 2012; Vanderwert et al., 2015), though studies are now required with human infants to further elucidate the genetic and environmental influences on the emergence of such systems. The influential research of Meltzoff and colleagues was discussed in a previous section of this chapter, where it was noted that neonatal imitation has been used as evidence suggestive of a mirror system in the neonate’s brain, even if neural data are required to strengthen this claim. Though the existence of neonatal imitation has been questioned (Anisfeld, 1996; Jones, 2009; Oostenbroek et al., 2016), individual differences in monkey neonatal imitation skill is correlated with important social-cognitive abilities later on, such as deferred imitation (Paukner, Ferrari, & Suomi, 2011), which may partly explain the variance in results from the human neonatal imitation literature. As such, it is argued that rather than dismissing neonatal imitation, investigations should focus on the causes and effects of individual differences in neonatal imitation (Simpson, Murray, Paukner, & Ferrari, 2014). These individual differences in imitation skill could in turn be due to individual differences in mirror system development, but the critical factor of how a mirror system could be pre-programmed to implement mappings between visual and motor representations of specific actions from birth is not clear at this time (Del Giudice et al., 2009) and thus requires investigation.

In any case, and as mentioned in the previous sections, most significant theories of mirror system development acknowledge that experience must play some role in the development of mirror systems, with learning processes undoubtedly involved to some degree. Nevertheless, it could be that despite genetic and learning processes both playing important roles in the development of mirror neurons, the degree to which these two components influence development could vary depending on the type of action they encode. Some researchers think that facial and manual mirror systems could emerge following two different developmental trajectories (and perhaps involving different but overlapping brain regions), with the former depending less on sensorimotor experience, and being more developed at birth (Casile et al., 2011). This does not, however, mean that a *mature* facial mirror system is innate, but that a rudimentary system for mapping between own and other facial expressions is present in the newborn, which is subsequently refined by experience. Interestingly, in macaques reared with no exposure to face stimuli, even deprivation periods of up to 2 years have been shown not to impede recognition and discrimination of facial stimuli (Sugita, 2008), which indicates that the basic mechanisms of face processing are at least somewhat independent and possibly prewired (Casile et al., 2011). Human infants are also apparently sensitive to facial stimuli at birth (Mondloch et al., 1999; Valenza et al., 1996), and the human brain contains specialized regions for face processing (Haxby, Hoffman, & Gobbini, 2000; Kanwisher, McDermott, & Chun, 1997) which use domain-specific visual mechanisms (Carmel & Bentin, 2002; Kanwisher & Moscovitch, 2000). Genetic influences could therefore guide mirror system development by, for example, providing coarse-grained connections between visual brain areas specialized for face processing and motor areas involved in controlling facial muscles at birth (Ball et al., 2014; Collin & van den Heuvel, 2013; van den Heuvel et al., 2015). Such crude connections could also explain why neonates might be capable of reproducing very basic adult facial gestures, but not more complex ones that might require fine-grained connections between specific neural subpopulations.

Although a mirror system for faces may be present in the newborn in a basic form, this system could still be, and likely needs to be, subjected to modification and development via experience. Clearly, learning that a specific facial expression (e.g. smiling) corresponds to a particular motor program or emotional state (e.g. happiness) could not occur via self-observation, and therefore an alternate idea has been proposed. This account posits that although infants cannot see themselves perform facial movements, the social environment provides them with biological mirrors separate from themselves, which allow them to observe the visual consequences of their own unobservable actions (Casile et al., 2011; Del Giudice et al., 2009; Heyes, 2001; Keysers & Perrett, 2004). In this case, the ‘mirror’ is provided by other individuals, with adults tending to imitate the facial expressions produced by an infant. In the majority of cases, an infant’s early social environment is comprised predominantly of face-to-face interactions with their mothers, and thus it is mothers who most often provide infants with this mirror for observing their own facial expressions. Via maternal imitation, then, infants can perceive the visual features that match their motor outputs when performing an expression, and therefore can build up an association between the two. This proposal does not reject the idea of any genetic involvement in development of the mirror system. For example, experiential canalization could be important for development of a facial mirror system in a number of ways: (i) the propensity of adults to imitate infants (Del Giudice et al., 2009) could in itself be an adaption, ensuring an infant receives the appropriate inputs for sensorimotor learning; and (ii), the attentional bias demonstrated by infants towards looking at faces (e.g. Valenza et al., 1996) could also ensure they receive the correct input for facial mirror system development (i.e. towards visual inputs that are contingent with their motor outputs). Also, a rudimentary system may be present in the infant at birth, but through maternal imitation, is further developed and refined (Ferrari et al., 2013; Vanderwert et al., 2015).

If this account of facial mirror system development is correct, it would be expected that differences in an infant’s early experience of being imitated by adults would predict differences in mirror system activation at subsequent points in development; i.e. if an infant did not experience their mother imitating their facial expressions as much as typically occurs during early interactions, activation of their mirror system would be less than expected during observation of others’ facial expressions. Currently, no study has explored this hypothesis in human infants, although as discussed previously, research has shown that sensorimotor experience can influence putative development of a mirror system for observable self-executed actions (e.g. Cannon et al., 2016; van Elk et al., 2008). In addition, although there has been no investigation into a mirror mechanism for mapping between own and other facial expressions at an early stage in human development, one study with infant macaques has demonstrated that the early social environment seems to affect development of a facial mirror system (Vanderwert et al., 2015). In this study, a group of infant macaques who had been raised with their biological mothers (so had the chance to be exposed to others producing facial gestures) were compared to a group who had been raised apart from their mothers. EEG was used to record mu rhythm modulation during infant observation and execution of facial expressions, which was revealed to be greater for the group of infants raised with their mothers. This suggests that the infants who had the opportunity to obtain more visual experience of their mother’s facial expressions had a more developed mirror system than those who had not had such experience. Along with the data showing neonatal macaque imitation of facial expressions, this suggests that a rudimentary facial mirror system could be present at birth, but that it is developed and modified through experience. Similar experiments must now be conducted with human infants to investigate whether social experience might also influence mirror activity in the same way. This could be achieved, for example, by looking at natural variations in maternal imitation during mother-infant interactions, or even by comparing a group of typical mother-infant dyads to a group where infants have no or impaired opportunities to visually perceive maternal imitation (e.g. infants with blind mothers, or in the context of postnatal depression).

Facial expressions are not the only action infants cannot see themselves perform. Another example is that of attention shifts, as indicated by an individual's eyes and head orientation. Though this has not been investigated as much as manual actions and facial expressions, some research does suggest that a mirror system may be involved in the mapping between own and other's direction of attention. In the macaque brain, single-cell recordings have revealed mirror neurons in LIP that respond both when a monkey looks in the neuron's preferred direction, and during observation of another monkey looking in the same direction (Shepherd et al., 2009), as well as grasping F5 mirror neurons that are modulated by gaze direction (Coudé et al., 2016). EEG studies with both human adults and infants have also found a greater reduction in mu power over central electrodes during episodes of joint attention (i.e. when the participant coordinates their attention towards an object with that of another individual) compared to no joint attention (Hoehl, Michel, Reid, Parise, & Striano, 2014; Lachat, Hugueville, Lemaréchal, Conty, & George, 2012), which suggests mirror system activation. As an action that cannot be directly perceived, it can be hypothesized that a mirror system involved in the processing of attention shifts may develop in a similar way to one for facial expressions. For instance, perhaps the observation of the mother looking in the direction they just did could serve to build up an infant's mapping between the motor commands they used to attend in a certain direction, and the visual representation of someone doing the same. One computational model (Triesch, Jasso, & Deák, 2007) has demonstrated how mirror neurons for mapping own and other's attention shifts could emerge via early mother-infant interactions, however, experimental studies are now needed in support of this idea.

1.4.4 VISUAL SYSTEM DEVELOPMENT AND MIRROR SYSTEMS

The visual system includes a number of cortical and subcortical areas, each with its own role in processing specific aspects of visual information (Braddick & Atkinson, 2011). Human visual cortex can be divided into a number of areas based on their retinotopic organization and functional selectivity. These are generally organized in a hierarchical manner, starting with early visual areas selective for simple visual features such as orientation and defined according to their retinotopic organization, then moving into extrastriate areas displaying weaker retinotopy and higher stimulus selectivity (Grill-Spector et al., 1998; Grill-Spector, Golarai, & Gabrieli, 2008). Regions at the top of this hierarchy include areas selective for objects, such as the inferior temporal cortex (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Kriegeskorte et al., 2008), for faces, such as the fusiform face gyrus (N. G. Kanwisher, McDermott, & Chun, 1997; Malach et al., 1995), and for body parts including faces such as the extrastriate body (EBA) area and STS (Kontaris, Wiggett, & Downing, 2009). Note that in contrast to STS, EBA seems to be decoupled from motor systems, and is limited to perceptual analysis of body-related visual input (Kontaris et al., 2009) such as identification of actor identity from morphological body features (Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007). The fusiform face gyrus also appears to be involved in identity processing, whereas subregions of the STS selective for faces appear to be involved in processing facial expressions (Haxby, Hoffman, & Gobbini, 2000; N. Kanwisher & Yovel, 2006).

Infants can see at birth, but neonatal vision is poor compared to adults in terms of acuity, contrast sensitivity, colour sensitivity, depth perception, and the field of view is much smaller (Johnson, 2011; Norcia, Tyler, & Hamer, 1990). Improvements in these visual skills, which occur gradually in the early postnatal years until reaching adult levels, arise predominantly from maturation of the eye and various cortical structures, but learning also plays an important role (Johnson, 2011). Clearly, the state of the infant’s visual system in the first months of life may have important implications for theories of mirror system development. For example, is visual perception good enough in the early months for social interactions to strengthen couplings between visual and motor representations of actions? Is the cortex developed enough in the early postnatal period and are there sufficient connections between visual and motor areas at birth for such mappings to develop?

Traditionally, visual perception was posited as being mediated primarily by subcortical structures at birth (Dubowitz, Mushin, De Vries, & Arden, 1986), which would make the possibility of a rudimentary mirror system existing in the neonate, or the potential to build up visuomotor mappings early on, very unlikely. However, a considerable body of research now suggests that visual cortex is functional in the neonate, albeit relatively immature, and is actively involved in the processing of visual information from very early on (Slater, 2002). Evidence in support of this includes visual memory capacities at birth, early learning about faces, and the flexibility of visual learning in very young infants (Slater, 2002). In particular, the very early-appearing sensitivity infants have to faces, including a newborn bias towards looking at faces (Pascalis & Kelly, 2009), early recognition of their mother's face (Pascalis & de Schonen, 1994), and perhaps, neonatal imitation (Meltzoff & Moore, 1977), is often used as evidence in support of this. Incredibly, there even seems to be a visual preference for face-like stimuli *in utero* (Dunn, Reid, Young, Amu, & Reissland, 2016), and it is hypothesized that the foetus may acquire visual experience of their own hands in the womb (Del Giudice, 2011). Furthermore, face-sensitive cortical areas such as the fusiform gyrus and superior temporal sulcus show a degree of facial tuning even in the first months of life (Farroni et al., 2013; Nakato et al., 2009; Otsuka et al., 2007; Tzourio-Mazoyer et al., 2002), and recent fMRI research shows that the spatial structure of responses to faces and natural scenes is very similar to that observed in adults (Deen et al., 2017). This actually extends to the whole cortex, including occipital, temporal, parietal and frontal regions, meaning basic aspects of functional organization are present from a very early age, despite anatomical maturation of human cortex being fairly slow (Deen et al., 2017; Keunen, Counsell, & Benders, 2017). Other work has shown that the sensorimotor, visual processing and auditory/language networks show adult-like topology at birth (W. Gao, Alcauter, Smith, Gilmore, & Lin, 2015; Keunen et al., 2017), with immature forms of these networks detected as early as 30 weeks in the foetus (Thomason et al., 2015).

Therefore, although many basic visual functions, such as visual acuity, are poor at birth, visual perception still appears adequate for allowing infants to perceive those aspects of the environment most relevant to them, e.g., objects which interact with them such as faces, with the occipital cortex seeming to mature more rapidly than other brain regions (Huttenlocher & Dabholkar, 1997; Kostovic & Vasung, 2009; Moeskops et al., 2015). Furthermore, although inter- and intraregional connectivity undergo extensive development in the first years of life, there is evidence for cortico-cortical connectivity from preterm and term neonates (Ball et al., 2014; Ratnarajah et al., 2013; Tymofiyeva et al., 2013), suggesting that coarse projections between cortical regions necessary for the strengthening of visuomotor mappings could be present from birth. Indeed, together with research concerning the development of the motor system and the state of various cortical regions at birth, the findings mentioned here suggest that the general organization required to match visual and motor representations of actions could be in place at birth, and that a rudimentary mirror system could take advantage of this organization in the early postnatal period. The fact that there is more evidence for face selectivity in visual regions than hand selectivity during early infancy, as well as the difference in early ability to produce movements with the face and hands, could support claims that a facial mirror system would appear much earlier than a manual mirror system; i.e. it could be that a basic facial mirror system is present at birth, or develops very quickly, but that a manual mirror system is more dependent on experience, and slowly emerging manual motor competence, so develops later. Note, mothers typically place themselves so their face is around 30cm from the infant's during interactions in the first months postpartum, which is the optimal distance in terms of visual ability at this age (Lavelli & Fogel, 2002; Schoetzau, 1979). By around 3-4 months, visual development is sufficient for infant's to see across a small room (Murray, 2014; Trevarthen & Aitken, 2001).

1.5 THESIS OUTLINE

In this introductory chapter, the significance that mirror neuron discovery has had for theories concerning the matching of self- and other-generated actions was discussed, as were the various properties and functions that have been ascribed to mirror systems in monkeys and humans. This was followed by a more detailed look at how EEG has been utilized to study putative mirror activity, and at the different explanations that have been proposed to explain how mirror neurons might develop. In the subsequent chapters of this thesis, a number of studies designed, conducted, and analysed by the current author are presented, in which human mirror system activity was investigated in very young children and infants. The overarching aim of these studies was to investigate mirror system involvement in the processing of opaque actions, namely facial expressions and attention direction. In addition, two out of the three studies considered how early experience might affect development of a mirror system.

As discussed in the literature review, although a mirror system may be involved in the processing of facial expressions, no study has really explored when and how this system may emerge in human development. Evidence does, however, support the idea that a mirror system for mapping between manual actions produced by self and other is present from quite early on in infants, with most studies having utilized EEG in order to explore this; i.e. have used decreases in mu rhythm power as an index of mirror system activity. Accordingly, the first study to be included in this thesis (***Chapter 2***) involved an EEG experiment to record changes in mu power during observation and execution of various facial expressions in 30-month-old children. 30 months is a much younger age than has been looked at in any prior investigations of facial mirror activity in humans. It is also a very interesting age, with children at this time becoming increasingly adept at recognising facial expressions and displaying behaviour indicative of empathic skill, even though their verbal skills are still very limited (Brownell & Kopp, 2007; Denham, 1998; Leppänen & Nelson, 2009). Therefore, 30 months seemed an appropriate age to explore mirror activity in response to facial expressions in a young human sample.

After this study with 30-month-old children, a longitudinal research programme was designed to explore putative mirror system responses to actions an infant cannot see themselves perform at an even earlier stage in development, and to investigate the influence of early mother-infant interactions on mu modulation. The design, recruitment process, sample characteristics, and general procedure for this longitudinal programme are described in ***Chapter 3.*** This wider programme encompassed two individual studies, which are presented in ***Chapters 4 and 5***. The first study (***Chapter 4***) involved an EEG experiment comparable to the one in Chapter 2, whereby modulation of the mu rhythm in 9-month-old infants was recorded, using EEG, during observation and execution of different facial expressions. These infants were also observed interacting face-to-face with their mothers at 2 months postpartum, with these interactions coded to identify instances of maternal mirroring of infant facial expressions. This coding was then related to the degree of mu power reduction during observation of facial expressions in the 9 month EEG experiment. The behavioural portion of the study was included to test the hypothesis that for facial expressions, mothers provide the necessary visual input that corresponds to their infant's motor output to strengthen the perceptual-motor couplings characteristic of a mirror system.

The second study from this longitudinal programme (***Chapter 5***) also involved mother-infant interactions and an infant EEG experiment. This study was designed to investigate mirror system involvement in the processing of others' attention shifts, which like facial expressions, are a type of opaque action. In this study, decreases in mu power were measured at 6.5 and 9.5 months postpartum during observation of an adult turning to look at an object the infant just looked at, compared to turning towards a different object. Behaviours related to attention direction were coded during interactions at 2, 3.5, and 6.5 months postpartum, which was then related to the EEG findings at the 6.5 and 9.5 month assessments.

The final chapter of the thesis (***Chapter 6***) summarises the results from the three experimental chapters. The findings from these studies are discussed in terms of what they add to current understanding of mirror systems in the developing brain, and limitations to the studies are considered. Finally, directions for future research are outlined and some general conclusions given.

2 STUDY ONE: MU DESYNCHRONIZATION DURING OBSERVATION AND EXECUTION OF FACIAL EXPRESSIONS IN 30-MONTH-OLD CHILDREN

2.1 INTRODUCTION TO THE STUDY

This chapter describes a study conducted by the current author in which EEG was utilized to record mu rhythm desynchronization in young children as they observed and executed various facial expressions (Rayson et al., 2016). The study was designed to extend previous research implicating a mirror system in the processing of facial expressions (Carr et al., 2003; Ferrari et al., 2012; Moore et al., 2012; van der Gaag et al., 2007; Vanderwert et al., 2015) in two ways: (i) via the exploration of putative mirror system activity in much younger human participants; and (ii), through the use of EEG to investigate mirror system involvement in processing both *emotional* and *non-emotional* facial expressions.

2.1.1 FACIAL EXPRESSION PROCESSING AND THE INVOLVEMENT OF A MIRROR SYSTEM

Facial expressions form a critical component of social interactions, providing a base from which to understand other people's feelings, and to infer their motivations or intentions. As such, accurate recognition and analysis of facial expressions is essential for the facilitation of appropriate behaviour within an interaction, and contributes significantly to the success of a social exchange. Facial expression processing is vital throughout the lifespan, but is particularly important during acquisition of social and communicative skills early on in development, with infants and young children understanding others predominantly via the 'reading' of faces before mastering language (Leppänen & Nelson, 2009). For example, towards the end of the first year postpartum, the facial expressions of caregivers can convey a wealth of information to their offspring in times of uncertainty, such as fear or happiness in order to signal the danger, or lack thereof, posed by a particular object or situation (Klinnert, 1984; Sorce, Emde, Campos, & Klinnert, 1985). Furthermore, difficulty recognizing and understanding facial expressions in early childhood has been associated with a range of adverse outcomes. This includes impaired social functioning and behavioural problems (Denham et al., 2003; Izard et al., 2001; Leppänen & Hietanen, 2001; Trentacosta & Fine, 2010), which highlights the importance of facial expression processing early in development.

As discussed in Chapter 1, the processing of facial expressions has been suggested to involve a mirror system. For instance, 'understanding' others' facial expressions may involve the mental simulation, or attempted simulation, of that same expression (Goldman & Sripada, 2005), with simulation theories positing that observation of someone performing a facial expression activates the observer’s sensorimotor representations involved in producing it themselves. This mental replication is thus thought to aid expression recognition (e.g. Adolphs, 2006; Gallese, 2007), perhaps via a mapping between the observed facial expression and other associated representations (e.g. emotional or communicative). Accordingly, the concept of a human mirror system has been proposed as a prospective biological mechanism underlying simulation or ‘embodied simulation’ theories of facial expression perception (Bastiaansen, Thioux, & Keysers, 2009; Gallese, 2007; Niedenthal, Mermillod, Maringer, & Hess, 2010), with the observation of another’s expression activating like neural processes in the observer as in the performer (Gallese & Sinigaglia, 2011). Some researchers have hypothesized that simulation processes within different modalities may be involved in this, with somatosensory, motor, and limbic systems all playing an important role (Keysers & Gazzola, 2009; Wicker et al., 2003). For example, premotor mirror neurons could represent the facial movement (Carr et al., 2003), insula mirror neurons the emotional content (Wicker et al., 2003), and somatosensory neurons the proprioceptive information contained in the observed facial movement (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000; Keysers et al., 2004). Note, ‘mirror neurons’ in all these areas may not be so in the classical sense of having visual and motor properties, but the type of representation they transform stimuli into (e.g. emotional, or proprioceptive) might be essential in the mirroring process (Pineda, 2008).

Although much mirror neuron research has focused on the study of hand actions, a number of studies with both monkeys and humans have now implicated a mirror system in the processing of facial expressions. In one of the first investigations, single cell recordings in the ventral premotor cortex (area F5) of macaque monkeys revealed mirror neurons for facial gestures (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003). Most of these neurons fired during live observation and execution of ingestive-related mouth actions (e.g. sucking or breaking food), but a subset was found to fire most effectively in response to live communicative gestures (e.g. lip smacking). Many fMRI studies with human adults have also found common activation of brain areas associated with a mirror system (such as IFG, STS, primary motor, somatosensory, premotor, and posterior parietal cortices, with the addition of the insula) during observation, execution, and imitation of facial expressions (Carr et al., 2003; Dapretto et al., 2006; Engell & Haxby, 2007; Hennenlotter et al., 2005; Kircher et al., 2013; Lee, Josephs, Dolan, & Critchley, 2006; Likowski et al., 2012; Pohl, Anders, Schulte-Rüther, Mathiak, & Kircher, 2013; van der Gaag et al., 2007). These human studies have demonstrated overlapping activation in response to a variety of different expressions (including happy, sad, angry, surprise, disgust, and fear), using both static and dynamic facial stimuli (e.g. Carr et al., 2003; and Leslie, Johnson-Frey, & Grafton, 2004, respectively).

The fMRI evidence cited above is further supported by TMS research designed to explore mirror system activation in relation to facial expression processing (Enticott, Johnston, Herring, Hoy, & Fitzgerald, 2008; Rochas et al., 2013). For example, TMS-induced MEPs have been shown to correlate with performance on facial emotion processing tasks (Enticott et al., 2008), and disrupting pre-supplementary motor area (SMA) activity with TMS has been found to disrupt recognition of happy faces (Rochas et al., 2013). Notably, one study with patients suffering from drug refractory seizures has also provided some evidence for the existence of a human facial mirror system using single-cell recordings, with activation in the SMA demonstrated during both performance and observation of emotional facial expressions (Mukamel et al., 2010).

Many facial expressions of course involve both motor and emotional components. Therefore, it could be that these aspects are processed by separate, but linked, mirror systems, which work together to contribute to facial expression processing (van der Gaag et al., 2007). In support of this idea, it has been shown that observation, imitation, and execution of emotional and non-emotional facial expressions result in overlapping patterns of neural activation, but that emotional facial expressions elicit more activation in regions such as the amygdala, insula, and IFG (Carr et al., 2003; Kircher et al., 2013; van der Gaag et al., 2007; Wicker et al., 2003). It has been proposed that the insula, which is associated with the feeling of emotion (Wicker et al., 2003) and recognition of facial expressions (Adolphs, Tranel, & Damasio, 2003), links the frontal component of the mirror system with the limbic system, thus providing a mapping from an observed expression onto internal emotional representations (Dapretto et al., 2006; Rizzolatti, Cattaneo, Fabbri-Destro, & Rozzi, 2014).

2.1.1.1 THE USE OF EEG TO INVESTIGATE FACIAL MIRROR SYSTEM ACTIVITY IN ADULTS AND INFANTS

Despite research on the human mirror system providing important information concerning a common neural substrate for facial expression observation and execution, its focus exclusively on adult participants leaves open the question of whether such a mechanism is functional from a much earlier age. This would also support the hypothesized presence of a simulative process for facial expression understanding in the developing brain (Decety & Meyer, 2008). As stated in Chapter 1, desynchronization of the mu rhythm, as recorded over central EEG electrodes, has been identified as an index of mirror system activity (Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy et al., 2004; Pineda, 2005, 2008), and is the preferred technique for investigating neural activity in more challenging populations. To reiterate briefly, the use of this measure is supported by a considerable body of evidence, including the fact that mu appears to be generated in the sensorimotor cortex (Babiloni et al., 2016; Hari et al., 1997; Pineda & Hecht, 2009; Salmelin et al., 1995), and is modulated during both action execution and observation (Kessler et al., 2006; Lepage & Théoret, 2006; Muthukumaraswamy & Johnson, 2004). Additionally, mu activity co-varies with BOLD activity in mirror system regions (e.g. inferior parietal lobule and dorsal premotor area), which have strong cortico-cortico connections with the primary sensorimotor region lining the central sulcus, during simultaneous EEG and fMRI acquisition (Arnstein et al., 2011).

Also noted in the introductory chapter, in infancy and early childhood, the mu frequency range is lower than in adults, gradually increasing over time (Berchicci et al., 2011; Marshall et al., 2002). The 6-9Hz range has been identified as functionally analogous to the adult 8-13Hz band in early development (Stroganova, Orekhova, & Posikera, 1999; Stroganova & Orekhova, 2007), and is considered appropriate for use with children up to 4 years of age (Marshall et al., 2002). As recommended by Cuevas et al. (2014), from here on the term mu ‘desynchronization’ is used where power is significantly decreased from a baseline period, and ‘suppression’ where mu power is significantly different between conditions or regions (i.e. one is significantly lower than the other) but not necessarily lower than baseline.

In human adults, the mu rhythm is sensitive to observation and mental imagery of orofacial movements (Muthukumaraswamy et al., 2006; Pfurtscheller, Brunner, Schlögl, & Lopes da Silva, 2006; Spiegler, Graimann, & Pfurtscheller, 2004), and the few studies that have investigated adult mu activity during observation of emotional facial expressions suggest mirror system involvement in the processing of them (Cooper, Simpson, Till, Simmons, & Puzzo, 2013; Moore et al., 2012). Moore, Gorodnitsky & Pineda (2012) found significant mu desynchronization in adult participants during observation of static happy and disgusted facial expressions. Interestingly, significant differences were found in the timing of the response to the two stimulus types, but only in the right hemisphere. In fact, some fMRI research concerning facial mirror system activity has also found right lateralization in certain regions during observation, execution, and imitation of facial expressions (Hennenlotter et al., 2005; Leslie et al., 2004). This is in keeping with other research demonstrating a right hemisphere dominance in face and emotion processing (Adolphs, 2002; Borod et al., 1998; Killgore & Yurgelun-Todd, 2007). No study utilizing EEG to explore facial mirror system activity has looked at non-emotional versus emotional expressions; therefore whether differences in mu modulation between the two would be found is currently unknown.

Around 8-14 months of age, human infants already demonstrate changes in mu rhythm power during observation and execution of manual actions (e.g. Cannon et al., 2016; Marshall et al., 2011; Nyström et al., 2011; Southgate et al., 2010, 2009), but despite the importance of face-face interactions during early childhood (Murray, 1992; Trevarthen & Aitken, 2001), mu responses to facial expressions in very young populations have not yet been explored. Ferrari et al. (2012) and Vanderwert et al. (2015) found evidence for mirror system involvement in observation and execution of facial gestures in newborn macaque monkeys, with desynchronization demonstrated in the 5–6 Hz EEG frequency band as infants viewed live human facial gesture performance (e.g. lip smacking). In order to look at both observation and execution in this study, video recordings of the macaques were made during EEG acquisition, which were then coded to identify any instances where infants performed the gestures being presented to them. As the 5–6 Hz band was found to become desynchronized both when the infant macaques executed and observed the facial gestures, it suggests this frequency band acts comparably to the mu rhythm in humans (Lepage & Théoret, 2006; Marshall et al., 2011; Muthukumaraswamy et al., 2006; Nyström et al., 2011; Pineda, 2005; Southgate et al., 2010), and is analogous with mu band in human infants. Findings from this research also indicate that a functioning mirror system could be present soon after birth in the macaque, and therefore may play a role in early facial gesture processing. Therefore, conducting similar studies with younger human populations is now critical in order to address the question of whether a mirror system might play a role in facial expression processing from early on in human development.

2.1.2 THE CURRENT STUDY

In this study, mu rhythm desynchronization in 30-month-old children was explored during presentation of video clips in which adults performed dynamic emotional and non-emotional facial expressions. Trials in which children spontaneously produced facial expressions were coded offline from video recordings, and were excluded from analysis of observation-only trials. The execution trials were then analysed separately in lieu of an explicit execution condition, as in the work with infant macaques (Ferrari et al., 2012; Vanderwert et al., 2015). While the age group included in this study is particularly difficult for EEG research, it is of importance because of the extensive emotional and social developments that occur during this period (Brownell & Kopp, 2007; Denham, 1998). Children of this age become increasingly adept at reading others' mental states and emotions

(Bartsch & Wellman, 1995; Phillips, Wellman, & Spelke, 2002), and, for example, begin to display more empathic behaviour towards parents (Zahn-Waxler, 1992), and sometimes even peers (Nichols et al., 2009; Spinrad & Stifter, 2006). Therefore 30 months constitutes an appropriate age to first explore potential mirror system activation during observation of facial expressions at an early stage in human development.

Based on previous EEG studies of hand action observation with young populations, and the facial expression studies with adults and infant macaques, mu desynchronization during both observation and execution of facial expressions in central clusters of electrodes was expected. In keeping with best practices suggested for mu rhythm research of the mirror system (Cuevas et al., 2014), dynamic stimuli including a pre-movement static neutral expression were utilized, as well as videos of facial expressions in which the face was scrambled. This enabled comparison of mu power changes relative to a baseline period and a control condition, which allowed the determination of whether any observed effects were simply due to observation of a face or any face-like stimulus performing meaningless movements.

2.2 METHODS

2.2.1 RECRUITMENT AND PARTICIPANTS

28 healthy children (15 male, 13 females) aged approximately 30 months took part in this study, which was approved by the University of Reading Research Ethics Committee (21.05.13). Participants were recruited from the Child Development Group (CDG) database, based in the School of Psychology and Clinical Language Sciences (SPCLS) at the University of Reading. For this database, mothers were approached by a member of the CDG on maternity wards at the Royal Berkshire Hospital soon after giving birth. The current author recruited mothers and infants for this database. Agreeable mothers gave permission to have their details stored in the CDG database, allowing SPCLS researchers to contact them if conducting any suitable research. For the research described here, mothers from the database with children aged around 30 months were contacted via telephone/email, and the study was described to them. Interested mothers were sent an information sheet outlining the study in more detail (see Appendix A, section 8.1), then a date for assessment at the University was arranged if they wished to take part. Mothers gave written, informed consent (see Appendix A, section 8.2) before participation, and all research was conducted in accordance with the Declaration of Helsinki.

10 participants were excluded before analysis due to excessive fussiness during net placement or throughout the experiment (N = 9), or technical difficulties (N = 1). This left a sample of 18 children (10 male, 8 female; age: M = 936.39 days, SD = 43.99), with the loss of data comparable to that in other EEG studies of the mu rhythm with younger populations (Cannon et al., 2016; Marshall et al., 2013; Reid, Striano, & Iacoboni, 2011; Saby, Marshall, & Meltzoff, 2012; Southgate et al., 2009; Warreyn et al., 2013). All mothers were given a gift voucher as compensation for their time.

2.2.2 EXPERIMENTAL STIMULI

Stimuli used in the EEG experiment consisted of short videos (2.5s) of female actors executing a number of facial expressions. Video clips were used rather than still images due to their greater ecological validity, and female-only actors were selected as all children had mothers as their primary caregiver; this has been linked to a preference for female versus male faces (Oakes, 2010; Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002). There were four different conditions included in the experiment: a positive condition, ‘happy’; a negative condition, ‘sad’; a non-emotional condition, ‘mouth opening’; and a control condition consisting of scrambled versions of the other videos (i.e. a version of each happy, sad, and mouth opening video). The scrambled versions of each video were produced by dividing the face region into square blocks (18 × 18 pixels), randomly shuffling these blocks in the first frame of the video, and then applying the same transformation to each subsequent frame. This resulted in a video with similar low-level visual and motion features as the original, but with an unrecognizable movement (see Figure 2.1). Previous studies have utilized static or non-biological moving stimuli in control conditions (Ferrari et al., 2012; Moore et al., 2012); however, the scrambled stimuli condition was used here instead to control for low-level visual features and overall movement across all experimental conditions.

The videos featuring positive and negative facial expressions were taken from the Amsterdam Dynamic Facial Expression Set (ADFES), which has been well validated in previous research (van der Schalk, Hawk, Fischer, & Doosje, 2011). Ratings of the mouth-opening videos on a scale of -2 (negative) to +2 (positive) by a panel of 20 adults confirmed that they represented non-emotional facial expressions (M = -0.10, SD = 0.07). These videos were made comparable with the ADFES stimuli in terms of onset, duration of movement, size, brightness, contrast, and spatial frequency. The brightness and contrast were confirmed to be similar to the ADFES videos by converting each frame of each video to greyscale, and then comparing the mean and standard deviation pixel values, respectively, over all frames. The spatial frequencies were computed by taking the Fourier transform of each frame, projecting the two dimensional spectrum to one dimension, and averaging over all frames. All videos started with 750ms of a static/neutral facial expression, followed by 500ms of movement, and 1250ms held at the movement peak (Figure 2.1).

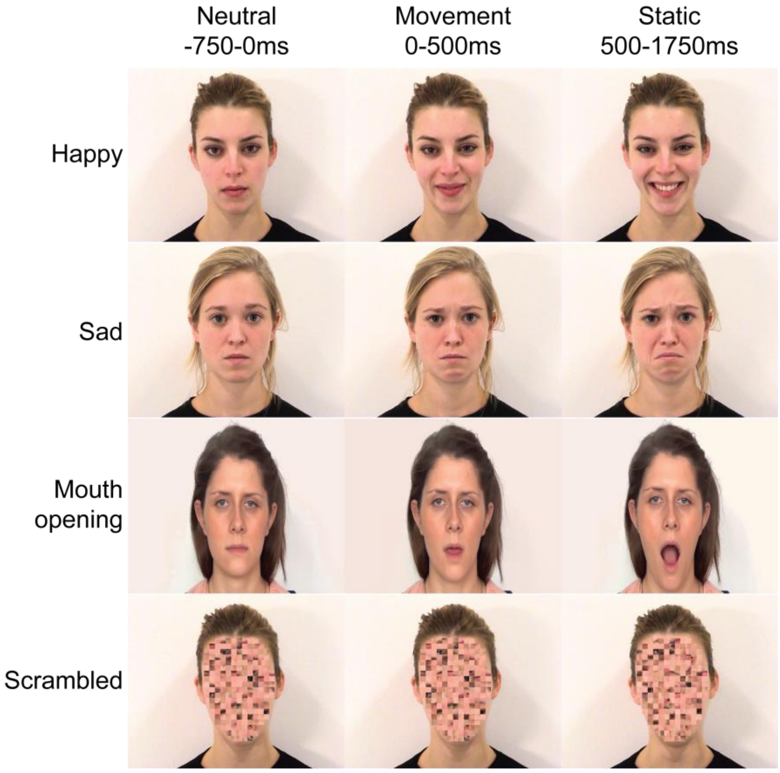

Figure 2.1: Time-course of stimuli in the four experimental conditions. Each condition included an initial, static neutral expression, followed by a facial movement which lasted approximately 500ms. After the movement peak, the expression was held for 1250ms.

2.2.3 DESIGN AND PROCEDURE

On arrival, children were given a selection of toys to play with, and were given time to become accustomed to the environment and feel comfortable with the two experimenters present (one of which was the current author). Once acclimated, children's heads were measured and the correctly sized EEG net selected for preparation. When the net was ready, children were taken into the testing area, which was in the same room but shielded from the surroundings. Children were seated on mothers' laps approximately 65cm from a computer monitor, and an experimenter fitted the EEG net onto their head. A popular children's cartoon was played during net placement to entertain participants, and a second experimenter was available to help distract and/or pacify the child if they became fussy or attempted to touch the net once in place. Any fussiness caused by net placement receded quickly for most children, however, the decision of whether to continue with the experiment was always left up to the mother. Mothers were asked to remain as still as possible and to not interact with their child during the experiment.

Stimuli were presented on the monitor using PsychoPy v1.80.04 (Peirce, 2008) in blocks of 6 video clips of the same facial expression (happy, sad, mouth opening or scrambled; 2 actors per block, 3 videos each). These clips were randomized within blocks, and blocks themselves were pseudo-randomized so that the same condition could not be presented more than twice in succession. The inter-stimulus interval was randomized between 800 and 1200ms. The experiment was terminated if the child became too inattentive, distressed, moved excessively, or once they had viewed 6 blocks of each condition. Between experimental blocks, static cartoon images were presented on the screen accompanied by sound effects, and children filled in an associated reward chart in order to retain focus. These cartoon images were presented in a randomised order, with the experimenter controlling when a 'reward' image was shown; children received a sticker for their reward chart when this image appeared. This approach proved very successful in maintaining child attention during the experiment.

2.2.4 EEG DATA ACQUISITION

EEG was recorded using a 128-channel Hydrocel Geodesic Sensor Net (EGI, Corp., Eugene, OR). All of the electrodes in this system are part of an elastomer geodesic net, with each electrode in the net surrounded by a sponge enclosed within a plastic pedestal. After measuring the child's head and selecting the correctly sized net, the entire net was soaked in an electrolyte solution made up of warm water, potassium chloride, and baby shampoo (Johnson & Johnson, New Brunswick, NJ), which increases the conduction between electrodes and the scalp. Such nets are particularly well suited for use with young populations due to the easy application procedure and comfortable fit compared with other EEG systems (Johnson et al., 2001).

The sensor net was then fitted on the child's head and plugged into an amplifier. This amplified, filtered, and sampled the EEG signal, with data transferred to a data acquisition computer to be visually monitored online and recorded. Data were sampled at 250 Hz with an analogue band-pass filter of 0.1–100 Hz, and were recorded with the vertex as a common reference. Impedances were measured before beginning the experiment, and were kept below 50 kΩ as far as possible. Note, 'impedance' here refers to the signal-to-noise ratio at each electrode, with high impedances resulting from poor contact with the scalp. When impedances were greater than 50 kΩ, extra electrolyte solution was applied to the electrode, and its position adjusted. The stimulus presentation script included event triggers at appropriate points of each trial (block onset, trial onset, video onset/offset, and block offset), which were sent via an Ethernet connection to the data acquisition computer. This enabled data to be segmented offline into epochs based on the timing of events during each trial. The PsychoPy script also sent trigger signals specifying the type of movement being shown in each video so that the trial type could also be determined from the data files. The data acquisition/stimulus presentation set-up can be seen in Figure 2.2.

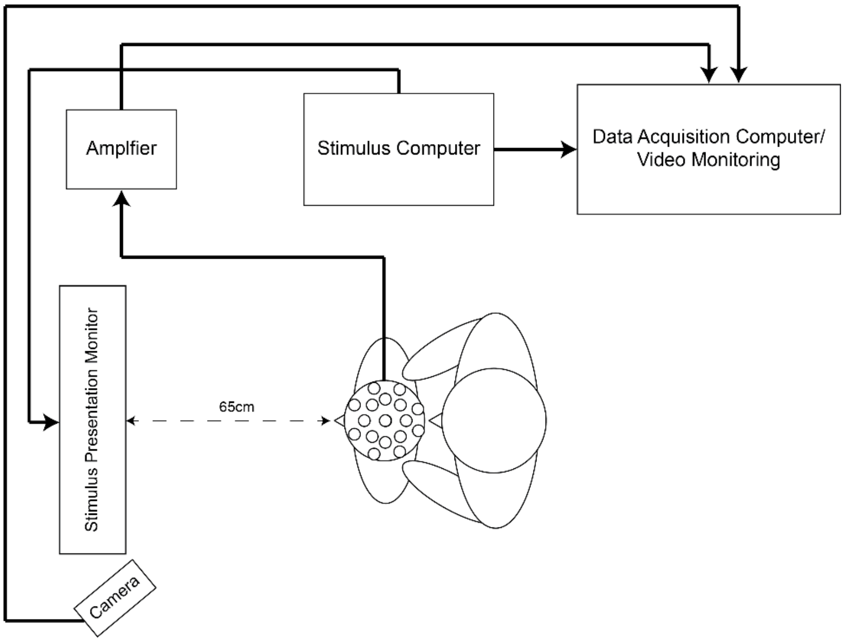

Figure 2.2: Schematic showing the organisation of the equipment used to run the experiment. The stimulus computer was connected to the computer monitor on which the stimuli were presented to the children. This computer also sent trial information to the data acquisition and video monitoring computer (used for online viewing of participants, and to record videos for offline coding). Children were seated on mothers' lap throughout the experiment around 65cm from the stimulus presentation monitor.

The experiment began when triggered manually by an experimenter who was watching the participant on a screen from another section of the room. Trial blocks were triggered as soon as the child was attentive to the monitor. Synchronous video recordings of the experiment were also examined offline to allow exclusion of trials in which the child was inattentive, and to enable execution of facial expressions to be coded.

2.2.5 BEHAVIOURAL CODING OF CHILD DURING THE EEG EXPERIMENT

In order to identify trials in which participants executed the facial expressions presented during experimental blocks, expressions (happy, sad, and mouth opening) were coded offline from the video recordings. Operational definitions were given for the expressions to be coded, and child expression levels were rated on a scale of 0-4 at the onset and offset of each movement in order to identify the magnitude of that movement (see Table 2.1 for mouth opening example). This was done in two phases; the first marking the onset and offset of the initial movement (i.e. when execution started and when the facial expression reached its peak), and the second marking the onset and offset of the return movement (i.e. when the movement began to return to its original position and when movement ceased). See Appendix B, section 9.1 for more details regarding this coding scheme.

All videos were coded by a research assistant blind to the study hypotheses and experimental condition being presented. Videos were viewed in real-time and frame-by-frame to accurately identify onsets and offsets of movements. To determine the extent to which the data coded in this study were correct representations of the variables measured, Cohen's kappa coefficient was calculated. Cohen’s kappa (κ) is a statistic measuring inter-rater agreement, and is considered a more robust measure than mere percentage agreement, as κ also takes into consideration any agreement occurring by chance. As such, a second independent researcher coded a random 20% of the EEG videos to establish inter-rater reliability, with good reliability obtained for timing of events and event type (time-unit κ = 0.86-0.88, event κ = 0.83).

Table 2.1: Examples of the different levels of mouth opening and their definitions

Rating	Description	Example
0	Mouth closed; neutral	
1	Lips very slightly parted; relaxed mouth	
2	Lips clearly parted; jaw slightly lowered	
3	Mouth half open (lips clearly parted; jaw clearly lowered, but not to maximal extent)	
4	Mouth fully open (lips clearly parted; jaw lowered to maximal extent)	

2.2.6 EEG PRE-PROCESSING AND ANALYSIS

After viewing the video recordings and marking periods of inattention using EGI software (NetStation v4.3.1; Electrical Geodesics, Inc., Eugene, OR), EEG data were exported and analysed using the EEGLAB v13.3.2. toolbox (Delorme & Makeig, 2004). Data were bandpass filtered at 2-35 Hz. Epochs ranging from 750ms before stimulus movement onset to 1750ms after movement onset from each trial were extracted. Epochs that contained previously marked periods of inattention and epochs in which more than 15% of channels exceeded +/- 250µV were excluded.

With EEG, each channel receives a mixture of signals from surrounding brain areas, and therefore independent components analysis (ICA) is often used to decompose these mixed signals into their underlying neural and artefactual components. This allows for the rejection of artefacts such as eye blinks and muscle movements which contaminate the data, leaving only components representing neural activity of interest. Therefore, a natural-gradient logistic infomax independent component analysis was performed on the data (the runica algorithm; Delorme & Makeig, 2004), and artefact components were identified and removed using the ADJUST algorithm (v1.1; Mognon, Jovicich, Bruzzone, & Buiatti, 2011). Finally, data were re-referenced to the average of all electrodes.

To compare power relative to baseline in the mu band, event related spectrums (ERSs) for each condition were computed using built-in EEGLAB procedures. Time-frequency decompositions were computed with a fast Fourier transform using a 1-second Hanning window with 50% overlap in 1Hz bins from 2-30Hz. To make the results comparable with those of other studies, log spectral power was converted to absolute power, and averaged across the 6-9Hz bins (e.g. Cannon et al., 2016; Marshall et al., 2013; Saby et al., 2012). Event-related desynchronization (ERD) was then computed as the percentage change of the average absolute power over a 0-750ms time window (from the onset of facial movement in experimental stimuli until 250ms after the peak of the full expression) from the condition-specific baseline averaged over -650ms to -50ms (prior to the onset of the observed facial movement; Pfurtscheller & Aranibar, 1979). The 6-9Hz range has been identified as suitable for use with participants up to 4 years of age (Marshall et al., 2002), and is the most commonly used frequency band in mu rhythm/mirror system studies with very young participants. However, because not a lot of research has looked at children aged 30 months, to confirm the suitability of the 6-9Hz band for use in this study, ERD during execution trials in the 6-9Hz and 10-13Hz (which covers the corresponding adult range) bands was calculated. There was indeed greater mu ERD in the 6-9Hz band (see Figure 2.3), with only ERD in this band significantly lower than baseline. Therefore this frequency range was used for the rest of the analyses.

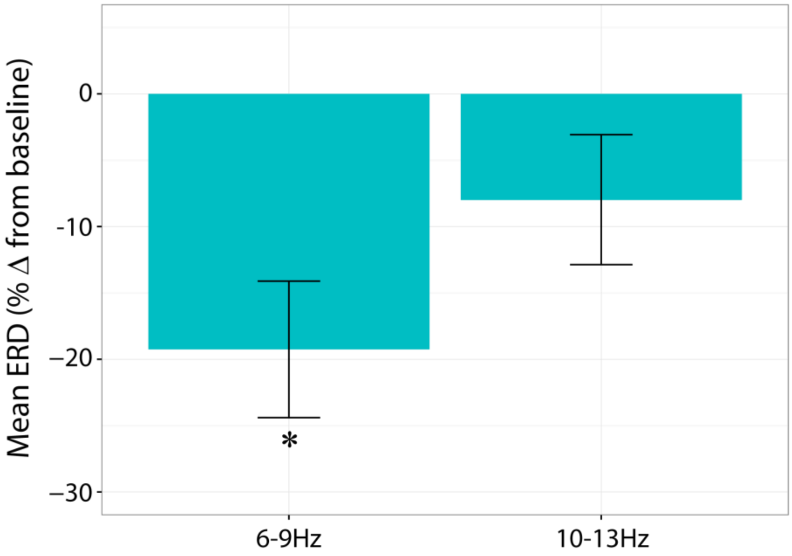

Figure 2.3: ERD in the central clusters during movement execution. Error bars represent the mean +/− standard error. Only ERD in the 6-9Hz band was significantly lower than baseline.

ERD was calculated for four clusters of electrodes. These were comprised of two central clusters (left and right hemisphere) located around standard C3 and C4 sites for mu rhythm recording, and two occipital clusters (left and right hemisphere) located around standard O1 and O2 sites to control for visual alpha responses (Figure 2.4; Umilta', Berchio, Sestito, Freedberg, & Gallese, 2012). For each cluster, in each experimental condition, the ERD values were calculated for each subject.

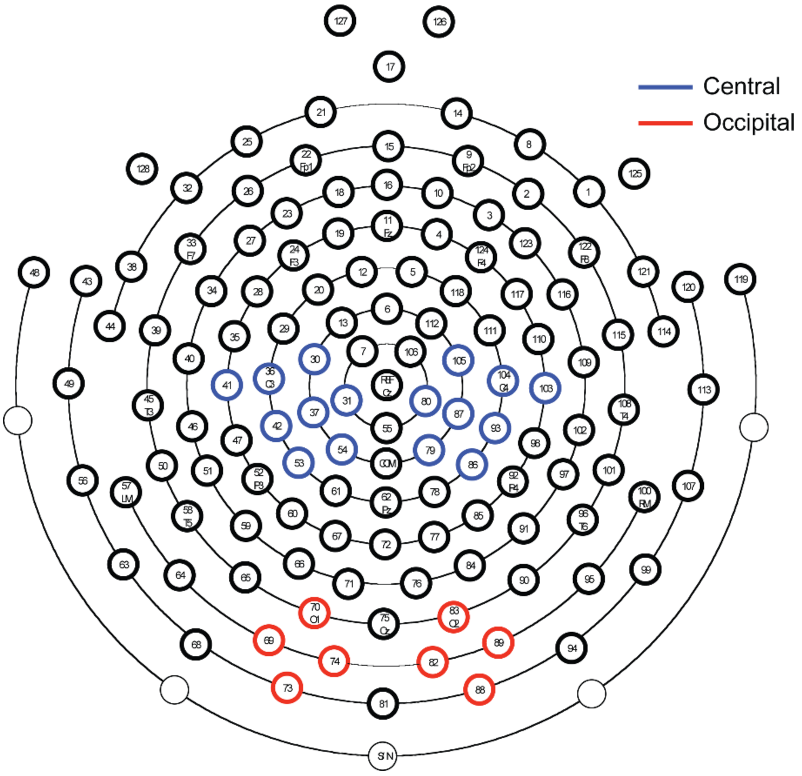

Figure 2.4: Location of channels included in the central (blue) and occipital (red) clusters.

2.3 RESULTS

In the following analyses, the α-level was set at 0.05 and all post-hoc tests were Bonferroni corrected. The Greenhouse-Geisser correction of degrees of freedom was used when the sphericity assumption was violated (indicated by ε).

2.3.1 OBSERVATION TRIALS

Children were required to have at least 5 trials per condition remaining after EEG pre-processing to be included in this analyses, in keeping with similar infant EEG studies (e.g. Cannon et al., 2016; Marshall, Saby, & Meltzoff, 2013; Southgate et al., 2009). This left a total of 15 children for analysis of the observation trials, which again, is comparable to numbers in previous research.

To investigate changes in mu power during observation of experimental stimuli, trials marked during behavioural coding as containing execution of mouth opening, happy, or sad expressions were excluded (leaving M = 14.12 SD = 4.09 observation trials per condition, per child). Before comparing conditions and clusters to each other, whether desynchronization indeed occurred relative to the baseline period was considered. Significant mu desynchronization was found in the left central cluster for mouth opening [M = -31.04, SD = 17.98; $t(14) = -6.69$, $p < 0.001$], but not for any other condition [all $p > 0.40$]. In the right central cluster, there was significant mu desynchronization for mouth opening [M = -26.20, SD = 17.25; $t(14) = -5.88$, $p < 0.001$], happy [M = -15.16, SD = 14.78; $t(14) = -3.97$, $p = 0.001$], and sad [M = -28.33, SD = 12.39; $t(14) = -8.85$, $p < 0.001$] conditions, with significant mu *synchronization* in the right central cluster for the scrambled condition [M = 2.55, SD = 3.28; $t(14) = 3.01$, $p = 0.01$]. There was no significant mu desynchronization in either occipital cluster relative to baseline [all $p > .20$], except for mu desynchronization in O1 for the sad condition [M = -15.42, SD = 20.26; $t(14) = -2.95$, $p = 0.001$].

Having established the presence of mu desynchronization, a 2 × 2 × 4 repeated-measures ANOVA was conducted, with region (central/occipital), hemisphere (left/right) and condition (happy/sad/mouth opening/scrambled) as within-subject variables. The ANOVA revealed a significant main effect of region [$F(1, 14) = 14.22$, $p = 0.002$, $\eta_p^2 = 0.50$] and of condition [$F(3, 42) = 5.76$, $p = 0.002$, $\eta_p^2 = 0.29$]. These results were qualified by significant region × hemisphere [$F(1, 14) = 10.30$, $p = 0.006$, $\eta_p^2 = 0.42$] and region × condition [$F(3, 42) = 6.05$, $p = 0.002$, $\eta_p^2 = 0.30$] interactions. A significant three-way region × hemisphere × condition interaction [$F(1.81, 25.38) = 6.30$, $p = 0.007$, $\eta_p^2 = 0.31$, $\varepsilon = 0.60$] was also revealed, which was followed up by conducting two separate repeated-measures ANOVAs for each region (central/occipital, Figure 2.5).

