THE UNIVERSITY OF CHICAGO

FROM ACTION TO ABSTRACTION:
THE DEVELOPMENT OF EARLY SOCIAL COGNITION

A DISSERTATION SUBMITTED TO
THE FACULTY OF THE DIVISION OF THE SOCIAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

DEPARTMENT OF PSYCHOLOGY

BY
COURTNEY FILIPPI

CHICAGO, ILLINOIS
JUNE 2016

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

The work described in this dissertation would not have been possible without the support of my friends, colleagues, and mentors—here I'd like to acknowledge those individuals who, whether they know it or not, were integral to this dissertation work. To Amanda, thank you for your unwavering support throughout my graduate career, your guidance, patience, and your time. The rough drafts were rough but your comments were an enormous help throughout the writing process. Thank you for allowing me to spend time training with Nathan and to do a dissertation on the EEG work that came out of this collaboration.

To Nathan, my time in your lab was short but what I've learned from that time was enormous. Thank you for taking me in and allowing me to learn in your lab full of wonderful individuals. To Sara, Lindsay, Kathryn, Sam, Fabrizia, Ty, Erin, Kayla & Tanya, you are all amazing scientists who, in my short time in the lab, challenged me, befriended me, and made me smile. I hope our friendship continues long after grad school. Special thanks to Sam, who taught me the ways of cdl code.

To Marc and Susan—thank you for your time and feedback. You've helped me develop a series of questions that I find truly interesting and your support during my proposal meeting gave me the confidence and jolt of energy that I needed to sprint to finish. To Sian, you asked me a question a couple of years ago and it sparked years of work and an entire chapter of my dissertation. Thank you for always modeling interesting questions and sharing your time. Thanks to Dan Margoliash, your behavioral neuroscience class was my favorite class in graduate school and it solidified my interest in neuroscience. I've never been more proud of any study that I've designed as I was for the one on baby electric eel motor control.

To the Woodward lab past and present—thank you for your patience and suggestions every quarter as I gave talks on “that brain stuff”. I know that discussing this work required many of you to step out of your comfort zones but you did. Special thanks to Amanda Favata; I would never have made it to 5th year without your support every single day (and sometimes twice a day). You always made everything better. To Nicole, thanks for being “darling”. To Miriam, thanks for being smart, strong, supportive, and “a real person”—I will always see you as my mentor.

To Shiva, mom, and dad—you all supported me even when it wasn’t easy. I couldn’t have gotten here if it wasn’t for you. Finally, to the one and only Jefferson—your puppy face lights up every room and cuddling with you cures everything.

ABSTRACT

Action is central to human experience. While considerable research suggests that action experience shapes cognition, we know relatively little about how this link emerges—particularly early in development when the action system undergoes dramatic change. In this dissertation, I integrate neural and behavioral measures to investigate how the action system is linked to social cognition in the first year of life. In chapter 1, I argue that in order to better understand the role that the action system plays in infant social cognition, we need clear evidence that the variability in the mu-ERD response is about infants' own motor development. To do so, I investigate the relation between the mu-ERD response and several aspects of motor development. I find a specific link between infants' ability to plan their actions and the sensorimotor mu-ERD response. In chapter 2, I investigate whether there is a functional link between the mu-ERD response and action encoding. I demonstrate that sensorimotor mu-ERD response is selectively present when infants encode others' goals. In chapter 3, I ask: how developmentally generative is the connection between the motor system and social cognitive development? Here I examine the longitudinal relation between the sensorimotor mu-ERD response in infancy and preschool theory of mind. This work suggests that the action system shows some links to children's explicit understanding of perception, but overall there are not strong links to abstract mental state reasoning. Taken together, these findings provide novel insight into the link between the infant mu-ERD response, action, and perception.

INTRODUCTION

Action is central to human experience. We act to obtain the objects we want, to get from one place to another, to solve problems, and to interact with people around us. Piaget was among the first to suggest that human cognition originates from action (Piaget & Inhelder, 1962). In many respects, Piaget's theory fits with what scientists now know about cognitive development. Research has shown that action experience is linked to developments across a broad spectrum of cognitive domains including action perception (Cannon et al, 2011, Gerson & Woodward, 2014a; Kanakogi & Itakura, 2011; Loucks & Sommerville, 2012; Sommerville et al, 2005; Sommerville et al, 2008), attention (Kretch, Franchak, Adolph, 2014; Libertus, Joh & Needham, in press; Soska, Adolph & Johnson, 2009), emotional development (Biringen et al, 1995; Campos et al, 2000), language development (He, Walle, & Campos, 2015; Iverson 2010; LeBarton & Iverson, 2013; Walle & Campos, 2014; Wang, Lekhal, Aaro, Schjolberg, 2014), memory (Clearfield, 2004; Howard, Riggins & Woodward, under review) and social skills (Clearfield, Osborne, Mullen, 2008; Karasik, Tamis-LeMonda, & Adolph, 2011; 2014; Libertus & Needham, 2011). Action also exerts its effects throughout the lifespan—action experience supports learning abstract concepts (e.g., physics and math; Kontra et al, 2015; Novack et al, 2014) and mature cognitive processing across a number of domains (Beilock & Goldin-Meadow, 2010; Beilock et al, 2008; Casasanto & Chrysikou, 2011; Casasanto & Dijkstra, 2010; Trofatter et al, 2014). In many cases, these effects suggest that people with different motor repertoires think differently (Casasanto, 2011). Despite considerable interest in the link between action and cognition, we know relatively little about how this link emerges—particularly early in development when the action system is first coming online.

In this dissertation, I ask: what can neural processing of action tell us about *how* action experiences influences early social cognition. To do so, I focus on one aspect of early social cognition that has broad implications on the development of complex abstract social reasoning: the perception of actions as goal-directed. I begin by outlining the behavioral evidence demonstrating that infants' action experiences influence this component of action perception.

Action Experience Shapes Early Action Perception

Learning to control one's actions is a central challenge for young infants and it's one that they are highly motivated to solve (Adolph, Cole, Vereijken, 2015; Adolph et al, 2012). Early in development, infants' motor control is limited and gradually becomes precise and controlled (von Hofsten, 1979, 1982, 1991). Research suggests that learning to move is linked to changes in infants' perception of others' action (See Woodward et al, 2009 for review). Evidence supporting this claim comes (largely) in two forms: experiments that manipulate infants' experiences in the lab and correlational measures examining the naturally occurring variability in infants' motor experience (e.g., comparing crawlers to walkers).

Experiments that use training paradigms show that active engagement with toys (e.g., Gerson & Woodward, 2014; Sommerville, Woodward & Needham, 2005) and tools (e.g., Gerson & Woodward, 2013; Sommerville et al, 2008; Sommerville & Woodward 2005), even if the training lasts a matter of minutes, facilitates changes in action perception. The first evidence demonstrating that action experience shapes infant perception came from habituation studies. In habituation, infants observed an experimenter act on one of two toys. Following habituation the objects switch places and the infant watches alternating trials where the experimenter either select the new object in the old location (new goal trials) or the old object in a new location (new location trials). Results indicated that infants who engage in active training, on average, look longer to actions that violate the goal structure of the event (i.e., new goal trials) relative to actions that violated the precise kinematics of the movement (i.e., new location trials). Relatively longer looking to violations of goal structure indicates that infants hold expectations about the goal-directedness of action[1]. In recent years, research has shown that infants also visually anticipate the target of an action before a person touches that target object (Cannon & Woodward, 2011; Krogh-Jesperson & Woodward, 2014) and respond selectively to others' goals (Hamlin et al, 2008). Action training facilitates anticipation of others' goals (Krogh-Jesperson & Woodward, in prep) and shapes infants' overt behavioral responses to others' actions (Gerson & Woodward, 2012).

In line with experimental work, research also has shown that the naturally occurring variability in infants' motor experience is related to perception. For example, infants who spontaneously point to objects at 9 months of age, understand pointing actions, but infants at the same age who do not yet point do not understand these actions (Brune & Woodward, 2007). Similarly, infants who are more planful in executing their own actions also understand others' actions better than less motorically planful infants (Sommerville, & Woodward, 2005). Eye-tracking work also has shown that developments in motor control are related the speed at which infants anticipate the outcomes of others' actions (Ambrosini et al, 2013; Filippi & Woodward, 2016; Kanakogi & Itakura, 2011). For instance, there is a correlation between how rapidly infants generate anticipatory saccades to others' action end-points and their own motor control abilities—such that those with better fine motor control show faster predictive saccades to the end-point of the action (Ambrosini et al, 2013; Filippi & Woodward, 2016). Thus, spontaneous developments in early motor behavior are related to the development of action perception.

---

[1] When an expectation is violated it is surprising and draws infants' global attention

This body of work demonstrates that both induced and spontaneous changes in motor abilities are linked to action perception. In what follows, I raise the question of how action experience may be translated into changes in perception.

Mechanism: Translating Action Experience into Perception

The link between action perception and action experience is clear—findings converge across a variety of motor skills and experimental methods (e.g., looking time measurements, imitation, eye-tracking). Nevertheless, the mechanism that translates action experience into changes in perception is still underspecified. Indeed, many explanations have been raised to explain this behavioral phenomenon (e.g.,Csibra, 2008; Ferrari et al, 2013; Kilner et al, 2007; Southgate & Begus, 2013; Woodward & Gerson, 2014). One possibility is that acting increases arousal and makes infants orient toward stimuli they view after training. If this were true, infants might show better responding to events following training. However, to date, behavioral coding has not revealed observable differences in global attention that could account for these effects (e.g., Cannon et al, 2011; Gerson & Woodward, 2012, 2014a). Nevertheless, it is still possible that attention plays a role that is not directly observable in infant's overt looking response.

Alternatively, some argue that action experience results in changes to the infant's own motor representations in an experience-specific manner—independent of attention. When infants subsequently observe an action that they've performed, their newly updated motor representation is recruited to support understanding of that action. This hypothesis is supported by neuroscientific evidence demonstrating that adults (and infants) recruit the sensorimotor system when they observe others' actions (See Fox et al, 2015 for review) and evidence that sensorimotor system activity during action observation is correlated with a person's level of experience performing that specific action (e.g., adults: Calvo-Merino et al, 2005; infants:

Cannon et al, 2015). But from these data it remains unclear whether attention could play a more fine-grained role in shaping changes in motor representations.

Indeed, there are a number of ways that action experience could shape infants' attention to others' actions. For instance, visual experience often co-occurs with manual experience. One possibility is that action experience provides infants with visual familiarity with actions, which enhances attention to the action when viewed in others (Cook et al, 2014). While it remains unclear how observing self-produced action is linked to differences in attentional processing in infancy (See de Klerk et al, 2015 for initial evidence), there is some evidence that enhancing infants' visual experience during training is not sufficient to observe differences in infants' looking time, online visual anticipation or imitative responses (e.g., Sommerville, Hildebrand & Crane, 2008; Krogh-Jesperson & Woodward, in prep; Gerson & Woodward, 2012). This work suggests that visual experience alone cannot predict changes in action understanding. Although, these findings do not speak to the extent to which visual and motor experience interact during action because infants in these studies only observed others' actions. This leaves open the possibility that coordinating the motor and perceptual systems shapes one's processing of others' actions.