The analysis of central clusters revealed significant main effects of both hemisphere [$F(1, 14) = 7.72$, $p = 0.02$, $\eta_p^2 = 0.36$] and condition [$F(1.62, 22.64) = 10.72$, $p = 0.001$, $\eta_p^2 = 0.43$, $\varepsilon = 0.54$], and a significant hemisphere × condition interaction [$F(2.09, 29.28) = 6.11$, $p = 0.006$, $\eta_p^2 = 0.30$, $\varepsilon = 0.70$]. Pairwise comparisons demonstrated that mu ERD was not significantly different in the left and right hemisphere for scrambled [$t(14) = -0.87$, $p = 0.40$] and mouth opening conditions [$t(14) = -1.35$, $p = 0.20$], but was significantly greater in the right hemisphere for happy [$t(14) = 2.19$, $p < 0.05$] and sad conditions [$t(14) = 3.44$, $p = 0.004$]. In the left hemisphere, ERD in response to mouth opening was significantly greater compared to scrambled [$t(14) = 6.01$, $p < 0.001$] and sad conditions [$t(14) = -3.82$, $p = 0.01$] (and approached significance for happy [$p < 0.06$]), and in the right hemisphere, ERD was significantly greater in all conditions compared to scrambled (mouth opening [$t(14) = 6.78$, $p < 0.001$]; happy [$t(14) = 4.42$, $p = 0.004$]; sad [$t(14) = 9.35$, $p < 0.001$]).

The analysis of occipital clusters revealed no significant main effects of hemisphere [*F*(1, 14) = 1.40, *p* = 0.26, η_p^2 = 0.09] or condition [*F*(3, 42) = 1.72, *p* = 0.18, η_p^2 = 0.11], and there was no significant hemisphere × condition interaction [*F*(3,42) = 0.88, *p* = 0.46, η_p^2 = 0.06]. This indicates that mu desynchronization was specific to central clusters and not due to changes in occipital alpha power.

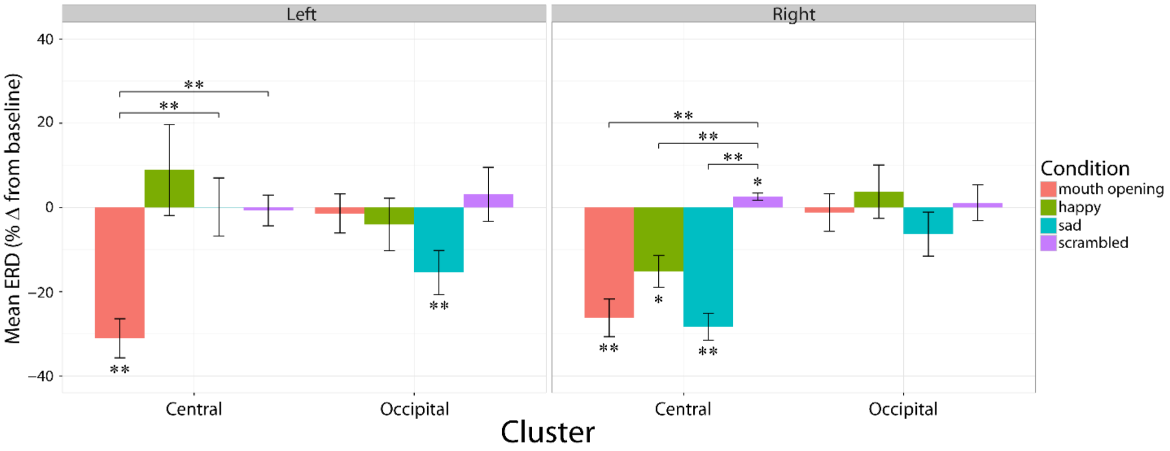

Figure 2.5: ERD for each condition in central and occipital clusters in the left and right hemisphere. Error bars represent the mean +/− standard error, * p < 0.05, ** p < 0.005. In the left central cluster, ERD in response to mouth opening was significantly greater compared to scrambled. There was no significant difference across conditions in O1 or O2.

2.3.2 EXECUTION TRIALS

To explore changes in the mu band while executing rather than observing facial expressions, separate analyses were conducted for 11 participants who performed happy, sad, or mouth opening expressions during the experiment (at any magnitude of movement). There were not enough instances of each expression to analyse separately (i.e. 5 trials per condition per child), therefore the conditions were collapsed across expression type. Children needed a minimum of 5 execution trials to be included.

For the coded execution trials (M = 11.65, SD = 10.89; per participant), significant mu desynchronization was found relative to baseline in the right central cluster [M = -19.26, SD=17.06; *t*(10) = -3.74, *p* = 0.004], but not for any other cluster [all *p* > 0.08]. To explore differences in mu ERD during execution of facial expressions, a 2 × 2 repeated-measures ANOVA was conducted, with region (central/occipital) and hemisphere (left/right) as within-subject variables (Figure 2.6). The ANOVA revealed a significant main effect of region [*F*(1, 10) = 6.05, *p* = 0.03, η_p^2 = 0.38], with relatively greater mu suppression in central [M = -17.57, SD = 19.62] compared to occipital clusters [M = -3.72, SD = 19.60].

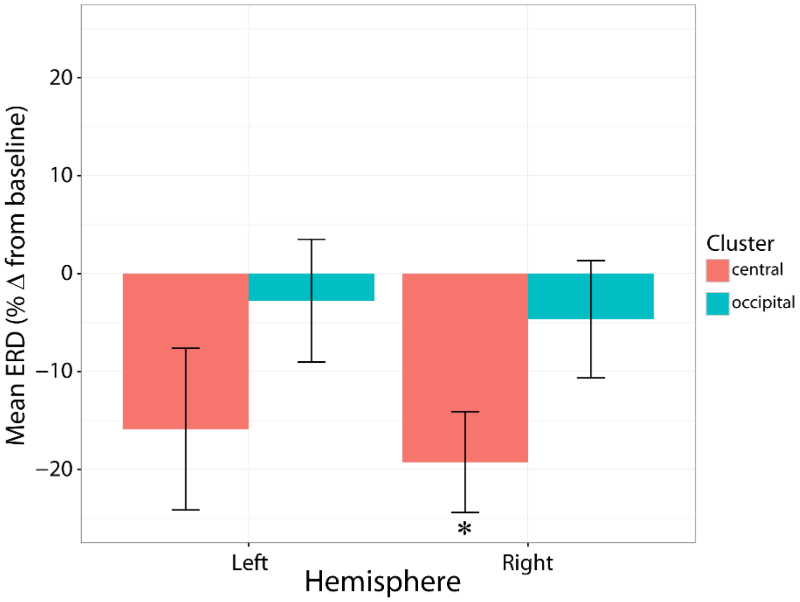

Figure 2.6: ERD in central and occipital clusters during movement execution in the left and right hemisphere. Error bars represent the mean +/− standard error, * p < 0.05, ** p < 0.005. There was relatively greater mu suppression in central compared to occipital clusters.

Having established that mu desynchronization occurred during execution trails, whether magnitude of movement was related to mu ERD was also investigated. Spearman's rho revealed no significant correlation between the magnitude of movement and mu ERD in C3 ($\rho = 0.23$, $p > 0.07$) or C4 ($\rho = -0.08$, $p > 0.55$). See Appendix C, section 10.1 for extra information regarding execution trials, including a histogram showing the frequency of movements at the various magnitudes.

2.4 DISCUSSION

Findings from monkeys and adult human studies suggest that a mirror system is involved in the processing of facial expressions (Carr et al., 2003; Ferrari et al., 2003; Moore et al., 2012; van der Gaag et al., 2007), but previous research has not explored whether this system is functional from an early stage in human development. The results of the present study suggest activation of the sensorimotor system during both observation and execution of facial expressions in children as young as 30 months, and therefore that a mirror system could indeed be involved in facial expression processing from a very young age.

Specifically, EEG was used to determine whether mu desynchronization occurs when children observe emotional (happy and sad) and non-emotional (mouth opening) dynamic facial expressions. The main finding was that significant mu ERD occurred in central clusters in response to all facial expressions during observation, relative to a static neutral face, but not in response to a scrambled control condition. Significant mu suppression (and desynchronization in the right hemisphere) was also demonstrated over central electrodes during execution of emotional and non-emotional expressions. Interestingly, whereas the effect during observation for mouth opening expressions was bilateral in central clusters, significant mu ERD during observation of happy and sad facial expressions was found in the right hemisphere only.

As well as being the first study to show mu desynchronization during observation of facial expressions early in childhood, the present study extends previous EEG studies of the facial mirror system by comparing emotional and non-emotional facial expressions. Additionally, most studies of mu rhythm activity use either observation of static stimuli or non-biological movement as control conditions (e.g. Ferrari et al., 2012; Moore et al., 2012), and thus do not address the specificity of the EEG response to biological movements (Cuevas et al., 2014). A recent meta-analysis on the mu rhythm has strongly recommended the use of multiple control conditions in order to assess EEG response specificity for the investigation of the mirror system (Fox et al., 2016). The use of a static neutral face baseline period and a scrambled facial movement condition controlled for observation of a face alone as well as observation of meaningless movement. The lack of significant mu desynchronization in response to the observation of scrambled facial expressions demonstrates that the significant mu ERD seen in the other conditions is not simply due to observation of a moving face-like stimulus or other attentional factors. Additionally, the lack of mu ERD in occipital regions during facial expression observation demonstrates that the effect seen in central clusters is not a result of alpha desynchronization in visual cortex, but is specific to somatomotor cortical regions.

In other studies, bilateral activation of human mirror system areas during action-observation has often been reported (for a review see Rizzolatti et al., 2014). However, most mirror system studies have investigated observation of hand actions, and therefore may not be directly comparable with the study presented in this chapter. The finding that mu desynchronization was right lateralized during observation of emotional expressions is in line with much research showing right hemisphere dominance for emotional facial processing (Adolphs, Damasio, Tranel, & Damasio, 1996; Calvo & Beltrán, 2014; de Haan & Nelson, 1998; Moreno, Borod, Welkowitz, & Alpert, 1990), and in fact, fMRI research has shown some right lateralization in certain mirror system-related regions during observation, execution and imitation of facial expressions (Hennenlotter et al., 2005; Leslie et al., 2004). Furthermore, other EEG studies of the facial mirror system have demonstrated differential mu responses to emotional facial expressions (Moore et al., 2012), and to faces associated with reward performing happy expressions (Gros et al., 2015), in the right hemisphere. Right lateralized ERPs have also been found during emotional facial expression discrimination in the somatosensory cortex, which is where the alpha mu rhythm is thought to be generated (Sel, Forster, & Calvo-Merino, 2014). In infants, EEG studies have shown the right hemisphere to be more sensitive to early emotional experience with caregivers (Bowers & Heilman, 1984; de Haan, Belsky, Reid, Volein, & Johnson, 2004), including exposure to maternal depression (Dawson, Klinger, Panagiotides, Hill, & Spieker, 1992; Jones, Field, & Almeida, 2009), and consistent with the results here, right lateralized ERPs have been found in children during observation of static facial expressions (Batty & Taylor, 2006; de Haan et al., 2004; Field et al., 1998).

Nevertheless, although these results are in keeping with previous research, the reason why right lateralization of mu desynchronization during observation of emotional facial expressions would be found here is not clear. Research investigating the effects of patients with brain lesions has demonstrated that the right somatosensory cortex is required for successful retrieval of conceptual knowledge about the emotions signalled by facial expressions (Adolphs et al., 2000). Given that the somatosensory cortex is thought to be a mirror system region, and is where the mu rhythm is generated, the right somatosensory cortex in particular could be important for linking simulated motor representations and emotional representations. As such, observing emotional facial expressions could result in, and indeed in the current study did result in, right lateralized sensorimotor activity. Non-emotional expressions, such as mouth opening, are likely not associated with any strongly lateralized representations (e.g. emotional), which may explain why bilateral activity was demonstrated during observation of mouth opening in the current study.

Changes in mu rhythm activity during observation of facial expressions might also, at least in part, be explained by covert imitation. In adults, the observation of facial expressions leads to subtle, measurable effects at the muscle level, similar to covert facial responses (Dimberg, 1982; i.e. facial mimicry; Dimberg, Thunberg, & Grunedal, 2002; Lundqvist & Dimberg, 1995). It is possible that in the current study children displayed such responses, but they were not detectable at the behavioural level. In other words, although the fine-grained behavioural analysis allowed the removal of any trials containing overt movements, the EEG responses described during observation trials may still partly reflect the synergy between observing and imitating facial expressions.

However, MEG research has shown that mu rhythm modulation can occur without significant facial EMG activity, and therefore decreases in mu power may not necessarily reflect covert imitation (Nishitani & Hari, 2002). Further research is clearly required to explore any relationship between mu rhythm responses in children and covert imitative responses.

One limitation of the present study is the lack of an explicit execution condition as it is difficult to instruct young children to perform such a task. Nevertheless, there were enough spontaneous instances of child happy, sad, and mouth opening expression production to combine them into an execution condition, with mu suppression demonstrated in central compared to occipital clusters. No significant relationship was found between the degree of mu desynchronization and movement magnitude during execution trials in the present study. This suggests that mu desynchronization here is an index of a motor representation that is more abstract than that of low level muscle commands (e.g. a representation for mouth opening rather than for extending the jaw by a certain amount). Additionally, while the results here indicate mirror system involvement in the processing of facial expressions in 30-month-olds, they do not give any indication of the functional role such a system might play. It is known that by 30 months of age, and indeed much earlier (Farroni, Menon, Rigato, & Johnson, 2007), children are capable of producing and implicitly recognizing all basic facial expressions, including those used in this study (Leppänen & Nelson, 2009). There are many event-related EEG studies that support implicit recognition of various facial expressions in infancy, which includes differentiation between emotional and neutral expressions (de Haan et al., 2004; Leppänen, Moulson, Vogel-Farley, & Nelson, 2007; Taylor-Colls & Fearon, 2015), as well as behavioural research showing that young children modulate their behaviour in response to others' emotional versus neutral expressions (Nichols et al., 2009, 2010). Therefore, although explicit recognition was not tested in this study, children at 30 months postpartum are very likely to implicitly recognize a number of facial expressions, and the differential mu desynchronization found in response to emotional and non-emotional facial expressions here could indicate a role for a mirror system in this process. Furthermore, infants as young as 2 months demonstrate disrupted behaviour when their mother responds negatively during an interaction, which suggests they are already sensitive to brief observation of facial expressions by this age (Murray, Fiori-Cowley, Hooper, & Cooper, 1996).

Many studies designed to investigate mirror system activity have been limited by their failure to include an execution as well as observation condition (Cuevas et al., 2014). This is particularly common in studies with very young children and infants, where it is much more difficult to ensure that participants perform the actions of interest. Therefore, the inclusion of any kind of execution condition in the study presented here, whereby spontaneous execution was identified and analysed separately from observation-only trials (as in the macaque work; Ferrari et al., 2012; Vanderwert et al., 2015) is a strength of the research. However, this method also has its limitations, in that for the majority of trials, infants would have also been observing the expressions they were producing. As such, it is not clear the extent to which mu desynchronization during execution was the result of motor or visual activity, or a combination of the two. This is an issue inherent to many studies of the mirror system (e.g. Carr et al., 2003; Leslie et al., 2004; van der Gaag et al., 2007; Ferrari et al., 2012; Vanderwert et al., 2015), where the execution condition is often imitative rather than 'purely' execution (i.e. a condition where the participant cannot see the action they must perform). Those such as Hennenlotter et al. (2005) have addressed this issue in adult fMRI research by including a pure execution, during which participants are cued to make an expression (e.g. using a cross for smile), rather than being shown the facial expression they need to execute. This has revealed similar results to those using the imitative paradigms, however such as design would not be possible with very young individuals. Note, during piloting for the study in this chapter, the current author did attempt to ask the 30 month olds to produce facial expressions (with and without giving an example), but this proved unsuccessful.

Although this limitation restricts the interpretation of results reported here, a number of points are worth mentioning. Firstly, we know that adults demonstrate sensorimotor activity during orofacial movement (Nakasato et al., 2001; Sakihara & Inagaki, 2015), and therefore 30 month olds, who are reasonably competent in the control of their own facial movements, would presumably demonstrate the similar activity. Additionally, modulation of the mu rhythm can be measured during manual action performance at 9 months of age (e.g. Southgate et al., 2009; 2010; Cannon et al., 2016), even though infants are capable of producing facial expressions long before they master execution of manual actions. Therefore, even without an execution condition at all, as mu desynchronization during observation of facial expressions suggests activation of the motor system, this would indicate that a mirror system is involved; this would not be possible to claim if mu ERD had been found during execution but not observation. The lack of alpha ERD in occipital clusters during observation and execution here also strongly supports the claim that responses were specific to sensorimotor regions, rather than mere recruitment of visual areas. The lack of mu ERD during the scrambled condition also suggests that the effect observed in the other conditions was not just due to other attentional factors, but reflected motor system activation.

It could also be the case that mu ERD during execution here reflected recruitment of the somatosensory cortex more strongly than primary motor cortex, and was therefore triggered by peripheral input from the face (i.e. the feeling of performing the facial movements). However, mu desynchronization was seen during observation in the present study, as it has been in other studies with adults and monkeys (Muthamukaswarmy et al., 2004; Ferrari et al., 2012; Vanderwert et al., 2015; Moore et al., 2012), with any overt movement excluded during observation-only trials. Adult research has also demonstrated that no overt muscle activity is required for mu ERD to occur during observation of facial expressions (Nishitani & Hari, 2002), which suggests that peripheral input to somatosensory cortex is not necessary, supporting the claim that mu ERD reflects activation of the motor system. Furthermore, somatosensory cortex receives collorary discharge from motor cortex, therefore even if mu rhythm is generated predominantly in somatosensory areas, its modulation is still likely to reflect activity in primary motor cortex (Pineda, 2005).

To summarise, results from this study revealed that in 30-month-old children, significant mu rhythm desynchronization occurred during observation and execution of emotional and non-emotional facial expressions compared to static neutral faces, but not during observation of comparable movement of a scrambled face-like stimulus. There was significant mu desynchronization in the left and right hemispheres during observation of non-emotional expressions, but desynchronization was right lateralized for emotional expressions, consistent with the concept of right hemisphere dominance in emotional face processing. These findings suggest activation of the sensorimotor system during observation and execution of facial expressions by 30 months of age, which is consistent with mirror system involvement in the processing of facial expressions from an early stage in human development.

3 LONGITUDINAL RESEARCH PROGRAMME: GENERAL METHODOLOGY AND STUDY DESCRIPTIONS

3.1 INTRODUCTION TO PROGRAMME

The EEG study presented in Chapter 2 revealed mu desynchronization during observation and execution of facial expressions (emotional and non-emotional) in 30-month-old children. These results are consistent with findings from the monkey and human adult literature (Ferrari et al., 2012; Moore et al., 2012; van der Gaag et al., 2007), and suggest that a mirror system may be involved in the processing of facial expressions from an early stage in human development. Following on from this study, a longitudinal research programme was designed to explore whether similar neural responses indicative of a mirror system would occur in infants at an even earlier age.

Two individual studies were included within this longitudinal programme, presented separately in the following two chapters (***Chapters 4 and 5***). Both of these focused on mirror system involvement in the processing of actions one cannot see oneself perform (‘opaque actions’). In the first study (***Chapter 4***), a very similar experimental paradigm to the one in Chapter 2 was utilized, with EEG recorded during observation and execution of facial expressions. However, participants in this new study were just 9 months of age, much younger than the 30-month-olds in Chapter 2. A different EEG experiment was conducted in the second study (***Chapter 5***), focused on the directing of attention rather than facial expressions. This experiment was carried out with the same group of infants as in Chapter 4, but was performed at 6.5 and 9.5 months of age. During this experiment, neural activity was recorded as infants observed an adult turn to look an object they had just looked themselves (i.e. the adult imitated or ‘mirrored’ the infant’s prior attention shift), compared to observation of an adult turning to look at a different object (i.e. the adult attended in the opposite direction to the infant’s prior attention shift).

In the introductory chapter of this thesis, it was noted that the development of mirror systems for opaque actions could be influenced by early interactions with a caregiver (Del Giudice et al., 2009). That is, mirroring of actions an infant cannot see themselves perform, by a caregiver, has been proposed to strengthen mappings between an infant’s visual representations of such actions and the motor commands used to perform them. In order to test this hypothesis, the two studies in ***Chapters 4 and 5*** not only involved recording of infant neural activity, but also video recordings of the same infants interacting with their mothers face-to-face at various ages. These videos were manually coded to identify behaviours that may impact the development of a mirror system, such as maternal imitation of infant facial expressions and infant observation of mothers following their previous attention shifts. Both of these are examples of an infant first executing an action, then observing their mother replicate the action they just performed. Therefore, both these examples enable the infant to observe the visual consequences of their own actions, and thus could strengthen the action-perception couplings characteristic of a mirror system. For that reason, the relationship between these coded behaviours during face-to-face interactions and the degree of infant mu desynchronization (used as an index of mirror system activity) in the EEG experiments was investigated in both the longitudinal programme studies; in an attempt to elucidate whether such early experiences influence putative mirror system activity later on in development.

In the remainder of this chapter, the design, recruitment process, and general procedure used in the longitudinal programme will be described in more detail, sample characteristics will be given, and brief outlines of the two studies contained within the programme presented. These studies will be described fully in the two experimental chapters that follow this one, including the findings obtained and their discussion.

3.2 LONGITUDINAL RESEARCH PROGRAMME DESIGN

Assessments were conducted with a group of mother-infant dyads at 2, 3.5, 6.5, 9, and 9.5 months postpartum. The 2 month assessment was conducted by a research assistant in mothers' homes, but all other assessments took place in a School of Psychology and Clinical Language Sciences (SPCLS) laboratory at the University of Reading. Two researchers were present during the University assessments, one of which was always the current author. Dyads engaged in a period of face-to-face play during the 2, 3.5, and 6.5 month assessments; and at the 6.5, 9, and 9.5 month visits to the University, infant EEG experiments were conducted. Mothers were also asked to fill in a number of questionnaires at these assessments concerning maternal mental health, general infant development, and demographic information (see section 3.5). Table 3.1 provides a summary of each assessment included in the longitudinal programme, including infants' age at each visit, the assessment location, the tasks conducted, and the questionnaires completed.

Table 3.1: Infant age at each visit, assessment location, and tasks

Infant age	Assessment Location	Tasks
2 months	Mothers' homes	• 3 minute face-to-face interaction • Two questionnaires (demographic information, maternal mental health)
3.5 months	University	• 3 minute face-to-face interaction • Questionnaire (maternal mental health)
6.5 months	University	• 3minute face-to-face interaction • Gaze EEG experiment • Two questionnaires (maternal mental health, general infant development)
9 months	University	• Facial expression EEG experiment • Questionnaire (general infant development)
9.5 months	University	• Gaze EEG experiment

3.3 RECRUITMENT AND PARTICIPANTS

Mothers who took part in this research programme were originally recruited for the Child Development Group (CDG) database by researchers from the SPCLS at the University of Reading, who approached mothers on maternity wards at the Royal Berkshire Hospital (as noted in Chapter 2, the author recruited for this database for approximately 2 years). Mothers agreed to have their details stored in the database, which enabled any SPCLS researcher to contact them if conducting research for which they might be suitable. For the research described here, mothers from the database were contacted via telephone/email by the author when infants were aged approximately 4 to 6 weeks old, and if agreeable, the research programme was described to them. Interested mothers were sent an information sheet (see Appendix A, section 8.3) outlining the study in more detail, and a date for the first assessment was then arranged if mothers wished to participate. The date and time for the next assessment was booked at the end of each visit, with mothers contacted again a few days before to remind them of the appointment and to rearrange if necessary. Mothers received a gift voucher at the 6.5 and 9.5 month assessments as compensation for their time, and were also given a selection of pictures from their assessments during the last visit. This research was approved by the University of Reading Research Ethics Committee (31.07.15), mothers gave written informed consent (see Appendix A, section 8.2) at beginning of every assessment, and all research was conducted in accordance with the Declaration of Helsinki.

50 infants (27 male, 23 female) and their mothers were originally recruited to take part in this research, however a number of dyads dropped out at a various stages. As such, a total of 43 dyads (100%) participated in the 2 month assessment (infant age: M = 65.81 days, SD = 6.49); 38 (88.37%) at the 3.5 months assessment (infant age: M = 112.87 days, SD = 5.61); 38 (88.37%) at the 6.5 assessment (infant age: M = 199.95 days, SD = 5.50); 34 (79.07%) at the 9 month assessment (infant age: M = 277.44 days, SD = 9.16); and 34 (79.07%) at the 9.5 months assessment (infant age: M = 295.00 days, SD = 7.99). The diagram in Figure 3.1 summarises recruitment and participation in the study at each stage of the research programme. More information regarding sample characteristics can be found later on in this chapter (section 3.6.).

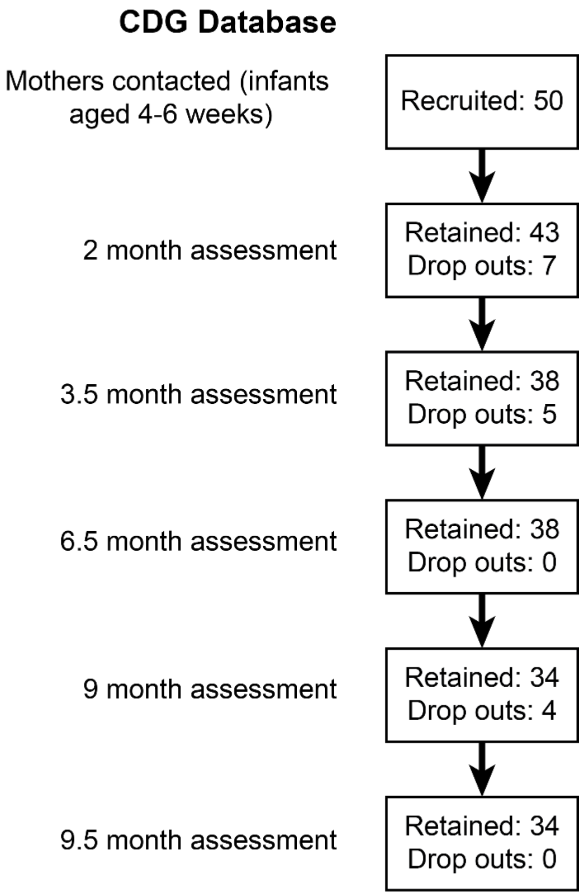

Figure 3.1: Diagram of recruitment and participation in the longitudinal study

3.4 GENERAL PROCEDURE

During the 2 month home assessments, mothers were asked to interact with their infants face-to-face for 3 minutes. During this interaction period, infants were laid semi-reclined on a changing mat and mothers knelt down so that their own face was positioned close to the infant’s, at a distance appropriate for infant visual acuity at this age. A camera was placed to capture a full-on view of the infant's face, as well as a side-view of the mother's face. A mirror was positioned behind infants to capture a full-on view of the mother, and a second mirror next to the infant's face in case they turned their head away from the camera (see Figure 3.2 for examples of this set-up). Mothers also completed two questionnaires at the 2 month assessment concerning symptoms of postnatal depression ('Edinburgh Postnatal Depression Scale' or EPDS) and demographic information. The EPDS was also completed at the following two visits to the University, with a general infant development (e.g. gross and fine motor development scales) questionnaire completed at the 6.5 and 9 month visits. Details about these questionnaires can be found in section 3.5.

Figure 3.2: Example images of the 2 month interaction set-up at mothers' homes

During the 3.5 and 6.5 month visits to the University, mothers were again asked to interact with their infants face-to-face for 3 minutes. During these interactions, mothers and infants were seated opposite one another; mothers on a chair and infants in an adjustable highchair suitable for all the ages assessed. This set-up can be seen in Figure 3.3. Two cameras were used to record these interactions, one directed towards the one infant and one towards the mother, which were later synchronized for manual coding. As noted in the introductory section of this chapter, all the interaction periods were included in order to investigate how early social environment (i.e. specific behaviours during early social exchanges) might be associated with infant mirror system development.

Figure 3.3: Example images of the interaction set-up at the University of Reading

During the 6.5, 9, and 9.5 month visits to the University, infant EEG experiments were conducted to investigate neural correlates of mirror system activity. During these experiments, infants sat on their mothers' laps approximately 65cm from a computer monitor, and were presented with various dynamic stimuli (see Figure 3.4). The data acquisition/stimulus presentation set-up was the same as in Chapter 2, and can be seen in Figure 2.2. As previously mentioned, these EEG experiments were included in the longitudinal research programme to investigate putative mirror system activity, which was then related to measures coded during the mother-infant interaction periods.

Figure 3.4: Example of an infant observing stimuli presented on a computer monitor during the 6.5 month EEG experiment

At the start of each University-based assessment, infants were given time to settle into the new environment, and to get used to the two researchers present. Mothers were given the information sheet once again to read, which outlined the longitudinal research programme as a whole. The researchers then went through the tasks to be completed during that particular visit in more detail, and mothers were encouraged to ask any questions they might have. Mothers were assured that they could have a break from, or stop, the tasks at any time. Finally, mothers were asked to sign a consent form before commencing with the tasks.

3.5 QUESTIONNAIRE MEASURES

Mothers completed questionnaires at the 2, 3.5, 6.5, and 9 month assessments, detailed below. See Appendix D, sections 11.1-11.3 for the actual questionnaires given to mothers.

3.5.1 EDINBURGH POSTNATAL DEPRESSION SCALE (EPDS)

The EPDS, first developed by Cox et al. (1987), is a widely used and well validated self-report questionnaire designed to identify those at risk of postnatal depression (Bunevicius, Kusminskas, & Bunevicius, 2009). The EPDS consists of 10 items, each asking the respondent about their feelings over the past week. Possible responses are scored on a scale of 0 to 3, with a maximum score of 30. This questionnaire was completed at all assessments where dyads engaged in a face-to-face exchange (2, 3.5, and 6.5 month visits) in order to explore any relationship that may exist between maternal interaction variables and depression scores. The reason for this is that research has consistently shown that postnatal depression disrupts early mother-infant interactions (e.g. Cohn et al., 1990; Murray et al., 1996), which has been linked to various poor psychological outcomes later on in childhood (Murray, Halligan, & Cooper, 2010).

3.5.2 AGES AND STAGES QUESTIONNAIRE-3 (ASQ-3)

The ASQ-3 (Squires & Bricker, 2009) is a questionnaire designed to identify the status of children in five developmental areas: communication, gross motor, fine motor, problem solving, and personal-social. Different versions of the questionnaire are available for various infant ages. Each question (30 in total) has three response options (yes, sometimes, not yet), which are converted to point-values and summed within each of the developmental areas assessed. The validity of this questionnaire has now been confirmed in a number of studies (e.g. Gollenberg, Lynch, Jackson, McGuinness, & Msall, 2010; Schonhaut, Armijo, Schönstedt, Alvarez, & Cordero, 2013). This questionnaire was completed at the 6.5 and 9 month assessments because it allowed any relationship between infant scores on the various developmental scales and EEG results to be considered. Of particular relevance here of course were the scales regarding motor development, as these might explain variation in the modulation of mu power recorded.

3.5.3 DEMOGRAPHICS QUESTIONNAIRE

Demographic information was obtained from mothers at the 2 month assessment via questionnaire, for example, maternal occupation and marital status (see section 3.6).

3.6 SAMPLE CHARACTERISTICS AND DEMOGRAPHIC DATA

The following information concerns the characteristics of the 43 mother-infant dyads who took part at the first visit (2 month assessment), where mothers filled in the demographics questionnaire.

3.6.1 INFANTS

Gestation and birth weight: All infants (19 female, 24 male) were born healthy, at an average gestation of 40 weeks, and average birthweight of 7lb 12oz. ***Birth order:*** Approximately 58% of infants were first-born, 35% second-born, and 5% third-born children. One infant in the sample was a fourth-born child (see Table 3.2).

3.6.2 MOTHERS

Age: At the time of their infant's birth, mothers were aged an average of 32.49 years. ***Ethnic origin:*** The majority of mothers (around 91%) identified their ethnic origin as 'White (British/Irish/other background)'. ***Education:*** Approximately 65% of mothers were educated to at least an undergraduate degree level, 21% to an A-level/NVQ level, and 14% of mothers to the level of GCSE/other. ***Marital Status:*** Around two thirds of mothers (67%) were married and cohabiting (see Table 3.2).

Table 3.2: Sample characteristics for infants and mothers

INFANT	
Gender	19 (44.19%) female 24 (55.81%) male
Average Gestation	40 weeks (SD= 1.63)
Birth weight	7lb 12oz. (SD = 0.08)
Birth order	25 (58.14%) first-born 15 (34.88%) second-born 2 (4.65%) third-born children 1 (2.33%) forth-born child
MOTHER	
Age	32.49 years (SD = 5.10)
Ethnic origin	39 (90.70%) British/Irish/other background 3 (6.98%) Mixed (White-Asian or White-Black) 1 (2.33%) Black (African/Caribbean or Black-British)
Education	27 (62.79%) at least a degree level 9 (20.93%) A-level/NVQ level 7 (16.28%) GCSE level/other
Marital Status	29 (67.44%) married and cohabiting 11 (25.58%) co-habiting but unmarried 3 (6.98%) single

3.7 INDIVIDUAL STUDIES

The two studies contained within this longitudinal research programme both focused on 'opaque' actions one cannot see oneself perform, namely facial expressions and the directing of attention. In Chapters 1 and 2, research suggesting mirror system involvement in the processing of facial expressions (Ferrari et al., 2003; van der Gaag et al., 2007; Vanderwert et al., 2015) was presented; however, no study had previously looked at this issue in very young human populations. The study described in Chapter 2 involving 30 months olds did just that, but nonetheless, it remained unknown whether a mirror system for facial expressions is present in the human brain at a much earlier age (i.e. in the first year, with evidence already suggesting manual mirror system activity in infants at this time), as well as how this system might develop. Additionally, evidence was presented in the introductory chapter for involvement of a mirror system in the mapping between own and others shifts of attention, in macaques and humans (Hoehl et al., 2014; Lachat et al., 2012; Shepherd et al., 2009). Actions that signal attention shifts are much less studied than facial expressions in the mirror system literature thus far, and while infant research suggests such a mechanism exists from an early age, limitations to previous studies restrict confidence in this interpretation. Again, there is no evidence as of yet concerning how such a mechanism may develop during infancy. Therefore, the studies presented in ***Chapter 4*** and ***Chapter 5*** were designed to both investigate mirror system activity during observation and execution of these two opaque actions, and the role of early mother-infant interactions might play in the development of such systems. Below are some very brief descriptions of the tasks included in each of these studies, which can also be found in Table 3.3.

3.7.1 STUDY TWO- MU DESYNCHRONIZATION DURING OBSERVATION AND EXECUTION OF FACIAL EXPRESSIONS IN 9-MONTH-OLD INFANTS: THE ROLE OF EARLY SOCIAL EXPERIENCE

This study (***Chapter 4***) involved the EEG experiment conducted at the 9 month assessment, which was designed to explore infant mu rhythm desynchronization during observation of both emotional (happy, sad) and non-emotional (mouth opening) facial expressions, as well as a scrambled control condition. The same dynamic facial stimuli from Chapter 2 were utilized, and again, infant execution of facial expressions during the EEG experiment were coded and analysed in lieu of an explicit execution condition. Video recordings of these infants interacting with their mothers previously at the 2 month assessment (see Figure 3.2) were coded on a second-by second basis to identify instances where mothers mirrored infant facial expressions, with coded measures then related to the degree of mu desynchronization during the 9 month EEG experiment.

This allowed the question of whether early maternal mirroring influences the development of a facial mirror system to be addressed, and for the following hypotheses to be tested: i) that infants whose mother mirror them more will demonstrate greater mu desynchronization during observation of facial expressions; ii), that additionally, infants whose mothers mirror particular expressions more will demonstrate greater mu desynchronization during observation of those expressions; and iii), based on the right lateralization found for emotional expressions at 30 months, that more maternal mirroring of emotional expressions will be linked to more right lateralized mu desynchronization in the 9 month sample. If the results confirmed these predictions, it would suggest that the postnatal environment is important for the refinement of facial mirror system responses, and that mothers do act as a biological mirror for their infant by allowing the infant to strengthen a mapping between the visual representations of facial expressions and their own motor representations.

3.7.2 STUDY THREE: MU DESYNCHRONIZATION IN INFANTS WHEN A SOCIAL PARTNER FOLLOWS THEIR DIRECTION OF ATTENTION: ROLE OF EARLY SOCIAL EXPERIENCE

This study (***Chapter 5***) was comprised of the infant EEG experiments conducted at both 6.5 and 9.5 month assessments (in which the same experimental paradigm was used), and the same infants interacting face-to-face with their mothers at 3.5 and 6.5months postpartum. The EEG experiment was designed to explore putative mirror system involvement in the mapping between own shifts in attention and the observation of someone else attending in that same direction. Infant attention was drawn to one of two objects displayed either side of an adults' face on a computer monitor, which was then followed by the adult turning in either a congruent or incongruent direction. Therefore, in each trial, infants first performed a head-turn, and then observed an adult turning in either the same (congruent) or opposite direction (incongruent). This meant that separate observation and execution conditions were not needed, as only in the congruent condition did the head-turn match the one the infant had just made. As such, it could be hypothesized that this would result in greater mu desynchronization. A scrambled control condition (i.e. scrambled versions of each congruent and incongruent video) was also included to test specificity of the response to a head turn, rather than just coherent motion.

During the interaction periods at the 3.5 and 6.5 month assessments, mother-infant dyads engaged in 3 minutes of face-to-face play. Mothers and infants were seated opposite each other in a small booth, with a number of colourful toys attached to the walls that would be likely to attract infant and maternal attention (see Figure 3.3). Mother and infant gaze behaviour was coded frame-by-frame from video recordings of these interactions, specifically, behaviours that could help to build a mapping between own and other attention shifts; e.g. infant follows mother's attention shift, infant sees mother look in the same direction they just did. These coded measures were then related to degree of mu desynchronization in the EEG experiments. Like in Chapter 4, the hypothesis was that infants who experienced more of the behaviours that might strengthen a mapping between own and other direction of attention during early interactions would demonstrate greater mu rhythm desynchronization in response to the congruent head turns of an adult (that is, the action that matched most closely to the action the infant just performed) in the EEG experiment. Specifically, it was hypothesized that infants who observed their mother following their attention shifts (i.e. whose mother followed their shift in attention, then the infant looked back at the mother to see her looking in the same direction) would demonstrate greater mu rhythm responses as this pattern of behaviour results in congruent and contingent visual and motor activation.

Table 3.3: Assessments for the two studies contained within the larger longitudinal research programme

	Assessment location	**Study One: Facial mirror system (Chapter 4)**	**Study Two: Attentional mirror system (Chapter 5)**
2 month assessment	Mother's home	3 minute mother-infant interaction Questionnaires: EPDS, demographics	
3.5 month assessment	University		3 minute mother-infant interaction Questionnaires: EPDS
6.5 month assessment	University		3 minute mother-infant interaction Questionnaires: EPDS, ASQ-3 EEG experiment
9 month assessment	University	Questionnaires: ASQ-3 EEG experiment	
9.5 month assessment	University		EEG experiment

4 STUDY TWO- MU DESYNCHRONIZATION DURING OBSERVATION AND EXECUTION OF FACIAL EXPRESSIONS IN 9-MONTH-OLD INFANTS: THE ROLE OF EARLY SOCIAL EXPERIENCE

4.1 INTRODUCTION TO THE STUDY

As frequently noted in the preceding chapters, research suggests that in both monkeys and human adults, a mirror system could be involved in the processing of facial expressions (Carr et al., 2003; Cooper et al., 2013; Ferrari et al., 2012, 2003b; Hennenlotter et al., 2005; Kircher et al., 2013; Leslie et al., 2004; Moore et al., 2012; van der Gaag et al., 2007; Vanderwert et al., 2015). Results from the EEG study in Chapter 2 advance understanding on this issue in relation to young children, with putative facial mirror system activity found at a much earlier age than has previously been investigated. Additionally, the Chapter 2 study extended prior EEG work on the human facial mirror system by being the first to explore any differences during observation of emotional versus non-emotional expressions. Specifically, significant mu rhythm desynchronization or suppression was found in 30-month-old children as they observed and executed happy, sad, and mouth-opening expressions. Interestingly, this desynchronization was right lateralized during observation of emotional expressions (happy, sad), but was bilateral during observation of non-emotional expressions (mouth opening). As such, these findings are in keeping with previous research implicating a mirror system in the mapping between self- and other-generated facial expressions, but also with the abundance of research demonstrating a right hemisphere dominance for emotional face processing (Adolphs, 1999, 2002; Adolphs et al., 1996; Calvo & Beltrán, 2014).

In this chapter (Chapter 4), a study will be presented in which facial mirror system activity was explored in an even younger sample of participants and, of particular note, also considered the influence of early social environment. The issue of facial mirror system development has not yet been explored in human infants, however, a number of theories have proposed that the development of mirror systems is influenced by caregiver imitation (or ‘mirroring’) of infant facial expressions (e.g. Casile et al., 2011; Del Giudice et al., 2009; Ferrari et al., 2013; Heyes, 2010). The hypothesis on which this claim is based is that via imitation of infant facial expressions, caregivers serve as ‘biological mirrors’ during early interactions (Del Giudice et al., 2009), allowing the infant to observe the visual consequences of their own, unobservable, actions. This is posited to strengthen a mapping between the infant’s visual and motor representations of facial expressions, aiding in the development of their facial mirror system. In order to test this hypothesis in the current study, a group of infants were observed interacting face-to-face with their mothers at 2 months postpartum. Any instances of maternal mirroring during the 2 month interactions were manually coded from video recordings, with coded variables then related to the degree of infant mu desynchronization during an EEG experiment conducted later on in the first year. Note, the sample of mother-infant dyads who participated in this study were taking part in the wider longitudinal research programme described in Chapter 3.

The EEG portion of this study took place when infants (i.e. those described above who were recorded interacting with their mothers at 2 months postpartum) were 9 months of age. Although the study in Chapter 2 was the first to provide results indicative of facial mirror system activity in very young children, the possibility remained that such a system may exist at an even earlier stage in development. Indeed, it has been proposed that a mirror system, at least in a rudimentary form, may be present in human infants at birth (e.g. Casile et al., 2011; Ferrari et al., 2013; Marshall & Meltzoff, 2011), and data support an infant mirror system for manual actions existing in the latter half of the first year (e.g. Cannon et al., 2016; Southgate et al., 2010, 2009). Therefore, to test the hypothesis that a mirror system may be involved in facial expression processing from a much earlier age, the current study utilized a very similar experimental paradigm as in Chapter 2 (i.e. EEG was recorded during observation and execution of emotional and non-emotional facial expressions), but with infants aged only 9 months. As mentioned in the previous paragraph, the results from this experiment were then explored in relation to early maternal mirroring of infant facial expressions, with the extent of mirroring predicted to influence mu desynchronization during observation of facial expressions later on in development.

In the rest of this introductory section, evidence for a facial mirror system in monkeys and humans will be reviewed, as will theories concerning how such a system might develop. This will be followed by a discussion of maternal mirroring during early mother-infant interactions.

4.1.1 EVIDENCE FOR A FACIAL MIRROR SYSTEM

The literature concerning facial mirror systems was explored in some depth in Chapters 1 and 2, so only a brief description will be given here. Processing others' facial expressions has been suggested to involve a mapping between own and other actions, and many have therefore hypothesized that a mirror system is involved (Carr et al., 2003; Casile et al., 2011; Ferrari et al., 2012, 2003; Moore et al., 2012; van der Gaag et al., 2007). Indeed, single-cell recordings have revealed mirror neurons selective for both ingestive and communicative mouth actions in area F5 of the macaque (Ferrari et al., 2003), and many human fMRI studies have demonstrated overlapping activation in mirror system-related brain regions (e.g. IFG, STS, primary motor, somatosensory, premotor, and posterior parietal cortices, with the addition of the insula) during observation, execution, and imitation of facial expressions (Carr et al., 2003; Engell & Haxby, 2007; Hennenlotter et al., 2005; Kircher et al., 2013; Lee et al., 2006; Likowski et al., 2012; Pohl et al., 2013; van der Gaag et al., 2007). TMS research supports these findings (Enticott et al., 2008; Rochas et al., 2013), with induced MEPs having been found to correlate with performance on facial emotion processing tasks (Enticott et al., 2008), and disruption to pre-supplementary motor area (SMA) activity found to interfere with recognition of happy faces (Rochas et al., 2013). One study using single-cell recordings has even provided some evidence for mirror neurons that encode emotional facial expressions in humans (Mukamel et al., 2010).

Adult EEG studies also indicate the involvement of a mirror system in the processing of emotional facial expressions (e.g. Cooper et al., 2013; Moore et al., 2012). These studies have utilized mu rhythm desynchronization as a proxy measure of mirror system activity, with a wealth of evidence now supporting this approach (Arnstein et al., 2011; Babiloni et al., 2016; Fox et al., 2016; Muthukumaraswamy & Johnson, 2004; Pineda, 2008) Furthermore, findings from the Chapter 2 EEG study suggest that a facial mirror system may be involved in the processing of emotional and non-emotional facial expressions by 30 months of age. Prior to this study, only fMRI research had looked at mirror system activity for emotional and non-emotional expressions (van der Gaag et al., 2007), with motor and emotional aspects of facial expressions suggested to be processed by separate, but linked, mirror systems (Dapretto et al., 2006; Rizzolatti et al., 2014). Additionally, EEG has been used to explore putative mirror system activity in macaque infants, with mu desynchronization during observation and execution of facial gestures found in the first days of life (Ferrari et al., 2012; Vanderwert et al., 2015). No comparable studies have been conducted with human newborns, however neonatal imitation of adult facial expressions has been interpreted as reflecting the existence of a facial mirror system, at least in a rudimentary form and for certain facial gestures, at birth (Casile et al., 2011; Marshall & Meltzoff, 2011). Note, macaque monkeys also engage in neonatal imitation of facial gestures (Ferrari et al., 2006; Ferrari, Paukner, Ionica, & Suomi, 2009; Paukner et al., 2011; Simpson, Fox, Tramacere, & Ferrari, 2014). As discussed in the introductory chapter, the existence of neonatal imitation has been questioned by some (Anisfeld, 1996; Jones, 2009), and consequently, the presence of a mirror system at birth has been doubted (e.g. Heyes, 2001). Such criticisms have been contested (Simpson, Murray, Paukner, & Ferrari, 2014), but neural data are required to elucidate when and how a mirror mechanism for mapping between own and other facial expressions might emerge in human development.

4.1.2 DEVELOPMENT OF A FACIAL MIRROR SYSTEM

In the first chapter of this thesis, various theories concerning mirror system development were discussed. Rather than a clear-cut division between theories emphasizing adaptive or learning components, as often portrayed by certain research groups, most accounts seem to attribute at least some role to both sensorimotor experience and genetics (e.g. the Hebbian learning and epigenetic hypotheses: Del Giudice et al., 2009; Ferrari et al., 2013). According to such theories, while learning processes that occur via sensorimotor experience are very important for mirror system development (Keysers & Gazzola, 2014; Keysers & Perrett, 2004), genetics also play an important guiding role by, for example, predisposing infants to attend to certain stimuli, or modulating the expression of certain genes. For instance, the Hebbian account asserts that mirror neurons are unique because of their synaptic connections, and therefore although genetics might not specify the fine grained connectivity between specific visual and motor neurons, they could bias infants towards looking at their own hands, and also provide the necessary brain architecture to form and strengthen visuomotor connections. This could ensure that the appropriate visual input is received to build up mappings between visual and motor representations of manual actions (Del Giudice et al., 2009). The epigenetic account states that mirror neurons are unique, not just because of their synaptic connections, but also because of the way in which experience modulates their genetic expression, which in turn, affects their activity. Thus, according to this view, even though there might be a rudimentary mirror system present at birth, subsequent experience is still essential for its development and refinement.

Research supports a role for sensorimotor experience in the development of a manual mirror system, with the degree of mu desynchronization during action observation correlated with own motor competence in infants as young a 9 months of age (Cannon et al., 2016). Many have suggested that a manual mirror system could develop via self-observation during action execution, which could facilitate the development of a mapping between visual and motor representations of actions. However, facial expressions are clearly different to manual actions, with infants unable to observe themselves performing facial expressions. Therefore, unlike actions involving the hand or other visible body parts, it is not possible via self-observation of facial expressions for infants to obtain the perceptual inputs required to strengthen links between corresponding visual and motor representations. Consequently, it seems likely that a mirror system for facial expressions develops differently from the one for manual actions (Casile et al., 2011).

Due to this correspondence issue, instead of developing via self-observation during action execution, as might be the case for a manual mirror system, the emergence of a facial mirror system has been hypothesized to be influenced by others' imitation of infant facial expressions (Casile et al., 2011; Del Giudice et al., 2009; Marshall & Meltzoff, 2011). As mentioned before, the basic idea behind this is that because mothers imitate their infant's facial expressions during early interactions (an event discussed more in the following section), they act as a 'biological mirror' for the infant. Through maternal mirroring of infant facial expressions, it is thus possible for infants to observe the visual consequences of their own facial expressions, and therefore strengthen the mapping between their visual and motor representations of that expression. This does not discount a role of genetics, e.g. the Hebbian hypothesis suggests that infants are predisposed to look at faces which canalizes sensorimotor learning (Del Giudice et al., 2009; Keysers & Gazzola, 2014), or the epigenetic account proposes that a rudimentary facial mirror system is present at birth and that experience modulates genetic expression (Ferrari et al., 2013). This idea is therefore in keeping with the general consensus in the literature that experience is vital for further development or refinement of mirror systems. However, it is possible that the facial and manual mirror system develop somewhat differently (they clearly involve some different areas of the brain), with the former perhaps relying more on sensorimotor learning, and thus developing more slowly, whereas the facial mirror system might be present in some basic form at birth (Ferrari et al., 2012; Vanderwert et al., 2015), but matures and become refined by experience after birth (Casile et al., 2011; Vanderwert et al., 2015).

The EEG studies with infant macaques certainly suggest that there could be a basic mechanism mapping between own and other facial expressions at birth (Ferrari et al., 2012; Vanderwert et al., 2015), and thus it seems fair to assume that this might be true in human infants as well. Further in support of a rudimentary mirror system at birth, lack of experience with facial stimuli does not seem to impede recognition and discrimination of facial stimuli in macaques (Sugita, 2008), indicating that the basic mechanisms of face processing are at least somewhat independent and potentially prewired (Casile et al., 2011), and human infants are also sensitive to facial stimuli from birth (Mondloch et al., 1999; Valenza et al., 1996). The human brain of course contains specialized regions for face processing (Haxby et al., 2000; Kanwisher et al., 1997), which use domain-specific visual mechanisms (Carmel & Bentin, 2002; Kanwisher & Moscovitch, 2000). Therefore, one possible idea is that genetic influences might guide mirror system development by providing coarse-grained connections between visual brain areas specialized for face processing and motor areas involved in controlling facial muscles at birth (Ball et al., 2014; van den Heuvel et al., 2015). These crude connections could also clarify why neonates may have the ability to produce very basic adult facial gestures, but not more complex ones that might require fine-grained connections between specific neural subpopulations, gained through experience.