This possibility has lead some to argue that selective attention could also be related, in functionally interesting ways, to motor experience. Some aspects of attention and motor abilities travel together. To illustrate, there is a tight coupling between the perceptual system and the motor system both in adults (Flanagan & Johansson, 2003; Johansen-Berg & Matthews, 2002) and in infants (Rosander & von Hofsten, 2011). In many cases, motor expertise requires coordinated shifts in attention (e.g., Vickers, 1992, 2006; Vickers & Adolphe, 1997) during action performance. Changes to one's motor repertoire over the course of skill learning could facilitate changes in attentional processing. Research with adults has shown that those with expertise performing specific actions (e.g., expert golfers, soccer players, etc) show a performance decrement when they attend to the specific movements they're performing as compared to when they focus their attention on their goal (Beilock, Carr, MacMahon, & Starkes, 2002; Beilock & Gray, 2012). Comparable findings can be seen in early skill acquisition—young infants learn new actions more rapidly when trained using methods that emphasize the goal of the action rather than the means needed to achieve the action (Gerson & Woodward, 2013).

In summary, while the behavioral literature has demonstrated that there is a link between infants' own action experience and action perception, it also raises questions about the mechanism that translates action experience into perception. In what follows, I review recent research that has begun to examine the neural mechanism that underlies early action perception.

Infant Neurophysiological Evidence Linking Experience and Perception

One method for investigating the mechanism that links action experience to action perception is to recruit neurophysiological methods to examine brain activity while individuals perform a task. Electroencephalography (EEG) is a widely used neurophysiological tool that is recruited to investigate the link between action and cognition. EEG passively records neural activity at the scalp and has been used extensively with infants. EEG also provides considerable information about the neural signal that underlies cognitive processing—EEG provides information about the timing of the neural signal and can provide gross descriptions of the spatial localization of the neural processing.

The EEG index used to examine the recruitment of the sensorimotor system is referred to as mu event-related desynchronization (mu-ERD). This index refers to instances where there is less EEG power in the frequency band of interest (i.e., the mu-frequency band) during a test event as compared to a baseline period (Pfurtscheller & Aranibar, 1979)[2]. Prior research has demonstrated that power in the mu frequency range (i.e., 8-13 Hz for adults) is reduced over central electrode sites when adults produce actions and when they observe other's goal-directed actions (Arnstein et al., 2011; Pfurscheller & Aranibar, 1979; Fox et al, 2015) and this pattern is similarly found in infants—although in a lower frequency range (i.e., 6-9 Hz; Cuevas et al., 2014; Marshall & Meltzoff, 2011; Southgate et al., 2010). This reduction in power over sensorimotor regions is thought to reflect sensorimotor cortical activity (Neuper, Wortz, Pfurtscheller, 2006; Arnstein et al, 2011)[3].

A growing body of work suggests that the mu-ERD response is present both when infants execute simple actions themselves and when they observe others' actions (See Fox et al, 2015 for meta-analysis). In addition to being present, this response is highly variable in infants (Filippi et al, 2016; Thorpe et al, 2015; Cannon et al, 2015; Marshall, Saby, Meltzoff, 2013; Saby, Marshall, Meltzoff, 2012). One important open question in the literature is whether the variability in the infant neural response is meaningful. Some recent evidence suggests that variability in the mu-ERD response could be meaningfully linked to action experience. Research suggests that action experience may modulate the mu-ERD response in both infants (Cannon et al, 2015; de Klerk et al, 2015; Saby et al, 2012; Upshaw, Bernier, Sommerville, 2015; van Elk et al, 2008) and adults (e.g., Cannon et al, 2014; Behmer, Jantzen, 2011). For instance, Cannon and colleagues (2015) found that infants with more developed reaching skill show a stronger mu-ERD response during the observation of others' reaching actions. Collectively this work has

---

[2] Instances where there is more power in a frequency band relative to baseline are referred to as event-related synchronization (ERS).

[3] Although there is discussion (particularly in the MEG literature but also in the EEG literature) about whether beta band activity might provide a better index of motor cortex activity and whether there are differences in the localization of the sources of mu versus beta band activity (For review: Hari, 2006).

shown that experimental manipulations of infants' experience (e.g., de Klerk et al, 2015; Saby et al, 2012) and spontaneous variability in infants' motor behavior (e.g., Cannon et al, 2015; Upshaw, Bernier, Sommerville, 2015; van Elk et al, 2008) correlate with the mu-ERD response during action observation. This pattern mirrors what has been found in the behavioral literature: greater action experience is correlated with changes in action perception (as indexed in habituation, eye-tracking and imitation studies). While this provides converging evidence for the claim that motor experience facilitates in action perception, to date, it remains unclear whether differences in the neural response during action observation are the result of changes in the neural encoding of one's own actions or whether other factors (such as attention) could also explain this neural response.

Some research suggests that in adults alpha band activity that peaks over occipital sites and shows a posterior to anterior gradient (a neural marker of visual attention) is functionally distinct from the mu response (See Manshanden et al, 2002; Pfurtscheller, 2003; Thorpe et al, 2015)[4]. However, less is known about the relationship between occipital alpha and mu-ERD over sensorimotor regions in infants. Some work suggests that the mu-rhythm responds differently than does the occipital alpha rhythm in infants (e.g., Stroganova, Orekhova, Posikera, 1999; Marshall, Bar-Haim, Fox, 2002 for review). Indeed, while these responses are thought to be functionally distinct, they are sometimes reported as both being present during action execution (Cannon et al, 2015; Marshall, Young, Meltzoff, 2011; Saby, Marshall, Meltzoff, 2012; Yoo et al, 2015) and observation (e.g., Cannon et al, 2015; Saby, Marshall, Meltzoff, 2012; Stapel et al, 2010; Paulus, et al, 2012; Yoo et al, 2015). This lack of spatial specificity of the infant mu-ERD response raises questions about the role of attention in action observation. It could be that the sensorimotor mu-ERD response in infants is modulated by attention. In adults,

---

[4] The alpha frequency band overlaps with the mu-frequency band.

the sensorimotor system response is modulated by changes in attention processing (e.g., Jones et al, 2010; Johansen-Berg & Matthews, 2002). To date, relatively little infancy research has compared the activity at occipital and sensorimotor regions during action observation. Rather, many studies examining the infant mu-ERD response report neural activity exclusively at central sites (for review: See Marshall et al, 2011; Cuevas et al, 2014) or report other regions but exclude occipital sites (See for example: Reid, Stiano, Iacoboni, 2011).

Since there is very limited evidence comparing the visual system response (over occipital sites) and the sensorimotor system response it is difficult to distinguish the role that attention could play in linking infants' experience to their action understanding. As such, throughout this dissertation, I examine how the sensorimotor mu-ERD response compares to the occipital mu-ERD response. In chapter 1, I directly investigate the relationship between motor behavior and both the sensorimotor mu-ERD response and the occipital mu-ERD response. In chapter 2, I investigate whether the sensorimotor mu-ERD response (and the occipital mu-ERD response) vary as a function of infants' social interactive behavior. In chapter 3, I use the functional distinction between the sensorimotor mu-ERD response and the occipital mu-ERD response to make two different predictions about the types of processing that might be relevant for social development later in life. This approach provides a foundation for thinking about the different aspects of action experience that might be relevant to social cognition.

Open Questions

There are at least three key gaps in the literature that make discerning the mechanism that links action experience to action perception difficult. One gap in the literature is that there is extremely limited evidence evaluating whether the variability in the mu-ERD response reflects variation in the maturity of the motor system and how this variability may relate to infants' own motor behavior. To date, we know very little about the neural response when infants act themselves. In adults, there is some evidence that the properties of adult action (e.g., the force used to generate an action) correlated with the strength of the mu-ERD response during action execution. For example, greater force and more movement complexity are positively correlated with greater mu-ERD (Stancak & Pfurtscheller, 1996; Manganotti et al, 1998). Evidence of this sort provides a link between effort exerted (one aspect of motor behavior) and the mu-ERD response. Demonstrating a link between the mu-ERD response and motor behavior is potentially even more critical in infancy because infants' motor skills develop rapidly. To date, the only evidence that suggests that motor behavior is linked to the infant mu-ERD response is from action *observation*: Infants who have more experience performing particular actions (de Klerk et al, 2014; Saby et al, 2012; van Elk et al, 2008) or more competence with those actions (e.g., Cannon et al, 2015; Upshaw, Bernier, Sommerville, 2015) show a stronger mu-ERD response when they observe those actions. In order to demonstrate that the sensorimotor system response during observation is about changes in infants' own motor representations, we should find that the variability in the mu-ERD response during action *execution* also maps onto individual differences in motor competence.

One reason that we know relatively little about the action execution neural response is because researchers use the action execution response as a functional localizer (See for example: Southgate et al, 2010; Southgate & Begus, 2013). Doing so allows researchers to identify the frequency band that is most likely to respond to self-produced action, to increase the chances of identifying a significant mu-ERD response to observed actions. While this method is popular and has informed our thinking about the properties of the mu-ERD response, this method assumes that the variability in the action execution response is meaningful—despite there being no evidence in the infancy literature to suggest that this is the case. This lack of evidence makes it difficult to know whether the neural system recruited during action performance is functionally linked the to the system recruited during action observation. Indeed, it still remains unclear if, in infancy, the neural response during action execution is correlated with the neural response during action observation (See Filippi et al, 2016 for some initial evidence).

A growing literature depends on the assumption that mu-ERD in infants indexes the development of the motor system, but there is little evidence to validate the assumption. In part 1 of this dissertation, I address this gap in the literature. I suggest that one method for testing whether action experience changes one's own motor representations is to investigate the neural correlates of motor planning behavior. If, as has been speculated, action experience changes one's own motor representations, then we would expect to find that as motor skill develops there is also greater mu-ERD during action execution. In chapter 1, I argue that demonstrating that variability in the mu-ERD response during reaching is linked to specific aspects of reaching skill (e.g., how likely infants are to plan their actions before they execute them) could provide initial evidence for understanding the relation between the representations of our own actions and the action observation response.

A second gap in the literature is that, to date, no infant EEG research has tested whether infants' neural response during action observation is selectively linked to their understanding the action that they've observed. Rather, researchers have largely recorded neural activity as infants observe two (or more) different events (e.g., Southgate et al, 2010, Southgate & Begus, 2013; Warreyn et al, 2013). If the mu-ERD response is present, researchers reason that this provides evidence the motor system encoded that event and did so by recruiting the same system the infant would use to execute the observed action. While this type of evidence typically converges with research demonstrating that *on average* infants have expectations about (and anticipate) some types of simple goal-directed action and not other more ambiguous actions, it does not demonstrate that motor system activity is selectively linked to a particular type of understanding[5]. To test whether infants understood the action they perceived requires combining concurrent independent behavioral assessments of infants' understanding and neural measures.

In chapter 2, I recruit this method to investigate the functional significance of the mu-ERD response for infant social perception. Specifically, I test the prediction that the mu-ERD response encodes one's understanding of others' actions. To do so, I examine how neural activity during action encoding differs as a function of infants' imitative responses to others' actions. By examining neural activity across the scalp, this work also provides evidence that the sensorimotor system and visual attention systems are both selectively recruited during goal encoding.

Cascading Effects on Development

A third open question is whether the link between the action system and social development extends beyond infancy. Some research suggests that it might—perceiving action structure in infancy is positively correlated with theory of mind abilities in childhood controlling for general developments in cognition (Aschersleben, Hofer, Jovanovic, 2008; Colonnesi, Rieffe, Koops, Perucchini, 2010; Welch-Ross & Miller, 2000; Wellman et al, 2004; Wellman et al, 2008; Yamaguchi, Kuhlmeier, Wynn, VanMarle, 2009). Despite considerable interest in the action system and its potential link to social cognition, there is little evidence supporting the hypothesis that the action system is connected to social cognitive development in early childhood. This leaves open the question of whether the motor system is linked selectively to

---

[5] This issue becomes particularly apparent when the neural activity measure directly conflicts with previous behavioral evidence (see for example: Southgate & Begus, 2013).

attending to action structure in the moment or whether motor development has broader implications for development. If the development of the action system sets the stage for later emerging developments in social cognition, then this could have implications for typical and atypical disorders of social cognition.

In chapter 3, I ask: how developmentally generative is the connection between motor system activation and social cognitive development? I address this question by examining the longitudinal relation between motor system activity in infancy and childhood theory of mind. I follow up by examining whether the relation between theory of mind abilities and motor system activation is modulated by domain-general developments in cognition. I focus on domain general developments in executive functioning and attention.

CHAPTER 1: Mu-ERD and infants' own motor behavior

In the first year of life, infants' motor abilities undergo fundamental change and these changes have cascading effects on cognitive development (Adolph & Robinson, 2015; Libertus, Joh, Needham, 2015). Despite considerable interest in how changes in infants' motor repertoire are linked to cognitive development, we still know relatively little about the neural mechanisms that support these links in infancy. One popular hypothesis is that the link between the motor system and cognition emerges from an inherent link in one's neural architecture: a shared neural system, sometimes referred to as the mirror neuron system. This shared neural system is thought to develop as infants' motor skills develop. With each new development in motor behavior, the neural system encoding one's own actions changes, which through reactivation enhances one's conceptual understanding of these same behaviors in others. In other words, this hypothesis proposes that there is a direct link between changes in infants' motor repertoires and changes in one's neural representation of action. While this hypothesis has received a lot of attention, the ontogenetic origins of this shared neural system and its function remains highly controversial (Cook, Bird, Catmur, Press, & Heyes, 2014; Csibra, 2008; Ferrari, Tramacere, Simpson, & Iriki, 2013; Hickok, 2014; Woodward & Gerson, 2014).

One reason that the shared neural system hypothesis remains controversial is because there are many open questions about a popular neural index of this putative shared neural system. Mu-ERD (i.e., mu- event related desynchronization), the most widely used neural index of motor system activity in infants, is a measure of relative EEG power in the alpha frequency band (6-9 Hz in infants; 8-12 Hz in adults). The mu-ERD response quickly became a widespread index of the mirror neuron system because the mu-ERD response is present when infants (and adults) act on objects and also when they observe others' action (e.g., Marshall & Meltzoff, 2011;

Pfurtscheller & Aranibar, 1979). While this is one central characteristic of the mirror neuron system, to date it remains unclear how exactly this response maps onto infants' experience performing actions. Since infants' motor skills develop rapidly, understanding how the mu-ERD response maps onto infants' own experience is critical for testing the hypothesis that a shared neural system supports advances in cognitive development.

Some evidence suggests that a link between experience and the mu-ERD response is possible. There is converging evidence that the sensorimotor mu-ERD response during cognitive tasks (e.g., action perception tasks) is positively correlated with infants' motor experience (Cannon et al, 2015; de Klerk et al, 2014; Saby et al, 2012; Yoo et al, 2016; van Elk et al, 2008). For example, those individuals with more experience performing an action (e.g., infants with relatively more crawling experience) show more robust mu-ERD when they *observe* those actions within their motor repertoire (e.g., infants: Cannon et al, 2015; Cannon et al, 2014; de Klerk et al, 2014; van Elk et al, 2008; adults: Quandt et al, 2011; Quandt et al, 2012; Quant & Marshall, 2014; Marshall et al, 2013). In many respects, this correlational evidence is quite compelling because it converges with research conducted on adults using fMRI (Calvo-Merino et al, 2005; Calvo-Merino et al, 2006). However, there are also many differences between what we know about how action is processed in the adult brain that we do not have direct evidence for in the infant brain. For adults, there is direct evidence demonstrating that the link seen between the brain's neural response during cognitive tasks is about action processing: fMRI demonstrates the activation seen during action observation occurs in regions directly linked to motor control, and activation of these regions correlates with motor expertise. Furthermore, we know that activity in these regions changes as a function of short-term motor experience (Grafton, Hazeltine, Ivry, 2002; Kim & Shin, 2014; Pollock et al, 2014; See Tanji, 2001 for review; Toni, Krams, Turner, Passingham, 1998)—providing a direct link (in these regions) between experience and the brain's neural response during action execution.

In infants, there is only clear evidence for one piece of the puzzle—that is, that mu-ERD during action observation tasks is linked to experience. If this correlation emerges because experience acting has shaped the motor system's response to actions broadly and the system between action and cognition is shared, then we should expect to find the same relationship between action experience and the recruitment of the motor system during *action* tasks (and/or we should find a correlation between the mu-ERD response during *action* tasks and *cognitive* tasks). However, to date, there is no direct evidence linking the mu-ERD response during action *execution* with infants' own experience. Only one study (i.e., Cannon et al, 2015) has systematically tested whether experience shapes the mu-ERD response during action execution and the results provided no evidence for this link (although see Filippi et al, 2016 supplemental materials for initial evidence for this link). This lack of evidence is particularly problematic for the infancy literature because, unlike in adulthood, the mu-ERD response during action execution is dispersed over several cortical areas (Filippi et al, 2016; Cannon et al, 2015; Marshall, Young, Meltzoff, 2011; Saby, Marshall, Meltzoff, 2012; Thorpe et al, 2015; Yoo et al, 2016[1])—rather than being regionally specific to sensorimotor cortical areas. Consequently, it is not clear whether the EEG data available from infants provides a clear measure of activity in the motor system or we're seeing a general pattern of alpha desynchronization (that could instead reflect attentional processing). Skilled action production requires tightly coordinated shifts in visual attention and as such, visual attention could change as a function of action experience.

---

[1] Thorpe et al, 2015 and Yoo et al, 2015 both show peaks in the mu-ERD response over central and parietal sites.

Raising the question: is this variability in the mu-ERD response about the maturity of infants' motor system or might it be reflect a general attention response?

One source of evidence that could help to clarify the significance of mu-ERD in infants is to investigate the relations between this neural response and motor development. Neuroscience has elegantly employed this strategy of linking a neural index with behavior in the adult and animal literature. To do so, researchers typically provide a cue to the participant (or animal) indicating that they should execute an action and researchers concurrently record the precise kinematics of the action (e.g., velocity and trajectory of the movement) and neural activity (See Saleh, Takahashi, Hatsopoulos, 2012; Georgopoulos et al, 1982; Moran & Schwartz, 1999; Evarts, 1968). There is known variability in the precise kinematics of an action on a given trial and at any given developmental time point[2]. By examining variability in the brain's neural response and behavior across a large number of trials and a large number of individuals, research has shown stable relations that emerge among different parts of the brain. For instance, adult EEG research using this method has found that individual differences in sensorimotor mu-ERD response do map onto some differences in motor behavior. For example, mu-ERD is positively correlated with force and movement complexity (Hummel, Kirsammer, & Gerloff, 2003; Stancak & Pfurtscheller, 1996) and the magnitude of the mu-ERD response diminishes as motor skills become automatized (Pollock et al, 2014). This provides some initial evidence that in adults that mu-ERD response is linked to particular aspects of mature motor behavior.

Chapter 1 recruits this logic to determine which aspects of motor behavior are related to the mu-ERD response in infants. To do so, I utilized data from studies of 7-, 9-, and 12-month-

---

[2] Developmental trajectories vary across individuals and are affected by many factors (Thelen et al, 1993) including: one's nervous system (Van Cutsem, Duchateau, Hainaut, 1998), environment (Thelen, Fisher, Ridley-Johnson, 2002), and body dimensions (Adolph & Avolio, 200; Thelen, Fisher, Ridley-Johnson, 2002).

old infants in which EEG was recorded as infants reached one at a time for toys. I coded several aspects of their reaching skill, and related this behavioral coding to the EEG data collected while infants reached. In this exploratory study, I examine the relation between neural and behavioral measures to provide the first systematic investigation of the neural correlates of motor learning across infancy. I reasoned that if the sensorimotor mu-ERD response is about motor development, then I should find that some aspects of motor competence map onto variability in the sensorimotor mu-ERD response. Alternatively, if the variability in mu-ERD over visual attention regions (e.g., occipital sites) also maps onto the same aspects of motor behavior, then the sensorimotor mu-ERD map may not be uniquely linked to developments in motor behavior.

In addition to asking whether the sensorimotor mu-ERD response in infants reflects developments in motor behavior, I can also ask whether the type of motor behavior that is linked to sensorimotor mu-ERD provides novel insight into the functional significance of this neural index. Some speculate that recruitment of the motor system indexes prediction (or expectations about others' goals) in the mature system (Kiler, Marchant, Frith, 2009; Kilner, Vargas, Duval, Blakemore, Sirigu, 2004; Prinz, 2006) and others have extended this argument to infants (Csibra, 2008; Southgate et al, 2010). Building on of this idea, I hypothesized that the link between the sensorimotor mu-ERD response might be specific to motor behaviors that reflect planning and holding your goal in mind. I further hypothesized that if there were a relation between motor planning and the sensorimotor mu-ERD response, I might be most likely to see it in infants' propensity to engage in hand pre-shaping behavior because hand pre-shaping requires not only planning one's action early in the reach but also holding that goal in mind. I expected to find that this relation should be functionally specific to sensorimotor regions. To test functional specificity, I compare the relation between motor behavior and mu-ERD at two scalp sites:

central sites (i.e., sensorimotor region) and occipital (visual system region) sites. I chose to compare mu-ERD at central sites to occipital mu-ERD because activity in the alpha-frequency band over occipital regions has been linked to visual attention processing (e.g., Stroganova, Orekhova, Posikera, 1999).