4.1.2.1 ***Maternal mirroring during early interactions and potential influence of infant mirror system development***

In infancy, the brain is generally considered to be at its most plastic (Johnson, 2001; Kolb & Gibb, 2011), and hence this is the time in which neural development is most susceptible (both positively and negatively) to the influence of the environment (Huttenlocher, 2002). The infant environment is comprised predominantly of face-to-face interactions with a primary caregiver (Murray, 1992), most often the mother, with an abundance of animal and human research attesting to the importance of early interaction quality for offspring development (Feldman & Eidelman, 2009; Kaffman & Meaney, 2007; Murray et al., 2011; Murray, Halligan, & Cooper, 2010). Indeed, disturbed early interactions are associated with poor child outcomes in both typical and atypical infant populations (Murray et al., 2008, 2011, 2010; Schmid et al., 2011), with even slight individual differences in maternal responses, which are to be expected (e.g. due to socio-cultural beliefs and expectations), having an impact on infant outcomes (Bigelow & Walden, 2009; Richman, Miller, & LeVine, 1992). This highlights the fundamental role played by early mother-infant interactions and the importance of such social experience for healthy child development.

Mother-infant dyads participate in complex and affectively rich social interactions from early on postpartum (Feldman, 2007; Gergely & Watson, 1996; Lavelli & Fogel, 2013; Tronick, 1989; Tronick & Cohn, 1989), with infants regularly directing a wide range of expressions towards the mother (Messinger, 2002). In the very first weeks, although infants appear sensitive to social stimuli such as faces, and parents intuitively respond to their infant in a social manner (e.g. if the infant makes eye contact, parents tend to make a clear greeting signal and exaggerated facial expression in response) infants do not play a very active role in face-to-face engagements. This changes at around 2 months of age, with the shift in infant social behaviour at this time often referred to as the beginnings of ‘primary intersubjectivity’ (Trevarthen & Aitken, 2001). For example, over the next couple of months, infants start to actively seek eye contact, and increasingly often, follow these looks to the caregiver with smiles, vocalizations, and more deliberate ‘pre-speech’ mouth movements. In terms of the mother's behaviour, mirroring/imitation of the infant is one type of response typically made during this early period. This refers to the marking of an infant's behaviour by means of its reproduction, reflecting back to the infant that particular behaviour (Gergely & Watson, 1999). This matching is often performed by the mother in a somewhat exaggerated manner (Bigelow & Walden, 2009; Stern, 1985; Trevarthen, 1985), such as in intensity and/or affect. For example, during a face-to-face interaction, if an infant opens their mouth the mother might immediately reproduce that action, but in doing so, extend the movement, and thus make it more noticeable to the infant (Gergely & Watson, 1999).

Mirroring is widely thought to represent a particularly enriching experience for infants during early interactions (Murray, 1989; Winnicott, 1967), and is proposed to facilitate the development of social expectations and more advanced social cognition (Gergely & Watson, 1996; Meltzoff & Moore, 1997). Others believe that mirroring may be no different from other examples of contingent responding (Moran, Krupka, Tutton, & Symons, 1987), however, research has shown that infants seem to respond differently to an adult who imitates them, compared to one who performs non-imitative but contingent actions (e.g. Meltzoff, 1990; see Nadel, 2002 for review). Of course, maternal mirroring is not the only type of response mothers can make during a social exchange with their infant. For instance, mothers often respond to their infant with other marking-type behaviours that are not imitative, but are still clear, expressive, events that draw attention to certain actions and affirm them (e.g. a strong smile in response to an infant's tongue protrusion, accompanied by a nod of the head, raised eyebrows, and a positive vocalization). However, as this chapter concerns how mothers may facilitate development of a facial mirror system via mirroring of infant expressions, this will be the response type focused on.

In the words of Winnicott, when an infant observes his/her mother mirroring their facial expressions, "what the baby sees is himself or herself", and when a mother looks at her baby, "what she looks like is related to what she sees there" (Winnicott, 1967, p. 131). This description fits well with the idea of mothers serving as biological mirrors for their infants, which could facilitate the strengthening of visual-motor couplings for opaque actions (Del Giudice et al., 2009). As noted before, this idea has been incorporated into many theories of mirror system development (e.g. Del Giudice et al., 2009; Ferrari et al., 2013; Heyes, 2001; Quadrelli & Turati, 2016), despite the fact that genetics is suggested to play slightly different roles in each.

During naturalistic face-to-face interactions, mothers indeed often try to shape social exchanges with their infants through inclusion of salient and fervent imitation episodes (Užgiris, Benson, Kruper, & Vasek, 1989), particularly in the form of facial or vocal mirroring during the first year of life (Gergely & Watson, 1999). Instances of imitation by mothers or infants have been shown to occur around once a minute during interactions between 4 and 10 months postpartum (Masur & Rodemaker, 1999; Pawlby, 1977), however, nearly all of these imitations (around 80%) are performed by the mother. Therefore, even though there is evidence that infants can imitate certain facial expressions from a very early age (or even from birth), research involving naturalistic interactions suggests that mothers imitate their infants much more than vice versa (Nadel & Butterworth, 1999; Užgiris et al., 1989).

In fact, Uzgiris et al. (1989) demonstrated that in early infancy, mothers were about five times as likely to imitate their infant as the infant was to imitate them, with a decrease in this proportion not occurring until towards the end of the year postpartum. Moreover, mothers appear to frequently search for opportunities to incorporate their infant’s behaviour in imitative exchanges. That is, when an infant is involved in repetitive facial play (e.g. body or vocal), mothers attempt to reproduce the infant’s action, which increases the opportunities for infants to concurrently act and observe an action (Pawlby, 1977). Mothers also seem to exploit opportunities to imitate their offspring more and more often as infants begin to increase their production of certain actions, and as infants are able execute a greater variety of actions with age (Flynn, Masur, & Eichorst, 2004; Užgiris et al., 1989).

Mothers seem particularly likely to mirror infant behaviours that are potentially communicative (Moran et al., 1987; Pawlby, 1977), such as smiles and vocalisations. For example, mothers have been found to produce more contingent imitations to infant’s emotional displays rather than random movements, such as twitches (Malatesta, Culver, Tesman, & Shepard, 1989; Malatesta & Izard, 1984). Other studies have also shown that mothers also mirror expressions reminiscent of sadness and anger (Tronick, 1989), with maternal responses to negative displays including mock expressions of negative affect (Malatesta & Izard, 1984). During interactions at 3 to 6 months postpartum, mothers respond to around 35% of infant’s emotional expressions with an imitation (Malatesta & Haviland, 1982)). Around a fifth of maternal responses to infant vocalisations at 10 months postpartum are also imitative (Masur & Olson, 2008), with infants found to be very responsive to such behaviours (e.g. responding to an imitation with a vocalisation or smile around 90% of the time; Masur & Olson, 2008).

Infants around 3 months of age have been found to look longer at their mothers, and to produce more smiles and vocalizations (Field, Guy, & Umbel, 1985; Striano, Henning, & Stahl, 2005), when mothers are instructed to mirror them compared to interacting naturally. Four-month-olds have also been found to engage more within a social interaction if their mothers mirrored them (Bigelow & Walden, 2009). In this study, infants were able to discriminate between live and replayed maternal interactions, whereas infants whose mothers did not mirror could not. The authors interpreted this as likely because maternal mirroring improves the infant's ability to detect reciprocity or contingency in turn-taking exchanges (Bigelow & Walden, 2009). Maternal mirroring of pre-verbal vocalisations has also been shown to aid an infant's linguistic development (e.g. Pelaez, Virués-Ortega, & Gewirtz, 2015; Tamis-LeMonda, Bornstein, & Baumwell, 2001), with a potential mechanism for mirroring in 'scaffolding' (Bruner, 1977) language development suggested via the guiding infant vowel prototypes to become clear vowels (Ishihara, Yoshikawa, Miura, & Asada, 2009).

One possibility is that maternal mirroring highlights an infant's own generation of the imitated action, which increases the infant's attention and awareness of their behaviour (Masur, 1987; Masur & Rodemaker, 1999; Užgiris, 1991). It has been proposed that imitation recognition (i.e. the awareness that one has been imitated, as indexed by an infant's responses) aids the development of understanding that others have mental states just as oneself does. That is, the temporal responsiveness of maternal mirroring is suggested to aid the infant in sensing the relation between their own behaviour and that of the mother (Neisser, 1993). In terms of emotional expressions, the marked nature often seen with maternal mirroring responses (e.g. exaggeration of an infant's behaviour) has been proposed to enable infants to associate those expressions with their own emotional states, but also to differentiate the mother's experience from their own (Gergely & Watson, 1999). In fact, the emergence of understanding that others are 'like me', hypothesized by Meltzoff and colleagues to provide a basis for development of more complex social-cognitive skills such as theory of mind (Meltzoff, 1996, 2002; Meltzoff & Decety, 2003), is suggested to be facilitated by maternal mirroring; with neonatal imitation also indicating that a basic mirror system could be in place, aiding the mapping between own and other actions from early on in life.

If maternal mirroring does highlight the infant's behaviour, it can be supposed this would be highly salient to the infant, thus eliciting changes in their reactions. Some research has shown that infant responses to being imitated as early as 2 months include increased looking and smiling (Nadel, 2002). Meltzoff (1990) also demonstrated that infants at 14 months smiled and gazed more at an adult who imitated their actions than one who performed non-imitative contingent actions. Such findings suggest that infants are particularly sensitive to the observation of other's actions that match their own. Currently, it is unclear at which cognitive level an infant might 'recognize' that they are being imitated. For example, it could be that, early on, this merely reflects a capacity to identify structural and temporal contingencies, with attribution of any imitative intentionality not necessary.

Some claim that if maternal mirroring strengthens the mapping between own and other executed actions (i.e. is involved in development and/or refinement of a mirror system) this should also be linked to more competent imitations skills demonstrated by infants themselves (Catmur, Walsh, & Heyes, 2009; Ray & Heyes, 2011). In support of this, a genetic twin study found that the largest source of variance (nearly half) when accounting for individual differences in imitation ability was related to the shared environment (McEwen et al., 2007). The rest of the variance was due to differences unique to each twin and genetic influence, which was around one quarter each. This was suggested to imply that differences in imitation ability are largely dependent on the degree to which infants have been imitated in early development (McEwen et al., 2007), although no measure of this was made in the study. A study by Masur (1987) also supports this idea, demonstrating that around 1 year postpartum, more imitative infants have the most imitative mothers. Research clearly demonstrates that infants exposed to atypical early interactions, such as in the context of postnatal depression or anxiety, demonstrate adverse developmental outcomes, and that this effect might be mediated by differences in maternal imitation. Indeed, Field et al. (2005) showed that in the case of comorbid depression, mothers who were highly anxious and angry spent less time imitating their infants, and that their infants also imitated them less. However, it should be noted that this type of imitation seen later in infancy is not necessarily the same as neonatal imitation; i.e. at birth, the matching of own and other facial expressions could rely on a very basic mirror system, whereas later on, imitation involves a more mature version of the system. For example, it could be that although a mirror system is very rudimentary at birth (neonates imitate only very simple and restricted expressions), this basic system means that infants have a 'mental readiness' to detect another's equivalent behaviour when someone imitates them. Thus maternal mirroring may echo what the infant is predisposed to expect, providing a direct connection between own and other actions (Murray, 2014).

Though no human studies have been conducted, one study with infant monkeys provides support for the hypothesis that early experience with caregivers influences the development of a facial mirror system. Vanderwert et al., (2015) used EEG to record the neural activity of two groups of infant macaques as they executed and observed facial gestures (e.g. lip-smacking). One of these groups had been reared with their biological mothers, but the other group had been reared separated from their mothers at birth. Like humans, macaques have an extended period of maternal care, and engage in complex mother-infant interactions, including mutual gaze, "motherese", and facial mirroring (Ferrari et al., 2009). In particular lip-smacking exchanges are often seen between macaque mothers and their infants, frequently in an exaggerated form by the mothers (Ferrari et al., 2009). Therefore in the Vanderwert et al. study, one group of infants had received the opportunity to experience facial gestures produced by their mother, but the other group did not. The group that had been reared by their biological mothers demonstrated greater mu desynchronization during observation of lip smacking compared to the other group, which suggests that early social experience had a significant impact on a mechanism for mapping own- and other-generated facial gestures. Whether differences in the early environment could also influence a human mirror system now needs to be explored. This could be done, for example, via investigation of natural variations in mothers' tendency to mirror, or by comparing a typical group of mother-infant dyads with one in which interactions are likely disturbed (e.g. in the case of postnatal depression).

4.1.3 THE CURRENT STUDY

In this study, EEG was used to record mu desynchronization as 9-month-old infants observed and executed both emotional (happy, sad) and non-emotional (mouth opening) facial expressions. A scrambled control condition was also included to explore the specificity of effects. At 2 months postpartum, the infants who took part in the 9 month EEG experiment had been observed interacting face-to-face with their mothers for 3 minutes. Videos of these interactions were coded on a second-by-second basis, and instances of maternal imitation of facial expressions noted. Measures of maternal imitation were then related to the degree of mu desynchronization at 9 months in order to test the hypothesis that greater experience of being imitated would result in greater mu desynchronization; i.e. putative mirror system activity. Note, the coding of infant expressions at 2 months included the identification of expressions equivalent to those presented in the 9 month EEG experiment. Therefore, any influence of maternal mirroring of specific expressions on infant neural activity during observation of those particular expressions could be considered, rather than just a generic, positive influence of maternal mirroring.

4.2 METHODS

4.2.1 RECRUITMENT AND PARTICIPANTS

34 healthy infants (19 male, 15 female) took part in the EEG experiment at approximately 9 months postpartum. Mother-infant dyads were recruited from the 'Child Development Database' housed in the School of Psychology and Clinical Language Sciences, at the University of Reading. Nine infants were excluded before analysis due to fussiness during the EEG net placement or experiment (N = 7), or technical problems (N = 2). This left a sample of 25 infants; however, after pre-processing of the EEG data, a minimum of five trials per condition during observation was also required for an infant to be included in any analyses (in keeping with other infant mu rhythm studies: e.g. Cannon et al., 2016; Marshall et al., 2011; Saby et al., 2012). Therefore, the final sample was made up of 19 infants (age: M = 275.42 days, SD= 7.88), with this loss of data comparable to that of other EEG studies that have investigated the infant mu rhythm (Cannon et al., 2016; Saby et al., 2012; Southgate et al., 2009). The 19 infants included had all previously been recorded interacting with their mothers at 2 months postpartum (age: M = 63.58 days, SD = 3.75). This research was approved by the University of Reading Research Ethics Committee (31.07.14), and mothers gave written, informed consent before participation. More information regarding recruitment and participants can be found in Chapter 3.

4.2.2 MOTHER-INFANT FACE-TO-FACE INTERACTIONS AT 2 MONTHS POSTPARTUM

4.2.2.1 Interaction periods: Design, procedure, and coding

Mothers were visited by a researcher at home when infants were aged around 2 months, and were asked to interact face-to-face with their infant for 3 minutes. During this interaction period, infants were placed on a semi-reclined changing mat, with mothers seated opposite them on the floor. A camera was positioned to capture a full-on view of the infant's face, as well as a side-view of the mother. Two mirrors were also utilized, one behind infants to capture a full-on view of the mother's face, and one next to the infant in case they turned away from the camera (see Figure 4.1 for an example of this set-up).

Figure 4.1: Example of the mother-infant interaction set-up at 2 months postpartum

The coding scheme used to identify instances of maternal mirroring was based on that of Murray and colleagues (Murray, Fiori-Cowley, Hooper, & Cooper, 1996; Stanley, Murray, & Stein, 2004: modified for the purpose of a current series of studies by Murray, L., Hawkins, L., & Bozicevic, L.), with videos coded on a 1 second time base using purpose built software (developed by Leonardo De Pascalis) for identifying associations between maternal and infant behaviours. This coding scheme identifies infant and maternal events that take place during social interactions in the first 9 weeks postpartum, based on the literature concerning early infant social development and early mother-infant engagement (e.g. Stern, 1985; Trevarthen, 1979). A number of infant behaviours are identified in this scheme, including vocalizations and facial expressions, with facial expressions the behaviour of interest in the present study. The infant facial expressions coded in this scheme include an equivalent of each expression included in the 9 month EEG experiment (mouth opening, happy, sad), as well as other facial movements, as follows: tongue protrusion, mouth opening, active movements of the lips and tongue, raised brow, smiles, non-social mouth movements (e.g., chewing or sucking), and negative expressions (cry face, negative mouth, and negative eyes) (Lavelli & Fogel, 2002, 2005; Messinger, 2002; Oster, Hegley, & Nagel, 1992; Trevarthen, 1979). A number of maternal responses to infant behaviours are also identified in this scheme, including maternal mirroring. ‘Mirroring’ here is defined as a maternal response that is an exact match of the infant’s behaviour, or a match of the main features with some minor modification; this could be an additional feature added to a direct match (e.g. a vocalisation to a clear mouth opening), the omission of some element (e.g. mirroring the facial expression of a cry but without sound), or slightly changing its form (e.g., responding to an infant ‘ooo’ vocalization with ‘goo’). Further details about this coding scheme can be found in Appendix B, section 9.2 and see Figure 4.2 for some mirroring examples.

Figure 4.2: Some examples of maternal mirroring of infant facial expressions during the 2 month interactions

All interaction videos were coded by a research assistant blind to experimental hypotheses. This researcher has already been established as reliable using this coding scheme; i.e. in another study, this individual and a second independent researcher coded a random 20% of a sample of mother-infant interaction videos (which involved the same set-up and infant age as the current study), with very good reliability scores obtained (infant events $\kappa = 0.90$; maternal events $\kappa = 0.83$).

4.2.2.2 Linking the interaction and EEG data

In Table 4.1, descriptive statistics are given concerning the proportion of infant facial expressions mirrored overall (number of maternal mirroring responses to any infant facial expression/number of infant facial expressions performed), the total proportion of maternal responses to infant facial expressions that were mirrored (number of mirroring responses to any infant facial expression/number of maternal responses of any kind to infant facial expressions), and the proportion of expressions included in the 9 month EEG experiment that were mirrored by mothers (mouth opening, smiles, negative expressions: number of maternal mirroring responses to a specific expression/number of times infant produced that specific expression).

Examination of responses to the different infant facial expressions revealed clear bi-modal distributions in each case, with mothers falling naturally into one of two groups in terms of how often they mirrored infant mouth opening and smiles (see histograms in Figure 4.3). Note, only two mothers ever mirrored an infant's negative expressions, so this behaviour was not considered when grouping the mothers or in the analyses of specific expressions. Additional histograms concerning maternal mirroring of negative expressions and more generally can be found in Appendix C, section 10.2, as well information concerning maternal mirroring of other infant expressions in Appendix C, section 10.3. Therefore, based on how often mothers mirrored mouth opening and smiles, if their infant had produced either of these expressions, dyads were split separately into two groups for analysis of how mirroring smiles and mouth opening related specifically to infant mu ERD during observation of these expressions later on. In accordance these groups were labelled as 'low mirroring' or 'high mirroring'. For mouth opening, there were 8 dyads included in the low group and 7 in the high; and for smiles, 10 in the low and 6 in the high mirroring group. Although it is not always ideal to dichotomize variables in such a way (e.g. if distributions were normal), considering the distribution of data points and the novel nature of this study, such an approach is appropriate here. Indeed, this type of group division is used very widely in the literature concerning links between maternal responses during early interactions and infant development (e.g. Field et al., 2005; Hofer, Hohenberger, Hauf, & Aschersleben, 2008; Legerstee & Varghese, 2001; Markova & Legerstee, 2006). These include studies about how often mothers imitate their infants during early social exchanges, where typically mothers have been found to fall into high and low groups (Bigelow & Walden, 2009; Field et al., 2005; Legerstee & Varghese, 2001; Wörmann, Holodynski, Kärtner, & Keller, 2012), and in the monkey literature (Ferrari et al., 2009; Paukner, Simpson, Ferrari, Mrozek, & Suomi, 2014; Simpson, Paukner, Suomi, & Ferrari, 2014), where such divisions are often used due to the nature of data available (e.g. to divide infant imitators and non-imitators of facial gestures for comparison).

Table 4.1: Means and standard deviations (SD) for maternal mirroring measures

	Mean (SD)
Percentage of all infant facial expressions mirrored	14.86% (11.99)
Percentage of mirroring responses (out of all response types) to infant facial expressions	73.35% (29.72)
Percentage of mouth openings mirrored	27.58% (24.24)
Percentage of smiles mirrored	55.49% (37.98)
Percentage of negative expressions mirrored	6.29% (19.27)

To test the hypothesis that more maternal mirroring of specific infant expressions would lead to greater mu desynchronization during observation of those expressions, and that greater mirroring of emotional expressions would also lead to more right lateralized desynchronization, differences between the two groups (i.e. low and high mirroring groups) were examined in the following analyses. Additionally, analyses were run to investigate whether there was a more generic relationship between early maternal mirroring and putative mirror system activity. In these analyses, the relationship between the proportion of all infant facial expressions mirrored by mothers and mu ERD overall in the happy, sad, and mouth opening conditions combined was investigated, as was the relationship between mu ERD in these conditions overall and the proportion of maternal responses to infant facial expressions that were mirrored.

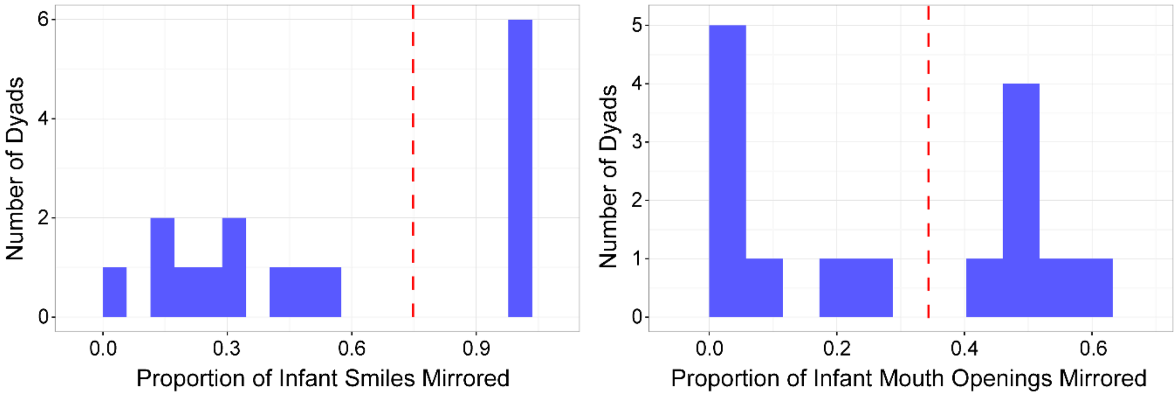

Figure 4.3: Proportion of infant smiles and mouth opening mirrored by mothers during face-to-face interactions at 2months postpartum. Mothers clearly fell naturally into high and low mirroring groups, with dotted lines designating where groups were split.

4.2.3 EEG EXPERIMENT AT 9 MONTHS POSTPARTUM

4.2.3.1 EEG Stimuli

The stimuli used were the same as in the EEG experiment presented in Chapter 2. To reiterate, these stimuli consisted of short videos (2.5s) of female actors executing various facial expressions, making up a total of four experimental conditions: a positive condition, 'happy'; a negative condition, 'sad'; a non-emotional condition, 'mouth opening'; and a control condition consisting of scrambled versions of the other videos (i.e. a version of each happy, sad and mouth opening video, whereby the face was split into a set of block regions which were randomly rearranged). As stated in Chapter 2, although previous studies have utilized static or non-biological moving stimuli in control conditions (Ferrari et al., 2012), these cannot control for both low-level visual features and overall movement across all experimental conditions. The scrambled control included used here instead controls for both these things. The videos featuring positive and negative facial expressions were taken from the Amsterdam Dynamic Facial Expression Set (ADFES), which has been well validated in previous research (van der Schalk et al., 2011). Ratings of the mouth-opening videos on a scale of -2 (negative) to +2 (positive) by a panel of 20 adults confirmed that they represented non-emotional facial expressions (M = -0.10, SD = 0.07). These videos were made comparable with the ADFES stimuli in terms of onset, duration of movement, size, brightness, contrast, and spatial frequency. All videos started with a static/neutral facial expression, followed by 500ms of movement, and 1250ms held at the movement peak (Figure 4.4).

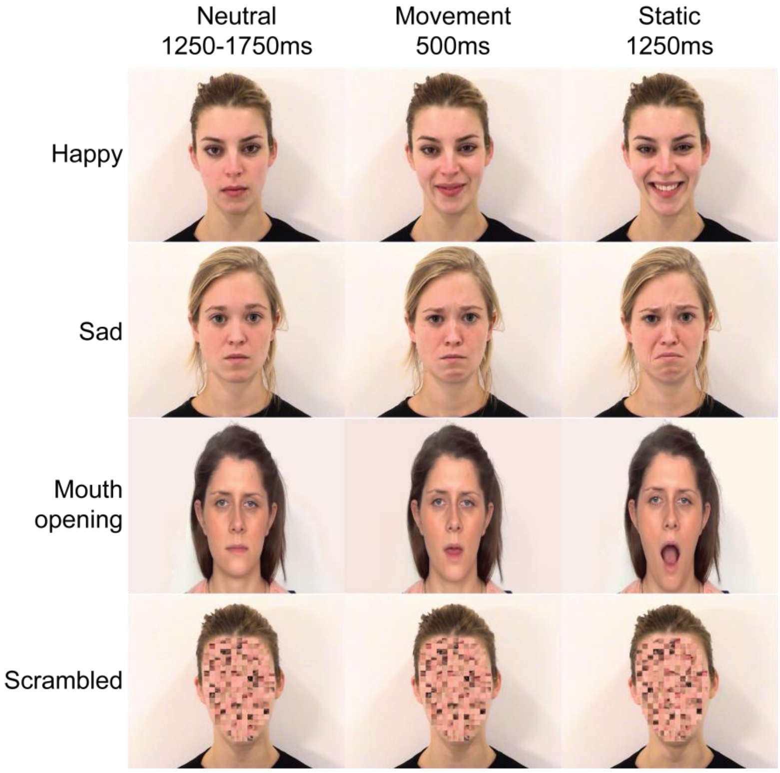

Figure 4.4: Time-course of stimuli in the four experimental conditions. Each condition included an initial, static neutral expression, followed by a facial movement which lasted approximately 500ms. After the movement peak, the expression was held for 1250ms.

4.2.3.2 EEG: Design and procedure

On arrival, infants were given time to settle into the environment and become comfortable with the two experimenters present (one of whom was the current author). When settled, an experimenter measured the infant's head and selected the correctly sized EEG net for preparation. When the net was ready, infants were taken into the testing area and seated on their mother's lap approximately 65cm from a computer monitor. An experimenter was available to help distract and/or pacify the infant if they became fussy during net placement, or attempted to touch the net once in place. Any fussiness caused by net placement receded quickly for most infants, however, whether to continue with the experiment was left to the mother's discretion. Mothers were asked to remain as still as possible and to not interact with their infant during the experiment.

Experimental stimuli were presented on the monitor using PsychoPy v1.80.04 (Peirce, 2008) in blocks of 4 video clips, one of each condition (i.e. one happy, sad, mouth opening, and scrambled per block; 2 actors per condition). These clips were randomized within blocks, and blocks themselves were pseudo-randomized so that the same condition could not be presented more than twice in succession. The inter-stimulus interval was randomized between 500 and 750ms, and the start of the movement was randomized between 1250 and 1750ms after the onset of the static face. Between blocks, moving shapes/patterns accompanied by sounds were presented to maintain infant attention, also presented in a randomized order. The experiment was terminated if the infant became too inattentive, distressed, moved excessively, or after 25 experimental blocks had been presented.

4.2.3.3 Acquisition of EEG data

EEG was recorded using a 128-channel Hydrocel Geodesic Sensor Net (EGI, Corp., Eugene, OR). After measuring the infant's head and choosing the correctly sized net, the entire net was soaked in an electrolyte solution to increase conduction between electrodes and the scalp. When the net was ready, it was fitted on the infant's head and plugged into an amplifier. Data were sampled at 250 Hz with an analogue band-pass filter of 0.1–100 Hz, and were recorded with the vertex as a common reference. Impedances were measured before beginning the experiment, and were kept below 50 kΩ, as far as possible. The stimulus presentation script included event triggers at appropriate points of each trial (block onset, trial onset, video onset/offset, and block offset), which were sent via an Ethernet connection to the data acquisition computer. This enabled data to be segmented offline into epochs based on the timing of events during each trial. The PsychoPy script also sent trigger signals specifying the type of movement being shown in each video so that the trial type could also be determined from the data files. An experimental block began when triggered manually by an experimenter who was watching the participant on a screen from another section of the room. Trial blocks were triggered as soon as the infant was attentive to the monitor. Synchronous video recordings of the experiment were also examined offline to allow exclusion of trials in which the infant was inattentive, and to enable execution of facial expressions to be coded.

4.2.3.4 Coding of infant facial expressions during EEG experiment

In order to identify trials in which participants executed the facial expressions presented during experimental blocks, expressions (happy, sad and mouth opening) were coded offline from the video recordings using the same procedure as in Chapter 2 (see section 2.3.5. and Appendix B, section 9.1 for more details). Again, all videos were coded by a research assistant blind to the experimental condition being presented. Videos were viewed in real-time and frame-by-frame to accurately identify onsets and offsets of movements. A second independent researcher coded a random 20% of the videos to establish inter-rater reliability, with very good reliability obtained (time-unit κ = .85-.86, event κ =.92).

*4.2.3.5 **Pre-processing and analysis of EEG data***

EEG was recorded using a 128-channel Hydrocel Geodesic Sensor Net (EGI, Corp., Eugene, OR). Data were sampled at 250 Hz with an analogue band-pass filter of 0.1–100 Hz, and were recorded with the vertex as a common reference. Impedances were kept below 50 kΩ. After viewing the video recordings of infants during the experiment and marking periods of inattention using EGI software (NetStation v4.3.1; Electrical Geodesics, Inc., Eugene, OR), EEG data were exported and analysed using the EEGLAB v13.3.2 toolbox (Delorme & Makeig, 2004). The PREP pipeline toolbox was used to identify and interpolate noisy channels, as well as to apply robust average re-referencing (Bigdely-Shamlo, Mullen, Kothe, Su, & Robbins, 2015). Data were then bandpass filtered at 2-35 Hz. Epochs ranging from 1s before the onset of the adult facial expression to 2s after the start of the movement were extracted. Epochs that contained previously marked periods of inattention and epochs in which more than 15% of channels exceeded +/- 250µV were excluded. A natural-gradient logistic infomax independent component analysis (ICA) was performed on the data (the runica algorithm; Delorme & Makeig, 2004) to decompose the EEG mixed signals into their underlying neural and artefactual components (such as eye and muscle movements). Artefact components were identified and removed using the ADJUST algorithm (v1.1; Mognon et al., 2011), as well as by applying a rejection threshold to the entropy of the activity of each component over all trials (8580), the kurtosis of the activity (82), as well as the kurtosis of the component’s spatial map (9.8; Delorme, Makeig, & Sejnowski, 2001).

To compare power relative to baseline in the mu band, event related spectrums (ERSs) were computed for each condition using built-in EEGLAB procedures. Time-frequency decompositions were computed with a fast Fourier transform using a 1-second Hanning window with 50% overlap in 1Hz bins from 2-35Hz. To make results comparable with those of other studies, log spectral power was converted to absolute power, and averaged across the 6-9Hz bins (corresponding to the mu range typically used in research with infants at this age: e.g. Cannon et al., 2016; Marshall et al., 2002; Nyström, 2008; Nyström et al., 2011; Saby et al., 2012). Event-related desynchronization (ERD) was then computed as the percentage change of the average absolute power over a 0-750ms time window (from the onset of facial movement in experimental stimuli until 250ms after the peak of the full expression) from the condition-specific baseline averaged over -650ms to -50ms (prior to the onset of the observed facial movement; Pfurtscheller & Aranibar, 1979).

As in Chapter 2, ERD was calculated for four clusters of electrodes. These were comprised of two central clusters (left and right hemisphere) located around standard C3 and C4 sites for mu rhythm recording, and two occipital clusters (left and right hemisphere) located around standard O1 and O2 sites to control for visual alpha responses (Figure 4.5; Umiltà, Berchio, Sestito, Freedberg, & Gallese, 2012). For each cluster, in each experimental condition, the ERD values were calculated for each subject.

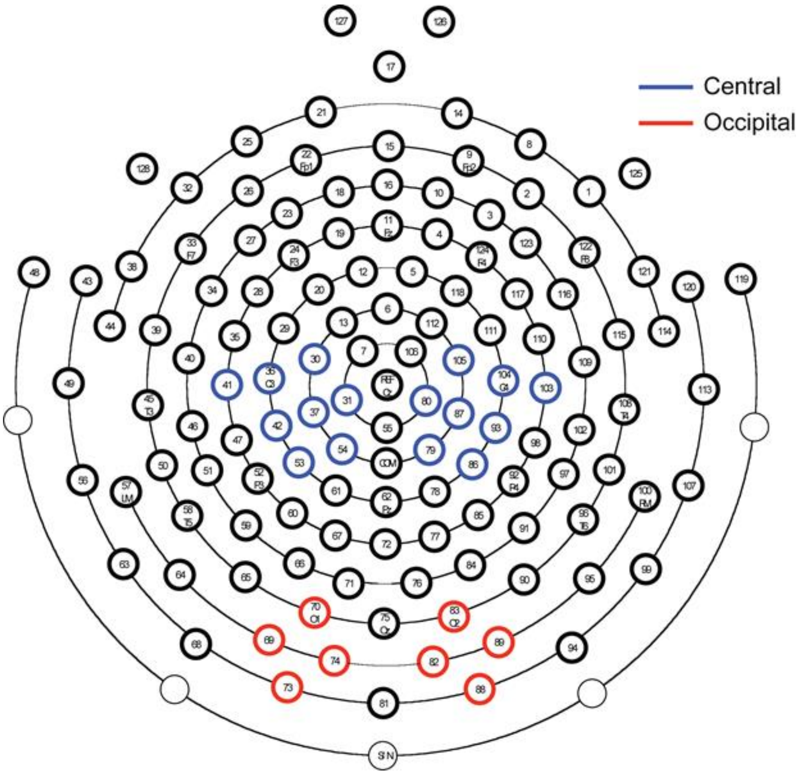

Figure 4.5: Location of channels included in the central (blue) and occipital (red) clusters.

4.2.4 QUESTIONNAIRES

At the 2 month assessment, mothers completed a demographics questionnaire and the 'Edinburgh Postnatal Depression Scale' (EPDS), and at the 9 month assessment, the 'Ages and Stages Questionnaire' (ASQ-3) in order to eliminate the possibility that these variables influenced putative mirror system responses. More detail on these questionnaires can be found in Chapter 3.

EPDS scores were compared between ‘low’ and ‘high’ maternal mirroring groups, as postnatal depression has been shown consistently in the literature to impact maternal responses during early interactions (e.g. Cohn, Campbell, Matias, & Hopkins, 1990; Field, 2010; Field et al., 2005; Murray et al., 1996, 2010). Additionally, even though the demographics questionnaire revealed a largely homogenous sample overall (see Section 3.6), as dyads were split into two groups for analysis of specific expressions here, potential differences were also investigated between the two (e.g. infant birth weight, gender, maternal education level); which could have also influenced early interactions (De Falco et al., 2014). Finally, relationships between the ASQ-3 scales (with those concerning motor development of particular interest here) and overall infant mu desynchronization during facial expression observation were examined in order to eliminate the possibility that these variables influenced putative mirror system responses.

Note, t-tests, Mann-Whitney tests, Pearson's Chi Square tests, and Fisher's Exact tests were used to investigate any differences between ‘low’ and ‘high’ mirroring groups, and Pearson’s or Kendall’s tau for any relationships with mu ERD. This depended on whether variables were normally distributed.

4.3 RESULTS

Below, findings from the 9 month EEG experiment will be presented first, followed by the results from the analysis comparing differences in mu desynchronization between infants with high and low mirroring mothers. In the next two sections, which concern infant mu desynchronization during observation and execution of facial expressions in the EEG experiment, the α-level was set at 0.05 and all post-hoc tests were Bonferroni corrected. The Greenhouse-Geisser correction of degrees of freedom was used when the sphericity assumption was violated (indicated by ε).

4.3.1 EEG: OBSERVATION TRIALS

To investigate changes in mu power during observation of experimental stimuli, trials marked during behavioural coding as containing execution of happy or sad expressions, or mouth opening movements were excluded. A minimum of 5 trials per condition was required for infants to be included in the analysis, which is in keeping with other research (e.g. Cannon et al., 2016). This left a total of 19 participants with an average of 34.21 trials (SD=13.66) overall (mouth opening, M = 8.63, SD = 3.93; happy, M = 8.05, SD = 3.64; sad, M = 8.84, SD = 3.24; scrambled, M = 8.68, SD = 4.14). Before comparing conditions and clusters to each other, mu power during each condition in each cluster was compared to the baseline period. Significant mu desynchronization was found in the left central cluster for mouth opening [M = -10.63, SD = 4.40; *t*(18) = -10.54, *p* < 0.0001] and sad expressions [M =-11.04 , SD = 4.95 ; *t*(18) = -9.73, *p* < 0.0001], but not for the happy or scrambled conditions [both *p* > 0.200]. In the right central cluster, there was significant mu desynchronization for mouth opening [M = -11.82, SD = 7.34; *t*(18) = -7.02, *p* < 0.0001], happy [M =-16.25 , SD = 8.01; *t*(18) = -8.84, *p* < 0.0001], and sad [M = -10.60, SD = 7.83; *t*(18) = -5.90, *p* < 0.0001] conditions, but again, not for the scrambled condition (p > 0.05). There was no significant mu desynchronization relative to baseline in either occipital cluster, for any condition (all *p* > 0.05). See Figure 4.6.

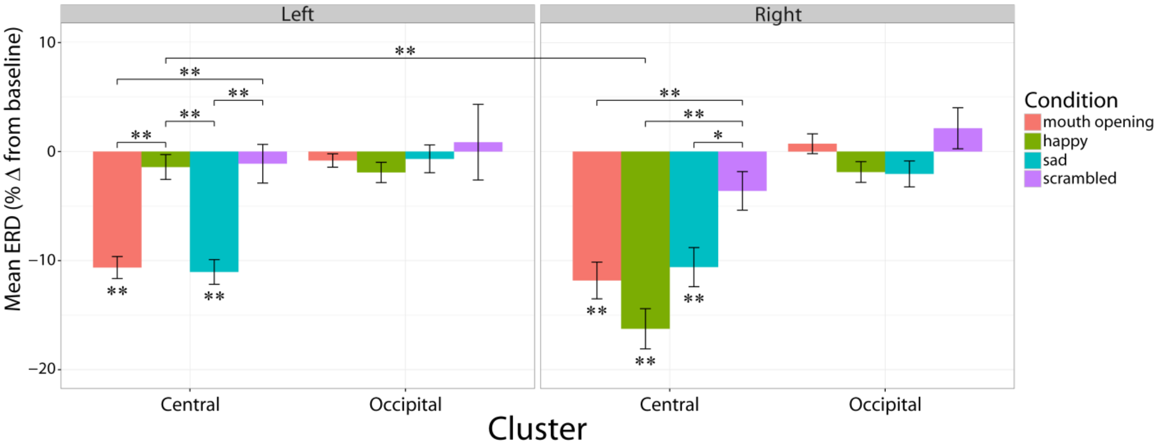

Figure 4.6: Mu ERD for each condition in central and occipital clusters. Error bars represent the mean +/− standard error, * p < 0.05, ** p < 0.005.

Having established the presence of mu desynchronization, a 2 × 2 × 4 repeated-measures ANOVA was conducted, with hemisphere (left/right), region (central/occipital), and condition (happy/sad/mouth opening/scrambled) as within-subject variables. The ANOVA revealed a significant main effect of hemisphere [*F*(1, 18) = 5.15, *p* = 0.04, η_p^2 = 0.22], region [*F*(1, 18) = 38.10, *p* < 0.0001, η_p^2 = 0.68] and condition [*F*(3, 54) = 27.05, *p* < 0.0001 η_p^2 = 0.60]. These results were qualified by significant hemisphere × region [*F*(1, 18) = 6.47, *p* = 0.02, η_p^2 = 0.26] and significant hemisphere × condition [*F*(3, 54) = 6.61, *p* = 0.001, η_p^2 = 0.27] interactions. A significant three-way hemisphere × regions × condition interaction [*F*(2.06, 37.13) = 5.25, *p* = 0.009, η_p^2 = 0.23, *ε* = 0.69] was also revealed, and was therefore followed up by conducting two separate repeated-measures ANOVAs for the two regions (central/occipital).

The analysis of central clusters (Figure 4.6) revealed significant main effects of both hemisphere [*F*(1, 18) = 16.85, *p* = 0.001, = 0.48] and condition [*F*(3, 54) = 15.59, *p* < 0.0001, η_p^2 = 0.46], and a significant hemisphere × condition interaction [*F*(3, 54) = 14.07, $p < 0.0001$, η_p^2 = 0.44]. Pairwise comparisons showed that mu ERD in the happy condition was significantly greater in the right compared to left hemisphere [*t*(18) = 6.38, $p < 0.0001$]. They also demonstrated that mu ERD in the left hemisphere, was significantly greater in the mouth opening condition compared to happy [*t*(18) = -5.91, p < 0.0001] and scrambled [*t*(18) = -5.09, $p < 0.0001$], and significantly greater in the sad condition compared to happy [*t*(18) = -6.33, $p < 0.0001$] and scrambled [*t*(18) = -4.75, $p < 0.005$]. In the right hemisphere, there was significantly greater mu ERD in all conditions compared to scrambled [mouth opening: *t*(18) = -5.03, $p < 0.005$; happy: *t*(18) = -4.93, $p < 0.005$; sad: *t*(18) = -3.25, $p < 0.03$].

The analysis of occipital clusters (Figure 4.6) revealed no significant main effects of hemisphere [*F*(1, 18) = 0.06, *p* = 0.81, η_p^2 = 0.003] or condition [*F*(1.97, 35.41) = 2.08, *p* = 0.14, η_p^2 = 0.10, *ε* = 0.66], and there was no significant hemisphere × condition interaction [*F*(1.51 , 27.12) = 0.34, *p* = 0.65, η_p^2 = 0.02, *ε* = 0.50]. This indicates that mu desynchronization was specific to central clusters and not due to changes in occipital alpha power.

4.3.2 EEG: EXECUTION TRIALS

To explore changes in the mu band while executing rather than observing facial expressions, separate analyses were conducted for participants who performed happy, sad or mouth opening expressions during the experiment. There were not enough instances of each expression to analyse separately; therefore execution was collapsed across expression type. This left 17 participants with a minimum of 3 execution trials each (M = 8.94, SD = 4.63); the required number for execution was lower than in Chapter 2 as infants tended to produce very few expressions, but is still in accordance with other research (e.g. Gerson, Bekkering, & Hunnius, 2015; Marshall et al., 2011; Saby et al., 2012).

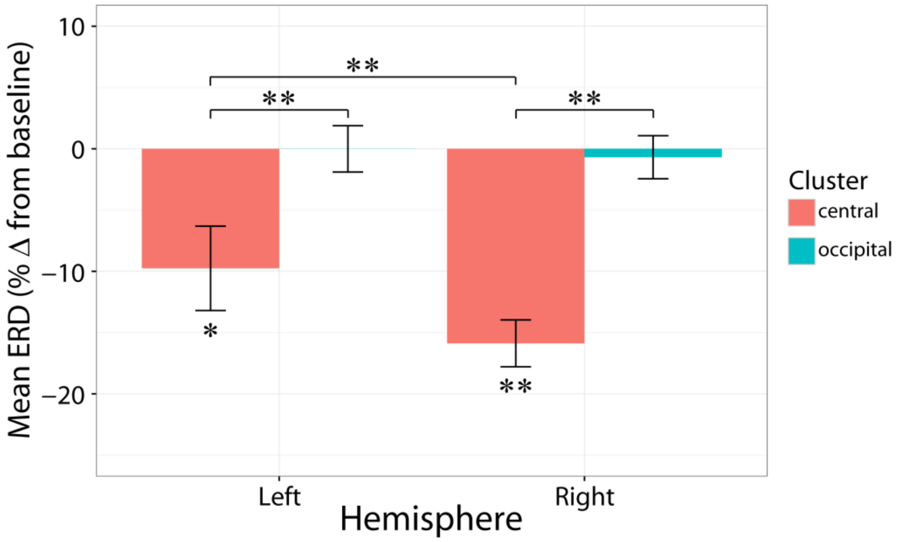

Figure 4.7: ERD in central and occipital clusters during movement execution. Error bars represent the mean +/− standard error, * p < 0.05, ** p < 0.005.

For the coded execution trials, significant mu desynchronization was found relative to baseline in the left central cluster [M = -9.76, SD = 3.44; *t*(16) = -2.84, *p* = 0.01] and the right central cluster [M = -15.88, SD = 1.91; *t*(16) = -8.30, *p* < 0.0001]. To explore differences in mu ERD during execution of facial expressions, a 2 × 2 repeated-measures ANOVA was conducted, with hemisphere (left/right) and region (central/occipital) as within-subject variables (Figure 4.7). The ANOVA revealed a significant main effect of region [*F*(1, 16) = 229.59, *p* < 0.0001, η_p^2 = 0.94], and a significant hemisphere × region interaction [*F*(1, 16) = 72.72, *p* < 0.0001, η_p^2 = 0.82]. Pairwise comparisons revealed significantly more mu ERD in the right compared to left hemisphere in the central regions [*t*(16) = 5.01, *p* < 0.0001], and there was significantly more mu ERD in both the left and right hemisphere for central compared to occipital regions [left: *t*(16) = -10.40, *p* < 0.0001; right: *t*(16)=-20.574, *p* < 0.0001].

4.3.3 INFLUENCE OF EARLY INTERACTIONS ON INFANT MU DESYNCRONIZATION

Before conducting analyses to investigate how maternal mirroring of specific expressions might influence mu ERD during observation of those expressions, linear models were used to investigate any generic relationship between mu ERD during observation of facial expressions and maternal mirroring of all expressions. Either the proportion of any infant facial expressions mirrored, or the proportion of maternal responses that were mirroring (in response to any infant facial expression), were included as predictors, with mu desynchronization averaged over hemisphere and the unscrambled conditions (mouth opening, happy, sad) as the dependent variable. Neither of these was found to be significant (both $p > 0.38$). This result is not surprising as mothers did not simply mirror infant expressions more or less often overall, but instead, mirrored particular expressions to varying degrees. In the case of mouth opening and smiles for example, dyads falling into a high or low group for one of these expressions did not necessarily fall into the same group for the other expression (e.g. mothers could have mirrored infant smiles very often, but not infant mouth opening). More details regarding the results from these general analyses can be found in Appendix C, section 10.4.

To investigate more specific effects, a linear mixed modelling framework was used to investigate the relationship between mu desynchronization in central clusters (left/right hemisphere) in the different observation conditions (mouth opening/happy) and early maternal mirroring of these expressions (low/high mirroring groups). The mothers were split separately for proportion of mouth opening and happy expressions they mirrored, with the group for each expression paired with central mu desynchronization in the corresponding experimental condition. A model with random subject-specific intercepts and hemisphere nested within subject was utilized, with condition, hemisphere, and maternal group (main effects and all interactions) as fixed effects. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. All *p* values were based on Kenward-Roger's corrected degrees of freedom, and all post-hoc tests (least-square means) were corrected for multiple comparisons using Tukey-Kramer contrasts. As noted previously, mu ERD during the observation of sad expressions was not included in the analysis as only two mothers in this sample mirrored negative infant expressions.

Significant main effects of condition [$F(1, 27.08) = 8.40$, $p = 0.007$], hemisphere [$F(1, 14.20) = 52.94$, $p < 0.0001$], and maternal group [$F(1, 37.94) = 5.14$, $p = 0.03$] were revealed. These results were qualified by significant condition × hemisphere [$F(1, 27.40)= 21.08$, $p < 0.0001$], hemisphere × maternal group [$\mathrm{F}(1.37, 37.27) = 6.09$, $p = 0.02$], and condition × hemisphere × maternal group [$F(1, 31.10)=7.31$, $p = 0.01$] interactions. This three-way interaction was followed up with planned pairwise comparisons. In the left hemisphere, there was significantly more mu desynchronization during the happy condition for those in the low compared to high mirroring group [$t(51.56) = 2.08$, $p = 0.04$], but significantly more during the mouth opening condition for the high compared to low mirroring group [$t(50.72) = -2.20$, $p = 0.03$]. In the right hemisphere, there was significantly more mu desynchronization during the happy condition in the high compared to low group [$t(51.56) =-2.64$, $p = 0.01$], and marginally so during the mouth opening condition in the high compared to low group [$t(50.72)= -1.98$, $\mathrm{p} = 0.053$]. See Figure 4.8.

Figure 4.8: Infant mu desynchronization during observation of mouth opening and happy conditions in the low and high maternal mirroring groups, in the left and right central clusters. Error bars represent the mean +/− standard error, * p < 0.05.

In order to confirm that the effects in the previous analysis were indeed due to maternal mirroring, control analyses were run in order to rule out any potential effects of purely motor or visual experience. Two linear mixed models were thus used in order to explore any potential relationship between base rates of mouth opening or smiles performed by the infant or mother during the two month interactions, and infant mu ERD in central regions during observation of those same expressions. Both the models included random subject-specific intercepts and hemisphere nested within subject, and either infant frequency per minute (mouth opening, M = 2.47, SD = 3.24: smiles, M = 1.82, SD = 2.13) or mother frequency per minute (mouth opening, M = 2.61, SD = 2.16: smiles, M = 4.11, SD = 1.12), along with condition, hemisphere, and their interaction as fixed effects. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. All *p* values were based on Kenward-Roger's corrected degrees of freedom. This revealed no significant main effects of expression execution base rates for infants or mothers, ruling out the possibility that any differences found in mu ERD during observation were influenced simply by the amount infants performed actions themselves, or by the opportunity to observe mothers performing the expressions (see Appendix C, section 10.4).

4.3.4 QUESTIONNAIRE MEASURES

There was no significant difference in the mean EPDS scores between mothers in the low and high mouth opening group [$U = 23.50$, $p = 0.63$]], or in the low and high smile group [$U = 27.50$, $p = 0.81$]. This suggests that differences in mu ERD between the low and high mirror groups were not driven by differences in maternal depression scores between the two groups. Additionally, no significant differences were revealed between low and high mirroring groups in terms of demographics (all $p > 0.07$).

The only significant relationship found between any of the ASQ-3 measures and mu ERD during facial expression observation was with scores on the fine motor development scale ($\tau = 0.39$, $p = 0.03$). As the correlation was positive (i.e. the greater the infant's fine motor score, the less mu desynchronization they demonstrated), higher scores on this scale could not have accounted for greater mu desynchronization during observation of the EEG stimuli.