While I suspect that the sensorimotor system should show a specific functional relation to motor behavior, it remains unclear what functional role the infant frontal and parietal mu-ERD response plays during action execution. Research has shown that, in addition to the sensorimotor system, there are stable relations been motor behavior and parietal cortex (Desmurget et al, 2009; Georgeopouloos, Kettner, & Schwartz, 1988), the cerebellum (for review: Robinson, 1995), and premotor cortex (e.g., Roland et al, 1980; Sadato et al, 1997). This raises the added question of whether the sensorimotor mu-ERD response accounts for all the variability in infants' motor behavior or whether different regions of the brain might be linked to different aspects of motor behavior. Since no research has systematically investigated the role that mu-ERD over other cortical regions (e.g., frontal and parietal) could play in motor development, in this exploratory investigation, I also ask which aspects of motor behavior map onto variability in frontal and parietal mu-ERD. In the case of frontal and parietal mu-ERD I do not have hypotheses of how these systems could be related to motor behavior. These supplemental analyses may provide a foundation for thinking about the role that the frontal and parietal systems play in motor development.

Method

Participants

126 full-term 7 to 12 months infants recruited from the Washington DC metro region (43 female) participated in EEG studies examining the neural correlates of action encoding. Of the

infants who participated, 90 met inclusion criteria for this study (*n*=35 7-month-olds, *n*=26 9-month-olds, *n*=29 12-month-olds). 36 infants were excluded for technical difficulties (*n*=6), fussiness shortly after net application (*n*=20), parental interference (*n*=1), fewer than 5 artifact free EEG trials (*n*=12), fewer than 5 trials of reaching (*n*=3). See Table 1 for descriptive statistics for the final sample of infants each age group.

Table 1.

Descriptive statistics for each age group in the final sample

	7-months	9-months	12-months
Mean (*M*)	7 months 9 days	9 months 6 days	12 months 2 days
Standard Deviation (*SD*)	14 days	12 days	10 days
Range	6 months 17 days – 8 months 5 days	8 months 18 days - 9 months 28 days	11 months 8 days - 12 months 19 days

Task of Interest

The current study examines neural activity and behavior from two different studies run in the same laboratory: one study designed for 7-month-olds and a second study designed for 9- and 12-month-olds. While both studies were designed to have action execution and action observation trials, the studies do differ in a few ways. In this section I describe the original study designs. In all studies, the infant was seated on their parent’s lap in front of a black stage with a rolling tray tabletop. In the study for 7-month-olds infants sat across the table from a presenter who passed toys (one at a time) to the infant. After the infant grasped the toy, a host experimenter came out from behind a curtain (located on the side of the stage) and took the toy away from the infant. The presenter was present throughout all action execution trials. This process was repeated twelve times. After all the action execution trials were completed, the host experimenter lowered a curtain (attached to the top of the stage) and the presenter set up for the action observation trials. The infant then observed several action observation trials (not described here—See Filippi et al, 2016 for more details).

In the 9- and 12-month-old studies, the infant was seated in front of the same stage. At the start of the session the host experimenter (hidden behind a large curtain to the side of the stage) lifted a curtain attached to the front of the stage to present either a still image of a shape on a card, a toy for the infant to grasp (i.e., action execution trial) or a presenter with a toy (i.e., action observation trial). In contrast to the 7-month-old study, in this study action execution trials and action observation trials were interspersed and presented pseudo-randomly so the infant was unable to predict the next trial type. Importantly, in this study the action execution trials were not done in the presence of an experimenter—rather a gloved hand (i.e., that of the presenter) covertly pushed a tray with the toy so that it was within the infants reach. This minimized the extent to which the experimenter was present. The toy was left in front of the infant until they grasped it. Following a grasp, the host experimenter came out from behind the large curtain to the side of the stage and took the toy from the infant. These interspersed trials of action execution and observation were repeated for as long as the infant was willing to participate.

In the current study, I examined infants' neural activity and behavior when they themselves execute simple goal-directed actions. By generating an index of infants' neural response during action execution and relating this index to infants' own behavior I can explore the nature of the relationship between motor behavior and mu-desynchronization in infancy. In the sections below, I provide more detail on the neural measure recruited and the behavioral coding used to evaluate infants' motor skill.

EEG collection and processing

EEG was recorded using a HydroCel Geodesic Sensor Net and sampled at 500 Hz via EGI software (Net Station Version 4.5.1; Electrical Geodesics, Inc., Eugene, OR). Since these data were collected as a part of two separate studies the size of the sensor net varied across samples. Data for the 7-month olds was collected using 128-channel HydroCel Geodesic Sensor Net and data for the 9- and 12-month-olds was collected using a 64-channel HydroCel Geodesic Sensor Net. With the exception of the net size, processing and collection was performed identically.

Impedance values for all EEG channels were below 100 kW at the start of data acquisition. All processing of the data was completed off-line in MATLAB (Release 2013a; The MathWorks, Natick, MA). Continuous data from the entire recording session were first baseline-corrected and forward/reverse Butterworth-filtered (pass band: 1–50 Hz; stop band: 0.1–59 Hz; 3-dB ripple; 10-dB attenuation from pass to stop band). By default, I excluded from analysis a set of 31 channels on the outermost ring of the sensor array, which lie furthest down on the head and nearest to the face and eyes, as they are heavily prone to artifact in infancy research. The continuous data were then artifact edited using a thresholding procedure that removed high-amplitude waveforms associated with egregious movement artifact. The procedure was applied as follows: First, the continuous data were broken into adjacent 250-ms epochs. Epochs for which 5 or more channels exceeded a threshold of 250 mV were removed from the record and the timestamp of all such discontinuities was recorded. Individual channels that exceeded the threshold on more than 10% of all epochs were deemed bad, and their data were interpolated (spherical spline) from the set of channels for all epochs. Data for channels not deemed bad for all epochs but which exceeded the threshold in individual epochs that had not been dropped were interpolated from the set of good subthreshold channels**.**

The resulting data were then average-referenced and decomposed into independent components using the fastica algorithm developed by Hyvärinen (1999). Components related to eye movement and net displacement over the front of the head were rejected using a twofold criterion. First, rejected components had to have their greatest loading magnitude at one of seven channels located over the most anterior part of the head (closest to the eyes). Second, rejected components had to have their greatest spectral power outside a band of interest from 4 through 16 Hz. This second criterion ensured that I rejected only those frontally dominant components with EEG that peaked either in the 0- to 4-Hz delta band (e.g., components related to blink or saccade waveforms) or above 16 Hz (e.g., components related to high-frequency broadband muscle artifact). Artifact-cleaned EEG data were then reconstructed in channel space from the remaining set of good components.

Next, I segmented the EEG data into intervals surrounding the events of interest. Two independent coders created markers for segmentation by viewing each video off-line, frame by frame, and identifying these events. The event of interest was the time when the infant first touched a toy. For 94% of the trials, the two coders agreed within three frames on the time of the first touch. If any trial showed disagreements that exceeded three frames, that trial was dropped (*n*=12 trials). EEG data were taken from the 1,000 ms window ranging from 1,000 ms prior to the touch through the touch. The baseline event for this action-execution test event corresponded to the moment before tray movement (this event occurred approximately 5,500 ms prior to the touch of the toy). For this marker, the two coders agreed within three frames on 94% of the trials. I took EEG data from a 1,000 ms window that corresponded to 3,000 to 2,000 ms prior to the first movement of the tray.

Any trials for which the artifact-editing routine resulted in a discontinuity in any of these intervals were excluded from analysis. For each trial, data from both the baseline and the test intervals were Fourier-transformed, and an ERD score was then computed as 10 times the log (base 10) ratio of power during the test interval to power during the baseline interval (i.e., decibel difference**).** Resultant ERD scores were averaged across the 6- to 9-Hz band. Thus, negative scores indicate desynchronization, and positive scores indicate synchronization, of band-specific EEG during action execution relative to baseline. Finally band-averaged ERD scores were averaged over groups corresponding to left and right central channels, parietal channels, frontal channels, and occipital channels (See Figure 1 for details).

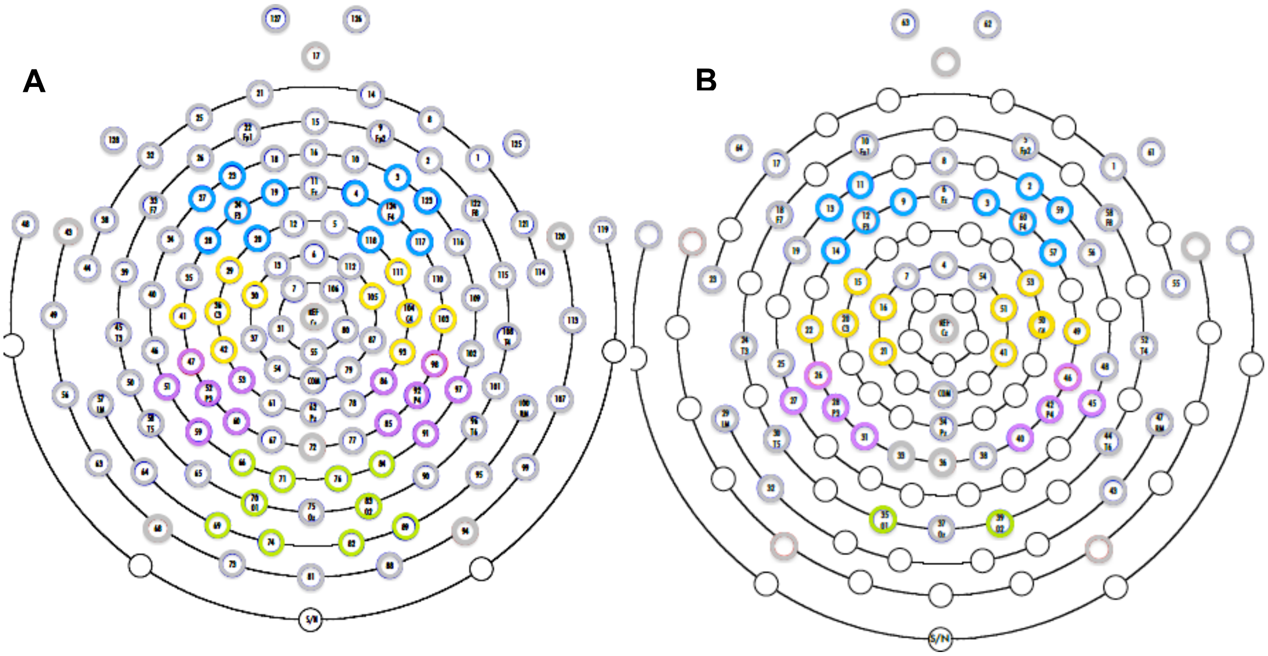

Figure 1. Depicts the site clusters on the 128-channel map (a) and the 64-channel map (b). Blue clusters index frontal sites, yellow index central sites, purple index parietal sites and green index occipital sites.

Behavior Coding

Infants' motor competence has been quantified using several metrics drawn from the motor development literature. Observers, who were unaware of the infant's EEG responses coded the video record of each infant's behavior. The aspects of motor behavior that were coded include: error rate, rate of successful grasping and lifting the toy, number of instances of withdrawing hand from its initial trajectory, unimanual reaching, instances of leaning on table (showing poor postural control), hand pre-shaping in anticipation of the toy, and speed of the reach. All coding was performed offline using Interact, a digital coding program (Mangold, 2010). A second coder independently coded 25% of the sample and was equally distributed across each age bin. Coding began by identifying whether or not the infant moved towards the toy at all when it was in front of them. If the infant did not move towards the toy at all[3], then the trial was marked as a mistrial and excluded from the total number of codeable trials. After it was determined that a trial was codeable, coders identified the first instance that the infant coordinated visual and manual contact with the toy and the first frame of the video where the infant was attending to the toy and their hand began moving toward the toy. Instances where the infant was banging on the table before reaching or when the infant was not attending to the object while reaching were deemed uncodeable behaviors. On average infants reached approximately 13 times during the testing session (range: 5 – 20) and produced an average of 11.48 useable EEG trials (range: 5 – 20). There were no statistically significant differences in the number of codeable trials as a function of age group ($F(2,87)=2.291$, $p<.107$)[4]. This provides

---

[3] This sometimes occurred if the infant became distressed during a trial. In these cases of fussiness, the infant turned toward the parent rather than the toy.

[4] There was however an effect of age group and the number of useable EEG trials. With 7 month olds producing fewer useable EEG trials ($t(29.77)=-2.879$, $p<.007$) when compared to 9-month-olds but comparable amounts of useable EEG data when compared to 12 month olds ($p<.183$). 9- and 12-month-olds didn't differ in the amount of useable EEG data extracted from the session.

initial evidence that despite this data coming from two unique studies the infants reached for a similar number of trials. Below I outline the criteria used for coding infants' behavior.

Error rate. As infant reaching develops it becomes more efficient resulting in successful contact with the toy on the first attempt and fewer misjudgments of distance and position (Fetters & Todd, 1987; McDonnell, 1975). To characterize infants' error rate in successfully contacting the toy, coders identified how many instances the infant reached too far to the right or left of the toy (i.e., position errors) and how many instances the infant undershot or overshot the reach (i.e., a distance error). Errors were identified up until the instance where the infant grasped the toy. To account for the number of errors per trial (i.e., error rate), I took the total number of errors (position errors plus distance errors) divided by the total number of codeable trials.

Rate of successful grasping to lift. Infants were not always able to lift the toys. To determine how successful the infant was in achieving the goal of grasping the toy, I coded whether or not the toy was successfully grasped and lifted. The proportion of trials that infants successfully grasped and lifted the toy was computed relative to the total number of codeable trials.

Trajectory changes. Early reaching is characterized by less smooth motion trajectory towards the target (Thelen, Corbetta, Spencer, 1996). To assess how often infants changed their trajectory during the course of reaching, I identified the total number of trajectory changes per trial. A trajectory change was defined as an instance where the infant was moving toward the object then withdrew their hand from its current trajectory before moving toward the object again. I started coding trajectory changes when the infant first moved toward the toy and stopped coding them when the infant made first contact with the toy.

Unimanual Reaching. The motor development literature suggests that as infants gain reaching proficiency, they begin to reach with one hand (i.e., unimanually) rather than with two hands (i.e., bimanually). Greater proficiency with unimanual reaching is indicative of increased motor coordination (Fagard & Jacquet, 1989; Fagard & Peze, 1997) and may involve advancements in inhibitory control (Barral, De Pretto, Debû, & Hauert, 2010; Liuzzi et al, 2011; Uehara et al, 2014). Coders identified whether infants reached toward the toy with one hand only, one hand initially but then the second hand came in to assist, or two hands initially. Coding ended when the infant made first contact with the toy. A single trial could only receive one of these codes. To create a composite score, I first grouped the instances where infants reached with one hand initially but the second hand assisted with the two-handed touches. Then I computed the proportion of instances where the infant reached with one hand using the number of one-handed reaches relative to the total number of codeable trials.

Leaning behavior. To index one large-scale motor behavior that may vary during reaching, I coded whether or not infants leaned on the table during the course of reaching. On every trial, the toy was within their reach. Nevertheless, some infants chose to lean on one of their hands during the course of reaching to stabilize their posture. Research has shown that postural control affects infants' goal-directed behavior in a variety of ways (Rachwani et al, 2015; Thelen & Spence, 1998). I coded whether on a given trial the infants placed one of their hands on the table to support themselves. Infants leaned on the table both prior to and during reaching. Each trial received a single code of either a leaning behavior present or absent.

Hand pre-shaping. I also coded one aspect of fine motor development—the ability to preshape one's hands in anticipation of objects. While infants' actions are prospective from very early in life (Claxton et al, 2003; von Hofsten 1980, 1993), hand pre-shaping behavior develops substantially over the course of the first year (Lockman et al, 1984; von Hofsten & Fazel-Zandy, 1984; von Hofsten & Ronnqvist, 1988; Morrongiello & Rocca, 1989). Research suggests that prior to the age of 9 months hand pre-shaping is an inconsistent behavior but by 13 months infants' hand pre-shaping behavior is reliable and compares to adult hand pre-shaping behavior (von Hofsten & Ronnqvist, 1988). Coders identified how infants made contact with the toy by watching the reaching action frame-by-frame to determine whether the infants' hand posture involved pre-shaping. I established three apriori criteria for evaluating the extent to which pre-shaping behavior was present—each codeable reach was given only one code to characterize the behavior leading up to the first touch of the object. The categories were as follows: pre-shaping present, no pre-shaping present but palm touched object first, no pre-shaping present and fingers bumped into toy. When pre-shaping was present, infants efficiently grasped the toy. When pre-shaping was not present one of two things happened: either the infant bumped into the toy making it impossible to grasp the object without a post-touch adjustment or infants managed to orient their hand so that their palm touched the toy first and they could grasp the object. As such, I reasoned that adjusting one's hand so that the toy first contacts the palm was the more efficient of the two behaviors. To create a pre-shaping composite, I added the total number of trials that infants' pre-shaped their hands with the total number of trials where the palm touched the toy first and divided by the total number of codeable trials. This estimate allows us to examine variability at all ages including 7-months, an age where hand pre-shaping is known to be inconsistent.

Speed of the reach. Another way of evaluating infants' reaching behavior is to characterize how rapidly they grasp the object. Research has shown that faster movements tend to be less accurate (Fitts, 1954) and reaching trajectories often require different strategies because faster movements are less straight and more difficult to stabilize in the moment (Thelen, Corbetta, Spencer, 1996). Furthermore, infants' latency to grasp an object was related to the mu-ERD response during action observation (e.g., Cannon et al, 2015; Yoo et al, 2015). To code the speed of infants' reaching behavior I only assessed instances where infants were able to grasp the toy. Coders identified the first frame that the tray with the tray began moving toward the infant as the start time[5] and coded the end time as the first frame when the infant lifted the toys.

Results

Preliminary Analyses: Mu-ERD Response

In these preliminary assessments of the mu-ERD response, I first examine whether the magnitude of the mu-ERD response changes as a function of developmental time. To date, few reports compare the strength of the infant mu-ERD response across developmental time (Cannon et al, 2015; Thorpe et al, 2015; Yoo et al, 2016). Nevertheless, there is some evidence in the adult literature that suggests that the mu-ERD response may diminish with automaticity of a motor skill (Pollock et al, 2014). Thus, I examine whether, in the data, there is any evidence for a decrease in the magnitude of the mu-ERD response. Concurrently, I examine whether the mu-ERD response is spatial localized to sensorimotor sites and whether spatial specificity of the mu-ERD response changes with development. Based on previous reports, I expected that the infant mu-ERD response would not yet be spatially localized to sensorimotor regions (Cannon et al, 2015; Filippi et al, 2016; Marshall, Young, Meltzoff, 2011; Saby, Marshall, Meltzoff, 2012; Thorpe et al, 2015; Yoo et al, 2016).

To examine whether the mu-ERD response changes as a function of development I compared the magnitude of the mu-ERD response across a (cross-sectional) sample of 7-, 9- and

---

[5] I chose to identify the time that the tray began moving toward the infant because the timing of the experimenter pushing the tray was highly consistent across all infants and trials.

12-month-old infants (See Figures 2). To do so, I conducted a repeated-measures ANOVA with average mu-ERD at all four scalp sites (frontal, central, parietal & occipital) as repeated measures and age group (7, 9 or 12 months) as a between subjects factor. Results indicated that the sphericity assumption was violated ($X^2(5)=12.512$, $p<.028$, $n=90$, $\varepsilon=.903$) so all statistics reported use the Greenhouse-Geisser correction. Results indicated that there was a significant effect of site ($F(2.710, 235.803)=13.281$, $p<.001$). There was no effect of age group ($p>.600$) and no site x age group interaction ($p>.148$). These findings suggest that the infant mu-ERD response did not diminish with age. This effect of site indicates that activity at one scalp site showed significantly greater mu-ERD response relative to other sites.

To further investigate the effect of site, I conducted several follow-up analyses. Follow-up analyses indicated that infants showed greater occipital mu-ERD relative to frontal ($t(89)=5.775$, $p<.001$), central ($t(89)=5.994$, $p<.001$), and parietal sites ($t(89)=5.901$, $p<.001$). This pattern of greater mu-ERD over occipital sites replicates findings in the literature (e.g., Yoo et al, 2015). To examine the magnitude of the mu-ERD response, I compared the mu-ERD response to 0 to see if there was significant desynchronization from baseline. Results indicated that for all age groups at all sites, there was significant desynchronization relative to baseline EEG activity (all ps<.006). This finding suggests that there is widespread and a robust average mu-ERD response across all scalp sites and this pattern holds across all age groups. Thus, this pattern of results suggests that the mu-ERD response is dispersed over several scalp sites and maximal over occipital cortex—a pattern that converges with prior research (e.g., Cannon et al, 2015; Filippi et al, 2016; Marshall, Young, Meltzoff, 2011; Saby, Marshall, Meltzoff, 2012; Thorpe et al, 2015; Yoo et al, 2015).

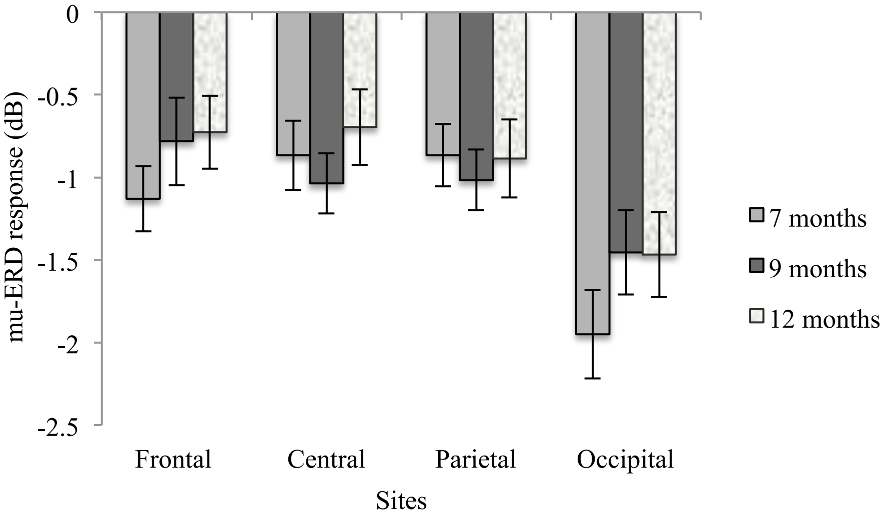

Figure 2. Average mu-ERD response across all scalp sites as a function of age (7-, 9- and 12-month-olds). Error bars represent one standard error.