4.4 DISCUSSION

Despite research with monkeys and human adults implicating a mirror system in the processing of facial expressions (Carr et al., 2003; Ferrari et al., 2003; Moore et al., 2012; van der Gaag et al., 2007), until the study presented in Chapter 2, no human research had investigated this in the developing brain. In the Chapter 2 EEG study, which involved a sample of 30-month-old children, results were indicative of facial mirror system activity, with right lateralized mu desynchronization revealed during observation of emotional expressions, but bilateral desynchronization during observation of non-emotional expressions. Findings from the research presented in this chapter were largely in keeping with these results, with mu desynchronization found during both observation and execution of facial expressions in 9-month-old infants, and thus is the first study to implicate a mirror mechanism in the mapping between own and other facial expressions at such an early stage in human development. Furthermore, this study is also the first to provide evidence for an influence of early social environment on putative facial mirror system activity in human infants, with measures of maternal mirroring at 2 months postpartum linked to the degree of mu desynchronization during observation of facial expressions later on in the first year of life.

The present study used EEG to record neural data from 9-month-old infants as they observed and executed both emotional and non-emotional dynamic facial expressions. The same stimuli were used, and a very similar experimental paradigm, to that utilized in Chapter 2 was employed. The key finding was that significant mu ERD was demonstrated in central clusters during observation of all types of facial expression relative to a static neutral face, but not in the scrambled control condition. Significant mu ERD was also found during execution of emotional and non-emotional expressions in central but not occipital regions. Therefore, these results are comparable to those obtained in the 30 month study, with the lack of mu desynchronization in response to the observation of scrambled stimuli suggesting that even at 9 months of age, significant mu ERD found during the other conditions was not a mere consequence of observing a moving face-like stimulus, or other attentional factors. There was still a lack of alpha ERD found in the occipital clusters during observation in the 9-month-old infants, which suggests that the response found in central clusters was not a result of alpha desynchronization in visual cortex, but was specific to sensorimotor cortical regions.

There was one key difference between the current study findings and the findings in Chapter 2. In the 30-month-old children, mu ERD during observation of mouth opening was bilateral in central clusters, whereas mu ERD during observation of happy and sad facial expressions was found only in the right hemisphere. This was in keeping with numerous studies showing a right hemisphere dominance for the processing of emotional facial expressions (Adolphs, 2002). In the 9-month-old infants, there was also right lateralization during observation of happy expressions, as well as bilateral desynchronization for mouth opening. However mu desynchronization in response to the sad expressions was bilateral rather than right lateralized in this younger sample. This finding could reflect a more refined response for happy expressions, perhaps a consequence of early experience, which will be discussed more below in regards to the early interaction data.

As well as investigating putative facial mirror activity in a much younger sample than has previously been looked at, the current study also explored, for the first time, how early face-to-face interactions might influence the development of a facial mirror system in human infants. By comparing ‘low’ and ‘high’ mirroring groups of mothers, the hypothesis that greater maternal mirroring of an infant facial expression would be linked to greater mu desynchronization during observation of that expression could be tested, and also that more right lateralization would be found in infants whose mothers mirrored emotional expressions more often. This second prediction was based on the results obtained from the Chapter 2 study with 30 month-old-infants, where mu desynchronization for both happy and sad expressions was right lateralized, but was bilateral for mouth opening (non-emotional). Unfortunately, only two mothers mirrored negative expressions, therefore analyses were based on mouth opening and smiles only. Findings revealed that infants whose mothers were in the high mirroring group for the corresponding expression showed greater desynchronization during observation of mouth opening and happy stimuli, and interestingly, desynchronization in the happy condition was more right lateralized in infants whose mothers mirrored smiles more often during early interactions. This could suggest that infants with high mirroring mothers were not only able to strengthen mappings between the visual and motor representations of the facial expressions investigated but, perhaps in regards to smiles, also the linkage between that expression and emotional representations in the right hemisphere. In accordance with this idea, the right hemisphere is thought to be specialized for emotional face processing (Adolphs et al., 1996; Calvo & Beltrán, 2014; de Haan & Nelson, 1998; Moreno et al., 1990). Additional analyses were also run to make sure that it was not simply higher base rates of infant expression execution or observation of maternal expressions that accounted for the greater desynchronization revealed, with no relationship revealed between these variables. Also, no general relationship was found between overall maternal mirroring and mu ERD, and therefore the effect of maternal mirroring on infant mu activity was specific to the action being mirrored, providing strong support for maternal mirroring facilitating the development of a facial mirror system.

Although highly speculative given the inability to include mu ERD during observation of sad stimuli in the analysis, it is intriguing that in the younger sample of infants, mu desynchronization in response to sad expressions was not right lateralized. Tentatively then, this could be linked to the lack of maternal mirroring seen in response to negative infant expressions. That is, if mothers tend to imitate smiles during early interactions more than negative expressions, the mirror system response during observation of smiles could be more refined by 9 months of age. Although mirroring of positive and negative expressions has not been looking at specifically, some research suggests that instead of simply responding to infants less often overall, depressed mothers respond to infant negative expressions more (e.g. frown and negate the infant verbally) than non-depressed mothers, but to positive expressions less . There was not a wide range of depression scores in the current sample, and there was no significant difference between low and high mirroring mothers in terms of depression. However, it would be interesting if future research compared a clinical group of mothers diagnosed with postnatal depression to a control group in order to explore potential differences in maternal mirroring of negative expressions and putative mirror system activity.

Results from this study, and the study in Chapter 2, could support a right hemisphere dominance for emotional face processing, as well as the idea that experience is important for learning about facial expressions (i.e. that perceptual dimensions relevant to various expressions are gradually discovered then used to differentiate perceptual inputs and associate them with different responses and consequences; Quinn & Johnson, 1997). Indeed, the lateralization revealed during observation of happy faces, but not sad, in nine month old infants also fits with idea that exposure to predominantly happy faces in the neonatal period is linked to a superior ability to process happy expressions from a very early age (Farroni et al., 2007). However, the potential challenges to a dominant right hemisphere interpretation posed by the difference found between nine and 30-month olds in terms of lateralization must also be considered. There are in fact a number of theories regarding hemispheric specialization for production of emotional facial expressions (which could, therefore, apply to observation of expressions), with three major positions (Cattaneo & Pavesi, 2014; Müri, 2016): i) control of emotional expression execution is lateralized to the right hemisphere (Borod et al., 1998); ii) the production of positive expressions is left lateralized and the production of negative expressions is right lateralized (Davidson & Fox, 1982); iii) the production of 'social' emotions acquired later during childhood, such as pride and embarrassment, are left lateralized, but production of more 'innate' emotions such as joy and sadness are right lateralized (Ross, Homan, & Buck, 1994). Related to this third option is the 'upper-lower facial axis' hypothesis of emotional expression (E. M. Murray et al., 2015), whereby the left hemisphere preferentially processes voluntary/social emotional displays enacted by the lower hemiface, or alternatively, that emotional displays in the upper hemiface are preferentially processed in the right and those in the lower hemiface in the left (Ross, Prodan, & Monnot, 2007; Ross & Pulusu, 2013). This fourth hypothesis is formulated in accordance with recent understanding of the different neuroanatomic connections for the upper versus the lower face (Müri, 2016).

So, how might results from the studies in Chapter 2 and 4 support these different theories? Again, the finding of right lateralization during observation of happy and sad expressions in 30 months old fits with specialization of the right hemisphere for emotional face processing (R Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000; R Adolphs, Damasio, Tranel, & Damasio, 1996; Borod et al., 1998; Dimberg & Petterson, 2000; Kucharska-Pietura, Phillips, Gernand, & David, 2003; Moreno, Borod, Welkowitz, & Alpert, 1990), as does the right lateralization during observation of happy expressions in the 9 month olds. Speculatively, it could be that mu desynchronization during observation of sad expressions was not yet right lateralized in the younger sample due to insufficient visuomotor experience, i.e., less maternal mirroring of such expressions, meaning that any links between emotional and motor representations in the right hemisphere were not that strong by nine months postpartum. Several adult studies have also shown right lateralization of motor regions during the observation of emotional facial expressions (Carr et al., 2003; Leslie et al., 2004; W. Sato & Aoki, 2006; Uono et al., 2016), whereas observation of non-emotional expressions activates such regions bilaterally (Buccino et al., 2001). It has thus been suggested that there may be a right hemisphere mirroring system that could provide a neural substrate for emotion and even empathy, which would fit with the idea that emotional and motor components of facial expressions may involve different but overlapping systems (van der Gaag et., 2007). Note, the fact that observation of sad expressions was not right lateralized in nine month olds does not automatically contradict this idea of a right hemisphere specialization for emotion processing. Indeed, this finding could fit with the perspective that whether or not newborns have some innate neurophysiological action patterns linked to discrete emotions, evolution could have prepared infants with innate action readiness patterns crucial for early mother-infant interactions, via which specific facial configurations are able to acquire functional significance and become associated with specific emotions (Cole & Moore, 2015; X. Gao, Maurer, & Nishimura, 2013; Leppänen & Nelson, 2009). Perhaps such development could lead to the gradual lateralization of motor representations for emotional expressions during execution and observation, with the process occurring much earlier for smiles. Or of course, mu desynchronization is used as an index of motor system activity, so even if emotional representations are right lateralized from birth, or early in the postnatal period, motor representations may not be lateralized until sufficient experience to link them to emotional representations has occurred, which is reflected in the lateralization of mu responses at various ages.

Findings from Chapters 2 and 4 don’t seem to fit with the hypothesis that positive emotional expressions are left lateralized and negative expressions are right lateralized, with observation of smiles resulting in right lateralization in both age groups; and sad expressions being bilateral in the nine months olds. However, it could be that different brain regions show distinct patterns of lateralization during emotional expression production and processing. For example, observing happy expressions results in activity in the left anterior cingulate gyrus, while observing sad expressions activates the right STS and bilateral IPL, but both expressions activate the right IFG (Harada, Hayashi, Sadato, & Iidaka, 2016). Similarly, parietofrontal regions show right lateralized activity during emotion discrimination, but ventral regions such as the inferior and medial cortex are more active in the left hemisphere for happy compared to neutral expressions (Nakamura, Maess, Knösche, & Friederici, 2014). This may indicate that while not all aspects of emotional processing are right-lateralized, the mirror system network in the right hemisphere is specialized for emotional expression processing (Leslie et al., 2004; Nakamura et al., 2014).

These results reported in Chapters 2 and 4 could fit with the idea of more ‘innate’ emotional facial expressions being represented in the right hemisphere and more social in the left, but social emotional expressions were not tested as the infants in these studies were too young to have had experience with them. However, as noted above, even if emotional representations were right lateralized much earlier than motor representations for facial movements, it could be that over time, motor representations form strong links with more innate emotional representations in the right hemisphere, so these results could fit with the idea that expressions such as joy and sadness are right lateralized whereas more social emotions are not. Furthermore, as mouth opening is non-emotional, even if it is mirrored a lot by mothers, there would be no reason according to lateralization theories that observation of this expression would be represented in one hemisphere over another. Perhaps if this gesture is associated with language it could become left lateralized over time, but this would not be seen until participants were older than 30 months.

Because the infants who took part in the study were already 9 months of age, results cannot help elucidate whether a facial mirror system is present at birth. However, the findings do indicate that a mirror system may be involved in the processing of facial expressions from a very early age, and that in accordance with a number of theories (Casile et al., 2011; Del Giudice et al., 2009; Ferrari et al., 2013; Heyes, 2010), early social experience plays a role in the development of such a system. It would be very challenging to obtain EEG data from newborn infants, however, future research should endeavour to obtain this in the neonatal period to further address the issue of genetic and environmental contributions to the development of mirror systems. Evidence from newborn macaque monkeys suggests that a mirror mechanism could be involved in the mapping between visual and motor representations of actions in the first days of life (Ferrari et al., 2012), and that early experience with their mother increases mu desynchronization during observation of facial gestures (Vanderwert et al., 2015), with the latter certainly in agreement with the findings presented here.

To conclude, the results from this study revealed significant mu rhythm desynchronization during observation and execution of emotional and non-emotional facial expressions in 9-month-old infants, but not during observation of meaningless biological movement of a face-like stimulus. This indicates activation of the sensorimotor system, and thus suggests involvement of a mirror system in the processing of facial expressions from very young age. Interestingly, mu desynchronization during observation occurred in both hemispheres for mouth opening and sad expressions, but was right lateralized for happy expressions. The extent to which mothers mirrored infant expressions during early interactions influenced the degree of mu desynchronization during observation of expressions in the EEG experiment, as well as the degree of right lateralization during the happy condition, which suggests that early interactions may be important for development and refinement of a facial mirror system.

5 STUDY THREE- MU DESYNCHRONIZATION IN INFANTS WHEN A SOCIAL PARTNER FOLLOWS THEIR DIRECTION OF ATTENTION: THE ROLE OF EARLY SOCIAL EXPERIENCE

5.1 INTRODUCTION TO THE STUDY

In Chapters 2 and 4, two EEG studies were presented in which mirror system involvement in the processing of facial expressions was explored in young children and infants. In these studies, findings consistent with sensorimotor cortex activation were revealed during observation and execution of emotional and non-emotional facial expressions, and thus are indicative of facial mirror system activity from a very early stage in development. In the latter of these EEG studies, which involved a sample of 9-month-old infants, mother-infant dyads had also been recorded interacting face-to-face at 2 months postpartum. These interaction periods were included in order to investigate the influence of early maternal mirroring on facial mirror system development, with video recordings manually coded to identify relevant behaviours. Interestingly, a link between early maternal mirroring of infant facial expressions during these early interactions and putative mirror system activity at 9 months was revealed. Infants whose mothers mirrored their mouth opening and smiles more at 2 months demonstrated greater mu desynchronization during observation of those particular expressions in the EEG experiment, and furthermore, infants whose mothers mirrored their smiles more often seemed to have greater right lateralization of the mu response during observation of happy expressions. Therefore, as well as providing evidence for a mirror mechanism mapping between own and other facial expressions at 9 months of age, results substantiate the hypothesis that mothers act as ‘biological mirrors’ for their infants during early interactions, enabling the infant to observe the visual consequences of their own facial expressions. This appears to strengthen the mapping between visual and motor representations of the facial expressions included in this study (and possibly emotional representations in the case of happy expressions), and thus to influence activation of the mirror system.

The results obtained in Chapter 4 constitute the first evidence of a relationship between early maternal mirroring and refinement of a facial mirror system in human infants. In this chapter (Chapter 5), another study designed to explore the link between early mother-infant interactions and infant mirror system activity is presented; however, the focus here is on the potential involvement of such a system in the matching of own and other attention shifts. ‘Attention mirroring’ has now been posited by a number of researchers to facilitate the processing of others’ shifts in attention (Lachat et al., 2012; Shepherd et al., 2009; Triesch, Jasso, & Deak, 2007). As another type of opaque action, which one cannot see oneself perform, if a mirror system is involved in a mechanism for matching own-other attention shifts, it can be hypothesized that early social experience with mothers might be related to activity in a similar way that facial expressions are.

5.1.1 THE IMPORTANCE OF GAZE AND ‘JOINT ATTENTION’

As emphasized throughout this thesis, accurate perception and analysis of non-verbal facial cues is an exceptionally important aspect of social interactions, providing a wealth of information concerning others’ feelings, motivations and intentions to the observer. Other than facial expressions, a non-verbal cue that is particularly instructive during a social exchange is that of *gaze*. Others’ gaze enables us to identify their focus of attention, as well as make inferences regarding their motor or behavioural goals, or communicative intents. Indeed, the importance of gaze is clear from the first days of life, with newborn infants demonstrating a preference for faces with eyes open rather than closed (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000). By 2 months postpartum, infants also tend to direct attention preferentially towards the eyes when looking at others’ faces (Hains & Muir, 1996; Lasky & Klein, 1979), and by 4 months of age, enhanced neural processing of mutual gaze compared to averted gaze is demonstrated (Farroni et al., 2002).

Two critical types of information can be extracted from another’s direction of attention, namely, that which can be inferred from direct, or from deictic (‘pointing’), gaze (Shepherd, 2010). Direct gaze is of great evolutionary significance, linked with predation and the probability of approach, and is thus associated with neural responses that are largely automatic (Senju & Hasegawa, 2005) and facilitated by evolutionarily preserved subcortical systems (Senju & Johnson, 2009). However, if a person’s gaze is not directed towards the observer, its direction signals a different target of attention, including the target of other facial signals, and can even be indicative of the other individual’s future actions (Shepherd, 2010). As such, it is clear that processing others’ shifts in attention is hugely beneficial for species such as human beings, whose actions are firmly embedded within their social environment, and for whom the ability to succeed in that environment depends on being able to recognize and interpret others’ actions during social exchanges. Indeed, humans have particularly visible eyes (e.g. white sclera) compared to other primates, making their presence very clear and others’ gaze direction far more salient (Kobayashi & Kohshima, 1997, 2001). Such colouration of the eyes may have evolved because it simplifies the task of determining the direction of another individual’s gaze, with many having proposed that eyes likely acquired a new social function in human evolution (Tomasello, Hare, Lehmann, & Call, 2007) to support cooperative and mutualistic social interactions.

‘Joint attention’ (JA) is the process through which an individual coordinates their own attention with that of another person towards a common object or event, and therefore plays a key role in the inter-individual synchronization required for successful social interactions (Lachat et al., 2012). Many believe that JA skills begin to emerge around 9-10 months postpartum (Mundy et al., 2007), with an infant’s ability to coordinate attention with a social partner around this age linked to subsequent acquisition of more complex social-cognitive abilities such as cooperative behaviour, social competence, self-regulation, theory of mind, and language learning (Baron-Cohen, 1991; Carpenter, Nagell, & Tomasello, 1998; Delgado et al., 2002; Morales, Mundy, Crowson, Neal, & Delgado, 2005; Mundy et al., 2007; Sheinkopf, Mundy, Claussen, & Willoughby, 2004; Smith & Ulvund, 2003). Additionally, difficulties or disinterest in JA is associated with autism spectrum disorders (ASD: Baron-Cohen, 1995; Dawson et al., 2004). Indeed, impairments in JA are considered one of the earliest indicators of ASD (Charman, 2003), and have been linked to a greater risk of ASD diagnoses later on in childhood (Charman, 2003; Poon, Watson, Baranek, & Poe, 2012). Altogether, this highlights the importance of JA for healthy development, and explains the great interest in the development of this ability in many research domains.

To be competent in JA, one must demonstrate the ability to both respond to (i.e. follow another’s direction of attention) and initiate JA (i.e. direct another’s attention). Research suggests that these two abilities involve overlapping and distinct processes, but that responding to and initiating JA may contribute somewhat independently to development of particular social and communicative skills later on in childhood (Mundy et al., 2007; Mundy & Jarrold, 2010). The process of JA can incorporate a variety of behaviours that signal one’s direction of attention (e.g. pointing of the finger, or body orientation), however most research has focused on the direction of gaze as signalled by eyes and/or head orientation. In fact, although infants follow another’s direction of attention to nearby targets during the first year postpartum (D’Entremont, Hains, & Muir, 1997), and to more distant targets around 12 months (Carpenter et al., 1998), they do not seem to reliably follow attention cued by the eyes only (i.e. with no accompanying head-turn) until they enter their second year of life (Corkum & Moore, 1995). In one direct comparison of head versus eye movement, Brooks and Meltzoff (2002) showed that infants around 12 months old followed gaze more frequently when an adult’s eyes were open versus closed, and by 14 months, when the adult’s eyes were uncovered rather than obscured by a blindfold. However, at least in the first year postpartum, others’ head-turns are especially important attention-directing cues during a social exchange (Caron, Butler, & Brooks, 2002; Corkum & Moore, 1995, 1998; Farroni, Johnson, Brockbank, & Simion, 2000; Johnson, Slaughter, & Carey, 1998).

5.1.2 MIRROR SYSTEM INVOLVEMENT IN THE PROCESSING OF ATTENTION SHIFTS

The ability to understand what someone else sees is multifaceted, requiring both perception and analysis of another's head, eye, and sometimes body position, in order to infer their direction of attention. At a lower level, this presumably requires detection of the congruence between another's attention direction and one's own (Lachat et al., 2012), which has been described as 'attention mirroring' (Gangopadhyay & Schilbach, 2012; Lachat et al., 2012; Shepherd et al., 2009; Triesch, Jasso, & Deak, 2007). This ability has been proposed to involve a neural mapping between other- and self-generated actions via a mirror mechanism (Bristow, Rees, & Frith, 2007; Frischen, Bayliss, & Tipper, 2007; Gangopadhyay & Schilbach, 2012; Iacoboni, 2009; Lachat et al., 2012; Lakin & Chartrand, 2003; Mundy & Jarrold, 2010; Shepherd et al., 2009; Triesch, Jasso, & Deak, 2007). For example, it could be that detecting that another person has turned their head in the same direction you just did requires a mapping of the visual representation of that observed head-turn onto the motor commands you used to turn your own head. Of course, it could be that individuals map between own and other gaze 'directions' (e.g. left/right) or 'targets' (e.g. toy/lamp) when they follow someone's gaze, or observe the other person following theirs, rather than mapping between actions. However, this might require much more complex processes, such as geometric reasoning and mental rotation, while a mapping between execution and observation of actions implemented by a mirror system may be more straightforward.

Most mirror system research thus far has focused on the study of manual actions (Cannon et al., 2016; di Pellegrino et al., 1992; Fadiga et al., 1995; Gallese et al., 1996; Gazzola & Keysers, 2009), and increasingly, on facial expressions (Carr et al., 2003; Ferrari et al., 2012, 2003b; Hennenlotter et al., 2005; Moore et al., 2012; van der Gaag et al., 2007). However, because the matching of own and other attention direction implies a dynamic perception-action mapping between social partners, it can also be hypothesized to be facilitated by a mirror system (Bristow et al., 2007; Frischen et al., 2007; Hoehl et al., 2014; Iacoboni, 2009; Lachat et al., 2012; Lakin & Chartrand, 2003; Mundy & Jarrold, 2010; Shepherd et al., 2009; Triesch, Jasso, & Deak, 2007), similar to that which operates for the hand and face. Indeed, a few studies have now investigated the involvement of a neural self-other matching mechanism in the processing of others' attention direction, both in monkeys (Shepherd et al., 2009) and humans (Hoehl et al., 2014; Lachat et al., 2012). In macaques, single-cell recordings have revealed that observed gaze direction modulates the activity of premotor mirror neurons selective for grasping (Coudé et al., 2016), as well as the existence of neurons with mirror properties in the lateral intraparietal sulcus (LIP, Shepherd et al., 2009), a region typically implicated in the control of eye movements. These LIP mirror neurons respond not only when a monkey orients their own gaze towards the neuron's responsive field, but also when they observe another monkey gaze in the same direction. Notably, in humans, one fMRI study has also shown that following a partner's gaze towards an object elicits activation in the left intra-parietal sulcus (Saito et al., 2010), a region thought to be homologous to macaque LIP (Culham & Kanwisher, 2001; Grefkes & Fink, 2005). Additionally, the frontal eye field (FEF) is a premotor cortical region that contains both visual and oculomotor neurons, and is active during covert shifts of attention and saccade preparation (e.g., Connolly, Goodale, Menon, & Munoz, 2002). Activation of the STS, which provides visual inputs to the manual and facial mirror systems, has also been reported during covert shifts of attention, gaze perception, and eye movements. Along with LIP, STS projects directly to the FEF (Grosbras et al., 2005), suggesting that FEF may be a candidate region for the premotor node of an attentional mirror system (Frischen et al., 2007).

If a mirror system is involved in detecting congruence between own and other attention shifts, it may also be important for both responding to and initiating JA. Both abilities require the capacity to infer others' attentional states and detect when those states correspond to one's own. While higher order social cognitive skills are needed to accomplish the former, the mirror system may implement the latter. Indeed, EEG data from human adults and infants during episodes of JA suggest mirror system involvement in the mapping between own and other direction of attention (Hoehl et al., 2014; Lachat et al., 2012), with greater mu rhythm desynchronization demonstrated in JA compared to no-JA conditions. For example, the mu rhythm is desynchronized significantly more when two adults turned to look at the same object, compared to when they looked at different objects (Lachat et al., 2012). Interestingly, Hoehl et al. (2014) obtained comparable EEG results from 9-month-old infants, while either observing an adult make direct eye-contact with them and then turn towards an object (JA condition), or gaze at a monitor on which an object eventually appeared, without ever making eye contact or turning the head (no JA). Like in Lachat et al., mu desynchronization was greater during episodes of JA versus no-JA over central areas, consistent with mirror system activity (Hoehl et al., 2014). However, this infant study involved a number of methodological factors that limit the possibility of making such an interpretation. For example, only in the eye-contact (JA) condition did infants and adults perform an actual movement by both turning towards the monitor on which an object was presented (in the no JA condition, adults were already looking at the monitor, and never performed a head turn), and the period in which mu desynchronization was analysed occurred after the object presentation rather than during observation of the movement (i.e. the object appeared after the adult's head turn towards the monitor on which is was presented). As such, infants did not engage in both observation and execution of the same action performed by the adult, only one condition included eye contact (which has been shown to modulate infants' neural processing: Csibra & Gergely, 2009), and the period of time analysed did not actually include observation of adult head-turns.

In an interesting study by Grossmann and colleagues (2013), near-infrared spectroscopy was used to investigate the neural activity of 5-month-old infants during observation of adult avatar head-turns. Two conditions were included in the experiment, one in which the avatar turned their head to look at an object the infant just looked at (congruent condition), and one in which the avatar turned to look at a different object (incongruent condition). Greater activation in the left prefrontal cortex was found during observation of congruent head-turns compared to baseline, but not during observation of incongruent head-turns, suggesting that infants were sensitive to another person following their gaze. These results correspond to adult fMRI research reporting activity in regions such as the left prefrontal cortex during both responding to and initiating JA (Schilbach et al., 2010). Therefore, findings in both adults and infants suggest a flexible engagement of neural processes common to own and other initiated interactions, with the left prefrontal region already sensitive to matching self-other head-turns in the first year of life. However, due to the limitations of their recording technique, Grossmann et al., did not record activity from any central areas, therefore without any evidence for differential activity in motor regions during congruent and incongruent conditions, nothing can be said about potential mirror system involvement. Also, while this study compared observation of congruent and incongruent head-turns, there was no condition to control for observation of congruent or incongruent *motion*. Without such a control condition, this study could indicate that the left prefrontal cortex is sensitive to any stimulus moving in a direction congruent to that the infant just looked in, but not necessarily a head-turn. Grossmann et al. also used avatars rather than video clips of real adults performing head turns, which as well as reducing ecological validity, may have influenced a system sensitive to biological motion.

5.1.3 ROLE OF EXPERIENCE IN DEVELOPMENT OF AN ATTENTIONAL MIRROR SYSTEM

Following others' gaze has been described as a form of imitation (e.g. Hoffman, Grimes, Shon, & Rao, 2006; Triesch, Jasso, & Deak, 2007), in that it involves the observation another individual's action (i.e. the shift of the eyes and/or head to a location in space) and the subsequent replication of it (Tomasello, 1999). This does not adhere to certain strict definitions of imitation as the action of the performer is somewhat different to any replication by the observer. That is, if two individuals sit facing each other and the 'performer' turns their head to the right, the 'imitator' would actually have to orient to their left to attend in the same way. For this reason, some may suggest that following someone's direction of attention involves the 'emulation' of the goal/outcome of the performer's action, rather than imitation of the action, which is to attend to a particular object or position in space. Nevertheless, it is argued that it is appropriate to consider gaze following as a type of imitation, with an exact replication in this case not useful for the observer (Triesch, Jasso, & Deak, 2007). This could therefore be conceptualized as a more 'functional' type of imitation, rather than a strict anatomical imitation. Indeed specular imitation (imitating as if looking in a mirror) activates classic mirror areas more strongly than anatomical imitation (Koski, Iacoboni, Dubeau, Woods, & Mazziotta, 2003), and is more natural for infants and young children (Bekkering, Wohlschläger, & Gattis, 2000; Gleissner, Meltzoff, & Bekkering, 2000; Schofield, 1976). If gaze following is considered a form of imitation, it would presumably develop and be refined in a similar fashion (Triesch, Jasso, & Deak, 2007), including the neural basis of such behaviours. Indeed, a number of studies with infants aged 9-20 months of age have found a relationship between other types of imitation and joint attention skills (Carpenter et al., 1998; Charman et al., 2000).

Although no experimental studies have been conducted to look at how early interactions may influence activity of an attentional mirror system, Triesch et al. (Triesch, Jasso, & Deak, 2007) used a computational model to demonstrate how mirror neurons for gaze following could emerge during early development. This model was designed to look at how gaze following may develop during infancy, based on the idea that infants gradually learn to use a caregiver's gaze direction to predict the location of interesting objects in the environment. The main structural components of the model consisted of two networks, one visual and one motor. The visual network (i.e. the system that processed infant's visual inputs) contained three subsystems: (i) a system for encoding the saliency of objects in particular locations, made up of neurons that each had a preferred location in space centred on the infant ('saliency map'); (ii) a system made up of neurons for encoding a caregiver's head direction; and (iii) a system made up of neurons for encoding a caregiver's eye direction. The motor network (i.e. the system involved in the execution of infant head/eye movements) was also comprised of neurons that had preferred locations, and was based in the same space as the saliency map in the visual network. Every neuron in the visual network projected to every neuron in the motor network, with connections between them modified using a reinforcement learning rule.

In the Triesch et al. (Triesch, Jasso, & Deak, 2007) set-up, infant and caregiver interacted with various objects that varied in visual saliency, with the partners placed opposite each other around 40cm apart. The caregiver and infant looked back and forth between the objects, and one another, depending on each object's saliency. Visual saliencies were attributed to the caregiver, infant, and objects, with most objects having a lower saliency than that of the infant and caregiver, but occasionally higher. The infant could only perceive objects directly within their field of vision (90° around the infant's current attention direction). At each time step the caregiver looked at the most salient object. Mirror neurons emerged in the model in two stages (though not necessarily in succession, i.e. there was some overlap). First, the model infant learned to orient its gaze toward salient stimuli in its field of view by mapping particular locations onto gaze shift motor commands. At first, although an object might be presented in the infant's visual field, because the connections between the visual and motor network were random, the infant did not know how to look at the object and therefore any gaze shifts made were also random. At this first stage, once in a while the infant would look at the presented object by chance, thus receiving a reward for looking at something salient and strengthening the connection between the saliency map neurons, which encoded the object location, and the corresponding neuron in the motor network used to look in that direction. If this occurred repeatedly, strong connections between each saliency map neuron and the corresponding motor neuron were formed, which meant the infant could now voluntarily look at an object in their visual field. In the second learning stage, the model learned to associate representations of the caregiver's gaze direction with the corresponding motor neurons. This process was propelled by the aim of maximizing reward, which here, was gained by looking at interesting visual stimuli. During interactions with the caregiver, by chance, the infant sometimes looks in the same direction as the caregiver; which resulted in the infant looking at a salient object, resulting in reward. This sequence of events thus strengthened connections between the visual neurons encoding the caregiver's eye/head direction and motor neurons for looking in that same direction, and after repeated occurrence, built up a mapping between these visual and motor neurons. Therefore after training, neurons in the infant's motor network behaved like mirror neurons, with such neurons activated when a salient object was in their preferred location, but even more when they saw the mother looking in that direction. This was the case because of the connections between both the saliency map and that motor neuron, as well as the connections between the neurons coding the caregiver's head/eye direction and that motor neuron.

Although it may be plausible that infants could strengthen a mapping between the motor and visual representations via reinforcement learning following the 'accidental' following of a caregiver's actions, with reward given by viewing interesting objects, Triesch et al. (Triesch, Jasso, & Deak, 2007) failed to acknowledge another potentially important aspect of early interactions that could strengthen such mappings: 'mirroring' of an infant's gaze direction by a caregiver and the infant observing this taking place. Because this type of attention event involves contingent and contiguous motor (from the infant's gaze shift) and visual (observation of the caregiver's following gaze shift) events, it could also help to form mappings between motor and visual representations in the infant. As this learning process would rely on the caregiver's responsiveness to the infant's attention shifts, rather than random exploration, it could hypothetically strengthen such mappings more efficiently. The resulting mirror mechanism could be important for both following another's attention and detecting whether someone has looked in the same direction, and therefore at least at a very low level, could contribute to both responding to and initiating JA. Certainly, as presented in the section below, there is some evidence already available in support of early maternal behaviour during face-to-face interactions influencing JA later on in infancy.

5.1.3.1 ***Evidence from infant studies***

In terms of JA development, most research focuses on changes from around 9 to 10 months onwards, with most agreeing that JA-type behaviours (e.g. responding to and initiating JA) begin to emerge at this age; and that from this time until about 18-24 months is the most formative developmental period in terms of JA ability (Brooks & Meltzoff, 2005; Carpenter et al., 1998; Mundy et al., 2007; Tomasello, 1995). It has been posited that the changes occurring at approximately 9 months reflect an infant's awareness, at least in a very basic or implicit sense, that a social partner is attending to the same thing as them (Bakeman & Adamson, 1984; Tomasello, Carpenter, Call, Behne, & Moll, 2005). In infant JA studies, an interchange of looks is usually required between an adults' face and object to classify an infant's behaviour as responding to or initiating JA. These interchanges start to appear around 9 months postpartum (Carpenter et al., 1998; Vaughan Van Hecke et al., 2007), and imply that the infant is 'checking' whether their social partner is attending to the same thing as them. This checking behaviour in both responding to and initiating JA could be built upon a basic mechanism for detecting matching attention direction (i.e. implicit recognition that someone's attention direction matches your own), which would fit well with the idea that some low-level component of JA is served by a mirror system. Prior to the shift at 9-10 months, although behaviours reminiscent or important for JA may be present, many believe that these behaviours are not cognizant (Butterworth, 2001; Deák, Krasno, Triesch, Lewis, & Sepeta, 2014).

For example, even though infants between 3 and 6 months old may follow another's attention shifts (D'Entremont et al., 1997; Hood, Willen, & Driver, 1998), this could be an example of more covert (reflexive) rather than overt (intentional) gaze following, which could occur due to the motion of an adult attention shift 'pulling' the infant's gaze in the same direction (Butterworth & Jarrett, 1991; Farroni, Johnson, Brockbank, & Simion, 2000). As such, although gaze following has been reported in the first year postpartum (Brooks & Meltzoff, 2005; Carpenter et al., 1998; D'Entremont et al., 1997; Hood et al., 1998; Mundy et al., 2007), many argue that infants do not have a basic understanding of the visual perceptual states of others until later on in development.

Despite the abundance of research concerning JA development from 9-10 months and its impact on later social-cognitive ability, very few studies have looked at potential precursors to JA. One behaviour that is clearly important is that of gaze following, which is distinct from responding to JA in that it could result from automatic low-level visuomotor processes without any representation of the other's attentional state, rather than from the intention to attend to the same object or direction as a social partner. Such precursors would not involve features such as the 'checking' behaviour often considered to reflect JA. A number of theories concerning the development of gaze following have been put forward, including that infants initially respond to others' looking behaviour as mere movements, with the strictest version claiming that young infants just visually track an adult's head movement in space; and as a result, their attention is 'pulled' into the correct hemi-field where they catch sight of the salient target object by happenstance (Butterworth & Jarrett, 1991; Farroni et al., 2000). This idea is similar to the Triesch et al. (Triesch, Jasso, & Deak, 2007) model in that it suggests that infants can learn, over time, that the adult's head turn is a reliable cue indicating where an interesting object can be seen (Moore, 1999), without the need to make any high-level attributions in terms of others' visual perception; but also extends the model in that the infant's attention is influenced by the adult's head motion, rather than relying on chance alignment of the infant's and adult's gaze direction. Other researchers embrace a more nativist position, positing that infants have an innate/very early emerging module that uses eye gaze as its input, which automatically makes attributions about others' visual experience (Baron-Cohen, 1995; Leslie, 1994). However, when exactly the ability to attribute visual perception to others emerges in development is not clear.

Other theories of gaze following, including hybrids of the above, have also been described in the literature (e.g. Csibra & Gergely, 2010), but note, most of these neglect the role of the caregiver's behaviour during early interactions. Even though few studies have investigated it so far, it has been hypothesized that JA development is facilitated by early mother-infant interactions. For instance, some suggest that mechanisms relevant to JA could be strengthened by reward during face-to-face interactions (Corkum & Moore, 1998; Gaffan, Martins, Healy, & Murray, 2010; Triesch, Jasso, & Deak, 2007), with infants perhaps experiencing particularly positive consequences when they attend to the same object or location as their caregiver. This reward could be extrinsic, such as sensory stimulation (Triesch, Jasso, & Deak, 2007) and praise from the caregiver, or intrinsic, with the experience of shared engagement pleasurable in itself. In the approach of Mundy and colleagues (e.g. Mundy et al., 2007; Mundy & Jarrold, 2010; Mundy & Newell, 2007), responding to JA and initiating JA rely on different but overlapping neural systems, with responding linked to a relatively involuntary posterior network (posterior parietal and superior temporal cortex), and initiating based on a later-developing, more volitional anterior network (dorsal and medial frontal areas and anterior cingulate cortex). These systems are thought to act together for fully competent JA skills, with social interactions between 3 and 9 months (while the anterior system matures) suggested to allow both neural systems to be integrated (Mundy & Newell, 2007). Therefore, this account also indicates that social experience is very important for JA development (Mundy & Jarrold, 2010), but the features of social interactions that might be important and the exact mechanisms they might influence are not made clear.

Some research has shown that adult behaviours can increase infant following of attention before 9 months of age (Corkum & Moore, 1998; Senju & Csibra, 2008), whether this is done covertly or overtly, but such investigations are very sparse. Even less work has focused on how naturalistic early interactions may influence JA development. A mother’s early interaction style has been widely shown to influence infant development (Murray et al., 1996, 2010b), and for instance, in research concerning JA in infants aged 12 months and above, young mothers’ interaction style (where this was insensitive) has been linked to less JA ability in their infants (Flanagan, Coppa, Riggs, & Alario, 1994). In one longitudinal study, mother-infant dyads were observed interacting with toys on a number of occasions between 2 and 9 months postpartum, with various aspects of infant JA and maternal responses manually coded from video recordings (Gaffan et al., 2010). Differences in JA at 9 months were found to be predicted by variations in maternal behaviour at 6 months. Maternal behaviours at 6 months that predicted more competent JA at 9 months included teaching, conjoint action on a toy, and global sensitivity, with other behaviours such as entertaining found to negatively predict JA. Indeed mothers’ entertaining (e.g. animating a toy) and active involvement (i.e. close physical proximity to the infant, active control of the interaction) both inhibited infant bids (behaviours to initiate JA). These behaviours that were negatively correlated with later JA ability are functionally similar, with mothers who are high on either measure taking the initiative in the interaction, which may prevent the infant from doing so themselves. Such results indicate that early maternal behaviour does indeed influence JA development, and are in keeping with theories that implicate social learning (Corkum & Moore, 1998; Moore & Corkum, 1994; Triesch, Teuscher, Deák, & Carlson, 2006) in the strengthening of JA abilities, though also elevates the role of caregivers in this process. Note, Gaffan et al. found almost no impact of infant characteristics on JA. The authors suggest that a sensitive mother is capable of teaching in a way that respects the infant's capacity and interest, and will avoid dominating the interaction through high levels of entertaining or active involvement which may interrupt infants, and inhibit their emerging ability to make joint attention bids. Results from these behavioural studies therefore suggest that maternal responses to infants are very important in the development of JA, and that 'following' the infant into attention states is crucial, rather than the mother simply attending to what she chooses to and ignoring the infant's own attention shifts. This may be important when considering how a mirror system may play a role in JA at a very low level (e.g. implicit detection of a match between own and other head turns), as it implies that the simultaneous visual and motor activity that would occur when an infant observes their mother follow their direction of attention might help to strengthen the mapping mechanism required of a mirror system.

5.1.4 **CURRENT STUDY: EEG**

This experiment was designed to extend previous research implicating a mirror mechanism in the mapping between own and other direction of attention during infancy. EEG was used to record mu rhythm desynchronization as 6.5- and 9.5-month-old infants observed an adult turn their head towards one of two objects displayed either side of the adult's face. Infants' attention was first drawn to one of these objects, and the adult head-turn that followed occurred in either a congruent or incongruent direction (as in Grossmann et al., 2013). This particular behaviour was chosen as a sensitivity to another person following your direction of attention clearly suggests a mapping between own and other actions, without the need to include separate observation and execution conditions. In a single trial, the infant first executes a head turn, and then observes a social partner either perform a matching (congruent) or mismatched (incongruent) movement. At the start of both congruent and incongruent conditions, the adult actor's gaze was directed towards the infant, and the amount of movement performed by the adult that followed was the same in each condition. Therefore, any differences revealed could not simply have resulted from whether or not eye contact was made by the adult, or from varying degrees of movement across conditions. Additionally, a scrambled control condition, as in the experiments presented in Chapters 2 and 4, was included to explore specificity of effects. To reiterate, the scrambled control stimuli were produced by creating a version of each of experimental stimulus (here, short video clips of adults performing head turns to the left and right), which involved dividing the face region into square blocks (18 × 18 pixels) and randomly shuffling these blocks in the first frame of the video. The same transformation was then applied to each subsequent frame, which resulted in a video with similar low-level visual and motion features as the original, but with an unrecognizable movement (i.e. there was still clear left or right motion, but it was not clear that this was performed by a person). It was hypothesized that there would be greater infant mu desynchronization during observation of the congruent compared to incongruent head turns, and that no real desynchronization would be shown in response to the scrambled stimuli. Additionally, it was expected that such differences would become more pronounced as infants aged, in line with the emergence of joint attention skills.

5.1.5 CURRENT STUDY: MOTHER-INFANT INTERACTIONS

In addition to the infant EEG experiments at 6.5 and 9.5 months postpartum, observations of mother-infant interactions were made when infants were aged 3.5 and 6.5 months old, which were manually coded from video recordings. The ages preceding the final EEG experiment at 9.5 months (which is when JA begins to emerge) were chosen because around 3.5 months is the time infants begin to lose interest in ‘pure’ face-to-face interaction (Murray, 2014; Trevarthen & Aitken, 2001), but begin to show more interest in other environmental features; participation in shared visual attention begins to occur more often around 6 months, increasing over the next few months (Adamson & Bakeman, 1991; D’Entremont et al., 1997); and maternal behaviours during interactions at 6.5 months have already been shown to predict infant JA at around 9 months postpartum (Gaffan et al., 2010). This element of the study was included in order to identify behaviours that may help to build an infant’s mapping between their own attention direction and that of an observed other, which was then related to degree of mu desynchronization in the EEG experiments. Previous research has already demonstrated how early social environment, specifically interaction with their biological mothers, can influence development of a putative mirror system for the processing of facial gestures in macaque monkeys (Vanderwert et al., 2015), and in Chapter 4, findings revealed that degree of mu desynchronization in human infants during observation a facial expressions was related to early maternal mirroring. No previous study has looked at actual mother-infants interactions and their potential relationship with a mirror mechanism for matching attention shifts, although this hypothesis has been explored using computational modelling (Triesch, Jasso, & Deak, 2007). As Triesch et al. (Triesch, Jasso, & Deak,

2007) acknowledge, however, this model neglects the role of the caregiver in this process. As mentioned above, mother-infant interactions similar to the congruent condition in the EEG experiment could serve to strengthen a mapping between own and other direction of attention. In these situations infants direct their gaze toward an object or location, the mother follows their gaze, and the infant looks back at the mother and sees her looking in the same direction they just did. It was therefore hypothesized that infants who experienced more interactions of this type would demonstrate greater mu desynchronization in response to congruent compared to incongruent head turn conditions, with only the former containing an action that directly matches the infants previous attention shift.

5.2 METHODS

5.2.1 GENERAL METHODS

The mother-infant dyads included in this study were taking part in the longitudinal research programme outlined in Chapter 3 (see for more details concerning general methodology). Briefly, these participants were recruited from the CDG database, based in the SPCLS at University of Reading. The research in this programme was designed to explore human mirror system activity in very young infants, and to consider how early experience might influence the development of such systems. The included tasks were comprised of face-to-face mother-infant interactions, infant EEG experiments, and the completion of various questionnaires. This programme was approved by the University of Reading Research Ethics Committee (31.07.14), and mothers gave written, informed consent before participation at each visit.

Two separate studies were contained within this wider longitudinal programme, the second of which is presented in this chapter. The study included two infant EEG experiments performed at 6.5 and 9.5 months postpartum, and periods of face-to-face mother-infant interaction at 3.5 and 6.5 months postpartum. Details about the included assessments are outlined in Table 5.1.

Table 5.1: Infant age at each assessment, assessment location, tasks performed, and sample size

Infant Age	Assessment Location	Tasks	Sample Size
3.5 months	University	• 3 min face-to-face interaction • EPDS questionnaire	N = 38
6.5 months	University	• 3 min face-to-face interaction • EEG experiment • EPDS and ASQ-3 questionnaires	N = 38
9.5 months	University	• EEG experiment • ASQ-3 questionnaire (ASQ completed at 9m assessment: see section 3.)	N = 34

Below, detailed information is first given regarding the specific methods, pre-processing steps, and analyses used for the EEG portion of the study. Following this, details are given regarding methods, event extraction, and analyses used for the early mother-infant interaction portion of the study, and analysis of early interaction effects on the EEG results.

5.2.2 EEG METHODS

5.2.2.1 ***Participants***

38 infants (22 male, 16 female) aged approximately 6.5 months took part in this experiment, with 34 of the same infants (19 male, 15 female) also participating at 9.5 months of age. 15 infants at 6.5 months, and 10 infants at 9.5 months, were excluded prior to analysis due to fussiness during net placement/throughout the experiment (6.5 months, N = 14; 9.5 months, N = 8), or technical difficulties (6.5 months, N = 1; 9.5 months, N = 2). This left a total of 23 infants (13 male, 10 female) at 6.5 months (age: M = 200.91 days, SD = 5.86) and 24 infants (11 male, 13 female) at 9.5 months (age: M = 292.92 days, SD, = 7.88). This loss of data is comparable with other EEG studies that have investigated the mu rhythm in early infancy (e.g. Cannon et al., 2016; Saby et al., 2012; Southgate et al., 2009).

5.2.2.2 ***EEG stimuli***

Stimuli consisted of short video clips featuring two female actors. All clips began with 500ms of a static face presented in the centre of the screen, with actors looking directly towards the infant. Located on either side of this face were two identical objects (colourful balls), which were displayed throughout the trial. After the static period, one of the two objects was highlighted and jittered slightly in order to attract infant attention. This attention grabbing sequence lasted for a maximum of 2.5s, and if the infant looked at the highlighted object within this time, one of three experimental conditions followed: congruent, incongruent, or a scrambled control (Figure 5.1). In the congruent condition, the actor turned to look at the object the infant just did (the one highlighted), but in the incongruent condition, the actor turned to look at the object on the opposite side to where the infant just looked (the non-highlighted object). Scrambled versions of the congruent and incongruent videos made up the control condition (i.e. a scrambled version of each left/right and actor1/actor2 versions of the congruent and incongruent videos). Previous studies have utilized static or non-biological moving stimuli in control conditions (Ferrari et al., 2012; Moore et al., 2012); however, the scrambled stimuli were used here in order to control for overall motion across all experimental conditions (Rayson et al., 2016). The scrambled versions of each video were produced by dividing the face region into square blocks (18 × 18 pixels), randomly shuffling these blocks in the first frame of the video, and then applying the same transformation to each subsequent frame. This process thus preserved coherent motion in the same direction as the head turn in the original video. It resulted in a video with comparable low-level visual and motion features to the original, but without higher order visual features that support recognition of the stimulus as a face.

In all videos, the head turn/scrambled movement lasted for 1s, with the end position held for a further 1.5s (see Figure 5.1 for the time-course). Before each trial, a colourful moving pattern was displayed in the middle of the screen for 1s in order to attract infant attention. One actor always looked in the congruent direction, one in the incongruent direction, with the identity of each actor counterbalanced across participants. Before each trial, a colourful screen-saver type pattern was displayed in the middle of the screen for 1s in order to attract infant attention to the centre.

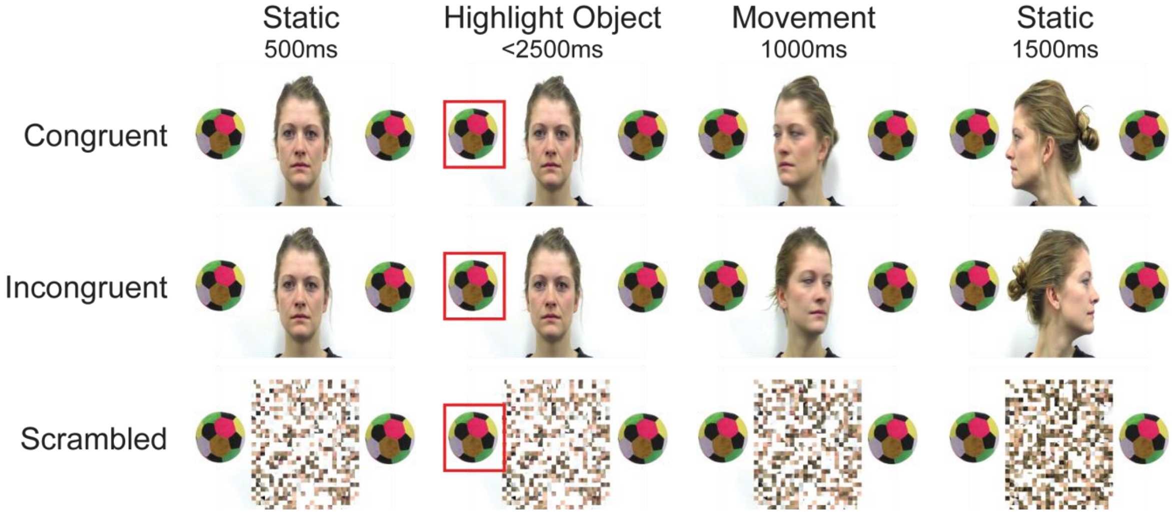

Figure 5.1: Time-course of EEG stimuli

5.2.2.3 ***Design and Procedure***

Once settled into the laboratory and made comfortable with the two experimenters present, infants' heads were measured and the correctly sized EEG net selected for preparation. When the net was ready, dyads were taken into the testing area, and infants were seated on mothers' laps approximately 65cm from a computer monitor. One experimenter then fitted the EEG net onto the infant's head. The second experimenter helped to distract and/or pacify the infant if the infant became fussy or attempted to touch the net once in place. Any fussiness caused by net placement receded quickly for most infants, however, the decision of whether or not to continue with the experiment was always left up to the mother. Mothers were asked to remain as still as possible and to not interact with their infant during the experiment.

Stimuli were presented on a computer monitor using PsychoPy v1.80.04 (Peirce, 2008). EEG stimuli were presented in blocks of 3 videos (one congruent, one incongruent, one scrambled), with presentation of these randomized within blocks. The inter-stimulus interval was a random length between 800 and 1200ms. Experimental blocks began when triggered manually by an experimenter, who was watching the infant live on a screen in another section of the room. Head-turns in the EEG stimuli were also triggered by the experimenter, who only did so if infants looked towards the highlighted object within the 2.5s attention-grabbing time-window. Between blocks, moving shapes/patterns accompanied by sounds were presented to maintain infant attention, also presented in a randomized order. The experiment was terminated if infants became too inattentive, distressed, started moving excessively, or once they had viewed 25 blocks.

5.2.2.4 ***EEG data acquisition***

EEG was recorded using a 128-channel Hydrocel Geodesic Sensor Net (EGI, Corp., Eugene, OR). Data were sampled at 250 Hz with an analogue band-pass filter of 0.1–100 Hz, and were recorded with the vertex as a common reference. Impedances were kept below 50 kΩ. Synchronous video recordings of the experiment (30 frames per second) were also examined offline to allow exclusion of trials in which the infant was inattentive, and to enable the coding of infant gaze behaviour during the experiment.