Preliminary Analyses: Motor Behavior

To begin, I compared motor behavior at 7-months, 9-months and 12-months. Then I examine correlations among motor behaviors within each age group. I used these preliminary analyses to determine whether, at any age, there were any behaviors that showed insufficient variability in measurement (e.g., if infants performed at ceiling or floor levels) and whether there were high correlations among any of the motor behavior measures. I chose to examine correlations within a given age band because I suspected, and the results confirmed, that over time infants would show less variability in the behaviors of interest. If a behavioral measure did not show sufficient variability, then it is highly unlikely that there will be sufficient variability to relate to the neural measures. I also reasoned that high correlations between measures could indicate that these behavior indices are pulling comparable variance, which could make modeling relationship between mu-ERD and motor behavior difficult.

Comparing Motor Behavior Across Age Groups. First, I examined how each of the motor behaviors that I coded compared across the 7-, 9-, and 12-month-old samples. Overall, results indicated that many behaviors showed significant age related differences. Table 2 provides descriptive statistics for all motor behavior variables.

Error rate. I examined whether age group and errors produced were independent. Results indicated that age and number of errors were related ($X^2(2)=182.46$, $p<.001$)—with older infants producing fewer errors during reaching. 7-month-olds produced errors in position and distance on approximately half of all trials, 9-month-olds produced errors on approximately 25% of all trials and 12-month olds produced errors on approximately 10% of all trials. Tests for equality of variance in error rate suggest that 12- month-olds show significantly less variance in error rate than both 7-month-olds ($F(1, 62)=16.743$, $p<.001$) and 9-month-olds ($F(1, 53)=7.805$, $p<.007$).

Rate of successful grasping. Results indicated that age and rate of successful grasping were independent ($X^2(2)=2.361$, $p<.307$). However, tests for equality of variance in the rate of successful grasping suggest that 9- and 12-month-olds show significantly less variance than 7-month-olds (*ps*<.025). 9-month-olds also showed significantly less variance in rate of successful grasping relative to 12-month-olds ($p<.002$).

Trajectory Changes. Results indicated that there were age related differences in rate of trajectory changes during reaching ($F(2, 87)=5.440$, $p<.006$). Follow-up t-tests indicated that there was no significant difference in rate of trajectory changes between 7-month-olds and 9-month-olds ($p>.440$). However, 7-month-olds produced more trajectory changes than did 12-month-olds ($t(62)=3.435$, $p<.001$) and 9-month-olds showed significantly more trajectory changes than 12-month-olds ($t(53)=2.302$, $p<.025$). Results also indicated that there was significantly less variance in 12-month-olds' rate of trajectory changes relative to 7-month-olds ($F(1,63)=4.192$, $p<.045$) and 9-month-olds ($F(1,53)=4.422$, $p<.040$).

Unimanual Reaching. Results indicated that age and unimanual reaching were not significantly related ($X^2(2)=4.574$, $p<.102$). Tests for equality of variance in the rate of unimanual reaching suggest that 9- and 12- month-olds show significantly less variance than 7-month-olds ($ps<.020$) but variance in unimanual reaching didn't differ between 9- and 12-month-olds.

Leaning. Results indicated that leaning behavior varied reliably across groups ($X^2(2)=13.465$, $p<.001$). Follow-up analyses indicated that 7-month-old infants leaned significantly more often than did 9- or 12-month-olds (ps<.001). However, 9- and 12-month-olds did not differ from one another ($X^2(1)=.742$, $p<.389$). Tests of equality of variance indicated no significant differences in leaning behavior between age groups.

Hand pre-shaping. Results indicated that infants' hand pre-shaping behavior varied as a function of age ($X^2(4)=313.13$, $p<.001$). These results suggest that 7-month-olds were much less likely than 9- and 12-month-olds to engage in hand pre-shaping behavior (ps<.001). Additionally, 9-month-olds showed less hand pre-shaping behavior than did 12-month-olds ($X^2(2)=64.719$, $p<.001$). Tests for equality of variance in the rate of hand pre-shaping suggest that 9-month-olds show significantly more variance than 7-month-olds ($F(1,59)=7.566$, $p<.008$)—there were no other significant differences in variance between the groups.

Speed. Next I examined whether there were significant age group differences in the speed of grasping the toy. Results indicated that there were no significant age group differences in how quickly infants grasped the toy ($F(2,87)=.942$, $p>.394$). Tests of equality of variance indicated no significant differences among age groups.

Table 2.
Descriptive Statistics (i.e., ***Mean*** *(SD), range) for each motor behavior as a function of age group.*

Motor Behavior	7-month-olds	9-month-olds	12-month-olds
Error rate	**.530** *(.393),* .08 – 1.83	**.255***(.306),* 0 - 1.0	**.108** *(.178),* 0 -.88
Rate of successful grasping	**.839** *(.184),* .25 – 1.0	**.977** *(.057),* .81 -1.0	**.933** *(.102),* .70 – 1.0
Rate of trajectory changes	**.192** *(.200),* 0 -.83	**.154** *(.207),* 0 - .88	**.056** *(.129),* 0 - .50
Unimanual reaching	**.873** *(.181),* .42 – 1.0	**.974** *(.084),* .62 – 1.0	**.943** *(.106),* .62 – 1.0
Leaning	**.167** *(.166),* 0 - .58	**.092** *(.147),* 0 - .46	**.104** *(.169),* 0 - .75
Hand pre-shaping	**.393** *(.178),* .10 - .75	**.542** *(.266),* .13 – 1.0	**.759** *(.233),* 0 – 1.0
Speed	**10.878** *(6.518),* 3 - 29.48	**8.80** *(5.527),* 3.40 – 23.69	**10.048** *(5.216),* 3.86 – 25.01

Correlations among motor behavior variables. Next, to determine whether any of the motor behavior variables were highly correlated with one another I ran bivariate correlation analyses for all seven behavioral measurements. See Table 3 for results. Results indicated that error rate showed strong negative correlations with rate of successful grasping and hand pre-shaping—indicating that infants who produced more errors were less likely to successfully grasp the toy and pre-shape their hands in anticipation of objects. There was also a strong positive correlation between error rate and rate of trajectory changes and speed—indicating that those infants who produced more errors also changed the trajectory of their reaches more often during the course of reaching and took longer to grasp the toy. There were also strong negative correlations among the rate of successful grasping and rate of trajectory changes and speed—indicating that those infants who were more successful at grasping the toy showed fewer trajectory changes and grasped the toy faster. The rate of successful grasping also showed a strong positive correlation with hand pre-shaping, indicating that those infants who were more successful at grasping the toy were more likely to pre-shape their hands in anticipation of the object. Furthermore, I found that leaning behavior correlated positively with rate of trajectory changes—indicating that those infants who showed less postural support during the testing session were more likely to change the trajectory of their reach during reaching.

Table 3.

Correlations between motor behavior measures. Bolded correlation coefficients indicate statistical significance.

	1	2	3	4	5	6
1. Error rate						
2. Rate of successful grasping	**-.465*** **					
3. Rate of trajectory changes (per trial)	**.583*** **	**-.227***				
4. Unimanual reaching	-.134	.023	-.113			
5. Leaning	.135	.013	**.312***	-.057		
6. Pre-shaping	**-.361*** **	**.286***	-.154	.031	.009	
7. Speed to grasp	**.221***	**-.379*** **	.204⁺	.150	.179	-.064

***p<.001, **p<.005, *p<.05, ⁺p<.06

Together these findings suggest that many of the motor behavior variables (e.g., error rate, rate of successful grasping) show consistent, strong correlations to other motor behaviors. This provides some evidence that the behavior variables that were coded are reliable indices of gross motor competence. These results also show that the strength of the correlation between error rate and rate of trajectory changes, was very high.

Using these preliminary assessments of motor behavior I decided to remove some motor behavior variables from further analyses. I decided to remove rate of successful grasping because performance was near ceiling across all age groups, showed minimal variability among the older age groups (i.e., 9- and 12-month-olds) and was highly correlated with other motor behaviors. Additionally, I removed error rate because it was highly correlated with many motor behaviors making it hard to capture unique variance across the measures. As a result, five motor behavior variables became the focus of the focal analyses: rate of trajectory changes, unimanual reaching, leaning, hand pre-shaping and speed. Among these five motor behavior variables only leaning behavior and rate of trajectory changes showed a correlation and this correlation was in the moderate range (r=.312, p<.003).

Focal Analyses

In the focal analyses I asked: does the mu-ERD response reflect developments in motor behavior? To do so, I first examined whether any aspects of infants' motor behavior predict the average mu-ERD response over central sites. Next, I examined whether this relation is functionally specific. To test the functional specificity of this relation, I asked whether the same relations emerged when I examined the link between mu-ERD over occipital sites and motor behavior. In this section, I also examined the possibility that the mu-ERD response over frontal and parietal regions is also linked to differences in infants' motor development.

Linking Mu-ERD to aspects of motor behavior. In this section, I directly examined whether the magnitude of the sensorimotor mu-ERD response is linked differences in motor abilities. I report these analyses two ways: first, I consider infants of all ages together to determine whether individual differences in different aspects of motor behavior that map onto the sensorimotor mu-ERD response. Second, I report the relation between motor behavior and the sensorimotor mu-ERD response for each age group separately.

To begin, I conducted a linear regression with average central mu-ERD as the dependent variable and motor behaviors (rate of trajectory changes, unimanual reaching, leaning, hand pre-shaping, speed) as predictors. Results indicated that there was a marginally significant effect of motor behaviors on average central mu-ERD ($F(5,84)=2.015$, $p<.085$). Follow-up analyses indicated that this marginally significant effect of the model was driven by a significant relationship between unimanual reaching and central mu-ERD. A model with unimanual reaching as the sole predictor of central mu-ERD was statistically significant ($F(1, 88)=7.895$, $p<.006$)[6]. Unimanual reaching accounted for 8% of the variance in central mu-ERD (See Figure 3).

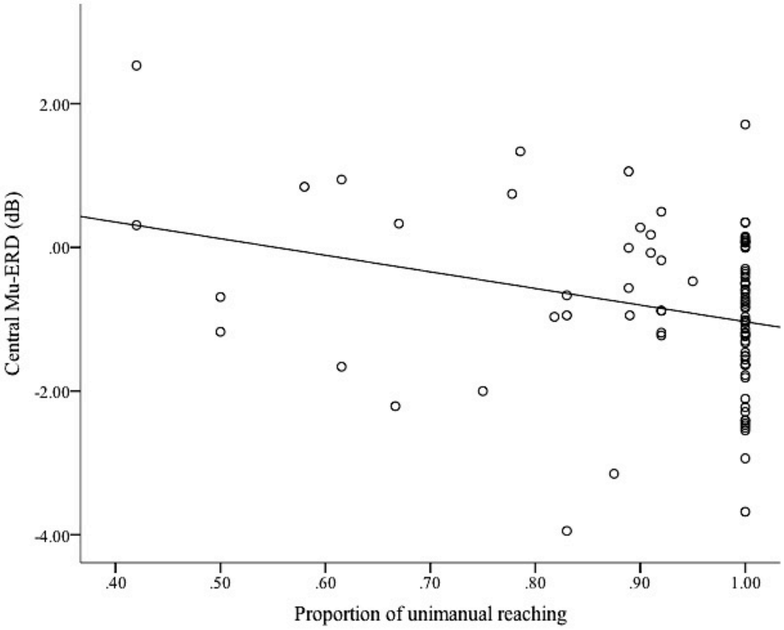

Figure 3. Depicts the relation between unimanual reaching and central mu-ERD.

---

[6] Results were identical when controlling for age.

I next asked whether this pattern held for infants of all ages. To do so, I conducted identical multiple regression broken up by age group.

7-month-olds. Results indicated that for the 7-month-old infants, hand pre-shaping (β = -2.352, *p*<.033) and unimanual reaching (β = -3.317, *p*<.004) both significantly predicted central mu-ERD (*F*(5, 29)=3.192, *p*<.020). This finding suggests that those infants who show more hand pre-shaping behavior and more unimanual reaching show a greater mu-desynchronization when they execute actions.

9-month-olds. I next examined the relation between motor behavior and central mu-ERD in 9-month-olds. Results indicated that the model with all motor behaviors as predictors did not significantly predict average central mu-ERD (*F*(5, 20)=1.363, *p*<.280)—suggesting that there was not a significant relation between motor behavior and central mu-ERD.

12-month-olds. Finally, I examined the relation between motor behavior and central mu-ERD in 12-month-olds. Results indicated that the model with all motor behaviors as predictors did not significantly predict average central mu-ERD (*F*(5, 23)=1.30, *p*<.299).

Functional specificity of these brain-behavior links. While these correlational analyses indicate that there may be some relation between the average central mu-ERD response and behavior, it could be that this link exists between mu-ERD at any site and behavior. To test the functional specificity of the link between central mu-ERD and aspects of motor behavior, I conducted a multiple regression with occipital mu-ERD as the dependent variable and motor behavior (rate of trajectory changes, unimanual reaching, leaning, hand pre-shaping, speed) as predictors. Results indicated that this model was not a good fit for the data (*F*(5, 84)=1.665, *p*<.152). These findings suggest that there is functional specificity in the link between motor behavior and central mu-ERD response.

As a follow-up, I conducted identical regressions for each age group separately. Results indicated that the model was marginally significant for 7-month-olds—indicating that a relation may exist between speed of grasping and occipital mu-ERD (β = .083, *p*<.051) but no relation between occipital mu-ERD and any other variables. There were no significant relations between motor behavior variables and occipital mu-ERD at 9 or 12 months. These findings indicate that the relation seen between the sensorimotor mu-ERD response and motor behavior may be functionally specific because this pattern doesn't emerge from a model examining the mu-ERD response over visual attention regions.

While these results suggest that the relation between the sensorimotor mu-ERD response and motor behavior may be functionally specific, it remains an open question whether the frontal and parietal mu-ERD response are related to developments in motor behavior. The frontal and parietal system have both been associated with motor control (e.g., Desmurget et al, 2009; Georgeopouloos, Kettner, & Schwartz, 1988; Roland et al, 1980; Sadato et al, 1997), however, to date, no research has investigated whether variability in the mu-ERD response over these regions is linked to motor behavior. To test whether there are relations between the mu-ERD response over these regions I conducted multiple regression analyses with frontal mu-ERD (model 1) and parietal mu-ERD (model 2) as the dependent variable and the five motor behavior variables as predictors. Results indicated that there were no significant relations between the motor behavior variables and frontal mu-ERD (p>.891) or parietal mu-ERD (*p*>.507). Together these results suggest that the relation between central mu-ERD and unimanual reaching is functionally specific.

Supplemental Analyses

In supplemental analyses, I examine each behavioral marker of motor behavior separately to ask whether the mu-ERD response over a particular site (frontal, central, parietal or occipital) uniquely predicts the variability in the behavior. If so, this could provide initial supporting evidence of the neural systems that support different aspects of motor control in infancy.

Neural correlates of each motor behavior. In a series of exploratory analyses, I also examined whether neural activity at any one site (frontal, central, parietal, occipital) uniquely predicted any aspects of motor behavior. To do so, five stepwise multiple regressions were conducted with site (frontal, central, parietal, occipital) as the predictors and motor behavior (either: rate of trajectory changes, unimanual reaching, leaning, hand pre-shaping, speed) as the dependent variable. I used a modeling method whereby the predictor with the highest significant correlation with the dependent variable was entered in step 1 and predictors were only added in step 2 if they significantly improve the model by accounting for unique variance.

When all age groups were considered together, results indicated that unimanual reaching was significantly predicted by central mu-ERD (Step 1; $\beta = -.036$, $F(1, 88)=7.895$, $p<.006$) and this model was significantly improved when (in step 2) parietal sites ($\beta = .039$) entered into the model ($R^2_{change}=.056$, $F(1, 87)=5.628$, $p<.020$). No other behaviors showed significant unique relations to the mu-ERD response at any site (*p*s>.10). Follow-up analyses indicated that this effect was largely driven by the 7-month olds—neural activity at central and parietal sites did not uniquely predict unimanual reaching at 9- or 12-months of age. I next conducted identical analyses broken up by age group.

7-month-olds. Results indicated that frontal site mu-ERD predicted hand pre-shaping at 7 months ($F(1, 33)=4.522$, $p<.041$). This relation was negative indicated that greater frontal mu-

ERD correlated with more hand pre-shaping behavior (β = -.053). Results also indicated that at 7-months occipital mu-ERD uniquely predicted speed to grasp the toy (β = 1.545, $F(1, 33)=5.189$, $p<.029$) and the rate of trajectory changes (β = .044, $F(1, 33)=4.319$, $p<.046$). There were no other significant relations between mu-ERD and motor behavior.

9-month-olds. When 9-month-olds were considered separately, results indicated that the mu-ERD response did not significantly predict the variability in any aspect of motor behavior.

12-month-olds. When 12-month-olds were considered separately, I found that some aspects of motor behavior did map onto variability in the mu-ERD response. In particular, results indicated that parietal mu-ERD predicted hand pre-shaping at 12 months of age ($F(1, 27)=4.701$, $p<.039$). This relation was positive (β = .072) suggesting that greater parietal mu-ERD was linked to less hand pre-shaping behavior. There were no other significant relations between mu-ERD and motor behavior.

These results provide initial evidence that different aspects of motor behavior may be predicted by the mu-ERD response at central, frontal, parietal and occipital sites. In particular, these effects seem to be most robust in the 7-month-old sample.

Discussion

How does the variability in the infant sensorimotor mu-ERD response relate to motor development? The current study is among the first to systematically investigate whether and how variability in the infant sensorimotor mu-ERD response during action execution is linked to motor development. To do so, I cross-sectionally sampled infants at 7-, 9- and 12-months to assess how the mu-ERD response and motor behavior change over the course of infancy. In this exploratory investigation, I demonstrate that there are links between some aspects of motor control and central mu-ERD. In particular, unimanual reaching behavior was correlated with the central mu-ERD response. This link was also specific—unimanual reaching behavior was not related to the mu-ERD response at occipital, frontal or parietal sites. The results further demonstrate that these links may be most robust in the youngest infants sampled (i.e., 7-month-olds). These results may suggest that early on in motor skill acquisition, the relationship between motor behavior and the mu-ERD response is clear—a more robust mu-ERD response is tied to advancements in motor maturity (unimanual reaching) and planning (hand pre-shaping).

With a new surge of interest in the neural correlates of action understanding, the mu-ERD response has become a particularly popular measure for indexing the sensorimotor system response. While there is strong evidence that the adult mu-ERD response over sensorimotor regions is linked to motor control (Babiloni et al, 1999; Hummel, Kirsammer, & Gerloff, 2003; Pfurtscheller, 2003; Stancak & Pfurtscheller, 1996), this relation is far less clear in infants. Infants' motor skills develop rapidly over the first year and to date, there is no evidence that as infants' motor skills change, there are changes in the magnitude of the sensorimotor mu-ERD response during action execution. This lack of a relation is puzzling given that there are numerous studies linking the magnitude of the sensorimotor mu-ERD response during action observation to infants' motor skills. In order to use the mu-ERD response to test the hypothesis that changes in one's neural representation of others' actions emerges from changes in one's motor representation of their own action, we need evidence that infants' sensorimotor mu-ERD response is linked to some aspect of motor development.

One reason that it's difficult to determine if the mu-ERD response is the same across adult and infant populations is because infants and adults show differences in the spatial specificity of the mu-ERD response (for review: Yoo & Fox, 2015). In adults, the sensorimotor mu-ERD response is largely localized to central sites during action execution (e.g., Hari et al, 1998; Pfurtscheller, 2003). Whereas, in infants, the sensorimotor mu-ERD response has been reported as dispersed across the scalp. This dispersed pattern of activity has lead some to speculate that the recorded response is the occipital alpha response "leaking" (or spreading) over toward central sites (See Pineda 2005 for review; Yoo & Fox, 2015). I replicate this effect—showing that infants in the sample show a global pattern of mu-ERD across all scalp sites. However, in addition to demonstrating that mu-ERD is present at all scalp sites, I also show that the sensorimotor mu-ERD response (i.e., the response over central sites) is specifically linked to one aspect of motor planning, unimanual reaching behavior. This provides novel evidence that the mu-ERD response over central and occipital sites are distinguishable—at least in terms of their relationship to motor behavior.

To further explore this response, I ask whether this pattern is driven by infants of any particular age. Results indicated that these effects were largely driven by variability in 7-month-old infants' motor behavior. When considered as an independent sample I don't find that motor measures predict the magnitude of the sensorimotor system response at 9 or 12 months of age. These null findings are consistent with Cannon and colleagues (2015) report that at 9- months there was no relation between motor behavior and mu-ERD during action execution. Thus, providing additional evidence that it is difficult to detect a relation between the mu-ERD response and motor planning at 9 and 12 months of age.

This raises the question of why there are developmental differences in the ability to detect a link between the mu-ERD response at 9- and 12-months and motor competence. While future research is needed to test this possibility, one possibility could be that the relation between mu-ERD and unimanual reaching is less robust at 9 and 12 months because in the sample there is somewhat less variability in infants' rates of unimanual reaching. In order to detect unique relations among behavioral variables, both sufficient variability in the measures and independence among measures is needed. One method of eliciting greater variability in infants' behavior at 9- and 12- months might be to experimentally manipulate some aspects of the action task. For example, tasks that involve infants reaching for objects of varying size and orientation, or that involve reaching around barriers might be some methods for eliciting greater variability in motor behavior.