5.2.2.5 ***EEG pre-processing and analysis***

After viewing the video recordings and marking periods of inattention using EGI software (NetStation v4.3.1; Electrical Geodesics, Inc., Eugene, OR), EEG data were exported and analysed using the EEGLAB v13.3.2 toolbox (Delorme & Makeig, 2004). The PREP pipeline toolbox was used to identify and interpolate noisy channels, as well as to apply robust average re-referencing (Bigdely-Shamlo et al., 2015). Data were then bandpass filtered at 2-35 Hz. Epochs ranging from 1s before the onset of the observed head turn movement to 2s after movement onset from each trial were extracted. Epochs that contained previously marked periods of inattention and epochs in which more than 15% of channels exceeded +/- 250µV were excluded. A natural-gradient logistic infomax independent component analysis (ICA) was performed on the data (the runica algorithm; Delorme & Makeig, 2004) to decompose the EEG mixed signals into their underlying neural and artefactual components (such as eye and muscle movements). Artefact components were identified and removed using the ADJUST algorithm (v1.1; Mognon et al., 2011), as well as by applying a rejection threshold to the entropy of the activity of each component over all trials (8580), the kurtosis of the activity (82), as well as the kurtosis of the component's spatial map (9.8; Delorme et al., 2001).

To compare power relative to baseline in the mu band, event related spectrums (ERSs) were computed for each condition using built-in EEGLAB procedures. Time-frequency decompositions were computed with a fast Fourier transform using a 1-second Hanning window with 50% overlap in 1Hz bins from 2-30Hz. To make the results comparable with those of other studies, the log spectral power was converted to absolute power, and averaged across the 5-9Hz bins (corresponding to the mu range typically used in research with infants and the mu peak identified at this age: e.g. Cannon et al., 2016; Marshall, Bar-Haim, & Fox, 2002; Marshall, Saby, & Meltzoff, 2013; Nyström, Ljunghammar, Rosander, & von Hofsten, 2011; Nyström, 2008; Berchicci et al., 2011; Southgate & Vernetti, 2014). ERD was calculated as the percentage change in average absolute power over the two time windows: 0-500ms and 500 to 1000ms after the onset of the observed movement, from the condition-specific (averaged across trials in that condition) baseline averaged over -500ms to 0ms (Pfurtscheller & Aranibar, 1979). These time windows were chosen based on visual inspection of ERD scalp maps showing activity averaged over participants (at both ages) and conditions.

ERD in the two time windows was calculated for 7 clusters of electrodes (see Figure 5.2). These were comprised of two lateral central clusters (left hemisphere, right hemisphere) and one medial central cluster, which were located around standard C3, C4, and Cz sites electrodes for mu rhythm recording; two prefrontal clusters (left and right hemisphere) located around standard F3 and F4 electrodes ; and finally, two occipital clusters (left and right hemisphere) located around standard O1 and O2 electrodes to control for visual alpha responses (e.g. de Klerk et al., 2015; Saby et al., 2012; Umiltà et al., 2012). The medial central cluster was selected for analysis, rather than just dividing central electrodes into left and right hemisphere clusters, because it has been recently shown that the neck is represented in the medial motor cortex, rather than laterally as was thought previously (Prudente et al., 2015). The frontal clusters were chosen based on the location of differential activity during observation of congruent and incongruent head-turns (Grossmann et al., 2013).

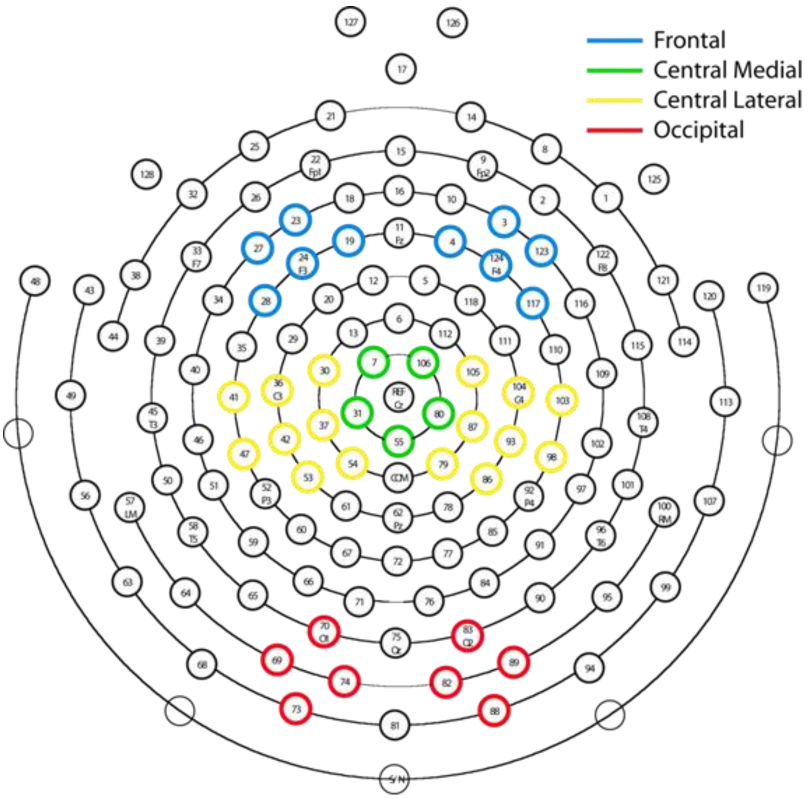

Figure 5.2: Clusters of electrodes used in the ERD analysis

A linear mixed modelling framework was used to investigate the relationship between experimental condition and mu desynchronization in the different clusters of electrodes. This was a two-level (clusters nested within participants) model with random intercepts and by-condition random slopes, with condition (congruent, incongruent, scrambled), cluster (C3, C4, Cmedial, F3, F4, O1, O2), and age (6.5, 9.5) (main effects and interactions) as predictors. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. All *p* values were based on Kenward-Roger's corrected degrees of freedom, and all post-hoc tests were corrected for multiple comparisons using Tukey-Kramer contrasts. The alpha level was set at 0.05.

5.2.2.6 EEG behavioural analysis

Looking time to the monitor and eye movements made in each experimental condition were manually coded from videos recorded during the EEG experiment (30fps) by a researcher blind to the condition being presented. Videos were viewed in real-time and frame-by-frame to accurately identify onsets and offsets of infant attention shifts (eye movements or head turns to the right, centre, left, or off-screen: see Figure 5.3). Unfortunately, although recording of simultaneous eye tracking was attempted during the EEG experiments here, due to serious technical difficulties and the general challenges presented by infant eye tracking research (especially in addition to EEG), not a lot of usable data was obtained. However, as some of the participants did have good data, the whole sample of videos was coded by hand and reliability with the eye tracker calculated: a Tobii (Stockholm, Sweden) TX300, which has a sampling rate of 300 Hz. To do this, eye tracking data from a random 10% of participants with EEG data at each age were compared to the manually coded data. Excellent reliability scores were obtained for both the 6.5 month (time-unit κ = 0.97-0.98, event κ = 0.83) and 9.5 month (time-unit κ= 0.98-0.99, event κ = 0.90) experiments, indicating that the manually coded data reflected an accurate representation of the variables of interest.

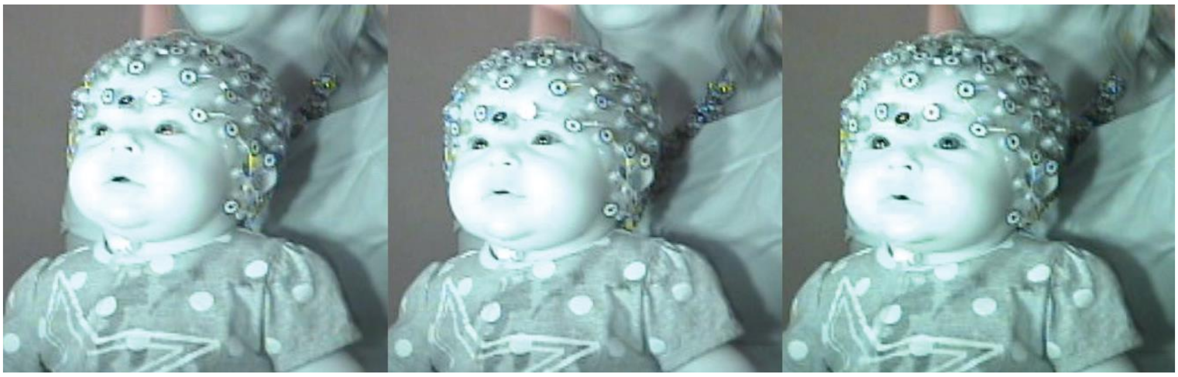

Figure 5.3: Examples of the different eye movements coded during EEG experiments. The left column shows a fixation to the right, the middle column a central fixation, and right column a fixation to the left.

To ensure any neural findings did not merely reflect differences in looking time towards the screen or variations in gaze behaviour during the three experimental conditions, repeated measures ANOVAs (condition as a within-participant factor: congruent, incongruent, scrambled) were conducted on the manually coded eye movement data.

5.2.3 MOTHER-INFANT INTERACTION METHODS

5.2.3.1 Participants

38 (22 male, 16 female) infants took part in this portion of the study at both 3.5 months postpartum (infant age: M = 112.87 days, SD = 5.61) and 6.5 months postpartum (infant age: M = 199.95, SD = 5.50) with their mothers. The infants who took part in the EEG experiment described above were from this same group (i.e. those participating in the longitudinal research programme outlined in Chapter 3).

5.2.3.2 ***Design and Procedure***

During visits to the University of Reading at both 3.5 and 6.5 months of age, infants were observed interacting face-to-face with their mothers for 3 minutes (see Figure 5.4). During these interaction periods, dyads were seated in a small booth (constructed out of poster boards) measuring 144 × 160cm, with 6 colourful toys attached to the walls. Mothers and infants were seated face-to-face; mothers on a chair, and infants in an adjustable highchair suitable for use with both age groups. Dyads were centred in the booth approximately 55 cm apart (see Figure 5.5 for booth dimensions). This set-up was chosen in order standardise and simplify the environment in which dyads interacted, as well as to provide ample opportunity for the attention events of interest (i.e. those that may strengthen visuomotor mappings characteristic of a mirror system) to occur.

Figure 5.4: Examples of the interaction set-up at the University and dyads looking around the booth.

The 6 colourful toys attached to the walls varied slightly from one another, but were comparable in salience, i.e., terms of size, colour, and pattern (toy position labels can be found in Figure 5.6). One camera was used to capture a full-on view of the infant's face, and a second camera was used to capture a full-on view of the mother's face. These videos were later synchronized for behavioural coding.

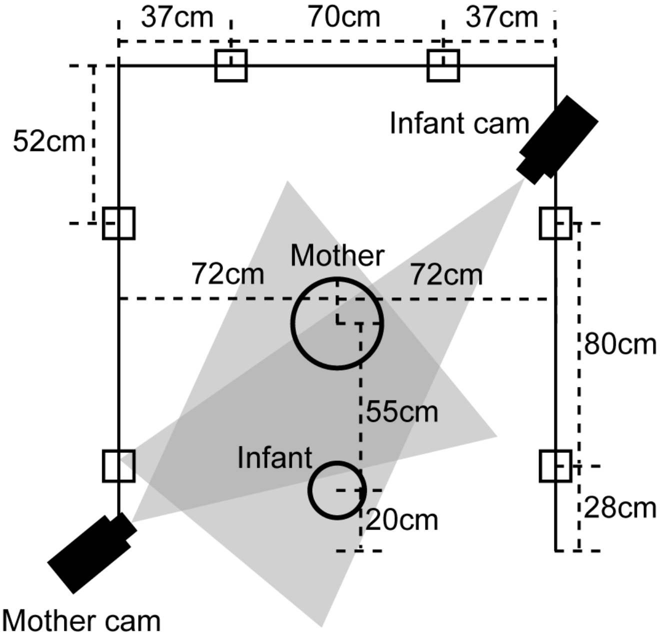

Figure 5.5: Booth set-up and dimensions. Empty squares represent the locations of toys hanging on the walls. Shaded areas represent the field of view of mother and infant cameras.

5.2.3.3 *Coding of mother-infant interaction videos*

A coding scheme was developed to identify instances of mother and infant attention-related behaviours during face-to-face interactions, with videos coded on a frame-by-frame (25fps) time base. For both infant and mother, the direction and target of gaze were coded for each frame of the video, as well as any head turns**.** Direction was specified in the horizontal and vertical dimensions as one of several discrete categories (see Figure 5.6). The gaze target was coded as one of several options such as left toy/mother's face/highchair (i.e. main features of the environment), ambiguous (i.e. target of gaze did not correspond to one of the available options, but the participant was clearly looking at something), or unknown (i.e. when an infant's eyes were unfocused/closed or a participant's face was occluded)**.** If the infant or mother were clearly looking at something that was not one of the pre-determined target categories, and the actual target was hence selected as ambiguous, the horizontal and vertical direction was still specified so it could still be known if the two social partners attended in the same direction. When the infant or mother's head was turning, no direction or target was coded as this could be determined from the directions and targets before and after the head-turn (i.e. frames were coded simply as ‘head turning’). More details about this coding scheme can be found in Appendix B, section 9.3.

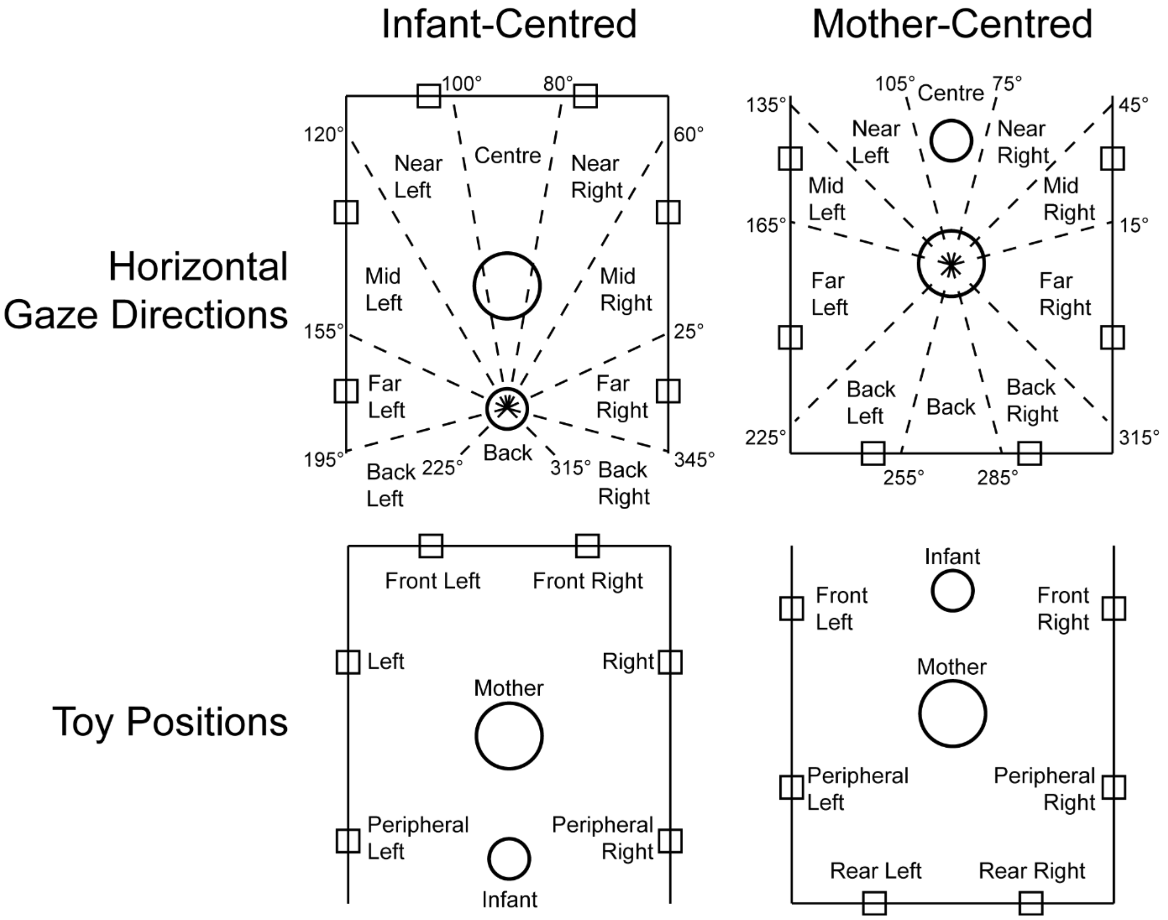

Figure 5.6: The top row shows the horizontal gaze direction codes for the infant (left) and mother (right). The bottom row shows the toy position codes for toys hanging on the walls, both for infant (left) and mother (right).

5.2.3.3.1 ***Reliability***

To determine reliability of the interaction coding, one researcher coded the whole sample of videos, and another independent researcher coded a random 10% of the videos at each age of assessment. Both were blind to the EEG results. This revealed very good reliability scores at each assessment for both mother and infant. These scores can be found in Table 5.2.

Table 5.2: Kappas for interaction measures at 6.5 and 9.5 month assessments

Infant	**3.5 month assessment**	**6.5 month assessment**
Horizontal direction	Time-unit κ = 0.90-0.91 Event κ = 0.91	Time-unit κ = 0.82-0.84 Event κ = 0.80
Vertical direction	Time-unit κ = 0.89-0.89 Event κ = 0.90	Time-unit κ = 0.88-0.92 Event κ = 0.86
Target	Time-unit κ = 0.83-0.83 Event κ = 0.85	Time-unit κ = 0.85-0.97 Event κ = 0.84

Mother		
Horizontal direction	Time-unit κ = 0.98-0.98 Event κ = 0.95	Time-unit κ = 0.88-0.88 Event κ = 0.89
Vertical direction	Time-unit κ = 0.96-0.98 Event κ = 0.93	Time-unit κ = 0.88-0.90 Event κ = 0.89
Target	Time-unit κ = 0.95-0.96 Event κ = 0.93	Time-unit κ = 0.87-0.87 Event κ = 0.88

5.2.3.4 Deriving attention events from the manual coding to relate to the EEG data

Here, interest was specifically on actions (or 'attention events') hypothesized to strengthen mappings between own and other direction of attention. As such, the key attention states selected for investigation were: *'infant follow mother'* (per mother gaze shift observed), '*mother follow infant*' (per infant gaze shift observed), and *'infant sees mother follow'* (per mother follow). 'Infant follow mother' was defined as the infant looking at the mother's face as she looked toward an object/in a certain direction, followed by the infant attending to the same thing/in the same direction without attending to any other objects/directions in between. 'Mother follow infant' was defined as the infant looking towards an object/in a certain direction and the mother looking at the infant's face, followed by the mother looking at the same object/the same direction as the infant. 'Infant sees mother follow' was defined as the infant looking towards an object/in a certain direction, followed by looking back at the mother within 3 seconds of their original attention shift, and seeing the mother looking at the same object/turning to look at the same object they just did. The 3 second time limit was used because infants of this age do not detect contingencies beyond this period (Gergely & Watson, 1999; Striano et al., 2005). Normalizing by gaze shifts observed and frequency of 'mother follow infant' enabled controlling for the opportunity infants had to engage in the behaviours of interest. 'Infant follow mother' could help strengthen visuomotor mappings by allowing the infant to see the mother perform an action and then perform it themselves (Triesch, Jasso, & Deak, 2007). Alternately, 'mother follow infant' could strengthen such mappings by increasing periods of shared attention and providing the infant with increased opportunities to observe the mother looking in the same direction they just did. However, one cannot be certain in this case that infants notice their mother following them, so the latter possibility was also specifically tested for by looking at 'infant sees mother follow', and normalizing by the frequency of 'mother follow infant'; which relies not only on the mother's behaviour, but also on the infant orienting toward the mother after she has followed their direction of attention. This may help strengthen visuomotor mappings by allowing the infant to observe mothers execute an action they just performed. For example, if this strengthening occurred via a Hebbian learning process, 'infant sees mother follow' would result in a motor trace of what the infant just did (i.e. shifted their attention towards an object) overlapping with the visual perception of the mother shifting her attention in the same way, and thus potentiating synapses between the visual and motor neural populations. As such, rather than happening occasionally in an accidental manner, this would depend based on contingency, and thus takes advantage of maternal behaviours versus infant random behaviour. These attention events were derived from combinations of frame-by-frame events that occurred in a particular order (see Appendix B, section 9.3 for more details).

In addition to the key attention events described above, the effect of '*infant gaze shifts per minute'* and '*observed mother gaze shifts per minute*' were also investigated to control for the possibility that simply performing or observing more or fewer gaze shifts had an effect on the EEG results. How all these behaviours during early interactions might predict EEG results at 6.5 and 9.5 months could then be considered, as well as the effect they might have on mu ERD concurrently at 6.5 months.

5.2.3.5 Analysis of interaction data: Linking to the EEG results

A linear modelling framework was used to investigate the relationship between the early interaction data and mu desynchronization in two electrode clusters of interest: a central electrode cluster (C3/Cmedial combined) and a left frontal electrode cluster (F3), with mu ERD (congruent minus incongruent condition) as the dependent variable. This was determined by the results from the EEG analysis (see Section 5.3.2. for details). Separate analyses were run for the central and frontal cluster.

The first analysis tested the influence of the interactions in the assessment at time t on the EEG results in the assessment at time t+1 (i.e. 3.5 month interactions were paired with 6.5 month EEG data, and 6.5 month interactions with 9.5 month EEG data). Separate linear mixed models were run in order to confirm that ‘infant gaze shifts’ and ‘observed mother gaze shifts’ alone were not related to mu ERD in central and frontal clusters. A random intercept (subject-specific) linear mixed model was used for the main analysis, with main effects of EEG age (6.5 and 9.5 months) and the coded mother-infant interaction measures from the previous assessment (‘infant follow mother’, ‘mother follow infant’, ‘infant sees mother follow’) included as predictors, as well as interactions between each coded measure and EEG age. Note, in order confirm that all the interaction variables should be included in the analysis, collinearity between them was tested via calculation of the variance inflation factor (VIF). This confirmed that none of the variables had a collinearity problem (all VIF < 2), and thus were retained in the model. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. All *p* values were based on Kenward-Roger's corrected degrees of freedom, and any significant interactions were followed up with Wald chi-squared tests to see if coefficients at each level of EEG age were significantly different from 0. The alpha level was set at 0.05.

The second analysis used a linear model to test possible concurrent effects of interactions at 6.5 months on the EEG results at 6.5 months. Again, separate linear models were run in order to confirm that ‘infant gaze shifts’ and ‘observed mother gaze shifts’ alone were not related to mu ERD in central and frontal clusters. The main analysis used a linear model with coded mother-infant interaction measures from the concurrent assessment (‘infant follow mother’, ‘mother follow infant’, ‘infant sees mother follow’) included as predictors. None of the variables had a collinearity problem (all VIF < 2), and visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality.

5.2.3.6 Questionnaires

At the 3.5 and 6.5 month assessments, mothers completed the ‘Edinburgh Postnatal Depression Scale’ (EPDS). At 6.5 and 9.5 month assessments (the latter was actually completed at a 9 month visit, but was not repeated at 9.5 months because of the short gap between the two assessments), mothers completed the ASQ-3, a questionnaire designed to score general infant development on a number of scales (e.g. gross and fine motor development). More details on the questionnaires used in the longitudinal research programme as a whole can be found in Chapter 3. As in Chapter 4, the questionnaires were examined here to make sure variables measured by these did not account for differences in putative infant mirror system activity. As such, the potential relationship between EPDS scores and infant mu ERD was explored, as was the relationship between scores on the various ASQ-3 scales and infant mu ERD, for all infants included in the early interaction/EEG analysis.

5.3 RESULTS

Below, findings from the EEG experiments will be presented first, followed by the results from the interaction/EEG analysis.

5.3.1 EEG: BEHAVIOURAL CODING

No significant differences were found in the amount of time spent looking at the screen during each condition at 6.5 months [*F*(2, 44) = 2.07, *p* = 0.14, η_p^2 = 0.09], or 9.5 months [*F*(2, 36) = 0.65, *p* = 0.28, η_p^2 = 0.02]. The number of participant attention shifts (i.e. to the left, right, and centre of the screen) made during the three experimental conditions was also investigated using repeated measures ANOVAs (with the same within-participant factors), which revealed significant differences between conditions at 6.5 months [*F*(1.35, 29.65) = 6.84, *p* = 0.008, η_p^2 = 0.24, ε = 0.67], but not at 9.5 months [*F*(2, 36) = 0.04, *p* = 0.96, η_p^2 = 0.002]. Pairwise comparisons at 6.5 months revealed that infants made more attention shifts during the scrambled condition than either the congruent (*p* = 0.03) or incongruent conditions (*p* = 0.03). Thus, neither the time spent looking at the screen, nor the number of attention shifts made during the three experimental conditions could account for any EEG differences found between the congruent and incongruent conditions at 6.5 months or any conditions at 9.5 months.

Additionally, the same repeated measures ANOVAs were conducted with the proportion of trials where infants looked back to the face (centre) after being cued to look at one of the two objects (left, right), and the percentage of trials where the infants' next look was in the direction the adult was attending to. This revealed that infants almost exclusively looked back to the face/scrambled stimuli after attending to the cued object (6.5 months, M = 98.94%, SD = 2.63; 9.5 months, M = 98.81%, SD = 2.43), with no significant differences found between conditions at 6.5 [*F*(2, 44) = 0.37, *p* = 0.96, η_p^2 = 0.002] or 9.5 months [*F*(1.19, 21.47) = 1.37, *p* = 0.26, η_p^2 = 0.07, ε = 0.60]. In the analysis of the proportion of trials infants next looked in the direction attended to by the adult, a main effect of condition was revealed at 6.5 [*F*(2, 44) = 4.19, *p* = 0.02, η_p^2 = 0.16] and 9.5 [*F*(2, 36) = 4.87, *p* = 0.01, η_p^2 = 0.21] months, however pairwise comparisons (Bonferroni corrected) demonstrated that there was only a significant difference between the congruent and scrambled conditions, with infants looking in the same direction attended to by the adult face in the congruent condition more than in the direction of motion in the scrambled condition (6.5 months, *p* = 0.02:

9.5 months, *p* = 0.001). Therefore, differences in the amount infants looked back towards the face could not account for any EEG differences found between conditions, and a difference between the numbers of times infants followed the adult's gaze could not account for any differences between congruent and incongruent conditions.

5.3.2 MAIN EEG RESULTS: ERD

To be included in the analyses below, infants were required to have a minimum of five trials per condition after pre-processing of the EEG data (in keeping with other infant mu rhythm studies: e.g. Marshall et al., 2011, 2013; Cannon et al., 2016). This left a total of 23 infants at 6.5 months and 19 infants at 9.5 months, with an average of 11.43 (SD = 3.44) trials per condition at 6.5 months (congruent, M = 11.48, SD = 3.44; incongruent, M = 10.78, SD = 3.54; scrambled, M = 12.04, SD = 1.55) and 12.49 (SD = 3.33) trials at 9.5 months (congruent, M = 12.53, SD = 3.63; incongruent, M = 12.05, SD = 3.54; scrambled, M = 12.89, SD = 3.43). Before comparing conditions and clusters to each other, analyses were conducted to establish whether mu desynchronization occurred relative to the baseline period. There was little modulation of mu ERD by condition in the 0-500ms time window (see Appendix C, section 10.5), so only results in the 500-1000ms are presented below.

At 6.5 months, in the ***500-1000ms*** time window (see Figure 5.7, left), significant mu desynchronization was found for the congruent condition in the left central cluster (C3) [*t*(22) = -4.46, *p* < 0.001], right central cluster (C4) [*t*(22) = -3.17, *p* < 0.01], medial cluster (Cmedial) [*t*(22) = -3.05, *p* < 0.0005], left prefrontal cluster (F3) [*t*(22) = -3.71, *p* < 0.005], and right prefrontal cluster (F4) [*t*(22) = -2.67, *p* < 0.05]. Significant desynchronization was also found for the incongruent condition in C4 [*t*(22) = -4.42, *p* < 0.0005] and in F3 [*t*(22) = -4.78, *p* < 0.0001]. There was no significant mu desynchronization for this time bin in either occipital cluster (O1 and O2) relative to baseline for congruent or incongruent conditions, and no significant desynchronization was found in any region for the scrambled condition.

At 9.5 months, during the ***500-1000ms*** time window (Figure 5.7, right), significant mu desynchronization was found for the congruent condition in C3 [*t*(18)= -3.34, *p* < 0.005], Cmedial [*t*(18) = -3.82, *p* < 0.005], F3 [*t*(18) = -9.10, *p* < 0.0001], and F4 [*t*(18) = -2.71, *p* < 0.05]. There was no significant mu desynchronization relative to baseline in any cluster for incongruent or scrambled conditions, and no significant desynchronization was found in O1 or O2 for any condition.

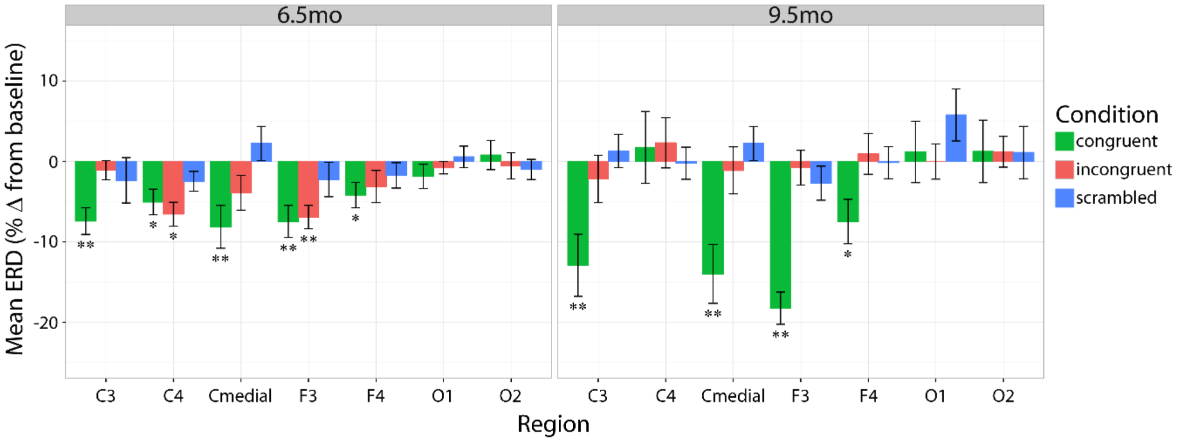

Figure 5.7: Changes in mu power at 500-1000ms for each electrode cluster, in each condition, at 6.5 months (left) and 9.5 months (right). Asterisks indicate where the percentage change is significantly different from baseline (** p<0.001, * p < 0.05). Error bars indicate +/- SE.

At <u>500-1000ms</u>, the linear mixed model revealed significant main effects of condition [$F(2,28.62) = 5.82$, $p = 0.008$], region [$F(6,14.33) = 7.22$, $p < 0.0001$], and age [$F(1,37.84) = 4.67$, $p = 0.03$]. These results were qualified by significant condition × region [$F(12,21.80) = 3.52$, $p < 0.0001$], condition × age [$F(2,37.04) = 3.02$, $p = 0.05$], and region × age [$F(6, 44.11) = 2.27$, $p = 0.04$] interactions, which were followed up with planned pairwise comparisons (see Table 5.3). For the ***condition × region interaction***, significantly more mu desynchronization was found in C3, Cmedial, and F3 for congruent compared to incongruent [C3: $t(14.61) = -3.24$, $p < 0.005$; Cmedial: $t(14.61) = -3.26$, $p < 0.005$; F3: $t(141.61) = -3.42$, $p < 0.005$], and congruent compared to scrambled conditions [C3: $t(126.74) = -3.60$, $p < 0.005$; Cmedial: $t(126.74) = -4.90$, $p < 0.0001$; F3: $t(126.74) = -3.828$, $p < 0.0001$]. For the ***condition × age interaction,*** significantly less desynchronization for the incongruent condition was found at 9.5 compared to 6.5 months [$t(342.11) = -2.90$, $p < 0.005$]. At ***9.5 months***, there was significantly more mu desynchronization in the congruent compared to incongruent [$t(54.29) = -3.39$, $p < 0.005$], and congruent compared to scrambled conditions [$t(48.2) = -3.66$, $p < 0.005$]. For the ***region × age interaction***, there was significantly less mu desynchronization in C4 at 9.5 months compared to at 6.5 months [$t(444.87) = -3.51$, $p < 0.0005$]. At ***6.5 months***, there was only significantly more mu desynchronization in F3 compared to O2 [$t(324.07) = -3.06$, $p < 0.05$], but at ***9.5 months***, there was significantly more desynchronization C3 compared to C4 [$t(336.8)=-3.09$, $p < 0.05$], O1 [$t(336.8)= -3.60$, $p < 0.01$], and O2 [$t(336.8) = -2.99$, $p < 0.05$], significantly more desynchronization in Cmedial compared to O1 [$t(336.8) = -3.45$, $p < 0.02$], and significantly more mu desynchronization in F3 compared to O1 [$t(336.8) = -4.92$, $p < 0.0001$] and O2 [$t(336.8) = -4.31$, $p < 0.0005$]. In Figure 5.8, a time-frequency plot is shown, illustrating the mu rhythm desynchronization that occurred in C3 during observation of the congruent, incongruent, and scrambled conditions, at both 6.5 and 9.5 months of age. Figures for the other clusters can be found in Appendix C, section 10.6.

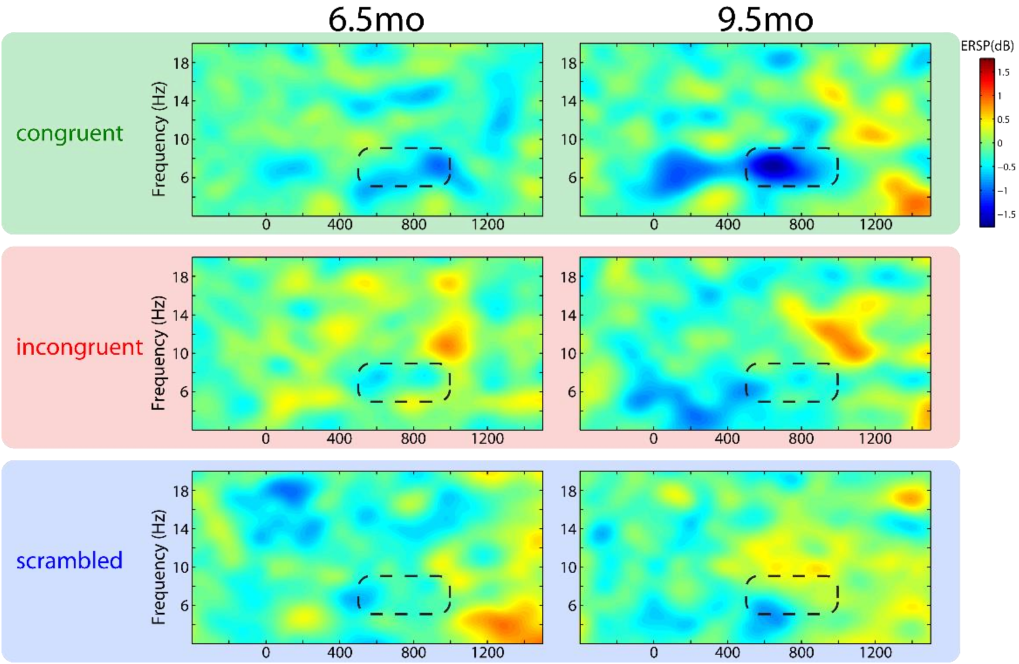

Figure 5.8: Time-frequency plot showing the pattern of activity in C3 during the congruent, incongruent, and scrambled conditions at 6.5 and 9.5 months. The plot shows baseline-corrected activity averaged over all the electrodes in that cluster, and over all infants in each condition. Zero represents the onset of the analysis period (i.e. when adults first started to turn their heads in the experimental stimuli). The dotted lines highlight the modulation of mu (5-9Hz band) during the 500-1000ms analysis period.

Table 5.3: Results from the linear mixed model used to investigate the relationship between condition and mu desynchronization at each age

Main effects	Interactions	Follow-ups
Condition [$F(2,28.62)=5.82$, $p = 0.008$] *Region* [$F(6,141.33)=7.22$, $p < 0.0001$] *Age* [$F(1,372.84)=4.67$, $p = 0.03$]	*condition × region* [$F(12,209.80)=3.52$, $p < 0.0001$]	*C3 congruent > C3 incongruent*: [$t(141.61)=-3.24$, $p < 0.005$] *C3 congruent > C3 scrambled*: [$t(126.74)=-3.60$, $p < 0.005$] *Cmedial congruent > Cmedial incongruent*: [$t(141.61)=-3.26$, $p < 0.005$] *Cmedial congruent > Cmedial scrambled*: [$t(126.74)=-4.90$, $p < 0.0001$] *F3 congruent > F3 incongruent*: [$t(141.61)=-3.42$, $p < 0.005$] *F3 congruent > F3 scrambled*: [$t(126.74)=-3.83$, $p < 0.0001$] *C3 congruent > C4, O1, O2 congruent*: C4 [$t(140.66)=-3.69$, $p < 0.01$], O1 [$t(140.66)=-4.09$, $p < 0.001$], O2 [$t(140.66)=-4.65$, $p < 0.0001$] *Cmedial congruent > O1, O2 congruent*: O1 [$t(140.66)=-4.44$, $p < 0.0005$], O2 [$t(140.66)=-5.00$, $p < 0.0001$] *F3 congruent > O1, O2 congruent*: O1 [$t(140.66)=-5.18$, $p < 0.0001$], O2 [$t(140.66)=-5.74$, $p < 0.0001$] *C4 congruent < Cmedial, F3 congruent*: Cmedial [$t(140.66)=4.04$, $p < 0.005$], F3 [$t(140.66)=4.78$, $p < 0.0001$]
	condition × age [$F(2,370.04)=3.02$, $p = 0.05$]	*Incongruent 9.5 months < incongruent 6.5 months*: [$t(342.11)=-2.90$, $p < 0.005$] *Congruent 9.5 months > incongruent 9.5 months, scrambled 9.5 months*: Incongruent [$t(54.29)=-3.39$, $p < 0.005$], Scrambled [$t(48.20)=-3.66$, $p < 0.005$]
	region × age [$F(6, 443.11)=2.27$, $p = 0.04$]	*C4 9.5 months < C4 6.5 months*: [$t(444.87)=-3.51$, $p < 0.0005$] *F3 6.5 months > O2 6.5 months*: [$t(324.07) = -3.06$, $p < 0.05$] *C3 9.5 months > C4, O1, O2 9.5 months*: C4 [$t(336.8)=-3.09$, $p < 0.05$], O1 [$t(336.8)=-3.60$, $p < 0.01$], O2 [$t(336.8)=-2.99$, $p < 0.05$] *Cmedial 9.5 months > O1* 9.5 months: O1 [$t(336.8)=-3.45$, $p < 0.02$] *F3 9.5 months > O1, O2 9.5 months*: O1 [$t(336.8)=-4.92$, $p < 0.0001$], O2 [$t(336.8)=-4.31$, $p < 0.0005$] *C4 9.5 months < F3 9.5 months*: [$t(336.8)=4.42$, $p < 0.0005$]

The previous analysis included congruent and incongruent motion directions within the scrambled control. In order to confirm that the lack of mu desynchronization found in this condition was not simply due to the congruent and incongruent stimuli cancelling each other out, an additional analysis was performed using the same linear mixed model as above to compare mu desynchronization during observation of the scrambled congruent compared to scrambled incongruent stimuli. 15 infants at 6.5 months and 14 infants at 9.5 months were included in this analysis, who had viewed a minimum of five scrambled congruent and five scrambled incongruent trials each. The average number of trials per infant was 7.07 (SD = 1.53) at 6.5 months (scrambled congruent, M = 6.60, SD = 1.56; scrambled incongruent, M = 7.53, SD = 1.88) and 7.32 (SD = 0.72) at 9.5 months (Scrambled congruent, M = 7.71, SD, 1.07; scrambled incongruent, M = 6.93, SD, 1.59). This revealed no significant differences between the conditions, confirming that the differences seen in the main congruent and incongruent head turn conditions are due to observation of the head turn itself and not just congruent or incongruent motion (Figure 5.9). Additionally, based on the manual coding of attention shifts during the EEG experiment, there were no differences between the congruent and incongruent scrambled conditions in the proportion of trials infants looked back at the scrambled face after looking at the cued object [6.5 months: *t*(22) = 1.80, *p* = 0.09; 9.5 months: *t*(18) = -1.82, *p* = 0.09], nor were there any differences in the proportion of trials in which infants then followed the direction of motion [6.5 months: *t*(22) = -1.15, *p* = 0.26; 9.5 months: *t*(18) = 1.14, p = 0.27].

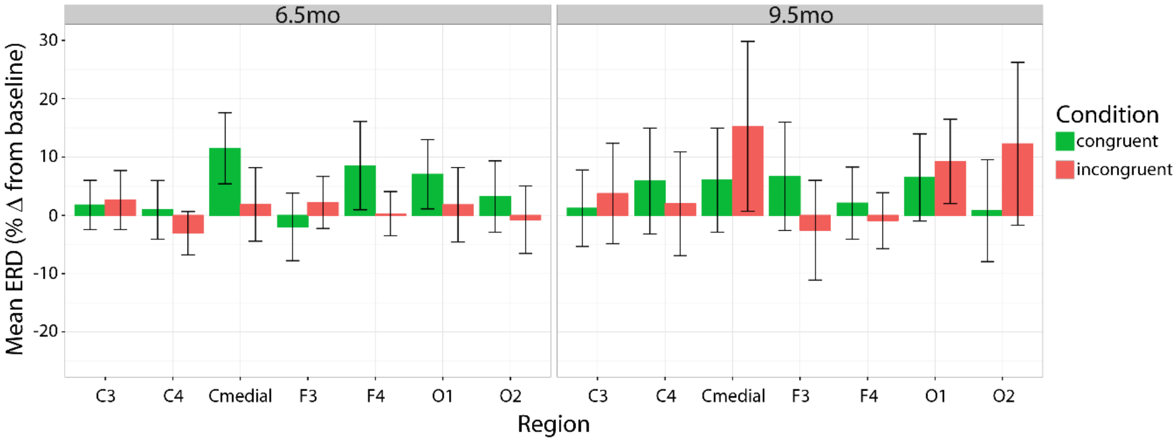

Figure 5.9: Changes in mu power at 500-1000ms for each electrode cluster in the congruent and incongruent scrambled conditions. Asterisks indicate where the percentage change is significantly different from baseline (p < 0.05). Error bars indicate +/- SE.

5.3.3 LINK BETWEEN EARLY FACE-TO-FACE INTERACTIONS AND EEG

5.3.3.1 Descriptive statistics and changes in attention-related behaviour over time

At 3.5 months, two dyads had to be excluded due to infant distress during the 3 minute interaction period, leaving a sample of 36 (infants: 21 male, 15 female). All 38 dyads completed the interaction period at 6.5 months. Before exploring how any interaction measures might have influenced the neural activity measured in the EEG experiments, some basic exploratory analyses were conducted to illustrate how dyads tended to behave during the interaction periods at the different ages, and to determine whether findings were consistent with previous research.

Figures 5.10-13 show the average amount of time infants and mothers spent looking towards different targets in the environment, the number of attention shifts each partner made, and the time dyads spent in various ‘attention states’. Means and standard deviations can be found in Tables 5.4-6. T-tests, Wilcoxon signed-rank tests, repeated measures ANOVAs, Pearson’s correlation coefficients, and Kendall’s tau were used to compare any differences and explore relationships between the two time points, depending on whether variables were normally distributed.

Table 5.4: Mean (SD) time infants spent attending to different targets/turning their heads, and number of attention shifts infants made per minute at 3.5 and 6.5 months

	3.5 months	**6.5 months**
Wall toys	31.47% (26.35)	40.17% (19.03)
Other objects	1.79% (7.43)	10.95% (12.93)
Ambiguous	5.03% (5.38)	3.36% (3.24)
Mother’s face	33.89% (23.38)	22.67% (13.57)
Mother (not face)	9.15% (11.50)	4.59% (4.40)
Self	11.58% (10.03)	4.64% (6.90)
Head turns	5.78% (3.34)	13.56% (4.64)
Unknown	1.31% (3.24)	0.07% (0.31)
Overall number of attention shifts	21.30 (7.73)	33.65 (9.25)
Number of eye movements	9.13 (4.63)	7.40 (3.19)
Number of head turns	12.17 (6.75)	26.25 (8.81)

Table 5.5: Mean (SD) time mothers spent attending to different targets /turning their heads, and number of attention shifts per minute at 3.5 and 6.5 months

	3.5 months	**6.5 months**
Wall toys	6.16% (8.06)	11.57% (10.24)
Other objects	0.55% (1.51)	1.79% (7.43)
Ambiguous	0.52% (1.18)	0.61% (0.70)
Infant's face	79.19% (11.60)	69.94% (12.80)
Infant (not face)	6.16% (5.00)	5.43% (5.03)
Self	0.48% (1.37)	0.43% (0.84)
Head turns	6.25% (4.88)	8.73% (5.69)
Unknown	0.14% (0.59)	0% (0)
Overall number of attention shifts	21.51 (9.37)	27.59 (8.91)
Number of eye movements	11.11 (7.85)	12.09 (6.77)
Number of head turns	10.40 (7.74)	15.50 (9.81)

In Figure 5.10, the amount of time infants spent looking at different targets can be found. The time infants spent attending to their mothers' face was found to decrease significantly between 3.5 and 6.5 months [$p = 0.02$]. By corollary, infants appeared to increase time looking towards objects other than the mother's face between 3.5 and 6.5 months (e.g. wall toys, other objects, and ambiguous combined: [$p = 0.002$] and spent more time turning their heads to attend to different features of the environment [$p < 0.0001$]. This is in keeping with previous research showing that around 4-5 months of age, infants start to look at others' faces much less than they did previously, and instead, look increasingly towards other objects in their visual field and toys/body parts introduced into games by a social partner (Cohn & Tronick, 1987; Murray, 2014).

Mothers (Figure 5.11) spent the majority of time looking at their infant's face at both 3.5 and 6.5 months, although this did decrease significantly between the two time points [$p < 0.0001$]. Although less than the infant, the time that mothers spent attending to other environmental features (wall toys, other objects, ambiguous: [$p = 0.001$]) and head turning [$p = 0.002$] also increased from 3.5 to 6.5 months. This again corroborates findings from other studies that have investigated the targets of mother and infant attention during early interactions at these stages in infant development (Brazelton, Koslowski, & Main, 1974; Cohn & Tronick, 1987; Deák et al., 2014).

Interestingly, for infants, there were no significant correlations (all $p < 0.14$) between the measures mentioned above (attention to social partner's face, other environmental features, or head turning) at 3.5 and 6.5 months (i.e. the measure at the first time point was not correlated with the same measure at the second). For the mothers, however, there was a significant correlation between the two time points for all three of these measures (all $p < 0.02$). This suggests that, whereas measures were more dependent on the specific age investigated for infants, they represent more pervasive characteristics of the mother's own interaction style. Similar results have been found in other research that has looked at the influence of early mother-infant interactions on infant joint attention (Gaffan et al., 2010), with maternal behaviour, rather than infant characteristics, found to specifically influence development.

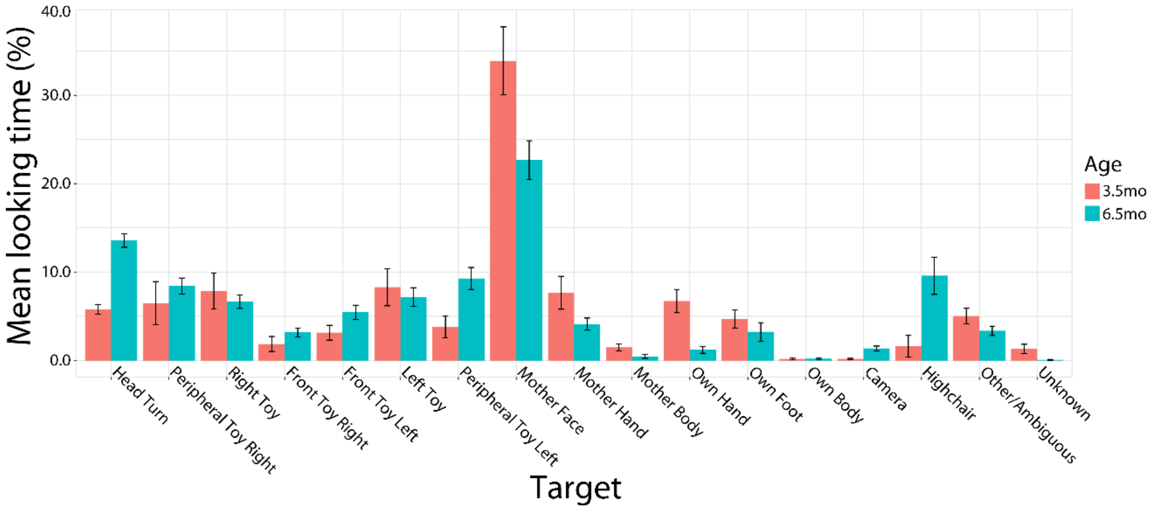

Figure 5.10: Time infants spent attending to different targets at 3.5 and 6.5 months.

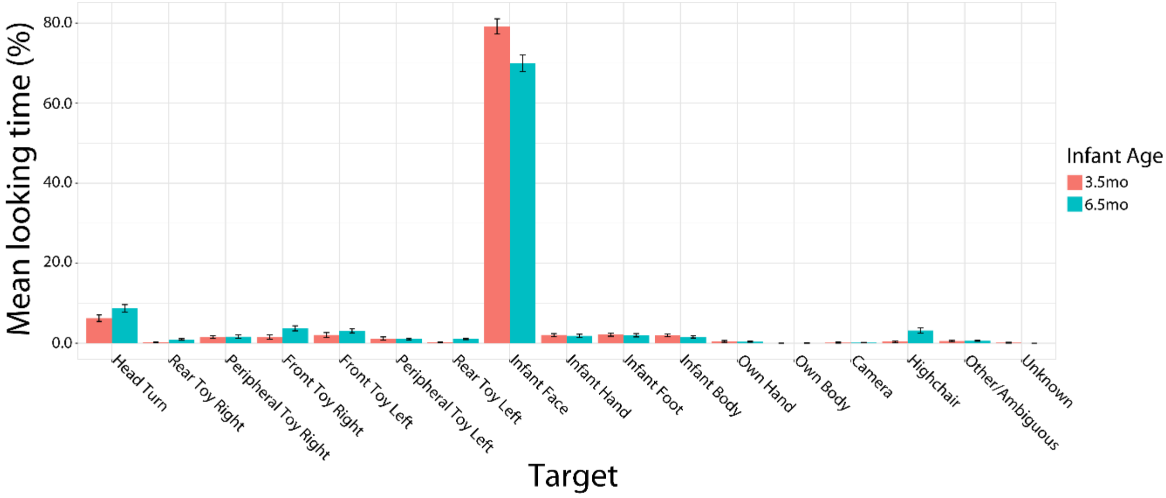

Figure 5.11: Time mothers spent attending to different targets at 3.5 and 6.5 months.

Figure 5.12 shows the number of attention shifts made per minute made by infants (left) and mothers (right). This includes eye movements (i.e. shifts in attention signalled by movement of the eyes only), head turns (i.e. shifts in attention signalled by head movement), and overall attention shifts (both eye movements and head turns). The overall number of attention shifts increased between 3.5 and 6.5 months for both infants [$p < 0.0001$] and mothers [$p < 0.0001$], with the number of head turns specifically increasing over time [infants, $p < 0.0001$]; mothers, $p < 0.0001$]. The number of attention shifts overall per minute actually seem very similar in both mothers and infants (3.5 months; infants, M = 21.30, SD = 7.73, and mothers, M = 21.51, SD = 9.37: 6.5 months; infants, M = 33.65, SD = 9.25, and mothers, M = 27.59, SD =8.91). Therefore, although mothers seemed to spend less time overall looking away from the infant than the infant did looking away from their mother, the frequency of attention shifts made by both partners appears comparable. Again, there were no significant correlations between these attention shift measures at the two ages for infants (all $p > 0.12$), but there were for all three measures in mothers (all $p < 0.01$), suggesting the number of attention shifts reflected a more long-lasting feature of maternal interaction style/individual differences, but specific developmental milestones for the infant.

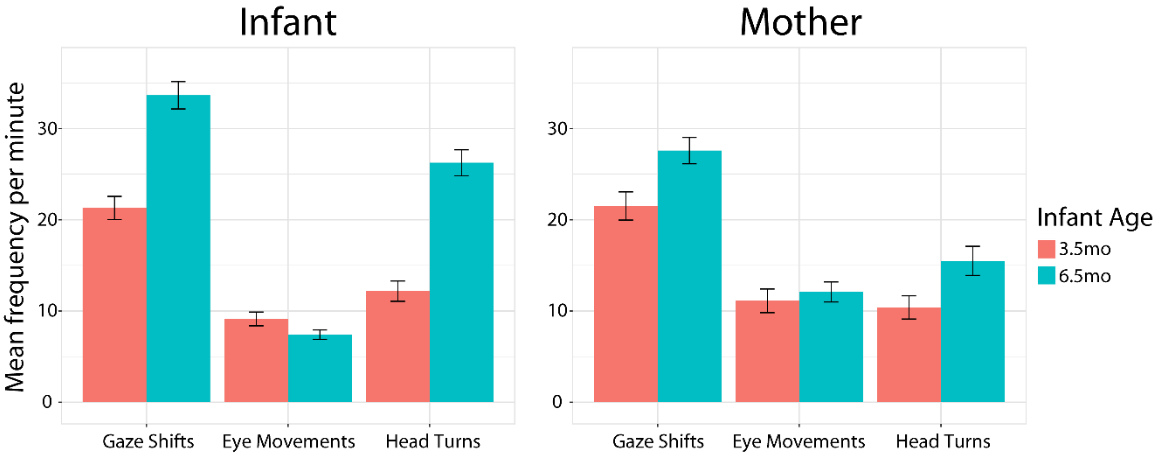

Figure 5.12: Shifts in attention (overall, eye movements-only, and head-turns) made by infants (left) and mothers (right) at 3.5 and 6.5 months.

A number of 'attention states' were also derived from the raw data, based on the coded target/direction of both mother and infant (see Figure 5.13). 'Shared gaze' here refers to periods where infant and mother attended to the same focus (but not to each other's face); 'mutual gaze' to periods where mother and infant were looking towards one another's face; 'different gaze' where the two partners were attending to different focuses (not including faces); 'infant face mother other' where infants looked at their mother's face while she looked elsewhere; and finally, 'mother face infant other' where mother's looked at their infant's face while the infant looked somewhere else (see Table 5.6).

Table 5.6: Mean (SD) time dyads spent in different attention states at 3.5 and 6.5 months

	3.5 months	**6.5 months**
Shared gaze	4.96% (5.58)	10.08% (6.59)
Mutual gaze	29.73% (21.37)	19.24% (12.94)
Different gaze	5.89% (3.91)	6.96% (3.25)
Infant face mother other	2.59% (2.79)	1.81% (1.38)
Mother face infant other	45.22% (18.30)	40.57% (10.58)

A 2 (age) × 5 (attention state) repeated measures ANOVA was conducted on these derived states to investigate how time spent in these states changed from 3.5 to 6.5 months. This revealed significant main effects of both age [$F(1, 35) = 68.54$, $p < 0.0001$, $\eta_p^2 = 0.66$] and attention state [$F(1.72, 60.03) = 129.15$, $p < 0.0001$, η_p^2 , 0.79, $\varepsilon = 0.43$], as well as an age × state interaction [$F(1.21, 42.21) = 4.86$, $p = 0.03$, η_p^2 , 0.12, $\varepsilon = 0.30$]. Pairwise comparisons (Bonferroni corrected) revealed that there was significantly more shared gaze at 6.5 compared to 3.5 months ($p < 0.0001$), and significantly less mutual gaze at 6.5 compared to 3.5 months ($p = 0.01$). At 3.5 months, there was less shared gaze than mother face infant other ($p < 0.0001$), significantly more mutual gaze than any other state (all $p < 0.0001$) apart from mother face infant other, and significantly less different gaze than mutual gaze and mother face infant other (both $p < 0.0001$). There was also more different gaze than infant face mother other ($p = 0.006$), significantly less infant face mother other than all other states (all $p < 0.01$) apart from shared gaze, and significantly more mother face infant other than all other states (all $p < 0.0001$) apart from mutual gaze. At 6.5 months, there was significantly less shared gaze than mutual gaze and mother face infant other (both $p < 0.03$), but significantly more shared gaze that infant face mother other ($p < 0.0001$); significantly more mutual gaze than all other states (all $p < 0.03$), apart from mother face infant other where there was significantly less ($p < 0.0001$); significantly less different gaze than mutual gaze or mother face infant other (both $p < 0.0001$), but more than infant face mother other ($p < 0.0001$); less infant face mother other than all other states (all $p < 0.0001$); and more mother face infant other than all other states (all $p < 0.0001$). These results are therefore in keeping with previous research showing that mutual gaze decreases between these two ages, but that shared gaze increases (e.g. Gaffan et al., 2010; Deak et al., 2014).

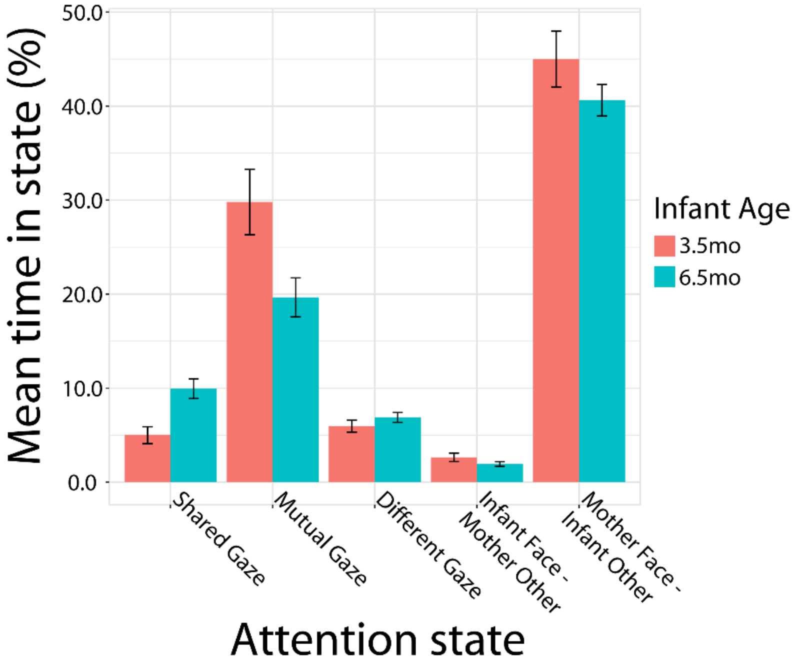

Figure 5.13: Time dyads spent in various attention states at 3.5 months and 6.5 months.

These results also allow some other general principles to be inferred about these early mother-infant interactions. For example, it seems that mothers tended to keep looking at their infant while infants look away much more than vice versa. Interestingly, even though mothers tended to look at their infants face most of the time, the amount of gaze shifts made by both partners was fairly similar, and both partners increased the number of gaze shifts they make between 3.5 and 6.5 months. Along with the fact that mothers followed infants much more than infants followed mothers, this indicates that mothers still followed infant gaze shifts very consistently, even if they did not spend as much time looking towards other aspects of the environment.

5.3.3.2 Attention events derived to explore relationship between early interactions and EEG

Wilcoxon signed-rank tests revealed that infants followed their mothers' attention direction (per mother gaze shift observed) significantly more at 6.5 compared to 3.5 months [*p* = 0.01] and, as noted previously, infants made significantly more gaze shifts at 6.5 compared to 3.5 months. No others differences were found for mothers or infants. The only significant correlation was between mother gaze shifts observed at the two ages (*p* = 0.01), therefore most of the behaviours seems specific to the time of the observed interaction. Means and standard deviations can be found in Table 5.7.

Table 5.7: Mean (SD) of attention events (frequency for the 3 minute interaction period, rates per minute, and proportions) at 3.5 and 6.5 months

	3.5 months				**6.5 months**			
	Frequency	**Per minute**	**Per gaze shift observed**	**Per mother follow**	**Frequency**	**Per minute**	**Per gaze shift observed**	**Per mother follow**
Infant gaze shifts	63.86 (22.88)	21.30 (7.73)			100.95 (28.12)	33.65 (9.25)		
Mother gaze shifts	64.54 (27.72)	21.51 (9.24)			82.76 (27.08)	27.59 (9.03)		
Mother gaze shifts infant observed	14.11 (15.71)	4.58 (5.22)			9.32 (7.16)	3.11 (2.38)		
Infant gaze shifts mother observed	49.78 (19.59)	16.59 (6.53)			70.08 (21.43)	23.35 (7.15)		
Infant follow mother	0.73 (1.57)	0.24 (0.52)	0.10 (0.22)		1.68 (1.56)	0.57 (0.52)	0.25 (0.33)	
Mother follow infant	10.43 (7.46)	3.48 (2.48)	0.27 (0.28)		17.42 (10.56)	5.80 (3.51)	0.28 (0.20)	
Infant sees mother follow	0.46 (0.77)	0.15 (0.26)		0.04 (0.08)	0.81 (1.02)	0.27 (0.34)		0.04 (0.06)

5.3.3.3 Results from interaction/EEG analysis

Separate models were run to explore the influence of attention events during interactions at the previous assessment (‘infant follow mother’, ‘mother follow infant’, ‘infant sees mother follow’) on infant mu desynchronization in the left frontal (electrode cluster F3) and the central regions (average of electrode clusters C3 and Cmedial) during the 6.5 and 9.5 month EEG experiments. These two regions were selected based on the results from the EEG analysis, where greater mu ERD in the congruent compared to incongruent condition was found overall, as well as in F3, C3 and Cmedial at 9.5 months. Accordingly, the dependent variable here was degree of mu ERD in the congruent versus incongruent condition (i.e. congruent minus incongruent). This analysis revealed some interesting effects of early interactions on mu desynchronization in the central cluster, presented below, however no significant effects were found for F3 (see Appendix C, section 10.7

for results). Note, for 'infant follow mother', 'mother follow infant' and 'infant sees mother follow', proportions (see Table 5.7) were used in all analyses instead of rates (raw frequencies per minute), in order to account for the varying opportunities dyads had to experience these events during the observed interaction. Rates (raw frequencies per minute) were used for 'infant gaze shifts' and 'mother gaze shifts infant observed'.

A significant interaction was revealed between EEG age (6.5, 9.5 months) and the interaction variables 'mother follow infant' [$F(1, 31.81) = 5.58$, $p = 0.02$] , and 'infant sees mother follow' [$F(1, 32.62) = 4.88$, $p = 0.03$]. Follow-up tests demonstrated that only at 6.5 months did 'infant sees mother follow' predict the degree of mu ERD in central regions at 9.5 months ($\chi^2_{(1)} = 4.61$, $p = 0.03$), with a higher frequency of 'infants sees mother follow' related to greater mu ERD in the congruent compared to the incongruent condition. Interestingly, more 'mother follow infant' at 6.5 months predicted less mu ERD at 9.5 months in the congruent compared to incongruent condition ($\chi^2_{(1)} = 6.09$, $p = 0.01$), however on inspection of the model coefficients, it appears that the absolute value of the coefficient for 'infant sees mother follow' at 9.5 months (-167.17) is much greater than for 'mother follow infant' at 9.5 months (39.51). Furthermore, the models run in order to see if simply 'infant gaze shifts per minute' or 'mother gaze shifts infant observed per minute' was related to mu ERD in the central cluster revealed no significant effects (see Appendix C, section 10.7).

As there was both a face-to-face interaction period and EEG experiment at the 6.5 month assessment, an additional model was run to see if concurrent interactions had an effect on mu ERD in the central cluster. This also revealed no significant effects, and neither did a model looking for effects of interactions at 3.5 months on mu ERD in the central cluster at 9.5 months (see Appendix C, section 10.7).

5.3.4 **QUESTIONNAIRES**

No significant correlations were found between EPDS scores and mu ERD (congruent minus incongruent in the combined central cluster and frontal cluster) (all $p > 0.39$), therefore differences in maternal depression scores could not have accounted for the relationship found between early interactions and infant neural activity. In regards to the ASQ-3, a relationship was revealed between fine motor development and mu ERD in the combined central cluster at 6.5 months ($p = 0.005$), and between gross motor development and mu ERD in the frontal cluster, and between problem solving development and mu ERD in the combined central cluster as 9.5 months (both $p < 0.02$). However, in all these cases, higher scores on the ASQ-3 scales was related to *less* mu desynchronization, therefore these measures were also unlikely to have influenced the relationship between early interaction variables and mu ERD.

5.4 DISCUSSION

5.4.1 EEG FINDINGS

Evidence from monkey and human research suggests that mapping between others' direction of attention and one's own could involve the flexible engagement of neural processes common to observer and performer (Grossmann et al., 2013; Hoehl et al., 2014; Lachat et al., 2012; Shepherd et al., 2009). The EEG study was designed to further understanding of these processes in human infants, including how such a neural matching mechanism might emerge over time. This study extends previous infant work concerning infants' sensitivity to a social partner following their gaze in several ways: one, via utilization of EEG to look at activation over the entire scalp; two, by using a scrambled condition to control for observation of congruent and incongruent motion; and three, by comparing neural responses at two different points in development.

Infant brain activity was recorded during observation of an adult turning their head to look at the same object the infant just looked at (congruent condition), compared to a turn towards an object in the opposite direction (incongruent condition). The most notable responses were found from approximately half-way through the adult head-turn until the end (500-1000ms), with significantly more mu desynchronization in the left and medial central, and left prefrontal clusters during observation of congruent compared to incongruent head-turns. At 9.5 months of age, infants demonstrated significantly less desynchronization during observation of incongruent head-turns compared to at 6.5 months, and there was also significantly more mu desynchronization during observation of congruent compared to incongruent turns by 9.5 months. These results indicate that infants are sensitive to another following their gaze from a very early age, and are consistent with theories emphasizing a dynamic perception-action mapping between interactive partners (Lachat et al., 2012). The pattern of increased mu desynchronization during observation of congruent compared to incongruent head turns, and not congruent compared to incongruent scrambled motion, is compatible with the idea of increased activity in sensorimotor regions that are involved in production and perception of actions and movements (Fox et al., 2016; Muthukumaraswamy et al., 2004; Pineda, 2008), and fits well with results showing greater infant mu desynchronization during observation of actions that match those that they have just performed (Reid et al., 2011;

Saby et al., 2012). This result also lends support to the hypothesis that a mirror mechanism aids this mapping between own and other attention shifts (Frischen et al., 2007; Grosbras, Laird, & Paus, 2005; Hoehl et al., 2014; Iacoboni, 2009; Lachat et al., 2012; Lakin & Chartrand, 2003; Shepherd et al., 2009). Findings therefore suggest that this mechanism emerges early in development and is gradually refined from 6.5 to 9.5 months.

Importantly, no significant mu desynchronization was found during the observation of scrambled stimuli at either age, even though 6.5-month-old infants made more attention shifts in the scrambled condition. In the majority of studies that have explored the infant mu rhythm, either static stimuli or non-biological movement has been used in control conditions (Ferrari et al., 2012; Moore et al., 2012). These do not therefore address the specificity of the EEG response to observation of comparable motion (Cuevas et al., 2014), with a recent meta-analysis recommending the use of multiple control conditions to assess this issue in investigation of mirror systems (Fox et al., 2016). The use of a static face baseline period (period before the adult moved their head, and when adult and objects were present) and a scrambled movement condition controlled for observation of the static face alone as well as observation of congruent or incongruent motion (Rayson et al., 2016). The lack of mu desynchronization in response to the scrambled stimuli demonstrates that the significant mu ERD seen in the other conditions is not simply due to observation of any movement or other attentional factors. The general lack of mu ERD in occipital regions during observation also indicates that the effects seen in central and frontal clusters are not a result of alpha desynchronization in visual cortex, but are specific to these clusters, and thus could not be explained by activity in early visual cortical regions.

The finding of greater mu desynchronization during observation of congruent head-turns could also reflect activation of a network implicated in oculomotor control. In the macaque, this circuit is comprised of the lateral intraparietal area (LIP) and the frontal eye field (FEF), and indeed mirror neurons for gaze direction have been found in LIP (Shepherd et al., 2009). This circuit interacts with the parietal-premotor mirror circuit, as the activity of grasp mirror neurons in area F5 is also modulated by the gaze direction of the observed grasp performer (Coudé et al., 2016). However, the FEF in humans is closer to the central sulcus than in macaques (Hutchison et al., 2012), therefore the activation found here in the left central and medial clusters might be reflective of FEF activity. Though the low spatial resolution of EEG makes it hard to make strong claims, the prefrontal cluster of electrodes in the present study was positioned around dorsolateral prefrontal area 46 (Koessler et al., 2009), which is projected to by FEF in both humans and macaques (Hutchison et al., 2012).

Therefore, mu desynchronization in the central and frontal clusters here could reflect activation of a LIP-FEF mirror circuit for gaze direction. A number of researchers have in fact hypothesized that FEF could represent a key region in an attentional mirror system (Frischen et al., 2007; Grosbras et al., 2005).

The significant decrease in infant mu desynchronization over all regions from 6.5 to 9.5 months during observation of incongruent head-turns, as well as the significantly greater mu desynchronization in the congruent compared to incongruent and scrambled conditions at 9.5 months, suggests development or refinement of a mechanism for matching others' direction of attention to one's own. By 9.5 months, significant desynchronization compared to baseline was found only for the congruent conditions, and only for left and medial central, and left and right prefrontal clusters. This desynchronization at 9.5 months was also greater overall in congruent compared to incongruent conditions, which was not the case at 6.5 months. This indicates that central and prefrontal areas were sensitive to observation of head-turns at 6.5 months, but the specific sensitivity to the congruence between the observed head-turns and those performed by the self was stronger by 9.5 months of age. The ability to match one's own direction of attention to others' direction of attention is presumably a prerequisite for responding to and initiating JA, and indeed, the differences found at 9.5 compared to 6.5 months in this study coincide with the age at which infants begin to demonstrate joint attention skills (Mundy et al., 2007; Tomasello, 1995). Note however, that the mirror mechanism may not necessarily play a high level role in JA (e.g. explicit recognition that someone has followed your gaze), but aids in an implicit mapping between own-other, other-own actions involved in directing attention, which may contribute to the ability to follow or initiate JA.

It is interesting that at 6.5 months, infants showed mu desynchronization to both congruent and incongruent head turns, but only to congruent head turns at 9.5 months. If a mirror system is involved in the processing of others' attentions shifts, you would expect to see it activated during observation of any type of head turn, at least to some degree. One possibility is that visual and motor neurons coding attention direction are tuned to particular directions, and that connections between the two populations are modified through experience, resulting in projections from visual neurons to motor neurons tuned to the same direction. Accordingly, if an individual looked in one direction and then saw someone else looking in that same direction, the same neural population would be activated during both execution and observation. However, if an individual looked in one direction and then saw someone look in a different direction, although mirror areas could still be activated during observation and execution, different populations of neurons sensitive to different directions would be activated. Therefore, observation of a congruent head turn would lead to greater activation in a particular population of mirror neurons, even if observing an incongruent one would still lead to some activation, i.e. activation of a different population of mirror neurons during observation and execution. Although EEG only provides an indirect measure of mirror system activity, other infant studies have found increased mu desynchronization during observation of an adult imitating them rather than producing some other contingent movement in response to the infants' own action (manual actions, Saby et al., 2012; any movement, Reid et al., 2011). As such, it follows that an increase in mu desynchronization could reflect the overlap in activity in a population of neurons when someone performs an action you just did, as in the study presented here.

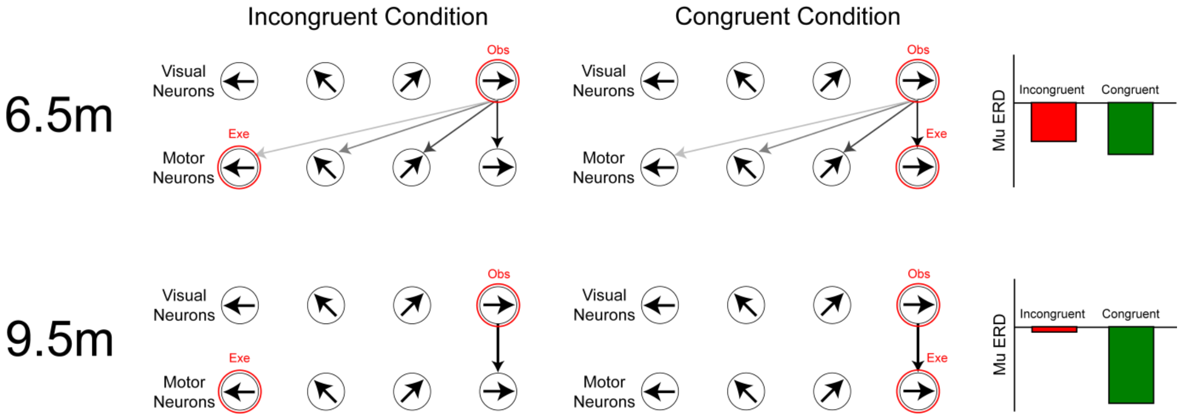

Figure 5.14: Possible explanation for the pattern of mu ERD at 6.5 and 9.5 months. Top row: At 6.5 months, projections from visual to motor neurons are not yet refined, and each visual neuron projects to several motor neurons with different directional tuning. The incongruent and congruent conditions therefore result in similar levels of mu ERD since the same neuron active during execution receives some excitatory input during observation in each condition. Bottom row: At 9.6 months, there are strong projections only between visual and motor neurons tuned to the same direction. Therefore in the incongruent condition, different motor neurons are activated during execution and observation, while in the congruent condition the same motor neuron is activated, resulting in much greater mu suppression in the congruent condition.

If more mu desynchronization reflects an overlap in neuronal population activation during observation of congruent versus incongruent actions, this, along with visuomotor experience during early interactions, could explain the difference in mu desynchronization seen for congruent and incongruent head turns between 6.5 and 9.5 months in this study. At 6.5 months, connections between visual and motor representations of attention direction may be roughly in place, but have not been refined because infants would not have had as much opportunity to observe mothers following their head turns. That is, at this age, connections between visual neurons and corresponding motor neurons could exist, but weak connections could also exist between visual neurons tuned to a specific direction of attention and motor neurons tuned to a range of directions (Figure 5.14, top row). Therefore at 6.5 months, because mu desynchronization in this experiment is measured relative to mu activity during execution (i.e. the baseline used is during infants' own execution, meaning any reduction in mu power during observation is in addition to the reduction during performance), mu desynchronization would still occur to a certain degree in the incongruent condition, although perhaps not as much as in the congruent condition (Figure 5.14, top right). At 9.5 months, connections between visual and motor representations could have been further refined via visuomotor experience during mother-infant interactions, eliminating weak connections between non-corresponding representations (Figure 5.14, bottom row). This could explain why at 9.5 months, mu desynchronization is no longer seen in the incongruent condition; it is not because there is no activation of mirror areas during observation at all, but because different neural populations are being activated during observation and execution, no desynchronization is seem relative to the execution baseline. In the congruent condition at 9.5 months, a visual representation may only activate the corresponding motor representation (more strongly than at 6.5 months too), resulting in increased mu desynchronization relative to execution (Figure 5.14, bottom right).

Less mu desynchronization was found in the right central cluster at 9.5 months compared to 6.5 months, reflecting increased spatial specificity. Left hemisphere dominance for mu desynchronization has been shown in infants of this age (Southgate et al., 2009), as well as adults during JA episodes (Lachat et al., 2012). A central medial cluster was included in the analyses, as recent research shows that this is where the neck representation is located in the motor cortex (Prudente et al., 2015). Significant desynchronization was found in this cluster at 6.5 and 9.5 months in response to congruent stimuli, which in addition to the decreased desynchronization in the right central cluster at 9.5 months, could signify the emergence of somatotopic organization. However, this issue requires more specific, in depth, investigations, and therefore interpretations remain speculative.

While the responses in the congruent condition could reflect involvement of a mirror system in mapping between the visual representations of a head-turn and the motor representations required to execute a head-turn in the same direction, additional processes could also be involved. One possibility is that mu desynchronization in the left frontal electrodes reflects a mapping between the perception of a head-turn and one’s own direction of attention, regardless of the actual movement (i.e. matching at a more abstract level, rather than gaze or head turn direction). This could involve other non-motor regions in the frontal lobe. The left dorsolateral prefrontal region, for example, is implicated in perceptual decision-making, such as the left/right categorization of moving stimuli, and this activity is independent of the specific response modality (Heekeren, Marrett, Bandettini, & Ungerleider, 2004; Heekeren, Marrett, Ruff, Bandettini, & Ungerleider, 2006; Heekeren, Marrett, & Ungerleider, 2008). The left prefrontal cortex is also involved in adult working memory (Curtis & D’Esposito, 2003; Rypma, Berger, & D’Esposito, 2002), and hence desynchronization in frontal electrodes in the current experiment during the congruent, but not incongruent, condition could reflect the matching of the object or location an infant sees the adult looking at, with the stored representation of the object or location they just looked at. Indeed, EEG research with infants aged 14 months indicates that left frontal activity is associated with the tendency to initiate JA at both 14 and 18 months of age (Mundy, Card, & Fox, 2000). Accordingly, the authors suggest that JA may involve working memory and representational demands, whereby infants maintain representations of their own focus of attention while attending to and interacting with others. Also noteworthy, infant and adult research has also shown that left prefrontal activity is related to a motivation to approach (Davidson & Fox, 1982; Harmon-Jones, 2003). Such an influence on motivational systems may play a role in guiding infant social behaviour by driving infants to interact with, learn from and share experiences with a cooperative partner (Grossmann et al., 2013; Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012), with the response found in this study perhaps reflecting a greater motivation to approach the adult in congruent compared to incongruent conditions.

A number of limitations to the present study should be noted. Firstly, although the design of the study ensured that infants both performed an action and then observed someone else performing a matching or non-matching action, it would also be useful to see if similar patterns of mu desynchronization are shown when infants voluntarily attend to an object, rather than be externally cued, before seeing an adult follow them. This would be more comparable to studies of joint attention in adults (Neufeld, Ioannou, Korb, Schilbach, & Chakrabarti, 2015; Schilbach et al., 2013). Additionally, although the results here concerning the refinement of a mechanism for matching own and other direction of attention coincide with the emergence of infant joint attention skills, one cannot know whether this corresponds to behavioural demonstrations of such abilities. It would therefore be interesting if future research looked at the relationship between infants’ ability to respond and initiate joint attention and putative mirror activity.

To conclude, findings from this study reveal that from 6.5 to 9.5 months of age, infants demonstrate significant mu rhythm desynchronization in central and left frontal electrode clusters during observation of an adult following their direction of attention, but not if the adult looks in the opposite direction. The differences between these conditions became more pronounced and spatially localized during this time, suggesting a refinement of a mechanism for matching observed attention direction with one's own. The lack of mu desynchronization in occipital clusters suggests that these results did not merely reflect changes in visual areas, and were specific to central (left and medial) and left frontal clusters. The absence of mu desynchronization in response to the scrambled condition at either age also indicates that this response was specific to the attention cues that were signalled by head turns, rather than a general cue indicating left or right motion. These findings suggest sensitivity of young infants' sensorimotor system to the observation of another person following their gaze, and are consistent with theories suggesting mirror system involvement in the mapping between self and other direction of attention.

5.4.2 LINK BETWEEN EARLY INTERACTIONS AND NEURAL RESPONSES

As is the case for most types of action, research concerning the development of a mirror system involved in the processing of attention direction is currently lacking. One computational model has shown how mirror neurons for gaze following could emerge via interactions with a caregiver (Triesch, Jasso, & Deak, 2007), however, no studies have tested this empirically, and the model in question neglected consideration of a role for the caregiver's gaze behaviour in response to the infant. Therefore, as well as being the first to provide persuasive evidence for mirror system involvement in the processing of attention shifts, the study presented here is also the first to have considered the influence of early social environment on development of this system. The key finding was that of a relationship between how often infants had previously seen mothers follow their direction of attention at 6.5 months, a type of event that could strengthen a mapping between self-generated and other-generated actions, and putative mirror activity during observation of a social partner following the infant's attention direction at 9.5 months postpartum. This suggests that maternal 'mirroring' of infant attention shifts during early social exchanges is important for building a mapping between own and other direction of attention.

In the EEG analysis, greater mu ERD in the congruent (where infants observed an adult match the attention shift they just performed) compared to incongruent (where adults attended in the opposite direction) condition was found, and by 9.5 months of age, more mu ERD in congruent compared to incongruent conditions in central medial, left central, and left frontal electrode clusters. As such, the analysis of previous mother-infant interaction effects (3.5 and 6.5 months) on mu ERD focused on neural activity during the congruent compared to incongruent condition, in central (medial/left central combined) and left frontal regions at both 6.5 and 9.5 months of age. 'Infant sees mother follow' (per mother follow) during the 6.5 month interaction was found to predict mu desynchronization in central regions during observation of adults' congruent head turns at 9.5 months, but no relationship was found with activity in the left frontal region. This suggests that the early interaction measures in this study specifically affected sensorimotor cortex activity and that the mu ERD in the left frontal electrode clusters reflects other cognitive processes. As suggested in the previous section, activity in the left frontal cluster could reflect activity of some processes such as working memory or perceptual categorization. The interaction behaviours selected for this analysis were ones hypothesized to strengthen a mapping between visual and motor representations, and therefore may not predict such frontal activity. Another possibility is that the left frontal activity does reflect activity of an attentional mirror system, but that for some reason, this activity was not influenced by infant-mother interactions in the same way as that in the central cluster.

It is interesting that early interactions at 3.5 months did not influence EEG activity at 6.5 months or 9.5 months in the same way as 6.5 interactions did EEG activity at 9.5 months. These findings suggest that motor representations of attention shifts were not developed enough to strengthen visuomotor mappings in 3.5 month old infants. Indeed, infants at 3.5 months have only just begun shifting their own attention to the environment during social interactions (Murray, 2014; Trevarthen & Aitken, 2001) and losing interest in 'pure' face-to-face interaction, and thus were unlikely to have had enough motor experience to build strong representations of related actions. However, as demonstrated in the control analyses presented here, it was not infants' pure motor experience that was linked to mu desynchronization during observation of others' attention shifts (or pure observational experience), but rather, observing that their mother had shifted attention in the same way they just did. Therefore, although having a strong motor representation is clearly important, these results indicate that motor experience alone is not sufficient for strengthening a mapping between visual and motor representations for opaque actions such as attention orienting. The lack of relationship found between interaction measures at 3.5 month and later mu desynchronization could also be explained, in part, by the lack of opportunities that mothers would have had to follow their infant's gaze at such an early age, and thus for their infant to see that they have followed (i.e. if infants have not been shifting/have only just begun to shift their attention away from their mother during 3.5 month interactions, mothers would have had fewer opportunities to mirror them). This is corroborated by the increase found in the rate (per minute) of 'infant see mother follow' between 3.5 and 6.5 months, even though the proportion of instances where infants saw their mothers follow their attention remained the same. This increase was driven by an increase in the number of gaze shifts made per minute by the infant between 3.5 and 6.5 months, as the number of times mother followed the infant's attention *per minute* increased between these ages, but the number of times the mother followed the infant's attention *per gaze shift observed* did not.

The EEG activity at 9.5 months was predicted by the 6.5 month interaction event 'infant sees mother follow' (per mother follow) on an individual basis, but there were no differences between the 3.5 and 6.5 month assessments in the frequency of this event over all infants as a group. This suggests that although the infants experienced these events at the same rate (relative to how often mothers followed them) at both ages, either certain developmental milestones had not been reached at the earlier time-point, or, as suggested by the previous paragraph, they had not gained sufficient experience until the later stage, and therefore the infant's brain was not yet prepared to benefit from the interactions in the same way. For example, only by 3 months does an infant's visual acuity begin to approach adult levels; around 4-5 months, infants begin to look around at the environment a lot more, gazing intently at objects in the distance, and exploring nearby features such as a strap on a chair; and around 4-5 months, infants show marked improvements in their attempts to reach and grasp objects (Murray, 2014; von Hofsten, 2004; von Hofsten & Rönnqvist, 1988). Caregivers also adapt to these changes in the infant by helping to create a sense of 'shared focus', such as following their infant's focus of interest more, bringing infant's objects of interest into play, or engaging in 'body games' (Murray, 2014; Trevarthen & Aitken, 2001). Therefore, it is not surprising that infants may not have been ready to benefit from the attention events considered in the research presented here.

Note, a relationship was also found between 'mother follows infant' (per infant gaze shift observed) at 6.5 months and mu desynchronization in central regions at 9.5 months, however this was found to predict *less* desynchronization during observation of congruent head turns in central regions. The reason for this is not clear, but it does suggest that rather than mothers simply following infants more, and therefore giving them the opportunity to observe them doing so, there is something particularly important about the infant looking back towards the mother after she has followed their gaze, as ‘infant sees mother follow’ (per mother follow) did predict less mu ERD in central regions at 9.5 months. For example, perhaps infants who do look back more have mothers who do something to draw infant’s attention back to them (e.g. make a positive vocalization), which could provide the infant with positive reinforcement for doing so, a possibility that could be looked at in future research (also see discussion of ostensive marking below). Additionally, the coefficients obtained for the ‘mother follow infant’ (per infant gaze shift observed) variable suggest that the influence of this event on mu ERD was much smaller than that of ‘infant sees mother follow’ (per mother follow). Therefore this behaviour may have partially reflected some other, unmeasured, variable. Nevertheless, because of the way ‘infant sees mother follow’ (per mother follow) was coded here, it could be that some instances were missed if infants saw mothers in their peripheral vision, but didn't covertly shift their attention back towards her. For example, by 3 months of age, infants can make two types of discrimination with their peripheral vision: between very different figures placed as far out as 30 degrees towards the periphery, and between more subtly divergent figures out to 10 degrees (Maurer & Lewis, 1979). This suggests that infants can readily process stimuli within their peripheral vision from early on. Perhaps in the future, for the mother-infant interactions observed here, potential instances of infant seeing mother follow (e.g. where infants be able to see her in the periphery) could also be noted, and whether or not this add to the effect on mu ERD explored.

Manual actions performed by mothers and infants were not coded for this study, even though mothers could still touch the toys on the wall or the infant, and infants could touch the highchair etc. This was because the study was designed to test specific hypotheses concerning the development of a mapping between others’ direction of attention, indicated by head/eye orientation and one’s own motor representations used to attend in the same direction. That is, behaviours during the mother-infant interactions that were the most similar, and which could therefore be hypothesised to strengthen relevant visuomotor mappings, to those that infants observed during the EEG experiment were selected for investigation. These are also the types of behaviour considered in the Triesch et al. (Triesch, Jasso, & Deak, 2007) model. Nevertheless, other research involving face-to-face mother-infant interactions, in which mothers were given toys and asked to engage their infants, has shown that the manual handling of objects by mothers may be important for the learning of gaze following (Deák et al., 2014). In this study, where infants were aged 3-11 months (3 groups: 3-5 months, 6-8 months, and 9-11 months), results were interpreted as suggesting infants receive the information needed to learn gaze following from adult direction cues, and that no innate knowledge about attentional states (i.e. understanding of visual perception of others) is required to do this. For example, if infants looked at their mother's face, the next look was usually to the toy she was handling. The authors also point out that even if there is sufficient information during interactions for infants to learn gaze following, they probably still take months to learn this because of 'sticky attention' in the first 3-4 months (Butcher, Kalverboer, & Geuze, 2000), and that their findings are consistent with the idea that because infants shift dyadic attention states less often before 3-5 months, infants have less opportunity to learn spatial associations between their own and others' gaze direction. Additionally, the rewarding sequences examined in the Deak et al., (2014) study did not happen frequently, and therefore it may have taken a lot of time to receive the required input for an attentional mirror system to build up the required associations. This is in accordance with the findings of the study presented in this chapter, in which mother-infant interactions at 6.5 months, but not 3.5 months predicted later infant mu ERD during observation of a social partner following their gaze.

Deak et al., (2014) claim their results are in keeping with the reinforcement learning idea proposed by the Triesch et al. (Triesch, Jasso, & Deak, 2007) developmental model of gaze following, in which this skill is acquired when infants learn that adults' gaze direction is likely to be aligned with interesting sights, resulting in the formation of mirror neurons for attention shifts. If this hypothesis was correct, adults should have tended to look at things that are salient to the infant, and infants should learn by detecting this tendency. The results in the Deak et al. study revealed that infants preferred watching their caregivers handle objects, which was strongly related to how mothers moved the object. Furthermore, when infants looked toward the caregiver, while she was looking at her own hands, the infant's next gaze shift was often toward the caregiver's object-handling. The authors argue that the behaviours observed ensured that infants received enough input to learn associations between their mother's gaze direction and the locations of interesting sights, and that this demonstrates that face-to-face toy-play could provide sufficient information for infants to learn gaze-following contingencies without any specialized or innate knowledge about mental states (e.g. 'intention'); or any understanding of visual perception or other people's gaze behaviours. They therefore claim that 'infants learn to follow gaze by watching their mother's hands'.

It is important to note that in the Deak et al. (2014) study, infants usually followed their mother into shared attention states, rather than mothers following infants. This is the opposite pattern to the one found in the study presented here, and is in fact rather anomalous in the literature. For example, research has shown that maternal 'maintaining' of infant attention (i.e. following the infant towards their target of attention and reinforcing the infant's engagement with it), is the only maternal behaviour (compared to directing the infant's attention, for example) to be related to infant JA at 9 months (Mendive, Bornstein, & Sebastián, 2013). This is in keeping with the general consensus that sensitive mothers follow infants into shared attention states (e.g. Gaffan et al., 2010; Murray, 2014; Trevarthen & Aitken, 2001), rather than the opposite way around. However significantly, in the Deak et al. study, mothers had been instructed to keep their infants engaged with the toys made available to them, rather than just interacting with their infant naturally. Accordingly, it could be that mothers tend to behave differently when not given instructions, with or without toys available, or that having more access to toys influenced the results in this case. In reality, mothers and infants would interact with and without toys, with much time spent interacting without toys occurring early in development, and gradual introduction of toys over time. It would be useful for future research to investigate mother-infant looking behaviour in both conditions, and see how they both might contribute to development of an attentional mirror mechanism.

In the study here, the proportion of 'infant sees mother follow' (per mother follow) was smaller than 'infant follows mother' (per mother gaze shift observed) at 6.5 months, yet the former had an influence on mu ERD at 9.5 months, while the latter did not. This suggests that this behaviour might be more influential on mirror activity than the random exploratory gaze following simulated by Triesch et al. (Triesch, Jasso, & Deak, 2007). However, these results do not completely exclude the possibility of reinforcement learning in shaping an attentional mirror system. It might be that infants are somehow rewarded by the mother's responses if they look back at her after she has followed their gaze, or something rewarding happens that attracts infant attention back to the mother. For example, ostensive marking (i.e. behaviours that can signal infant-directed communication, such as direct eye contact, eyebrow raises, infant directed speech, contingent responses, positive vocalization) tend to elicit positive affective responses, (primarily smiling) in infants, and thus seem to act as rewards (Csibra & Gergely, 2010). Interestingly, by 6-7 months, adult ostensive marking can increase infant gaze following (Senju & Csibra, 2008). It would therefore be valuable to code ostensive marking in future studies, and consideration given to whether these maternal behaviours influence infant gaze behaviour, and in turn, attentional mirror system activity. For instance, perhaps ostensive marking such as infant-directed speech happens more often after the mother follows the infant's direction of attention, which then draws the infant's attention back towards the mother, increasing the proportion of 'infant sees mother follow' (per mother follow). Perhaps seeing mothers follow them is particularly rewarding to infants because it is an example of contingent responsiveness, and specifically, mirroring, which has been suggested by some to be a particularly enriching form of maternal responsiveness compared to non-imitative but contingent actions (Meltzoff, 1990; Nadel, 2002).

It could also be that infants seeing their mother follow them is more dependent on the infant's own behavioural tendencies, or a mixture of both maternal and infant responses. For example, perhaps infants who see mothers follow more tend to look at their mothers more generally as well, and therefore are more likely to look back and see that mothers have followed them, or just react more positively to their mother's ostensive cues. This would be interesting to code in the future. Extra coding of the early-mother infant interactions would be interesting to try and further prise apart what 'infant sees mother follow' and 'infant follow mother' relates to . For instance, where a target location lies along the infant's scan path may influence how likely they are to follow their mother (e.g. Butterworth & Cochran, 1980; Butterworth & Jarrett, 1991), or indeed where the mother lies on the scan path along with other targets may influence how likely they are to look back at her.

5.4.3 GENERAL CONCLUSIONS

To conclude, findings from the EEG experiments presented in this chapter suggest that a mechanism for matching own and other shifts of attention may exist from very early on in infancy, and that this matching may involve a mirror system. This is in keeping with other research implicating the flexible engagement of neural processes implicated in the understanding of self- and other- generated attention shifts, but goes even further in that they demonstrate a refinement of the response between 6.5 and 9.5 months, which coincides with the emergence of joint attention skills. This does not suggest mirror system involvement in knowledge about the visual perception of others, but does suggest that the matching between own and other attention implemented by such a system could form a low level basis for responding to and initiating JA. The relationship revealed between early mother-infant interactions and mu desynchronization in the EEG experiment, also indicates that the early social environment plays an important role in the development of this system, and, like results in Chapter 4, suggests that mothers act as biological mirrors for their infants during early interactions, which facilitates the strengthening of mappings between motor and visual representations.

6 DISCUSSION

The overarching aim of the research presented in this thesis was to investigate mirror system involvement in the processing of actions one cannot see oneself perform, from very early stages in human development. Facial expressions and attention directing were the specific actions of interest, with such ‘opaque’ actions relatively unexplored in the mirror system literature compared to manual actions, especially in young children and infants. In addition, although a small number of macaque and human infant studies have been conducted (e.g. Cannon et al., 2016; Vanderwert et al., 2015), and a number of theoretical accounts put forward (e.g. Cook et al., 2014; Del Giudice et al., 2009; Ferrari et al., 2013), very little empirical research thus far has investigated how mirror systems may develop. Therefore, an additional aim of the research presented here was to investigate the role early social experience may play in the development of human mirror systems. Specifically, two studies looked at how early mother-infant interactions might relate to infant mirror system activity , with particular behaviours that occur during such face-to-face exchanges thought to provide infants with the visual feedback necessary to strengthen visuomotor mappings in the case of unobservable self-performed actions.

In the next section of this final chapter, the rationale behind each of the studies that make up this thesis, along with the main results, will be summarised. The implications of these findings will then be considered in terms of how they further understanding on infant mirror systems, limitations to the studies acknowledged, and ideas for future work discussed. Finally, some general conclusions will be given.

6.1 SUMMARY OF MAIN RESULTS

The first study presented in ***Chapter 2*** was designed to explore putative facial mirror system activity in a much younger human population than has previously been investigated. This was achieved via recording of EEG from 30-month-old children as they observed different facial expressions, with mu desynchronization in central clusters of electrodes used as an index of mirror system activity (Cuevas et al., 2014; Fox et al., 2016; Muthukumaraswamy & Johnson, 2004; Pineda, 2005). Any instances where infants produced the emotional (happy, sad) or non-emotional (mouth opening) expressions they were presented with were coded offline from videos made during the EEG experiment. This allowed such trials to be removed and analysed separately as an execution condition. Results revealed significant mu desynchronization during observation of all the facial expression types; however, whereas desynchronization was bilateral for mouth opening, it was right lateralized for both happy and sad expressions. No significant differences between conditions were found in occipital regions, which suggests that modulation in the mu band was specific to central regions, and not simply due to changes in visual alpha. Additionally, no significant desynchronization was found during observation of a scrambled control condition, so findings in the other conditions appeared specific to the expressions observed, rather than observation of just any comparable motion. Finally, significantly more mu suppression was found in central compared to occipital regions during execution, therefore a general overlap in the cortical regions activated during observation and execution was demonstrated. These results indicate that the sensorimotor cortex is activated during both execution and observation of facial expressions in children aged only 30 months, and thus that a mirror system may be involved in facial expression processing from an early age in human beings (Rayson et al., 2016).

Following on from the Chapter 2 study in which evidence was provided for the presence of a facial mirror system in human children, a longitudinal research programme (see ***Chapter 3*** for general methodology details) was designed to investigate mirror system activity related to opaque action processing at an even earlier stage in development, i.e. around the same age other studies have obtained findings consistent with manual mirror system activity (e.g. Cannon et al., 2016; Nyström, 2008; Nyström et al., 2011; Southgate et al., 2010, 2009). Two studies were included in this wider research programme, the first of which (***Chapter 4***) looked at mu desynchronization in 9-month-old infants during the observation and execution of facial expressions. This EEG experiment was almost identical to the one presented Chapter 2, albeit with a much younger sample. Again, participants were presented with happy, sad, mouth opening, and scrambled stimuli, with any instances of infant execution coded manually from video recordings made during the experiment. Interestingly, results were very similar to those obtained from the 30-month-old sample. That is, mu desynchronization in central clusters of electrodes was revealed during both observation and execution of facial expressions, but no significant desynchronization was found in occipital clusters or during observation of the scrambled control condition. There was one key difference, however, with mu desynchronization during observation of sad expressions found to be bilateral instead of right lateralized in the younger sample (mouth opening was bilateral and happy right lateralized in the 9-month-olds, as they were in the 30 month sample). Together, these findings suggest that a mirror system may be involved in facial expression processing as early as 9 months postpartum in human infants, but also indicate that the system undergoes some refinement between 9 and 30 months of age. Indeed, as well as the difference in lateralization of the sad condition, it seems that, generally, mu desynchronization was greater during observation of facial expressions at 30 months compared to 9 months of age . This is in keeping (as was the magnitude of mu rhythm desynchronization in the Chapter 5 gaze study at 9.5 months of age), with previous research suggesting there is an increase in mu power suppression during observation and execution of actions throughout development, with similar percentages seen in other mirror system studies with infants around 9-30 months of age (e.g. Marshall et al., 2011; Southgate et al., 2009; Warreyn et al., 2013). Again, these results indicate that developmental changes take place in a neural system that facilitates the matching of own and other actions (Marshall & Meltzoff, 2011), but, of course, no definitive conclusions can be based on either the work here or on previous studies due to the various methodological differences between them.

The study in ***Chapter 4*** also considered how early maternal mirroring of infant facial expressions may have influenced results in the 9 month EEG experiment. Based on the proportions of infant mouth opening and smiles mirrored by mothers during interactions at 2 months postpartum, dyads were split into low and high mirroring groups. In support of experimental hypotheses, infants whose mothers mirrored certain facial expressions more during early interactions were found to demonstrate greater mu desynchronization during observation of those specific expressions at 9 months and, furthermore, they showed more right lateralization of mu desynchronization in the happy condition if mothers had mirrored smiles more often. As such, findings from this chapter not only provide evidence indicative of a facial mirror system in very young infants, but suggest that early maternal mirroring may indeed play a role in the development of this system in infants, by strengthening the mapping between visual and motor representations of opaque actions.

Based on the findings from Chapters 2 and 4, and as mentioned above, it appears that a mirror system involved in facial expression processing undergoes further refinement between 9 and 30 months of age, which may result from a combination of both more experience with different facial expressions (maternal mirroring) and cortical maturation. These possibilities were not tested in the studies here, however, so this suggestion remains tentative. It is also possible that neural mirroring activity during observation of sad expressions becomes right lateralized later in development (by 30 months but not by 9 months) than that during observation of happy expressions because mothers mirror infant negative expressions less during early interactions. This fits with previous research suggesting that mothers do mirror infant negative expressions, but less often than positive ones (Malatesta & Haviland, 1982; Malatesta & Izard, 1984; Tronick, 1989), which was also the pattern revealed in Chapter 4 during the early mother-infant interactions. Theoretically, such mirroring could strengthen connections in the infant brain between visuomotor action representations and emotional representations in the right hemisphere, which is the hemisphere thought to be specialized for emotional processing (Adolphs, 2002). Therefore, neural activity during observation of sad expressions would become lateralized more slowly due to there being fewer opportunities for the infant's mirror system to receive visual inputs corresponding to their own expression execution.

In the second study (***Chapter 5***) encompassed within the longitudinal programme, the involvement of a mirror system in another action that is unobservable when performed by the self, the directing of attention, was examined. During an assessment at both 6.5 and 9.5 months postpartum, infants took part in an EEG experiment where their attention was drawn to one of two objects presented either side of a screen, followed by an adult turning their head in a congruent direction (i.e. the same direction the infant just did, and hence 'mirroring' the infant's direction of attention) or an incongruent direction (i.e. the opposite way to the in which the infant just attended). Critically, then, each trial in this experiment contained both execution (infant directing their own attention towards an object) and observation (the infant then seeing an adult attend in a congruent or incongruent direction), but only in the congruent condition did the executed and observed actions match. A scrambled control condition was also included, as in the Chapter 2 and 4 studies. The results obtained from this experiment suggest that a neural mechanism for matching own and other attention direction is present early on in infancy, and that the pattern of activity is consistent with mirror system involvement in this matching process. The matching mechanism seemed to be refined between 6.5 and 9.5 months of age, with a much clearer response pattern found in central and frontal regions by 9.5 months. More precisely, significantly more mu desynchronization was demonstrated in the congruent compared to incongruent condition overall and, by 9.5 months, this difference was significantly greater in central medial and left clusters of electrodes specifically, and in a left frontal cluster of electrodes (see Figure 4). No significant desynchronization was found in occipital regions or during the scrambled control condition, and the response seemed to become more localised with age (i.e. there were no longer any significant changes in the right central cluster by 9.5 months). This refinement in the response between 6.5 and 9.5 months coincides with the emergence of joint attention skills (Gaffan et al., 2010; Mundy et al., 2007); therefore, it could be that the matching mechanism reflected by this activity could contribute, at least at a low level, to the mapping between own and other shifts of attention. Such an implicit ability is presumably required for both responding to and initiating joint attention.

The ***Chapter 5*** study also looked at how early mother-infant interactions at 3.5 and 6.5 months postpartum may have related to the pattern of mu desynchronization (congruent relative to incongruent) revealed in the central and left frontal clusters of electrodes during the EEG experiments. A coding scheme designed to explore mother-infant attention-related behaviours was used to extract relevant events during the early social interactions; i.e. events that could be hypothesized to strengthen an infant's mapping between own and other direction of attention, such as 'infant follows mother' and 'infant sees mother follow'. A relationship was revealed between the amount infants saw mothers follow their direction of attention at 6.5 months and the EEG results at 9.5 months, which suggests that this attentional event during early interactions could play a role in the development of a mechanism for matching one's own attention shift to another individual's. No relationship was found between interactions at 3.5 months and infant mu desynchronization later on in infancy. These findings fit well with the timing of joint attention skill emergence in the first year postpartum (Mundy & Jarrold, 2010), as well as research demonstrating a link between mother-infant interactions around 6 months and joint attention skills at 9 months (Gaffan et al., 2010). One computational model has considered the influence of early social interactions on the development of a mechanism for mapping between own- and other-generated attention shifts, with mirror neurons for gaze following emerging in the infant via the 'accidental' following of a caregiver's gaze direction (Triesch, Jasso, & Deák, 2007). However, in this model, the role of the mother was neglected, and although the results presented here do not entirely discount the potential importance of the infant following their mother's direction of attention, they do suggest that observing their mother 'mirroring' their attention shifts is particularly key for building up mapping between own and other actions in the infant.

6.2 MIRROR SYSTEMS AND THEIR DEVELOPMENT IN HUMAN INFANTS

Altogether, the findings described in the previous section make a significant contribution to the existing literature concerning neural mirror systems and their development. Although research with adult humans and adult/infant macaques has provided considerable evidence for the involvement of a mirror system in facial expression processing (e.g. Carr et al., 2003; Ferrari et al., 2012, 2003; Moore et al., 2012; van der Gaag et al., 2007; Vanderwert et al., 2015), the studies in Chapters 2 and 4 are the first to do so in regards to a human facial mirror system in the developing brain. Furthermore, these were the first EEG studies to consider potential differences in mirror system activity during observation of emotional versus non-emotional facial expressions, providing support for the idea that processing of the two may involve separate or overlapping representations. The study in Chapter 5 focused on a relatively unexplored type of action in terms of mirror system research, the directing of attention. Previous work with adult monkeys and adult/infant humans has provided some evidence for the involvement of a mirror system in the matching of own and other attention direction (Coudé et al., 2016; Hoehl et al., 2014; Lachat et al., 2012; Shepherd et al., 2009), however the study in this thesis was the first infant study to deliver more direct support for this hypothesis.

A particular strength of all the EEG studies included here was the use of a scrambled control condition in addition to a static baseline period, in accordance with the strongly recommended use of multiple control/baseline conditions in order to assess mirror system response specificity (Cuevas et al., 2014; Fox et al., 2016). Although a few studies of putative mirror system activity in infant macaques have adopted this type of design (Ferrari et al., 2012; Vanderwert et al., 2015), the EEG studies presented here were the first do so with human infants. The studies here also go further than previous research in that they not only allowed comparison of movement observation with a static baseline, but the use of scrambled control conditions also enabled comparison of naturalistic (experimental conditions) versus meaningless motion (scrambled condition) while controlling for low-level visual features (e.g. overall movement) at the same time. More precisely, the movement that occurred in the scrambled conditions was made as similar as possible to the unscrambled conditions, and in the facial expressions studies, other-low level features such as size and shape of the stimulus were also controlled for. This, as well as the use of a static frame of the experimental and scrambled conditions as the baseline, ensured that the control condition/baseline periods were as near to the experimental conditions as they could be, which is in line with ‘best practices’ recommended in the literature (Cuevas et al., 2014; Fox et al., 2016). Notably, the use of a scrambled control condition allows stronger claims to be made about response specificity (mirror system involvement), with activity in the experimental conditions unlikely to have resulted from just any comparable motion. The static baseline condition controls for the appearance of a face-like stimulus in the facial expression studies, as well as the appearance of potential gaze targets in the attention shift study.

Another strength of the EEG study designs used in this thesis was that activity in occipital regions was considered in all of the EEG studies, with a lack of mu desynchronization in these areas suggesting neural activity was specific to central regions (and thus was likely to reflect sensorimotor cortex activation), rather than changes in visual regions. Many studies do not report this (e.g. Paulus, Hunnius, van Elk, & Bekkering, 2012; Southgate et al., 2010, 2009), however, a number of researchers now argue that this is very important if one is going claim findings are reflective of mirror system activity. This is because modulation in the mu band is required to occur in central regions to be interpreted as putative mirror system activity, as this suggests sensorimotor cortex activation rather than activity in visual areas (Cuevas et al., 2014; Marshall & Meltzoff, 2011). In other words, if there is desynchronization in the same band as mu in occipital regions, any modulation in central regions could actually reflect visual cortex activity. Note, increased attention or cognitive load has been related to decreases alpha power, which is most evident in occipital areas (Perry & Bentin, 2009), therefore, the lack of mu desynchronization in occipital regions in any experimental conditions here indicates that the observed responses in central regions were not simply due to these factors.

The EEG studies presented here are some of only a few in the mirror system literature to date that consider age-related differences over development (see Yoo, Cannon, Thorpe, & Fox, 2016 for a recent example concerning manual actions, which involved two separate groups of 9- and 12-month-old infants). This strength is most applicable to the gaze EEG experiment in Chapter 5, which was longitudinal in its design: that is, EEG was recorded from the same group of infants at both 6.5 and 9.5 months, which meant differences in mu desynchronization between the two time points could be looked at in subsequent analyses. In the Chapter 2 and 4 facial expression experiments, where participants were aged 30 and 9 months respectively, although the same participants did not take part at both ages and there were slight differences in the design, the experiment was extremely similar in both. Therefore, even though no statistical tests could be performed, it is still appropriate to discuss apparent differences in putative mirror responses during these two studies.

Finally in regards to the EEG experiments specifically, the inclusion of execution conditions is another strength of the research presented here. The failure to do this is a shortcoming of many studies that have endeavoured to investigate human mirror system activity (e.g. Moore et al., 2012; Nyström, 2008; Nyström et al., 2011; van Elk et al., 2008; Virji-Babul, Rose, Moiseeva, & Makan, 2012). Overlapping activity in brain regions during observation and execution of actions is characteristic of a mirror system, and therefore the absence of an execution condition means it is more difficult to make strong claims in terms of mirror activity; i.e. if activity is modulated during observation only, it might simply suggest that the frequency band of interest is sensitive to motion or other visual properties of the observed movement rather than neural mirroring. In Chapters 2 and 4, mu desynchronization during execution of facial expressions was considered in addition to observation via the coding of any instances where infants performed the facial expressions presented to them. This did reveal overlapping activity in central clusters of electrodes during observation and execution, which certainly suggests mirror activity, but the merging of conditions (mouth opening, happy, sad) means it cannot be known if there were any differences in terms of more precise areas activated for different expressions. For example, if the conditions were looked at separately, perhaps there would have been right lateralization during execution of emotional expressions, as was found during observation of happy and sad expressions in the 30-month-old children, and of happy expressions in the 9-month-old infants. This would have enabled even stronger claims to be made in terms of action specificity, but unfortunately, it is not feasible to include an explicit execution condition where participants are so young, which would increase the numbers of usable trials obtained.

The second major theoretical contribution of this thesis research is the potential role revealed for early social interactions in the development of mirror systems for opaque actions, with the studies in Chapters 4 and 5 being the first to do so in regards to human infants. Results from these studies suggest that maternal mirroring of infants is particularly crucial for the strengthening of visuomotor mappings representative of a mirror mechanism, above and beyond simple observation and execution of opaque actions early postpartum. Therefore, in the case of unobservable self-performed actions, it seems that mothers do act as a ‘biological mirror’ for their infant (Del Giudice et al., 2009; Ferrari et al., 2013), and even though the studies here do not address the question of whether a mirror system exists at birth, the provision of visual inputs that correspond to the infant’s own actions during early social exchanges does at least seem to play a role in mirror system development. This role could be divergent for facial expressions and attention directing behaviours. A rudimentary mirror system at birth may be involved in facial expression processing (Ferrari et al., 2012; Vanderwert et al., 2015), but not in the matching of attention shifts performed by self and other until later on in infancy, as might be the case for manual actions (Casile et al., 2011; Triesch, Jasso, & Deák, 2007). However, results from Chapters 4 and 5 do both provide evidence for the influence of early experience on putative mirror activity in young infants. This finding is in accordance with the majority of accounts attempting to elucidate potential mechanisms through which mirror systems may develop, nearly all of which ascribe some role to experience.

In the 2 month interactions periods that made up part of the Chapter 4 study, ecological validity was improved by visiting mothers at home (Lavelli & Fogel, 2002), with mothers perhaps more relaxed and inclined to act naturally than they would have been in the University laboratory. EEG assessments had to take place in the laboratory, and the ‘gaze’ interactions in Chapter 5 were conducted in this location in order to standardize the environment and elicit more gaze orientating behaviours. Before all the interaction periods, mothers were simply asked to interact with their infant as they would do normally, and therefore were not encouraged in any way to produce the behaviours of interest. Research has shown that during spontaneous home based observations and more structured face-to-face play like the approach used for all interaction periods here (at home or in the lab), mothers show consistent behaviour within their own interactions, demonstrating a continuity across situations (Belsky, 1980; Cohn, Matias, Tronick, Connell, & Lyons-Ruth, 1986). Note, brief early interactions (i.e. maternal behaviours during face-to-face exchanges) as used in the research here have consistently been shown to predict later child outcomes, both on behavioural and neural measures (e.g. Cohn et al., 1986; Diego, Field, Jones, & Hernandez-Reif, 2006; Feldman, Greenbaum, & Yirmiya, 1999; Hohenberger et al., 2012; Legerstee & Varghese, 2001; Murray et al., 1996; Murray, Kempton, Woolgar, & Hooper, 1993; Murray, Woolgar, Cooper, & Hipwell, 2001; Taylor-Colls & Fearon, 2015; Wörmann et al., 2012).

In the introduction to this thesis, a number of theories concerning mirror system development were discussed, but how do results from the research presented here fit with those accounts? First of all, a very simplistic representation of the two major positions was outlined, whereby on one side, mirror neurons are proposed to be innate and not subject to experience (the ‘adaptive’ hypothesis), and on the other side, mirror neurons are posited as being the result of sensorimotor learning only (the ‘associative hypothesis’). If this dichotomy is treated seriously, it could be argued that the findings in Chapters 4 and 5, where more maternal mirroring of infant actions was related to greater infant mu ERD during observation of similar actions, support the associative account, with contingent visuomotor experience helping to form the visuomotor couplings characteristic of a mirror system. However, because putative mirror system activity was not measured until 6.5, 9 and 9.5 months of age, there is no way of knowing whether similar motor responses would have occurred much earlier in the postnatal period, and thus whether a rudimentary mirror system could have existed in the infants from, or very soon, after birth.

As stressed in Chapter 1, the portrayal of adaptive and associative hypotheses above is extremely simplistic, with most major accounts acknowledging at least some role for both genes and environment in the development of mirror neurons. In fact, even early proponents of the associative account have now conceded that coarse connections between visual and motor areas would be required at birth for mirror neurons to develop in the way they suggest (Cook et al., 2014), which some may argue as constituting a very basic neonatal mirror system. Again, as the EEG experiments in Chapters 4 and 5 did not involve neonates, it is not possible to make any strong claims about genetic *versus* learning contributions to mirror system development based on the results from this thesis. Nevertheless, results here do suggest that experience plays an important role in this process, whether or not this development builds on an existing rudimentary mirror system. The fact that motor or visual experience alone during early interactions was not related to mu ERD in either the facial expression or gaze study suggests that, at least in the case of opaque actions, visuomotor experience was the key factor in development of a mirror mechanism.

As such, the findings from Chapters 4 and 5 support the Hebbian, Neuroconstructivist, Epigenetic, and Associative accounts to a degree, with all of these positing that early maternal mirroring could strengthen a mapping between self- and other-generated facial gestures (e.g. Heyes et al., 2011; del Giudice et al., 2009; Ferrari et al., 2013; Tramacere et al., 2016; Quadrelli & Turarti, 2016). The fact that maternal mirroring of facial expressions at a mere two months was related to mu ERD at nine months could indicate that the infant's brain is at least capable of capitalizing on relatively infrequent visuomotor contingencies to strengthen visuomotor mappings for particular facial expressions. This suggests that a basic mirror system could already be present at this age, and thus that there could be some genetic factors that constrain the environmental input infants receive and/or that provide the fundamental structures necessary to develop a facial mirror system. This could be used in support of the Hebbian and Neuroconstructivist accounts, both of which emphasize the canalization of early experience (e.g. genetic predisposing of mothers to imitate their infant or for infants to look at faces). While such a finding also fits with the Epigenetic account, which claims there must be some kind of rudimentary mirror system very soon after birth, it is not known whether early experience altered genetic expression in any way, which is a central claim of the Epigenetic hypothesis.

Finally, perhaps a distinction can be made between mirror system involvement in the perception of faces versus gaze shifts' based on results in Chapters 4 and 5. In the gaze study, interactions at 6.5 months were related to mu ERD later on in infancy, but 3.5 month interactions were not. Therefore, a mirror system involved in processing attention shifts could depend on experience to a greater degree than a facial mirror system, with less of a genetic basis. This is similar to the distinction proposed between a manual and facial mirror system (Casile et al., 2011). More sepcifically, infants are capable of producing a number of facial movements before they can competently orient attention to aspects of the environment other than people's faces. Additionally, mothers have more opportunity to mirror infants' expressions early on postpartum than follow infant shifts in attention, thus the experience necessary to develop a mirror mechanism for faces is likely to develop first.

6.3 LIMITATIONS AND FUTURE WORK

There are some limitations to the studies included in this thesis that should be noted. For example, *a priori* criteria based on previous research were used to select the mu frequency band for analysis. However, this means that the extent to which neural activity associated with action execution might have differed between participants is unclear. In studies such as those by Southgate and colleagues (2010, 2009), the frequency band in which mu power modulation was analysed was determined on an individual basis, dependent on the modulation revealed during action execution. The frequency band with the most desynchronization compared to baseline, along with 1Hz above and below, was then chosen for analysis of the observation condition. This ensured that any changes in mu power revealed during action observation would be common to both observation and execution conditions, and that individual differences in participant mu frequency could be considered. The frequency band investigated in the present studies could have been influenced somewhat by differences between participants, weakening the ability to detect any influence on action observation in the group data. However, with a small number of execution trials available, an approach such as that of Southgate et al. (2010, 2009) was not the most appropriate in the current body of work, and besides, the action of interest here was facial expressions rather than manual actions, which are far more difficult to elicit from very young participants. The use of the 6-9 or 5-9Hz frequency band is very commonly used in mirror system literature involving infants and children of the ages investigated here (i.e. it is the standard approach: e.g. Cannon et al., 2016; Marshall et al., 2011; Nyström, 2008; Nyström et al., 2011), with longitudinal research supporting the use of these particular bands (Berchicci et al., 2011; Marshall et al., 2002). As research involving 30-month-olds is much less common than with infants around 9 months, even though studies on the development of mu strongly suggest that the 6-9Hz band is the most appropriate for use at this age, for the study in Chapter 2, mu modulation in the 10-13Hz band (thus covering the adult frequency band also) during execution of facial expressions was also explored. This demonstrated that there was indeed greater mu desynchronization in the 6-9Hz band than the 10-13Hz band, and only in the 6-9Hz band was desynchronization significantly lower than baseline. Furthermore, even though the peak of each infant's mu band may not have been in the centre of the a priori bands selected for use in the studies here, there was still clearly an overlap in the central regions activated during observation and execution.

Another limitation to the research here is presented by the use of EEG itself, although this still is the most practical way to investigate mirror system activity in difficult populations such as infants and young children. The spatial resolution of EEG is inferior to techniques such as fMRI, and therefore even though analysing particular electrode clusters and comparing different regions (particularly occipital with central areas in mirror system studies) is very useful for estimating the cortical areas activated during action observation and execution, the exact regions from which activity arises cannot be identified. Therefore, although this is currently the most useful and reasonable way to explore infant mirror systems, it would be interesting if future EEG studies increasingly utilized other analysis techniques such as cortical source localization to identify more precisely the areas of the brain activated. This type of analysis exploits high-density EEG recordings and quantitative models to identify dipole sources that account for the EEG data obtained, and these sources can then be related to neural activity in either the time domain or different experimental conditions. This would be very challenging for research such as that included here for a number of reasons, including the small amount of data that one is usually able to collect and analyse in such studies, and the need for structural MRIs. The second point concerns the fact that calculating the head shapes of individual participants is critical for cortical source localization (Michel et al., 2004), hence the need for structural MRIs, but obtaining the scans necessary to do this is of course very hard with younger participants. Some infant research has simply used adult models for the electrical and spatial characteristics of the head in order to conduct this type of analysis, or even just a single example of an infant at the right age, but the use of individual MRIs is considered far superior, and thus would be ideal. Additionally, magnetoencephalogram (MEG) and near-infrared spectroscopy (NIRS) are two techniques that are becoming more feasible possibilities for use with infants, which may help to elucidate the exact brain areas activated in infants during action observation and execution. However, for number of reasons EEG remains by far the most useful tool to explore putative mirror system activity in infants at this point, including that it is relatively inexpensive, is non-invasive, is less sensitive to movement, provides a direct measure of neural activity, and allows collection of neurophysiological data in a relatively unconstrained environment. Note, fNIRS, similar to fMRI, does not give a direct measure of neural activity, and MEG involves a lot of participant restraint.

Due to relatively low levels of execution, mouth opening, happy and sad conditions had to be combined for analysis in the EEG experiments in Chapters 2 and 4. Research suggests that infants aged 1-2 years old tend to imitate live models more often than televised ones (Hayne et al., 2003; Nielsen et al., 2008). No such evidence had been provided for infants around 9 months of age, but perhaps children/infants in the studies presented here would have produced more expressions if they had observed them being performed live by the experimenter versus video clips. This has been the approach used in infant macaque research (Ferrari et al., 2012; Vanderwert et al., 2015). Nonetheless, if infants here had produced expressions too often, analysis of observation-only conditions may not have been possible, and live presentation of facial expressions would have been less standardized across participants. Perhaps in future work it would be interesting to compare spontaneous facial expressions performed during live presentation with presentation on a monitor to see if there are any differences, but also to increase the chance of obtaining more useable execution trials. Note, in the gaze EEG experiment in Chapter 2, a separate observation and execution condition was not necessary as infants performed an action and observed an adult performing an action in each trial. It would still be interesting though if future research compared mu desynchronization during gaze following and seeing someone else follow one's own gaze without being cued (i.e. infant voluntarily looking at an object before observing someone else do the same), which would more comparable to adult studies (e.g. Neufeld et al., 2015; Schilbach et al., 2013), but this may be difficult to achieve with very young samples.

The mu rhythm actually consists of two spectral peaks, with its arch-like appearance resulting from activity in two frequency bands: i) alpha range activity, and ii) beta range activity (Lopes da Silva & Niedermeyer, 2005). In common with the majority of infant studies, this thesis focused only on the former. However, a number of adult mirror system studies have looked at the beta band (e.g. Cannon et al., 2014; Cooper et al., 2013; Gros et al., 2015; Muthukumaraswamy & Singh, 2008; Orgs et al., 2008), which is also modulated during observation and execution of actions (Babiloni et al., 2002; Muthukumaraswamy & Singh, 2008), and in fact, some research suggests that investigation of desynchronization in the beta frequency may be more sensitive to action observation (Hari et al., 1998). Nevertheless, the few infant studies that have looked at beta have produced mixed results (Nyström, 2008; van Elk et al., 2008; Virji-Babul et al., 2012). The reason beta was not analysed in this thesis is because much less is currently know about this frequency band compared to alpha activity during action observation in infants, and the functional significance of the beta band is not clear, even in the adult mirror system literature (Cuevas et al., 2014). The alpha portion of mu in infants is evidently at a lower frequency than in adults, and has been shown to be functionally equivalent to the adult band, however, it is not known what the functionally equivalent band for beta is in infants. The infant studies that have looked at beta have simply investigated the same band as in adults, but to make such investigations more interesting and valid, perhaps future research should try to establish what frequency range in the developing brain should be considered as equivalent to the beta portion of mu in adults.

Concerning alpha and beta components of the mu rhythm, there is some evidence suggesting that the alpha portion of mu originates largely from the primary somatosensory cortex, whereas the beta portion arises from primary motor cortex (Avanzini et al., 2012; Hari et al., 1997; Ritter, Moosmann, & Villringer, 2009; van Schie et al., 2008). Additionally, combined EEG and fMRI research has revealed that modulation of mu in the alpha frequency band correlates with the BOLD signal in various mirror system areas, such as the inferior parietal lobule, dorsal premotor and primary somatosensory cortex during action observation and execution (Arnstein et al., 2011). This could mean that alpha mu suppression reflects downstream modulation of the sensorimotor cortex by mirror neuron areas in the parietal and frontal cortex (Arnstein et al., 2011; Babiloni et al., 2003; Hari et al., 1998; Muthukumaraswamy et al., 2004; Nyström et al., 2011; Perry & Bentin, 2009). The mirror system literature that has looked at beta modulation has mostly focused on manual actions, though some adult research has been conducted in regards to facial expressions (Cooper et al., 2013). Whereas other studies have found alpha mu modulation during observation of facial expressions (Moore et al., 2012), Cooper et al., only found modulation in the beta band. The authors conclude this might mean their results reflected greater motor compared to somatosensory activation, noting that differential functions of alpha and beta portions of mu during action observation/facial expression observation warrants further investigation.

In relation to the interaction periods, it also might be interesting in the future to use a different type of scheme to code the early mother-infant in order to capture facial movements of the social partners in more detail; i.e. perhaps there is some more fine-grained matching/mirroring going on which can’t be identified by a scheme that identifies higher-level discrete events/facial expressions. For example, an approach more similar to that presented by the ‘Facial Action Coding System’ (FACS: Ekman, Friesen, & Hager, 2002) could be utilized. A modified version of this system is also available for use with infants and young children (Oster, 2003). FACS enables almost any anatomically possible facial expression to be coded by identifying individual muscle movements that occur in sequential time steps, and combined can result in particular expressions. As certain facial expressions involve overlapping sets of muscles, using such a coding scheme may allow something to be said about the level of representation a facial mirror system is functioning at; i.e. whether it codes particular muscle movements or coordinated sets of muscle movements that comprise particular expressions or higher-level movements. For instance, if mother and infant facial movements were coded separately in each second/frame of a recorded interaction (e.g. movement of the eyes, brow, mouth etc.), events could then be extracted from criteria based on overlaps in the coding of mother and infant (similar to the gaze coding scheme used in Chapter 5).

Although the research reported in this thesis uncovered evidence for neural activity that would be expected if a mirror system was involved in the processing of observed facial expressions and attentional actions, it did not address the question of function and how this system might be linked to the emergence of social-cognitive abilities. These abilities could be low-level action recognition, goal inference, prediction of an action outcome, or higher level abilities such as imitation learning, empathy, or theory of mind skills, in which either lower or higher level functions could be played by a mirror system. As noted in the introductory chapter, many potential functions for mirror systems have been hypothesized, however, no agreement has been reached. Some investigations into the link between mirror system activity and behavioural measures of social cognition have been conducted, implicating a number of potential roles, however, more research is clearly required if questions concerning the functional role a mirror mechanism may play are to be addressed, especially in early development. For example, adult TMS research has shown that premotor cortex disruption both impedes an individual's ability to recognize actions (Michael et al., 2014), decreases the speed at which one can generate visual predictions about action outcomes (Stadler et al., 2012), and when applied to the hand versus leg motor area, produces deficits in predictive saccades while watching a reaching hand (Elsner, D'Ausilio, Gredebäck, Falck-Ytter, & Fadiga, 2013). One fMRI study has also demonstrated differential activation in mirror regions if an individual is asked to think about how an action was performed or why it was performed (Iacoboni et al., 2005). As noted in Chapter 2, the 'understanding' of others facial expressions is widely thought to involve a simulation, or 'embodied simulation', mechanism (Bastiaansen et al., 2009; Gallese, 2007; Niedenthal et al., 2010), which is thought to occur via coupling perceptual and motor representations. The facial mirror system is thus thought to be involved in facial processing and empathic ability (Tramacere & Ferrari, 2016). For example, if covert emotional states such as happiness are associated with overt motor behaviours (e.g., smiling), an observer could simulate the unobservable emotional states of others by embodying their observable motor behaviour; i.e. mentally replicating the observed facial expression. Indeed, some research has demonstrated a link between putative mirror system activity and empathy in adults (Braadbaart et al., 2014; Gazzola et al., 2006; Schulte-Rüther, Markowitsch, Fink, & Piefke, 2007). However, the techniques used in studies such as these (e.g. TMS to disrupt motor activity, the explicit instruction to think about why actions are performed or to deliberately empathize, or the use of Baron-Cohen and Wheelwright's (2004) 'Empathy Quotient' questionnaire) are not possible for use with very young populations, making investigation of the involvement of a mirror system in social cognition very challenging.

Despite the difficulties presented, a few studies concerning manual actions have now also provided some evidence for the function of a mirror system in human infants. For instance, some EEG research has found mu desynchronization in 9-month-old infants as they observed a hand ‘reaching’ (i.e. posed as if to grasp an object) behind a barrier, but not during observation of a hand reaching to an empty location or when the hand moved in an ambiguous way rather than reaching (Southgate et al., 2010). This might suggest that a mirror system selective specifically for representing goal-directed actions was activated (Woodward & Gerson, 2014), or could indicate that the infant was predicting the outcome of the action rather than analysing the goal per se (Southgate et al., 2010). In either case, this could play an important role early on in development by contributing to the ‘understanding’ of others’ actions or facilitating responses to those actions, but the divergence in opinion highlights an issue generally found in the mirror system literature; wherein it is still debated what exactly is ‘mirrored’ by mirror mechanisms; e.g. the precise kinematics, the action goal, or a combination of the two (Gazzola et al., 2007), or even whether a goal might be identified outside the mirror system, with the motor system then predicting, for instance, the unfolding kinematics or emulating what the observer would do to achieve the identified action goal themselves (Csibra, 2007; Southgate, 2013). Therefore, an important question to answer now is also what is being mirrored in the developing brain.

The research presented here was designed to investigate whether a mirror system in young children and infants might be involved in the processing of opaque actions in some way, rather than the precise function it might play, and whether early experience might influence the development and refinement of such systems. Despite this, it is still interesting to speculate about the way in which a mirror mechanism might do this and the functional role it plays. As implied above, for example, the ‘direct matching hypothesis’ states that during observation of others’ actions, the visual representation of that action is mapped directly onto a corresponding motor representation (which could for example, be at the level of movement or a motor goal) which leads to a direct ‘understanding’ of that action (Gallese et al., 1996; Rizzolatti & Sinigaglia, 2010). Alternative theories of mirror system function include predictive and emulative accounts (Csibra, 2007; Southgate, 2013), which posit that action mirroring is a consequence of action/goal understanding, that this is already in place very early in development, and that mirroring may be vital for engaging in joint action. The neuroconstructivist account (Quadrelli & Turati, 2016) suggests that both direct-matching and emulative or predictive processes might play a role in action/goal understanding, hypothesizing that at first, top-down processes drive infants’ understanding of others’ actions, and that observed actions have to be reconstructed based on previously identified goals and other significant features. Then, later in development, bottom-up mechanisms could start operating in response to actions that have become familiar to the infant due to active and observational experiences. Therefore the ‘understanding’ of highly experienced actions may eventually bypass ‘top-down’ processes, and occur via the generation of a more speedy and direct motor ‘resonance’ response to observed actions, facilitated by a mirror mechanism.

How can such theories of mirror system function be applied to other types of action, such as facial expressions and attention orienting? Of course, it has to be kept in mind that manual actions and facial expressions are very different, and therefore the mirror systems for each type of action are likely to work in different ways, as well as develop somewhat differently (Casile et al., 2011). Manual actions have the potential to act upon and manipulate objects, while facial expressions (with the exception of gestures such as biting and ingestive actions) do not, and therefore mirror system theories about goal inference and emulation do not seem as relevant to facial expressions. As face-to-face interactions comprise the majority of an infant’s early environment, a mirror system for faces present early on in life may play an important role in detecting the congruence between own and other actions through direct matching (Ferrari et al., 2013; Marshall & Meltzoff, 2011), which could aid early social exchanges, and thus contribute to the development of more demanding abilities, such as empathy and the attribution of mental states. Such a system could be present in rudimentary form at or soon after birth, and thus could also contribute to neonatal facial imitation, however, this could then be further developed via experience of maternal mirroring. Perhaps a mirror system for facial expressions could also work in a predictive fashion, predicting the final expression from an initial observed facial movement, thus facilitating smooth interactions. A different experience-dependent system might subserve visuomotor couplings in the case of manual actions, with development of specific motor abilities over a greater time period causally connected to the development of related perceptual abilities (Casile et al., 2011). Attention direction involves different processes and brain regions from both facial and manual actions, and thus also likely functions and develops in divergent ways. On one hand, attending towards an object is clearly object/goal orientated, and therefore even though an attentional mirror system may still develop somewhat differently to a manual mirror system (e.g. be more influence by maternal ‘mirroring’, rather than self-observation, as it is an opaque action), it could potentially work in a predictive or emulative fashion. On the other hand, saccades and head turns may occur too quickly to predict the target from the initial movement, and complex geometric reasoning is required to determine the target of another’s gaze in an emulative fashion. Therefore an attentional mirror system could work via directly matching the observed movement onto corresponding motor representations in order to determine the target of attention.

There are a number of potential ways future research could look at how a putative infant mirror system activity related to the processing of facial expressions or attention shifts may relate to the development of various social-cognitive abilities. For example, a study could be designed to investigate whether greater mu desynchronization during observation of different facial expressions was related to the ability to recognize expressions. In preverbal infants, perhaps this could be done using a preferential looking paradigm, which could test the infant's implicit ability to discriminate between different expressions (such as in Kotsoni, de Haan, & Johnson, 2001). In older children (e.g. around 4 years of age), a more explicit measure could be used, such as the categorizing of expressions into different groups, or asking children to label the emotion an individual is feeling based on short demonstrations using puppets or on pictures/cartoons (e.g. Cheal & Rutherford, 2011; Denham, 1986; Pons, Harris, & de Rosnay, 2004). If a relationship between early empathy measures and mirror system activity was to be looked at, an approach such as that used by Knafo et al. (2008) could even be used with children around 3years of age, where the child's reactions to their mother/experimenter simulating distress are coded. In terms of attention direction, if a mirror mechanism is involved in the matching of this type of own and other actions, and thus is important at a low-level for responding to and initiating joint attention (JA), it would be expected that the degree of mu desynchronization during the experiment in Chapter 5 would be related to individual differences in JA development. This could be explored by the manual coding of infants' JA behaviours during a naturalistic interaction (e.g. Gaffan et al., 2010), or by using more standardized interactive measures such as the 'Early Social Communications Scales' (ESCS; Mundy et al., 2003).

Additionally, although the research encompassed within this thesis revealed something about how early experience may influence mirror system development, and in doing so, suggest that mirror systems for opaque actions seem to be present in the brain from early on in infancy, this still does not address whether or not a rudimentary mirror system may exist at birth in human beings. Typically, motor output is suppressed during action observation (Mancini, Ferrari, & Palagi, 2013), but many suggest that a mirror system, along with other motor regions, could be involved in overt production of observed behaviours for the purposes of imitation (Kraskov et al., 2009). In the developmental literature, a mirror mechanism has been implicated in neonatal imitation (Ferrari et al., 2012), with those such as Lepage and Theoret (2007) putting forward an interesting idea concerning how a mirror system may be involve in neonatal imitation. They claim that this behaviour, while not reflexive, could reflect the activation of an automatic observation-execution matching mechanism. That is, although evidence that infants imitate a variety of gestures means it is unlikely that behavioural matching occurs via purely reflexive means, it does not mean it is under direct volitional control either. The authors argue that activation of a mirror system is largely automatic and pre-attentive, and that that subthreshold activations occur in response to the passive observation during non-imitative contexts. Indeed, spontaneous covert mimicry of facial expressions in adults may reflect this automatic and largely subthreshold activation, and perhaps it is the case that in very early infancy, overt imitative behaviours occur because frontal inhibitory mechanisms are not yet developed enough to suppress activation of motor representations triggered during observation of others facial expressions. Although neonates have the capacity to perform volitional actions (van der Meer, 1997; van der Meer, van der Weel, & Lee, 1995), according to this view the infant does not have to intentionally match another’s facial expression because the corresponding motor output is automatically activated (Lepage & Théoret, 2007). This could explain why the occurrence of infant imitation decreases 2 months postpartum (Field, Goldstein, Vega-Lahr, & Porter, 1986; Fontaine, 1984), and then seems to reappear in a more complex, intentional form later on after the mirror system and related inhibitory mechanisms have developed further.

Clearly, it would be very difficult to obtain neural data from newborn infants, however, this is required to elucidate the genetic and learning components required for emergence and refinement of mirror systems. This could potentially be achieved using a similar approach to that used with macaque infants, with EEG used to record putative mirror system activity in infants soon after birth, and even linking it to neonatal imitation ability. This may help to address whether a mirror system is involved in facial processing from birth, as well as if the neonatal imitation phenomenon really does represent a basic mechanism for mapping between own and other actions from birth. Also, as proponents of the epigenetic theory of mirror neuron development suggest (Ferrari et al., 2013), it would be interesting if future work looked more at the complex relationship (not dichotomous and exclusive) between innate and acquired, adaptive and plastic, and genetic and environmental influences on mirror system development. This could include looking at molecular differences between postnatal and adult mirror neurons, or testing of environmental stimuli that may trigger specific patterns of molecular alterations that underlie mirror neurons (Ferrari et al., 2013; Tramacere et al., 2015). In a similar vein, although base rates of mother and infant behaviours were considered in these studies along with maternal imitation, it would be interesting if future research also considered the influence of infant imitation of mothers on development of the mirror system. Whether or not infants do this from birth (or even if they can do it but do not tend to in early interactions) or if this happens 'by accident' as in the Triesch et al. (2007) developmental model of gaze following mirror neurons, observation of maternal production and subsequent infant production of the same facial expression could strengthen a mapping between visual and motor representations. Perhaps a mirror system is more developed in certain infants than in others from birth due to genetic or prenatal experiential reasons (Simpson, Fox, Tramacere, & Ferrari, 2014; Simpson, Murray, Paukner, Ferrari, et al., 2014), which might explain why neonatal imitation is not always found on a population level. If neonatal imitation does involve this system, infants' ability to imitate early on might mediate the influence of subsequent interactions with their mothers. This is a slightly different question to the one addressed in this thesis, which focused specifically on the influence of mothers on 'opaque' actions that cannot be seen by infant. It would also be interesting if future work looked at other maternal behaviours that may impact the relationship between maternal mirroring and mirror system activity, e.g. ostensive marking in addition to maternal imitation which might make the response more noticeable to the infants, or in addition to 'mother follow infant' which may make it more likely that an infant will look back towards the mother and see that she has followed.

In this thesis, rather than a single mirror system, mirror systems have been presented as separate for manual, facial, and attention-related actions. This is because the processing of such actions likely involves both distinct and overlapping regions of the brain, and thus a mirror mechanism implemented in these areas may function and develop in slightly different ways. Indeed, this proposal has been suggested by a number of researchers (e.g. Casile et al., 2011; Del Giudice et al., 2009), with a rudimentary mirror system involved in facial expression processing perhaps being present very soon after birth and subsequently refined via maternal mirroring of infant facial expressions, and a manual mirror system emerging later in the infant based on observation of self-generated actions. Therefore, it would be fruitful if future work specifically compared development of a mirror system for opaque actions to one involved in the processing of actions one can see oneself perform. For example, if a facial mirror system is present in the neonate in some form, but a manual mirror system emerges later based more on sensorimotor experience (Casile et al., 2011), presumably a neural response indicative of mirror activity would be demonstrated much earlier in development for facial expressions, and early experience would influence the two systems differently. This could be looked at using a longitudinal design similar to the one used here (see Chapters 3, 4, and 5), whereby mothers and infants are observed interacting at various times points over the first year (i.e. at time points where infants have differential experience of manual and facial actions), and a number of infant EEG experiments conducted. During these interactions (perhaps with and without toys), the dyad's facial expressions could be coded and instances of mirroring identified, as well as any manual actions, looks to own/other hands, and any mirroring of manual actions noted. These measures could then be compared to activity in the EEG experiments, where either the same or separate groups of infants observed (live or video) both facial expressions and manual actions, e.g. grasps infants can and can't do at that age, emotional and non-emotional facial expressions, familiar and non-familiar facial expressions. Execution of facial expressions could be coded from videos during these experiments or via encouragement of a live model on a separate occasion, and execution of grasps via an experimenter demonstrating this with toys. It might be interesting if EMG could be used with the same infants during the EEG experiment, or even with another group who observed the same stimuli, to see if covert mimicry was contributing to, or occurring as a result of, the effect during observation. In terms of manual actions, theories of mirror system development thus far have focused on the role self-observation may play in the strengthening of visual-motor couplings, however, the observation of mothers 'mirroring' infant manual actions during joint action could also theoretically have an effect, and perhaps even contribute to a generalization process in the mirror system in order to process others' actions observed from a different perspective than when observing oneself.

Finally, it may help to further elucidate the impact of early environment on development of a facial, manual, or attentional mirror system by comparing a typical group mother-infant dyads with a group where interactions are likely disturbed, e.g. in the context of postnatal depression. Depressed mothers often smile less and interact with their infants in a withdrawn and muted style (Cohn et al., 1986; Delgado et al., 2002; Field, Diego, & Hernandez-Reif, 2009), with infants of these mothers often exposed to more sad, angry, and neutral facial expressions compared to other infants (Dawson et al., 2003). Research also suggests that depressed mothers mirror infant facial expressions less (Field et al., 2005), and respond more often to negative rather than positive expressions (Field, Healy, Goldstein, & Guthertz, 1990; Murray et al., 1996). Young infants of depressed mothers have also been shown to look at sad facial expressions for less time than infants of non-depressed mothers (Field et al., 1998), and to have difficulty discriminating neutral and smiling facial expressions (Bornstein, Arterberry, Mash, & Manian, 2011). Depressed mothers also seem to experience more difficulty compared to non-depressed mother in establishing and maintaining joint attention, and generally providing contingent responses to their children's behaviours (Goldsmith & Rogoff, 1997; Jameson, Gelfand, Kulcsar, & Teti, 1997). As such, they often engage in less coordinated joint attention and maintenance of their child's attention focus when competing focuses of attention are present (Goldsmith & Rogoff, 1997; Jameson et al., 1997). Such disturbed interactions are unsurprisingly related to less feedback and reinforcement of infant behaviours like exploration and manipulation of objects, with less engagement in joint activity also demonstrated overall. Maternal depression has also been linked to poor infant motor development (Cornish et al., 2005), perhaps because mothers provide suboptimal levels of stimulation for their infants (Field et al., 1998; Murray et al., 1996). Therefore, infants of depressed mothers tend to experience an atypical social environment, which has been linked to poor child outcomes, and thus would provide an ideal opportunity to investigate how differences in early social environment may influence mirror system activity in relation to various actions.

6.4 CONCLUSIONS

Overall, results from the studies that comprise this thesis suggest activation of the sensorimotor cortex during observation and execution of opaque actions, in very young children and infants. This research is therefore the first to provide evidence consistent with mirror system involvement in the processing of such actions from an early stage in human development. Additionally, findings revealed a link between early social experience and putative mirror system activity, and thus are the first to support the hypothesis that mother-infant interactions play an important role in the development of such systems for opaque actions in humans. While such results cannot answer questions concerning the status of the system at birth, they do suggest that a mirror system, or systems, are present in the brain from an early age, and that whether or not a rudimentary mirror system exists in the newborn, maternal mirroring plays a significant role in the strengthening of visuomotor mappings linked to unobservable self-performed actions.

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8 APPENDIX A: INFORMATION SHEETS AND CONSENT FORMS

8.1 30 MONTH EEG STUDY INFORMATION SHEET

Project Title: An Investigation of Infant Psychological Development

Thank you for agreeing to receive this information about the research we discussed together previously. Before you decide whether or not you want to take part in this study, we would like to explain in more detail why we are planning this research and what it would involve for you. We hope this information sheet will help you decide whether you would like to take part, but one of our team would be happy to talk with you and answer any questions you may have.

What is the research for?

We know that the first years of a child's life are an important time for developing many basic psychological skills and social relationships. In this study, we are interested in learning more about the development of social and cognitive skills in the first two and a half years of life.

Why have I been invited?

We are inviting all the mothers with children of the right age who agreed at the Royal Berkshire Hospital to have their details stored on the SPCLS Child Development Database.

Do I have to take part?

It is up to you whether or not to take part in this study. Before participating, we invite you to read this information sheet that describes the research. We will also call you by telephone in order to answer any questions you may have. If you decide to participate and then change your mind, you are free to withdraw from the study at any time, without giving a reason. You are free to decide if you would like your child to take part in some, but not all, assessments.

What will happen to me if I take part?

Taking part in this study will involve coming to the University of Reading when your child is 30 months old. The visit should take up to 1 hour 30 minutes, although this may depend a little on catching your child when he/she is ready. We will refund all your travel costs. You will be present in the room with your baby throughout the session, and will be free to stop the tasks at any time. If your child becomes upset at any time, the researcher will of course stop and wait until they are settled and ready to start again. We will video your child throughout the session using video cameras.

This visit will be divided in two parts. In the first part, we will invite you and your child to take part in a play session with one other mother and child of a similar age, who have also been involved in the study. In the second part (involving only you and your own child), you will be asked to talk to your child about an everyday experience using two picture books. Your child will then be shown videos of faces performing different expressions on a screen, during which we will record his/her brain activity. To record this brain activity, a soft cap will be placed on your baby's head, as in the picture below. This brain recording method is frequently used in research with children, and should not cause any discomfort or upset.

What are the benefits of taking part?

Although there won't be any direct benefit for you, we hope that the research will help us to better understand the early years of development, and therefore may result in better support for other families in the future.

To thank you for giving up your valuable time to take part in the research we will also give you a £10 Mothercare voucher.

What are the potential disadvantages of taking part?

We have thought very carefully about this study and do not anticipate any disadvantages for you or your family. There is a time commitment required for the research visit, but all travelling expenses will be refunded.

What will I have to do?

A few days after you receive this information sheet, we will contact you by telephone and will explain the study in more detail, and will be able to answer any questions you might have. At this point, if you are happy to be involved, we will arrange your visit to the University. When you come to the University, we will go through the research with you again, and you will be asked to sign a consent form to show that you have understood what taking part involves. We will always try to make these visits as easy as possible for you by finding a time which will fit in with your own and your baby's routine.

What will happen if I don't want to carry on with the study?

If you decide to take part but then change your mind, you can withdraw from the study at any time. You don't need to give a reason.

What if there is a problem?

If you wish to complain about any aspect of the way in which you have been approached or treated during the course of the study, you can either contact our research team directly, or contact the Head of the University of Reading Research Governance office, Dr. Mike Proven on 0118 3787119 or by email to m.j.proven@reading.ac.uk. Given the nature of this study, it is highly unlikely that you will suffer harm by taking part. However, the University has arrangements in place to provide for harm arising from participation in studies for which they are the Research Sponsor.

Will my participation be confidential?

If you decide to take part in this study, all information collected will remain strictly confidential. We will use a unique participant number to identify you so that your name and address will not be stored with any other confidential information that you provide. All data will be kept in a secure place, separate from any other identifying details. Responsible members of the University of Reading may be given access to data for monitoring and/or audit of the study to ensure compliance with regulations. All data will remain entirely confidential. Copies of the data, including the audio-visual material, will be kept securely and confidentially by the University of Reading and will be destroyed within five years of the study's completion.

What will happen to the results of this study?

The information will be used to develop our understanding of the first two years of a child's development. It will be written up for other professionals working in the research field, published in academic journals, and presented at conferences. None of the participating families will be identifiable from any information that is published or made available to other professionals. Participants can request a summary of the research results once the study is complete if they wish.

Who is organising and funding this research?

The costs of this research will be met by a studentship award to Ms. Holly Rayson from the Medical Research Council (UK). It is organised by Professor Lynne Murray (University of Reading).

Who has reviewed this study?

This study has been reviewed by both the University of Reading Research Ethics Committee and has been given a favourable ethical opinion for conduct (University of Reading number: 13/29).

What happens next?

You will receive a call from one of the research team shortly to make sure you received this letter, and we will answer any questions you may have. You can let us know then if you would be interested in participating or not, or if you would like more time to think about it.

Thank you for taking the time to read this information and considering taking part in the study. If you have any immediate queries, you can contact Holly Rayson who is working full time on the study, via the email address (h.rayson@pgr.reading.ac.uk) or contact number (+44 (0)118 378 6487).

8.2 CONSENT FORM

Title of Project: An Investigation of Infant Psychological Development

1. I confirm that I have read and understand the information sheet dated.................... (version.....) for the above study. I have had the opportunity to consider the information, ask questions and have had these answered satisfactorily. ☐

2. I understand that my participation is voluntary and that I am free to withdraw from the research at any time without giving any reason without prejudice. ☐

3. I agree to my GP being informed of my participation in the study, and, in consultation with you, of results of any assessments of clinical relevance. ☐

4. I am happy for my baby and myself to be video-recorded during the research visit, and I am aware that this footage will only be accessed by the research team and will be stored anonymously and securely. ☐

5. I agree on behalf of my baby and myself to take part in the above study. ☐

OPTIONAL I am happy for anonymous, but potentially identifiable, video recordings to be used, only by members of the study research staff, for teaching or training purposes, or to be presented at scientific meetings. ☐

Name of Infant: ……………………………………………………………

Name of Mother: ………………………………………………………….

Date:…………………………………………………………………………….

Signature:…………………………………………………………………….

Name of Person taking consent: …………………………………………..

Date: ……………………………………………………………………………

Signature: ……………………………………………………………………

8.3 LONGITUDINAL STUDY INFORMATION SHEET

An Investigation of Infant Psychological Development

Thank you for agreeing to receive this information about the research we discussed together previously. We would like to explain in more detail why we are planning this research and what it would involve for you if you agreed to take part.

What is the research for?

We know that the first years of a child's life are an important time for developing many basic psychological skills and social relationships. In this study, we are particularly interested in learning more about the development of babies very early on, in the first 10 months of life, as well as how the evolving relationship between mothers and their babies supports this development.

Why have you been invited?

We are inviting mothers of infants who are the required age for this study, who kindly signed up to the University of Reading's Child Development database whilst on the maternity ward at the Royal Berkshire Hospital.

Do I have to take part?

It is up to you whether or not to take part in the study.

What will happen to me if I take part?

Taking part in this study will involve a researcher coming to visit you at home when your baby is around 2 months old, and then you coming to the University of Reading when your baby is 3 ½ , 6 ½ , and 9-9 ½ months old. The 2 and 3 ½ month visits will take around 1 hour 30 minutes, the 6 ½ month visit around 2 ½ hours, the 9-9 ½ month visit a bit longer, though this may depend a little on catching your baby when he/she is ready. As there are quite a few assessments at the 9-9 ½ month visit, we plan to complete these over two visits. You will be present in the room with your baby throughout the sessions, and you will be free to stop the tasks at any time. If your baby becomes upset at any stage, the researcher will, of course, stop and wait until they are settled and ready to start again. We will video your baby throughout the session using both hand held and wall mounted cameras.

At each visit, we will ask you to play with your baby, with and without toys, and in different situations, and we will also ask you to fill in four questionnaires; two about your baby's general behaviour and development, and two about moods and feelings in motherhood.

At the 6 ½ , 9-9 ½ month visits, we will record your baby's looking behaviour and brain responses while they look at different things presented on a computer monitor and/or by an experimenter (e.g. people displaying different facial expressions). This will be done using an eye-tracker and a soft cap to measure brain activity. These eye-movement and brain recording methods are frequently used in research with infants. They are completely safe and should not cause any discomfort or upset to your baby.

Additionally there will be a number of brief and simple activities for your baby to do with the researcher. These will include showing your baby a new toy and asking him to wait for a brief period before playing with it, and watching a researcher manipulate different objects.

What are the benefits of taking part?

Although taking part in the research won’t be of any direct benefit for you, we think you will find the assessment sessions interesting. We hope that the research will help us to gain a better understanding of the early months of development, as well as help us understand how to improve on support to other families in the future. To thank you for giving up your valuable time to take part in the research, at the 6 ½ month visit you will receive a £5 gift voucher, and at the final visit a £10 voucher.

What are the potential disadvantages of taking part?

We have thought very carefully about this study and do not anticipate any disadvantages for you or your family, other than the sacrifice of your time.

What will I have to do?

If you are happy to take part, please contact Holly Rayson, who will arrange the first visit to you home for when your baby is around 2 months old. We will go through the different assessments with you again before going ahead. At the end of the session we will arrange a date for your next visit to the University. We will always try to make these visits as easy as possible for you by finding a time which will fit in with your own and your baby’s routine.

What will happen if I don’t want to carry on with the study?

If you decide to take part but then change your mind, you can withdraw from the study at any time. You don’t need to give a reason.

What if there is a problem?

If you wish to complain about any aspect of the way in which you have been approached or treated during the course of the study, you can either contact our research team directly, or contact the Head of the University of Reading Research Governance office, Dr. Mike Proven on 0118 3787119 or by email to m.j.proven@reading.ac.uk.

Will my participation be confidential?

If you decide to take part in this study, all information collected will remain strictly confidential. We will use a unique participant number to identify you so that your name and address will not be stored with any other confidential information that you provide. All data will be kept in a secure place, separate from any other identifying details. Responsible members of the University of Reading may be given access to data for monitoring and/or audit of the study to ensure compliance with regulations. All data will remain entirely confidential. Copies of the data, including the audio-visual material, will be kept securely and confidentially by the University of Reading and will be destroyed within five years of the study’s completion.

What will happen to the results of this study?

The information will be used to develop our understanding of the first 10 months of a baby’s development. It will be written up for other professionals working in the research field, published in academic journals, and presented at conferences. None of the participating families will be identifiable from any information that is published or made available to other professionals. Participants can request a summary of the research results once the study is complete if they wish.

Who is organising and funding this research?

The costs of this research will be met by a studentship award to Ms. Holly Rayson from the Medical Research Council (UK). The research will be carried out under the supervision of Professors Lynne Murray and Peter Cooper (University of Reading).

Who has reviewed this study?

This study has been reviewed by the University of Reading Research Ethics Committee and has been given a favourable ethical opinion for conduct (University of Reading number: 14/35).
All investigators on this project have had criminal records checks and have been approved by the School to work with children.

Thank you for taking the time to read this information and considering taking part in the study.
If you have any queries, you can contact Holly Rayson who is working full time on the study, via the email address (h.rayson@pgr.reading.ac.uk) or contact number (+44 (0)118 378 6487).
If you wish to proceed with taking part in this study please contact Holly Rayson.

9 APPENDIX B: EXTRA CODING SCHEME DETAILS

9.1 CODING OF INFANT FACIAL EXPRESSIONS DURING EEG EXPERIMENTS IN STUDIES ONE AND TWO

Coding Instructions

- One individual should code the entire sample, another 20% for reliability
- Coders will be given videos and corresponding event files showing the start and end times of experimental blocks
    - Coders should be blind to the facial expression being shown to participants on the monitor during the experimental block
- Any instances of happy, sad, and mouth opening expressions (the expressions viewed during the experiment) performed by participants within experimental blocks should be coded
    - See below for movement definitions
        - Expressions at the start and end of each movement coded on a scale of 0-4
        - These values will be used to calculate the magnitude of the movement
- Videos should be watched in real-time and frame-by-frame to accurately identify onsets and offsets
    - This improves accuracy and helps to avoid behaviours from being misinterpreted

Expression definitions

- **Mouth opening**
    - Parting of the lips and lowering of the jaw
        - 0 = Mouth closed; neutral
        - 1 = Lips very slightly parted; relaxed mouth
        - 2 = Lips clearly parted; jaw slightly lowered
        - 3 = Mouth half open (lips clearly parted; jaw clearly lowered, but not to maximal extent)
        - 4 = Mouth fully open (lips clearly parted; jaw lowered to maximal extent)

- **Happy**
    - From a slightly upturned mouth with no cheek elevation and no change in brow region, to a very upturned mouth (often with mouth open) with cheek elevation and raised eyebrows/raised in middles and down at corners

        - 0 = Neutral
        - 1 = Slightly upturned mouth; closed lips
        - 2 = Slightly upturned mouth, can be closed or slightly open lips; some cheek elevation; eyebrows not clearly raised
        - 3 = Clearly upturned mouth, slightly open lips; cheek elevation; eyebrows slightly raised
        - 4 = Clearly upturned mouth, widely open lips; cheek elevation; eyebrows clearly raised
- **Sad**
    - From a slightly furrowed brow and/or slightly downturned/pouted lip, to an extremely furrowed brow with a very downturned/pouted lip
        - 0 = Neutral
        - 1 = Slightly downturned mouth and/or slightly pouted lip; OR slight furrowing of brow (eyebrows often raised or lowered in the centre)
        - 2 = Clearly downturned mouth and/or pouted lip (lips can be slightly parted); OR clear furrowing of brow (eyebrows often raised or lowered in the centre)
        - 3 = Clearly downturned mouth and/or pouted lip (lips can be slightly parted); AND clear furrowing of brow (eyebrows often raised or lowered in the centre); perhaps slight narrowing of the eyes
        - 4 = Clearly downturned mouth and/or pouted lip (lips can be parted); AND clear furrowing of brow (eyebrows often raised or lowered in the centre); narrowing of the eyes

Movement Time Course

- Each of the expression described above will be coded as consisting of 3 phases:
    - (1) The initial movement
    - (2) The hold of the expression
    - (3) The return movement
- Coders will mark the onset and offset of phases 1 and 2
    - E.g. for mouth opening
        - Onset of initial movement starts when the jaw begins to drop and the lips part
        - Offset of initial movement starts when the mouth opening movement reaches its peak

        - Onset of return movement starts when the mouth begins to close
        - Offset of return starts when this movement end
            - That is, it doesn't matter if the mouth is not fully closed
- Coders will rate the expression on a scale of 0-4 at the onset and offset of phases 1 and 2
    - E.g. for mouth opening
        - At the initial movement onset the infant is at a level 1
            - Lips very slightly parted
                - Note, the initial movement onset does not necessarily have to be 0
        - At the initial movement offset the infant is at a level 4
            - Lips clearly parted and jaw lowered to maximal extent
        - At the return movement onset the infant is still at level 4
            - The return movement onset should always be the same as the initial movement offset, otherwise another movement has occurred
        - At the return movement offset the infant is at level 0
            - Mouth closed
                - Again note though, the return movement offset does not necessarily have to be 0

9.2 CODING OF MOTHER-INFANT INTERACTIONS AT 2 MONTHS IN STUDY TWO

Coding instructions

- One individual should code the entire sample, another 20% for reliability
- Coding should start 10 seconds following the start of video recording
    - Infant distress lasting longer than 10 seconds should be excluded
    - Periods in which the mother engages in non-standardised activities with the infant (e.g. including a toy in the interaction period or holding the infant) should be excluded
- The infant's behaviour should always be coded first
    - The image of the mother should be covered on the screen and the first viewing of the video should be without volume to avoid bias
        - For subsequent viewings of the video, volume will be necessary to code infant vocalisations, however the coder should ignore the mother's speech
- Coded behaviours should be observable as discrete events when the film is viewed live

    - The film speed should also be varied during coding (for example viewing with both natural speed and frame by frame)
        - This improves accuracy and helps to avoid behaviours from being misinterpreted
    - If the onset of a behaviour spans 2 sequential seconds, the behaviour should be linked to the second in which the event is first identifiable as the coded behaviour

Infant Behaviours

Coded behaviours are mutually exclusive, representing distinct, discrete events with clear onsets, and thus would be easily identified by the mother in live time. In addition to the infant facial expressions listed in Chapter 4, the following infant behaviours are also identified in this scheme:

- Vocalizations (positive and negative)
- Biological events (e.g. sneezing and hiccoughs)

Maternal Behaviours

At the age this scheme is aimed at (up to 9weeks postpartum), infants do not seem able to detect events as contingent if they occur three or more seconds after their own behaviour (Gergely & Watson, 1999). Additionally, mothers almost exclusively respond to infants within 2 seconds of infant expression (Nicely, Tamis-LeMonda, & Bornstein, 1999), therefore maternal responses were only coded as contingent if they occurred within two seconds of the infant's behaviour. Other non-contingent, spontaneous maternal responses were still coded (which usually take place in a way that signals maternal effort to engage with the infant), including vocalizations and nods of the head.

As well as mirroring, the following contingent maternal responses to infant behaviours are also identified in this scheme:

- <u>Marking</u>
    - Affirming responses that are of same valence and intensity as the infant's behaviour and that affirm that behaviour, but differ in form and involve 'attention-attracting' cues (Csibra & Gergely, 2009).
        - I.e. responses that single out an infant's behaviour without mirroring it, for instance, a response to an infant sneeze whereby the mother opens her mouth wide, nods her heads, and smiles saying 'what a big sneeze'.
- <u>Negative</u>
    - These could be rejecting or misattuned responses in terms of valence or intensity

        - E.g. the infant displays distress and the mother smiles/laughs or the mother responds to a strong positive vocalization with a very flat smile

9.3 CODING OF MOTHER-INFANT INTERACTIONS AT 3.5 AND 6.5 MONTHS IN STUDY THREE

Coding instructions

- Coding should start 10 seconds following the wall toy revelation (covered until interaction starts)
    - Infant distress lasting longer than 10 seconds should be excluded
- Mother and infant gaze behaviour during interactions should be coded independently
    - Infant behaviours should always be coded first
- Videos should be viewed without volume to avoid bias
- Each frame of the videos is to be coded (25 fps)
    - Should be viewed in real-time and frame-by frame to improve accuracy and correct interpretation
- Blinks should be included in the previous direction/target code unless it is immediately clear that the infant/mother is looking at something else after eyes open
- When the infant or mother makes an eye movement without a head-turn, it is often difficult to code the direction/target of gaze during the eye movement: i.e. there can be some frames when they are not clearly looking in/at either the previous or next direction/target because the eyes are moving
    - Therefore a new direction/target should be coded from the moment the eyes leave the previous target (the time during the movement counts as fixation in/at the next direction/target)

Deriving and defining events

- Purpose built software was used to extract events of interest based on mother and infant attention targets/directions. This allowed the attention events and states of interest to be extracted for analysis, such as ‘infant sees mother follow’ and ‘mutual gaze’

- ‘Attention events’ were defined as follows (note, ‘looking’ here refers both to eye movements and turns of the head):
  - <u>‘Infant follow mother’</u>
    - Infant looking at their mother’s face as she looks toward an object/in a certain direction, followed by the infant attending to the same thing/in the same direction without attending to any other objects/directions in between
    - This was normalized by the number of mother gaze shifts that the infant observed, which was defined as the number of times the infant was looking at the mother’s face while she made a head turn or eye movement
  - <u>‘Infant sees mother follow’</u>
    - Infant looking towards an object/in a certain direction, followed by looking back at the mother within 3 seconds of their original attention shift. When the infant sees the mother, she is looking at the same object/turning to look at the same object they just did
      - 3 seconds selected because infants of this age do not detect contingencies beyond this period (e.g. Gergely & Watson, 1999; Henning & Striano, 2011)
    - This normalized by the frequency of ‘mother follow infant’, described below
  - <u>‘Mother follow infant’</u>
    - Infant looking towards an object/in a certain direction and mother looking at the infant’s face, followed by the mother looking at the same object/the same direction as the infant
    - This was normalized by the number of infant gaze shifts that the mother observed, which was defined as the number of times the mother was looking at the infant’s face while they made a head turn or eye movement
  - <u>‘Infant gaze shifts’</u>
    - The amount of eye movements and head turns infants made per minute

- <u>‘Observed mother gaze shifts’</u>
    - The amount of eye movements and head turns mothers made while their infant looked at the mother’s face

10 APPENDIX C: EXTRA STUDY RESULTS

10.1 RELATIONSHIP BETWEEN EXECUTED MOVEMENT MAGNITUDE AND INFANT MU ERD IN STUDY ONE

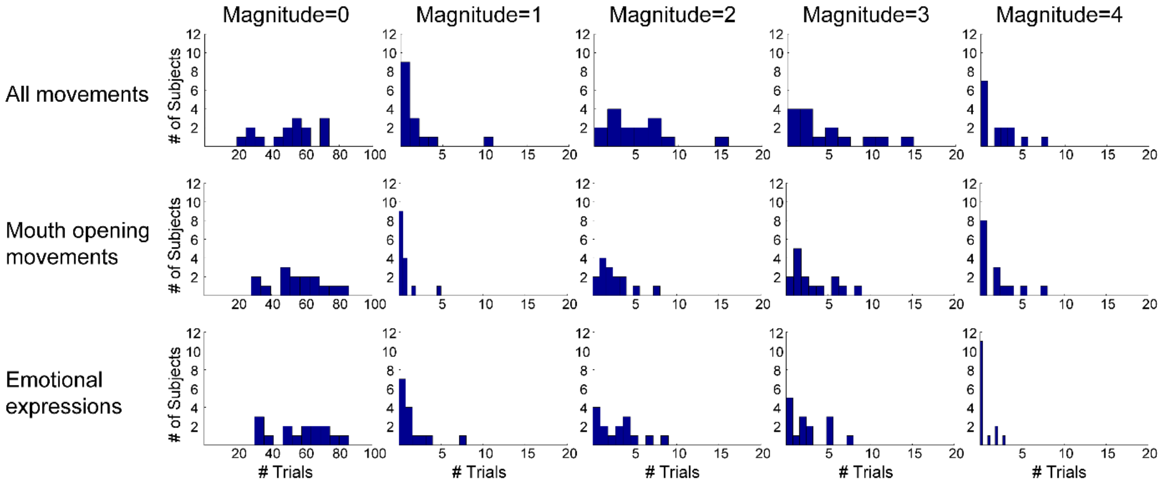

Figure C.1: Histogram of number of subjects with trials containing movements at each magnitude. Magnitude 0 = no movement. Top row is all movements, middle row is mouth opening movements, and bottom row is emotional expressions (i.e. happy and sad).

Spearman's rho revealed no significant correlation between the magnitude of movement and mu ERD for mouth opening in C3 ($\rho = 0.24$, $p > 0.08$) or C4 ($\rho = 0.06$, $p > 0.66$), or between magnitude of movement and mu ERD for emotional expressions in C3 ($\rho = 0.26$, $p > 0.07$) or C4 ($\rho = 0.16$, $p > 0.27$). Note, happy and sad faces were grouped together as 'emotional expressions' here due to the small number of trials/infants with happy and sad trials (sad, range = 0-8, M = 1.53, SD = 2.39; happy, range 0-18, M = 5.00, SD = 5.50; mouth opening; range = 0-22, M = 7.33, SD = 6.63).

10.2 MONTH MOTHER-INFANT INTERACTION DISTRIBUTIONS IN STUDY TWO

Below, the proportions of infant expressions mirrored by mothers that correspond to the stimuli used in the 9month EEG experiment (happy, sad, mouth opening) are presented. Mothers were split into 'low' and 'high' mirroring groups based on natural splits in the data for smiles and mouth opening. This split tended to fall above around the mean, with 10 mothers in the low and 6 in the high group for smiles, and 8 in the low and 7 in the high group for mouth opening. Note, only two mothers mirrored negative expressions so this was not looked at further, and dyads who were included in the high group for one expression were not necessarily in the high mirroring group for the: e.g. only 2 dyads were included in the high group for both smiles and mouth opening.

PROPORTION OF MATERNAL RESPONSES THAT WERE MIRRORRING

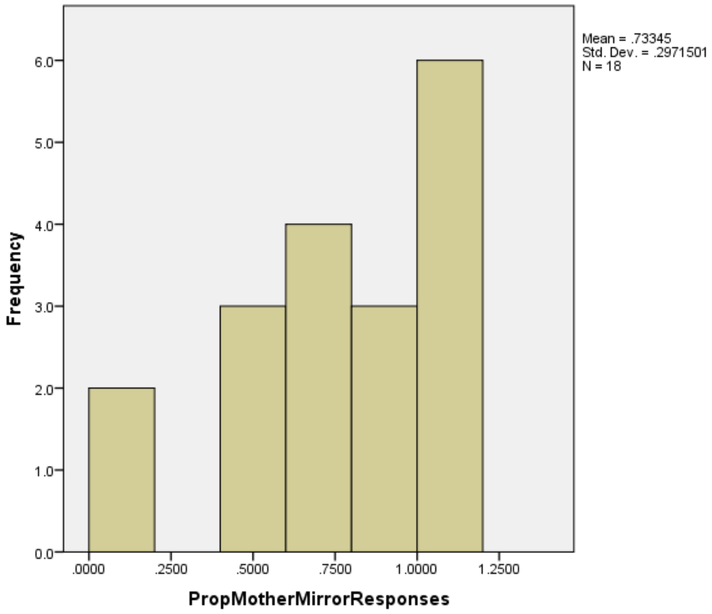

Figure C.2: Proportion of infant facial expressions that were responded to via maternal mirroring during the mother-infant interaction at two month postpartum.

PROPORTION MOTHERS MIRRORED INFANT FACIAL EXPRESSIONS OVERALL

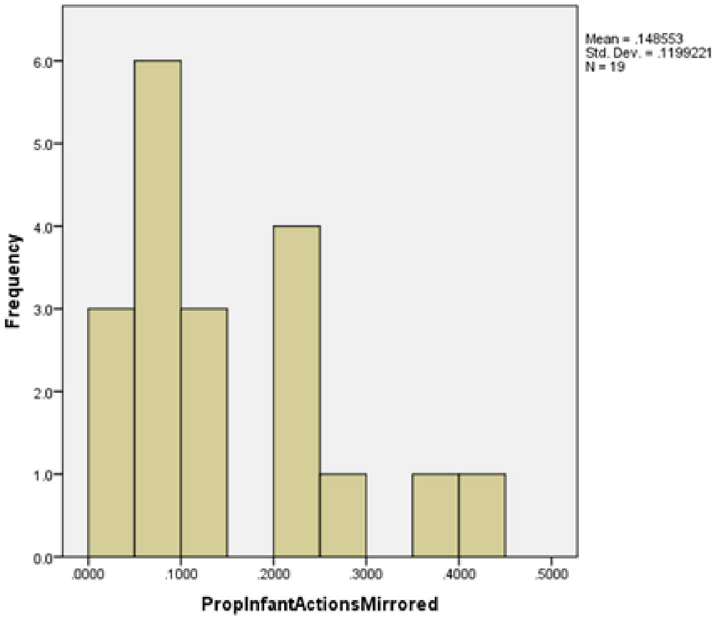

Figure C.3: Proportion of facial expressions mirrored by mothers during the mother-infant interaction at two months postpartum.

PROPORTION MOTHERS MIRRORED INFANT NEGATIVE FACIAL EXPESSIONS

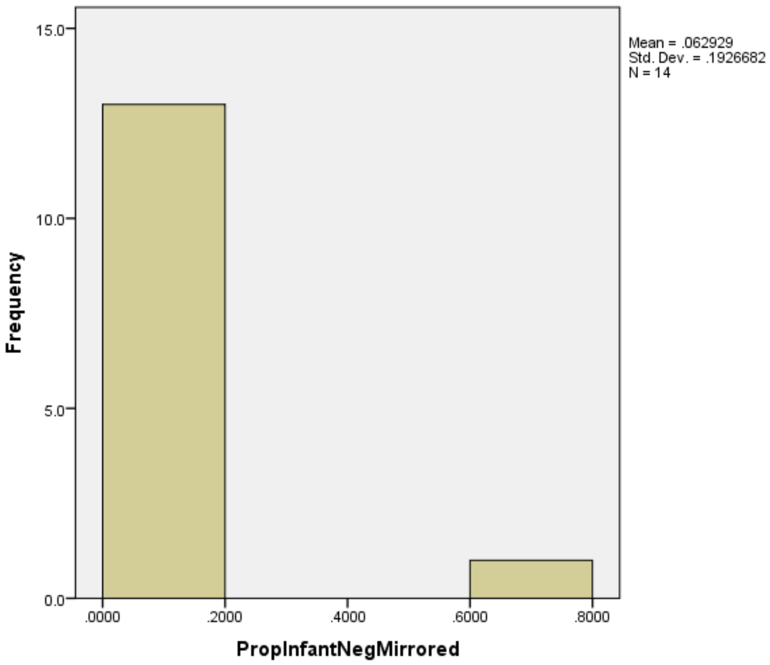

Figure C.4: Proportion of infant negative expressions mirrored by mothers at two months postpartum.

10.3 MEAN FREQUENCY OF INFANT EXPRESSIONS AND PROPORTION OF MATERNAL MIRRORING IN STUDY TWO

Table C.1: Average proportion of infant expressions mirrored by mothers at two months postpartum.

Infant Expression	**Mean Frequency Per Minute (SD)**	**Mean Percentage Mirrored (SD)**
Non-social mouth movement	4.04 (1.97)	1.50% (3.08)
Tongue protrusion	0.21 (0.32)	0.0% (0.0)
Mouth opening	2.47 (3.24)	27.58% (24.24)
Yawn	0.11 (0.19)	0.0% (0.0)
Active lips / tongue movement	0.0 (0.0)	N.D.
Smile	1.82 (2.13)	55.49% (37.98)
Raised brow	0.19 (0.28)	4.17% (11.78)
Negative mouth	0.23 (0.35)	14.29% (37.80)
Negative eyes	1.60 (2.29)	1.81% (6.03)
Cry face	0.93 (2.23)	11.11% (27.22)

Table C.1 summarises the amount that infants performed the various expressions identified in the coding scheme, as well as the percentage of these individual expressions that were mirrored by mothers. Clearly, the expressions that were included in the EEG experiment stimuli at 9 months were the ones (apart from non-social movements) produced by most infants during early interactions, with mouth opening and smiles mirrored most often by mothers. The interaction findings are in accordance with previous research demonstrating that mothers tend to mirror expressions that can be perceived as communicative (Malatesta et al., 1989; Malatesta & Izard, 1984; Moran et al., 1987; Pawlby, 1977), and with studies concerning the frequency of maternal responses (e.g. emotional expressions were mirrored around 31% of the time, similar to other research: Malatesta & Haviland, 1982).

10.4 RESULTS FROM EEG/INTERACTION ANALYSIS IN STUDY TWO

No influence of infant smile or mouth opening frequency on mu ERD in central clusters of electrodes

```
                Effect       df F.scaling         F p.value
1            Condition 1, 30.29      1.00   7.80 **    .009
2           Hemisphere 1, 15.27      1.00 28.94 ***  <.0001
3     InfantFreqPerMin 1, 31.31      1.00      2.18     .15
4 Condition:Hemisphere 1, 29.24      1.00  11.08 **    .002
```

No influence of mother smile or mouth opening frequency on mu ERD in central clusters of electrodes

```
                Effect       df F.scaling         F p.value
1            Condition 1, 30.56      1.00    4.17 *     .05
2           Hemisphere 1, 15.28      1.00 28.96 ***  <.0001
3     MotherFreqPerMin 1, 40.71      1.00      0.98     .33
4 Condition:Hemisphere 1, 28.83      1.00  11.16 **    .002
```

No relationship between the proportion of all infant facial expressions mirrored and mu ERD (averaged over hemisphere and unscrambled conditions) in central region

```
                          Estimate Std. Error t value Pr(>|t|)
(Intercept)                -10.922      1.283  -8.513 1.55e-07 ***
PropInfantActionsMirrored    4.234      6.791   0.623    0.541
```

No relationship between the proportion of maternal responses to infant facial expressions that were mirroring and mu ERD (averaged over hemisphere and unscrambled conditions) in central region

```
                          Estimate Std. Error t value Pr(>|t|)
(Intercept)                -11.259      2.303  -4.890 0.000164 ***
PropMotherMirrorResponses    1.327      2.921   0.454 0.655709
```

10.5 MU ERD IN THE 0-500ms TIME WINDOW IN STUDY THREE

At 6.5 months, during this time window compared to baseline, significant mu desynchronization compared to baseline was only found for the scrambled condition in the right occipital cluster (O2) [*t*(22) = -2.61, *p* < 0.05]. At 9.5 months, in this time window, significant mu desynchronization relative to baseline was found only for the congruent condition in F3 [*t*(18) = -2.92, *p* < 0.01], and for the scrambled condition in O2 [*t*(18) =-3.2, *p* < 0.005] compared to baseline (Figure 1).

In the analysis comparing mu desynchronization in the different conditions and clusters, at 0-500ms, only a significant main effect of region [*F*(6,138.27) = 2.38, *p* < 0.05] was revealed, with significantly less mu rhythm desynchronization in F4 compared to O2 [*t*(138.27) = 3.59, *p* < 0.01].

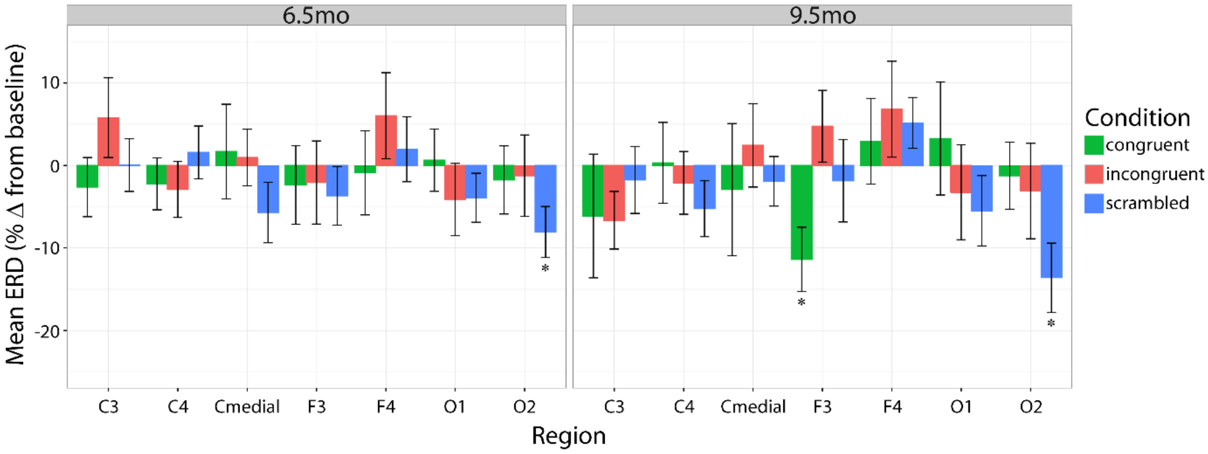

Figure C.5: Changes in mu power at 0-500ms for each electrode cluster, in each condition, at 6.5 months (left) and 9.5 months (right). Asterisks indicate where the percentage change is significantly different from baseline (** p<0.001, * p < 0.05). Error bars indicate +/- SE.

10.6 TIME-FREQUENCY PLOTS FOR THE DIFFERENT EEG ELECTRODE CLUSTERS AT 6.5 AND 9.5 MONTHS IN STUDY THREE

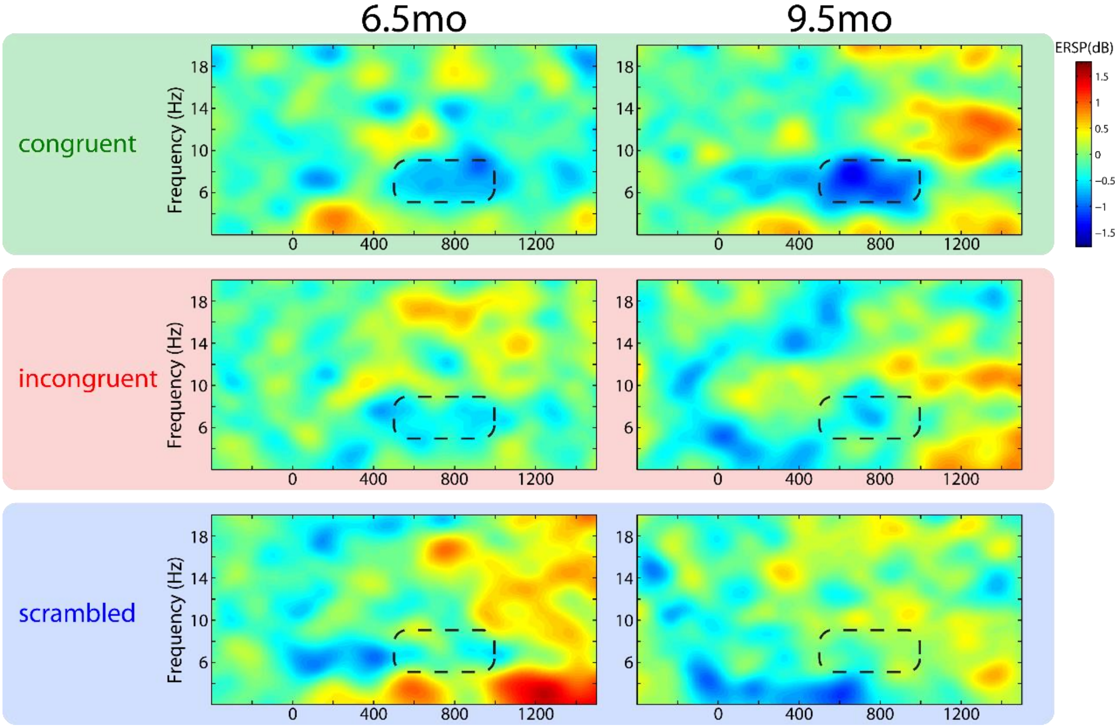

Figure C.6: Mu desynchronization in the Cmedial cluster.

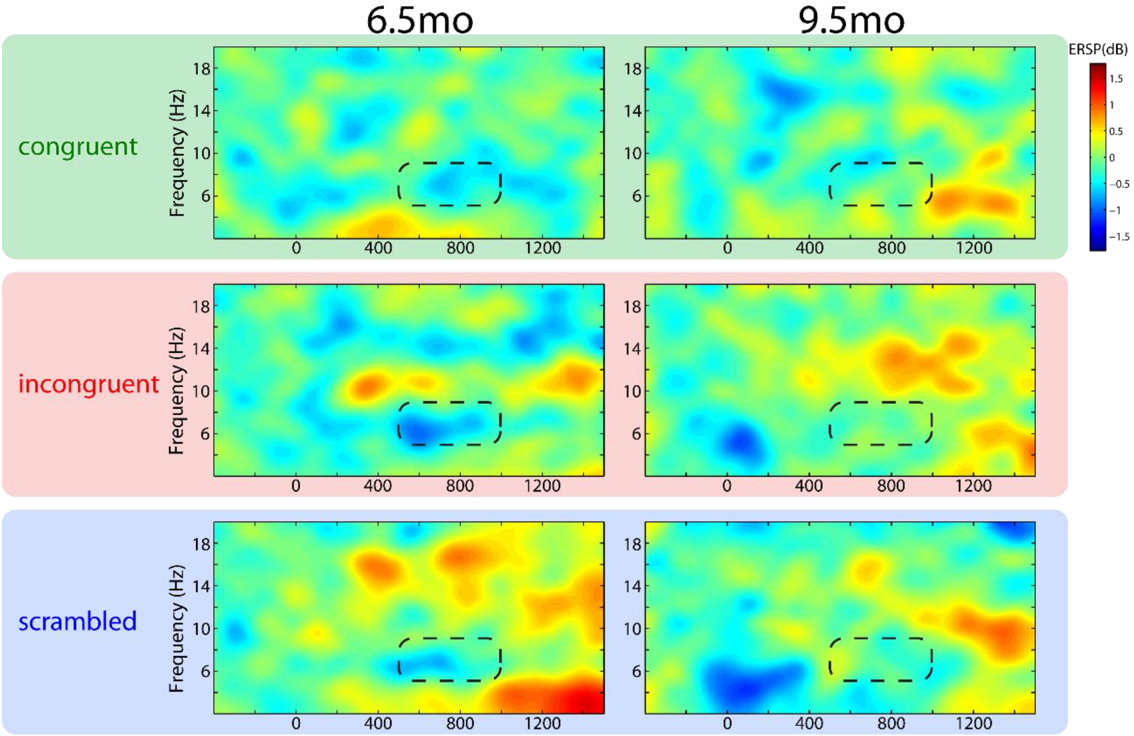

Figure C.7: Mu desynchronization in the C4 cluster.

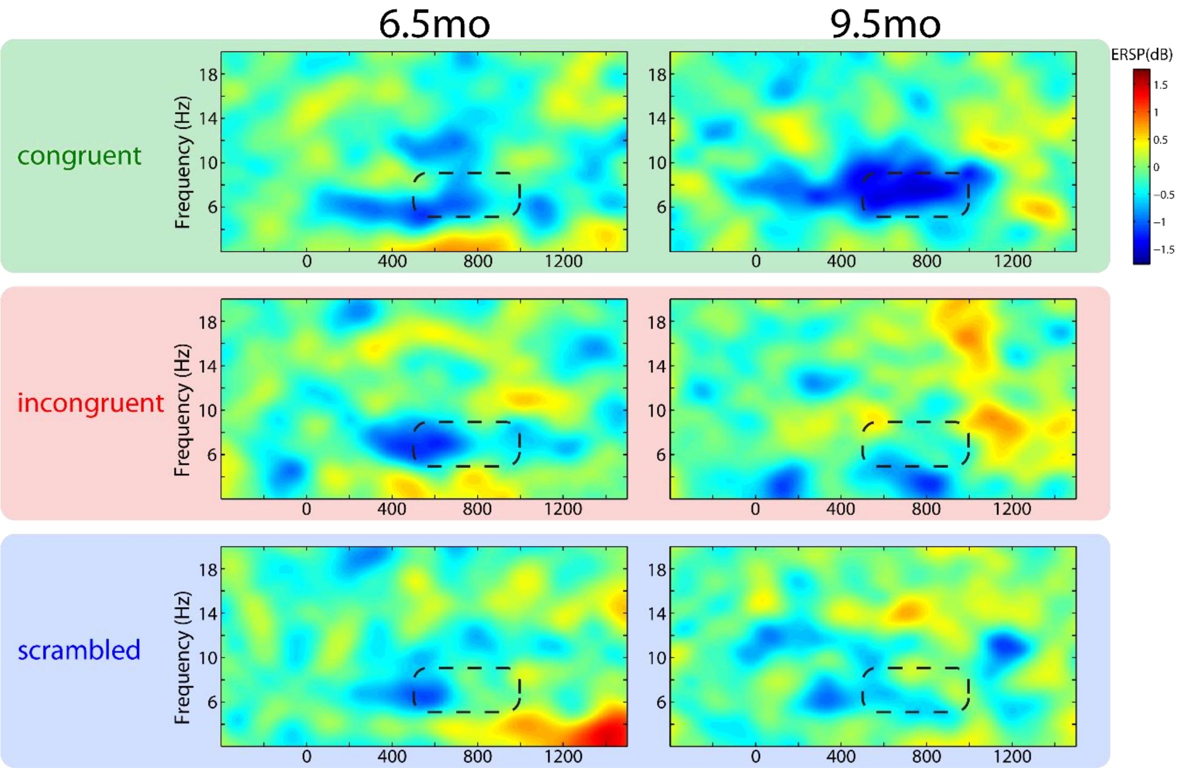

Figure C.8: Activity in the F3 cluster at 6.5 and 9.5 months.

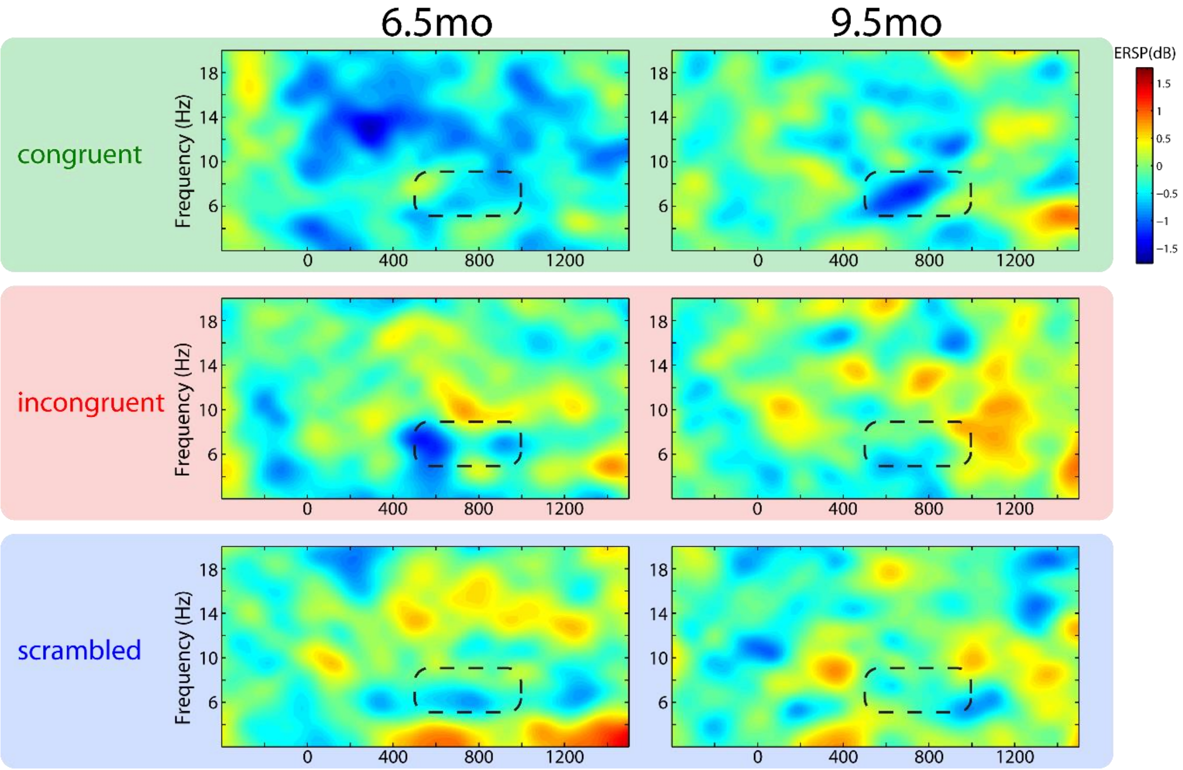

Figure C.9: Activity in the F4 cluster at 6.5 and 9.5 months.

10.7 RESULTS FROM EEG/INTERACTION ANALYSIS IN STUDY THREE

F3 (LEFT FRONTAL CLUSTER) AT BOTH AGES

No influence of infant gaze shifts on mu ERD:

```
Effect       df F.scaling       F p.value

1                            EEGAge 1, 25.88      1.00 9.67 **    .005

2        PrevInfantGazeShiftsPerMin 1, 33.08      1.00    0.13     .72

3 EEGAge:PrevInfantGazeShiftsPerMin 1, 29.25      1.00  3.55 +     .07
```

No influence of observed mother gaze shifts on mu ERD:

```
Effect       df F.scaling       F

1                                          EEGAge 1, 22.47      1.00 9.84
**

2       PrevMotherGazeShiftsInfantObservedPerMin 1, 36.15      1.00   0.15

3 EEGAge:PrevMotherGazeShiftsInfantObservedPerMin 1, 31.92     1.00   0.39

  p.value

1    .005

2     .70

3     .53
```

No influence of key attention events identified during early interactions on mu ERD:

```
                                             Effect      df F.scaling     F

1                                               EEGAge 1, 19.43      1.00
5.98 *

2          PrevMotherFollowInfantPerGazeShiftObserved 1, 25.01       1.00
0.00

3          PrevInfantFollowMotherPerGazeShiftObserved 1, 31.91       1.00
0.25

4           PrevInfantSeesMotherFollowPerMotherFollow 1, 30.38       1.00
1.31

5  EEGAge:PrevMotherFollowInfantPerGazeShiftObserved 1, 31.87        1.00
0.13

6  EEGAge:PrevInfantFollowMotherPerGazeShiftObserved 1, 21.46        1.00
0.01
```

```
7   EEGAge:PrevInfantSeesMotherFollowPerMotherFollow 1, 32.41        1.00
0.10

  p.value

1     .02

2     .97

3     .62

4     .26

5     .72

6     .91

7     .75
```

C3/CMEDIAL COMBINED (CENTRAL CLUSTER) AT BOTH AGES

No influence of infant gaze shifts on mu ERD:

```
                            Effect       df F.scaling    F p.value

1                           EEGAge 1, 36.39      1.00 1.38     .25

2        PrevInfantGazeShiftsPerMin 1, 36.63      1.00 1.72     .20

3 EEGAge:PrevInfantGazeShiftsPerMin 1, 36.63      1.00 1.81     .19
```

No influence of observed mother gaze shifts on mu ERD:

```
                                          Effect       df F.scaling    F

1                                         EEGAge 1, 26.36      1.00 1.30

2        PrevMotherGazeShiftsInfantObservedPerMin 1, 36.64      1.00 0.32

3 EEGAge:PrevMotherGazeShiftsInfantObservedPerMin 1, 36.64      1.00 0.00

  p.value

1     .27

2     .58

3     .98
```

CONCURRENT ANALYSIS AT 6.5 MONTHS

C3CMEDIAL:

Infant gaze shifts (no influence)

```
Coefficients:

                       Estimate Std. Error t value Pr(>|t|)
```

```
(Intercept)            -5.37517    7.70565  -0.698    0.493
InfantGazeShiftsPerMin  0.00295    0.22231   0.013    0.990

Residual standard error: 10.5 on 21 degrees of freedom
Multiple R-squared:  8.384e-06,     Adjusted R-squared:  -0.04761
F-statistic: 0.0001761 on 1 and 21 DF,  p-value: 0.9895
```

Observed mother gaze shifts (no influence)

```
Coefficients:
                                     Estimate Std. Error t value Pr(>|t|)
(Intercept)                           -2.1740     3.1209  -0.697    0.494
MotherGazeShiftsInfantObservedPerMin  -1.1200     0.8327  -1.345    0.193

Residual standard error: 10.08 on 21 degrees of freedom
Multiple R-squared:  0.07931, Adjusted R-squared:  0.03546
F-statistic: 1.809 on 1 and 21 DF,  p-value: 0.193
```

Predictor collinearity

```
                              Variables      VIF
1 MotherFollowInfantPerGazeShiftObserved 1.042914
2 InfantFollowMotherPerGazeShiftObserved 1.385498
3  InfantSeesMotherFollowPerMotherFollow 1.346064
```

Main analysis (no influence of face-to-face interactions)

```
Coefficients:
                                       Estimate   Std.   Error   t   value
Pr(>|t|)
(Intercept)                               1.307      4.262   0.307   0.7625
MotherFollowInfantPerGazeShiftObserved  -18.368      9.509  -1.932   0.0684
.
InfantFollowMotherPerGazeShiftObserved    2.253      6.861   0.328   0.7462
InfantSeesMotherFollowPerMotherFollow   -28.867     37.051  -0.779   0.4455
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 9.863 on 19 degrees of freedom
```

```
Multiple R-squared:  0.2022,  Adjusted R-squared:  0.0762
F-statistic: 1.605 on 3 and 19 DF,  p-value: 0.2214
```

F3:

Infant gaze shifts (no influence)

```
Coefficients:
                       Estimate Std. Error t value Pr(>|t|)
(Intercept)              7.8565     9.5426   0.823    0.420
InfantGazeShiftsPerMin  -0.2532     0.2753  -0.920    0.368

Residual standard error: 13.01 on 21 degrees of freedom
Multiple R-squared:  0.03872, Adjusted R-squared:  -0.007053
F-statistic: 0.8459 on 1 and 21 DF,  p-value: 0.3682
```

Observed mother gaze shifts (no influence)

```
Coefficients:
                                     Estimate Std. Error t value Pr(>|t|)
(Intercept)                            0.4143     4.0981   0.101    0.920
MotherGazeShiftsInfantObservedPerMin  -0.3510     1.0935  -0.321    0.751

Residual standard error: 13.23 on 21 degrees of freedom
Multiple R-squared:  0.004882,      Adjusted R-squared:  -0.0425
F-statistic: 0.103 on 1 and 21 DF,  p-value: 0.7514
```

Main analysis (no influence of face-to-face interactions)

```
Coefficients:
                                        Estimate   Std.   Error   t   value
Pr(>|t|)
(Intercept)                             -1.1666     5.9559  -0.196    0.847
MotherFollowInfantPerGazeShiftObserved   4.9350    13.2868   0.371    0.714
InfantFollowMotherPerGazeShiftObserved   0.8682     9.5870   0.091    0.929
InfantSeesMotherFollowPerMotherFollow  -27.8626    51.7718  -0.538    0.597

Residual standard error: 13.78 on 19 degrees of freedom
Multiple R-squared:  0.02359, Adjusted R-squared:  -0.1306
F-statistic: 0.153 on 3 and 19 DF,  p-value: 0.9264
```

ANALYSIS OF 3.5 MONTH INTERACTIONS AND 9.5 MONTH EEG

C3CMEDIAL:

Infant gaze shifts (no influence)

```
Coefficients:
                       Estimate Std. Error t value Pr(>|t|)
(Intercept)             11.1303    15.3996   0.723    0.480
InfantGazeShiftsPerMin  -0.9972     0.6630  -1.504    0.152

Residual standard error: 16.3 on 16 degrees of freedom
  (1 observation deleted due to missingness)
Multiple R-squared:  0.1239,  Adjusted R-squared:  0.06913
F-statistic: 2.262 on 1 and 16 DF,  p-value: 0.152
```

Observed mother gaze shifts (no influence)

```
Coefficients:
                                     Estimate Std. Error t value Pr(>|t|)
(Intercept)                          -13.5619     5.6492  -2.401   0.0289
*
MotherGazeShiftsInfantObservedPerMin   0.7004     1.2165   0.576   0.5728
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 17.23 on 16 degrees of freedom
  (1 observation deleted due to missingness)
Multiple R-squared:  0.0203,  Adjusted R-squared:  -0.04093
F-statistic: 0.3315 on 1 and 16 DF,  p-value: 0.5728
```

Predictors collinearity

```
                               Variables      VIF
1 MotherFollowInfantPerGazeShiftObserved 1.000584
2 InfantFollowMotherPerGazeShiftObserved 1.010347
3  InfantSeesMotherFollowPerMotherFollow 1.010230
```

Main analysis (no influence of face-to-face interactions)

```
Coefficients:

                                        Estimate Std. Error t value
Pr(>|t|)

(Intercept)                            -11.96231    6.83422  -1.750
0.102

MotherFollowInfantPerGazeShiftObserved  -2.00383   14.44723  -0.139
0.892

InfantFollowMotherPerGazeShiftObserved   0.01993   18.79603   0.001
0.999

InfantSeesMotherFollowPerMotherFollow   27.75450   60.73548   0.457
0.655


Residual standard error: 18.46 on 14 degrees of freedom

  (1 observation deleted due to missingness)

Multiple R-squared:  0.0163,  Adjusted R-squared:  -0.1945

F-statistic: 0.07731 on 3 and 14 DF,  p-value: 0.9712
```

F3:

Infant gaze shifts (no influence)

```
Coefficients:

                        Estimate Std. Error t value Pr(>|t|)

(Intercept)            -15.51223    9.24180  -1.678    0.113

InfantGazeShiftsPerMin  -0.07322    0.39788  -0.184    0.856


Residual standard error: 9.779 on 16 degrees of freedom

  (1 observation deleted due to missingness)

Multiple R-squared:  0.002112,      Adjusted R-squared:  -0.06026

F-statistic: 0.03387 on 1 and 16 DF,  p-value: 0.8563
```

Observed mother gaze shifts (no influence)

```
Coefficients:

                                      Estimate Std. Error t value
Pr(>|t|)
```

```
(Intercept)                            -16.96186    3.20860  -5.286 7.38e-
05 ***
MotherGazeShiftsInfantObservedPerMin  -0.06114    0.69093  -0.088
0.931
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 9.787 on 16 degrees of freedom
  (1 observation deleted due to missingness)
Multiple R-squared:  0.0004892,     Adjusted R-squared:  -0.06198
F-statistic: 0.007831 on 1 and 16 DF,  p-value: 0.9306
```

Main analysis (no influence of face-to-face interactions)

```
Coefficients:
                                        Estimate Std. Error t value
Pr(>|t|)
(Intercept)                              -20.482      3.668  -5.584 6.74e-
05 ***
MotherFollowInfantPerGazeShiftObserved    4.963      7.755   0.640
0.532
InfantFollowMotherPerGazeShiftObserved    4.821     10.089   0.478
0.640
InfantSeesMotherFollowPerMotherFollow    34.180     32.600   1.048
0.312
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 9.908 on 14 degrees of freedom
  (1 observation deleted due to missingness)
Multiple R-squared:  0.1037,  Adjusted R-squared:  -0.08833
F-statistic: 0.5401 on 3 and 14 DF,  p-value: 0.6626
```

11 APPENDIX D: QUESTIONNAIRES

11.1 EDINBURGH POSTNATAL DEPRESSION SCALE (EPDS)

As you have recently had a baby, we would like to know how you are feeling. Please UNDERLINE OR CIRCLE the answer which comes closest to how you have felt IN THE PAST 7 DAYS, not just how you feel today.

Here is an example, already completed.

I have felt happy:
Yes, all the time
<u>Yes, most of the time</u>
No, not very often
No, not at all

This would mean: “I have felt happy most of the time” during the past week. Please complete the other questions in the same way.

In the past 7 days:

1. I have been able to laugh and see the funny side of things:
    a. as much as I always could
    b. Not quite so much now
    c. Definitely not so much now
    d. Not at all

2. I have looked forward with enjoyment to things
    a. As much as I ever did
    b. Rather less than I used to
    c. Definitely less than I used to
    d. Hardly at all

3. I have blamed myself unnecessarily when things went wrong
    a. Yes, most of the time
    b. Yes, some of the time
    c. Not very often
    d. No, never

4. I have been anxious or worried for no good reason
    a. No, not at all
    b. Hardly ever
    c. Yes, sometimes
    d. Yes, very often

5. I have felt scared or panicky for no very good reason
    a. Yes, quite a lot
    b. Yes, sometimes
    c. No, not much
    d. No, not at all

6. Things have been getting on top of me
    a. Yes, most of the time I haven't been able to cope at all
    b. Yes, sometimes I haven't been coping as well as usual
    c. No, most of the time I have coped quite well
    d. No, have been coping as well as ever

7. I have been so unhappy that I have had difficulty sleeping
    a. Yes, most of the time
    b. Yes, sometimes
    c. Not very often
    d. No, not at all

8. I have felt sad or miserable
    a. Yes, most of the time
    b. Yes, quite often
    c. Not very often
    d. No, not at all

9. I have been so unhappy that I have been crying
    a. Yes, most of the time
    b. Yes, quite often
    c. Only occasionally
    d. No, never

10. The thought of harming myself has occurred to me
    a. Yes, quite often
    b. Sometimes
    c. Hardly ever
    d. Never

11.2 AGES AND STAGES QUESTIONNAIRE-3 (ASQ-3): 6MONTH EXAMPLE

On the following pages are questions about activities babies may do. Your baby may have already done some of the activities described here, and there may be some your baby has not begun doing yet. For each item, please fill in the circle that indicates whether your baby is doing the activity regularly, sometimes, or not yet.

Yes Sometimes Not yet

○ ○ ○

COMMUNICATION

1. Does your baby make high-pitched squeals?

2. When playing with sounds, does your baby make grunting, growling, or other deep-toned sounds?

3. If you call your baby when you are out of sight, does she look in the direction of your voice?

4. When a loud noise occurs, does your baby turn to see where the sound came from?

5. Does your baby make sounds like “da,” “ga,” “ka,” and “ba”?
6. If you copy the sounds your baby makes, does your baby repeat the same sounds back to you?

GROSS MOTOR

1. While your baby is on his back, does your baby lift his legs high enough to see his feet?
2. When your baby is on her tummy, does she straighten both arms and push her whole chest off the bed or floor?
3. Does your baby roll from his back to his tummy, getting both arms out from under him?
4. When you put your baby on the floor, does she lean on her hands while sitting? (If she already sits up straight without leaning on her hands, mark “yes” for this item.)
5. If you hold both hands just to balance your baby, does he support his own weight while standing?
6. Does your baby get into a crawling position by getting up on her hands and knees?

FINE MOTOR

1. Does your baby grab a toy you offer and look at it, wave it about, or chew on it for about 1 minute?
2. Does your baby reach for or grasp a toy using both hands at once?
3. Does your baby reach for a crumb or Cheerio and touch it with his finger or hand?
(If he already picks up a small object the size of a pea, mark “yes” for this item.)
4. Does your baby pick up a small toy, holding it in the center of her hand with her fingers around it?
5. Does your baby try to pick up a crumb or Cheerio by using his thumb and all of his fingers in a raking motion, even if he isn’t able to pick it up? (If he already picks up the crumb or Cheerio, mark “yes” for this item.)
6. Does your baby pick up a small toy with only one hand?

PROBLEM SOLVING

1. When a toy is in front of your baby, does she reach for it with both hands?
2. When your baby is on his back, does he turn his head to look for a toy when he drops it? (If he already picks it up, mark “yes” for this item.)
3. When your baby is on her back, does she try to get a toy she has dropped if she can see it?
4. Does your baby pick up a toy and put it in his mouth?
5. Does your baby pass a toy back and forth from one hand to the other?
6. Does your baby play by banging a toy up and down on the floor or table?

PERSONAL-SOCIAL

1. When in front of a large mirror, does your baby smile or coo at herself?
2. Does your baby act differently toward strangers than he does with you and other familiar people? (Reactions to strangers may include staring, frowning, withdrawing, or crying.)
3. While lying on her back, does your baby play by grabbing her foot?
4. When in front of a large mirror, does your baby reach out to pat the mirror?
5. While your baby is on his back, does he put his foot in his mouth?
6. Does your baby try to get a toy that is out of reach? (She may roll, pivot on her tummy, or crawl to get it.)

11.3 DEMOGRAPHICS QUESTIONNAIRE

CHILD

Date of Birth

Gestational age at birth

Birthweight

Gender

- Male
- Female

This child is my

- First
- Second
- Third
- Fourth or more

Feeding Method

- Breast
- Expressed breast milk in bottle (EBM)
- Formula
- Both EBM and formula

Does this child have any medical problems or needs? If so, please describe.

____
____
____
____

____
____
____

__MOTHER__

Date of Birth

Highest Level of Education
None
GCSEs/ O-levels or equivalent
A-level or equivalent
NVQ, HND or equivalent
Degree
Postgraduate Degree
Other (please give details): _______________________________
____

Marital Status

Single
Unmarried & Co-habiting
Married & Co-habiting
Married & Living Apart
Separated
Divorced
Widowed

Ethnic Origin

Asian (Indian/Pakistani/other Asian background) or Asian British
Black (African/ Caribbean) or Black British
Mixed (White-Asian or White-Black)
White (British/Irish/other White background)
Chinese
Any other ethnic group
I do not wish to disclose this