In considering the differences across the 7-, 9- and 12-month-old samples, it is also important to remember that the 9- and 12- month sample did execute actions in a slightly different context as compared to the 7-month-olds. At 7-months, infants executed actions in the context of an experimenter—a context that is considerably more social than the context that the 9- and 12-month-old infants experienced. Since these data were taken from 2 different studies, the study designs were slightly different. At 9- and 12-months engaged in actions in a non-social context—that is, an experimenter's gloved hand pushed the tray with the toy towards the infant but the infant didn't observe an experimenter during the action context. Also, at 9 and 12 months the action execution and observation trials were interspersed rather than blocked (as in the 7-month study)—this is another difference that could have impacted the failure to find a relation between motor behavior and the mu-ERD response. As such, we cannot rule out the possibility that the reason there are differences in the relation between the mu-ERD response and motor behavior is, in part, due to the differences in the context of infants' reaching behavior. If this is the case, then this might suggest that reaching in a social context provides unique variance in the mu-ERD response and this variance is tied to infants' own motor behavior.

This work raises questions about the type of variability that matters for detecting a relation between mu-ERD and motor behavior as infants' motor skills develop. Here I assess infants' average mu-ERD response—the most common measure reported in the literature—but it could be that at 9 and 12 months, this average mu-ERD response does not map onto variability in behavior but variability at the trial level is a better index of small variations in behavior. One novel approach to examining these data might be to let a computational model examine the trial level data to look for patterns between brain activity and behavior. Considerable adult and non-human primate research has successfully recruited this method to decode the neural response that maps onto motor planning—even among individuals with highly automatized motor planning abilities (e.g., Saleh, Takahashi, Hatsopoulos, 2012). This approach could provide additional detail about the nature of the relation observed at 7-months and the nature of the variability in infants behavior. Alternatively, it could be that the time course of the neural signal is a better predictor of motor behavior in infancy. Future research should examine how the time course of infants' neural activity changes as a function of development and how these changes map onto differences in motor competence. Combining these methods with the use of motor behavior manipulations could also provide further insight into the link between motor planning and the sensorimotor mu-ERD response.

In this exploratory investigation of the relation between the mu-ERD response and motor behavior, I also report whether neural activity at any particular site uniquely predicts behavior. The findings again demonstrate that the variability in the mu-ERD response at 7-months showed the most robust links to behavior. At 7-months, the frontal mu-ERD response predicts the most unique variance in hand pre-shaping a result suggests that while both central and frontal site mu-ERD predicts hand pre-shaping, the correlation between frontal mu-ERD and hand pre-shaping is stronger and accounts for the most unique variance. This result provides initial evidence that the frontal mu-ERD response shows a strong link to planning behavior in infancy. At 7-months, the occipital mu-ERD response uniquely predicted the most variance in trajectory changes and speed to grasp the toy. This could indicate that those aspects of motor behavior that map more closely onto coordinating your visual and manual modalities efficiently map onto the variability in the visual attention systems response during action; although further research is needed to directly investigate this possibility.

In supplemental analyses, I also show that at 12-months parietal mu-ERD is positively correlated with infants' likelihood of pre-shaping their hands in anticipation of objects. Interestingly, I found that this correlation was positive indicating that infants who show less mu-desynchronization (or more mu-synchronization) are more likely to engage in hand pre-shaping behavior. This raises new questions about the link between the parietal mu-ERD response and the central mu-ERD response in infancy. A couple of recent reports suggest that in young infants the mu-ERD response peaks at central and parietal regions (e.g., Thorpe et al, 2015; Yoo et al, 2015). Some researchers speculate that parietal desynchronziation could reflect computations of translating the visual system information into a three-dimensional space representation (e.g., Thorpe et al, 2015). It could be that this is a computation that the parietal system is engaged in during action tasks—however it remains an open question as to why less mu-desynchronization maps onto better motor performance. Mounting evidence has begun to consider the mu-ERD response as an integrated network (See Bowman et al, in press; Thorpe et al, 2015). The supplemental analyses provide general support for this idea.

Overall, these findings suggest that there is some evidence that the sensorimotor mu-ERD response is about motor planning behavior—particularly behaviors that involve planning how to grasp an object. Indeed, the strongest effects link the sensorimotor mu-ERD response to unimanual reaching. Unimanual reaching is linked to inhibitory control and general motor competence early in development (Barral, De Pretto, Debû, & Hauert, 2010; Liuzzi et al, 2011; Uehara et al, 2014) and involves planning how many hands may be necessary to obtain an object. This pattern seems to be most robust early in development before motor plans become automatized. Together, these results lend some initial support to the idea that the mu-ERD response could index a shared neural system that supports both action execution and perception but also raise questions about how the mu-ERD response changes over development. In particular, these findings also raise new questions about the relationship between the mu-ERD response and infants' own behavior as reaching become automatized, and how best to capture variability in infants' sensorimotor mu-ERD response.

CHAPTER 2: Mu-ERD predicts goal imitation in infancy[1]

The ability to interpret social partners' actions in terms of goals is fundamental to human experience and is foundational to human development (Woodward & Gerson, 2014). This ability emerges early in ontogeny; by the age of 6 months, infants attend and respond selectively to the goal structure of others' actions (Hamlin, Hallinan, & Woodward, 2008; Woodward, 1998). Despite considerable interest in infants' action understanding and its implications for later development (Meltzoff, 1995; Wellman, Phillips, Dunphy-Lelii, & LaLonde, 2004; Woodward & Gerson, 2014), the neural mechanisms underpinning this critical social-cognitive ability are poorly understood. Activating one's own motor system while observing someone else acting is one neural process that is hypothesized to support action understanding (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Even so, there is active debate about whether motor system activation could facilitate action understanding in adulthood (Cook, Bird, Catmur, Press, & Heyes, 2014; Hickok, 2014) or during development (Csibra, 2008; Ferrari, Tramacere, Simpson, & Iriki, 2013; Woodward & Gerson, 2014).

One source of debate is that studies on this topic often lack independent assessments of neural activity and behaviors that index social-cognitive functions (Hickok, 2014; Woodward & Gerson, 2014). Researchers sometimes interpret differential activation of the sensorimotor system during action observation as indicating that this system functions to facilitate action understanding. However, without behavioral measurements to assess participants' social cognition, the functional significance of this activity is unclear. Recent research with adults has addressed this issue by using transcranial magnetic stimulation (TMS). When the sensorimotor cortex is temporarily disrupted using TMS, adults are slower to visually anticipate an actor's

---

[1] This work is a published paper. See Filippi, Cannon, Fox, Thorpe, Ferrari & Woodward (2016). Motor system activation predicts goal imitation in 7-month-old infants. *Psychological Science.* doi: 10.1177/0956797616632231

goal (Stadler et al., 2012) and worse at recognizing others' actions (Michael et al., 2014). These findings indicate a functional link between action understanding and motor system activation by showing that particular behavioral responses are contingent on motor system recruitment.

A growing body of research has documented that infants, like adults, recruit the motor system when viewing other individuals' actions (e.g., Southgate, Johnson, Karoui, & Csibra, 2010). However, there is currently no evidence from infants that goes beyond simply measuring motor system responses during action observation. In part, this reflects the restricted range of experimental tools that can be used in infancy research. Even so, infants offer a vantage point on this issue that adults cannot: In adults, the perception of goal-directed action is automatic and robust (Spunt & Lieberman, 2013), but during infancy, when this ability first emerges, it may be more variable (Woodward & Gerson, 2014). Indeed, infants are variable in their behavioral responses to others' goal-directed actions, and this variation is meaningful for understanding developmental processes, both concurrently and longitudinally (Sommerville & Woodward, 2005; Wellman et al., 2004). More generally, behavioral variability, both between children and across time within the behavior of an individual child, is inherent to developmental change and can be harnessed to understand developmental mechanisms (Siegler & Shipley, 1995; Smith & Thelen, 2003). In the current study, I used infancy as a test case, examining whether developmental variability in goal imitation, a selective behavioral response to the goal structure of an observed action, reflects variation in motor system activity.

The ability to imitate other people's actions is critical in early development. Converging behavioral research shows that infants do not automatically copy the actions they observe. Rather, they selectively reproduce the goal-relevant aspects of the actions (e.g., Hamlin et al., 2008; Meltzoff, 1995). For example, Hamlin et al. (2008) demonstrated that when 7-month-old infants see a person grasp one of two objects, they systematically act on the same goal object t that the actor grasped. This response is specific to well-formed, goal-directed actions. When infants observe an actor perform an ambiguous action or observe inanimate objects move, they do not respond this way—despite the fact that these events are identical to the action in terms of their patterns of movement and contact and entrain infants' attention similarly**]** (Gerson & Woodward, 2012; Mahajan & Woodward, 2009). These findings indicate that infants' engage in goal imitation. Although there is open debate about the richness of infants' understanding of others' intentions (Lou & Baillargeon, 2010; Meltzoff, 1995; Woodward & Gerson, 2014), at the very least these behavioral responses indicate that infants are sensitive to the goal structure of others' actions.

I examined whether infants' goal imitation is linked to recruitment of the sensorimotor system. To do so, I used the paradigm from Hamlin et al. (2008) with 7-month-old infants, while collecting electroencephalography (EEG). I hypothesized that recruitment of the motor system would selectively predict infants' goal imitation. I evaluated variability in motor system recruitment by examining mu desynchronization over sensorimotor regions when infants observed an experimenter choose between two objects. If motor system activation supports goal imitation, then within subjects, we would expect that infants' mu desynchronization during action observation would be greater when the infant subsequently imitated the goal (i.e., *goal response*) than when the infant subsequently generated an action directed toward the other object (i.e., *nongoal response*). Further, I predicted that between-subjects variability in the robustness of infants' motor system activity during action execution would also relate to their tendency to imitate an observed goal-directed action.

Method

Participants

Thirty-six full-term 7-month-old infants from a metropolitan area (15 female mean age = 7 months 8 days, range = 6 months 17 days–8 months 5days) were included in the final sample of the study. An additional 27 infants were tested but excluded from the final sample (*n* = 11 females) because of technical error (*n* = 1) or because they became distressed shortly after application of the EEG electrode net (*n* = 7), or they did not meet the inclusion criteria established for the experiment (*n=19*). In order for infants to be included in the final sample they needed to: provide at least six trials of codeable behavioral data (*n*=8 excluded; *See Behavior Coding*), infants could not show a side bias during behavioral testing (i.e., if infants selected all or all but one toy on the same side of the tray they were identified as having a side bias; *n*=6 excluded), and infants needed to provide at least six trials of artifact-free and movement-free EEG data during action observation (with a minimum of two goal response trials and two non-goal response trials; *n*=5 excluded). Importantly, very few infants included in the final sample (*n*=7) only had only two trials to contribute to either the goal response trial bin (*n*=3) or the non-goal response trial bin (*n*=4). This rate of data loss is similar to that of other infant EEG studies (e.g., Saby, Marshall, & Meltzoff, 2012).

Procedure

Each infant sat on his or her parent's lap in front of a black-curtained puppet stage (99 cm wide ´ 61 cm deep ´ 89 cm tall), where the infant observed reaching actions performed by an experimenter who acted as the *presenter*. Each testing session was recorded on video. First, the infant was fitted with a 128-channel EEG net. Once the net was in place, the infant was familiarized with each of the 12 toys that would be used during the procedure. During this familiarization period, the infant observed the presenter place a single toy on a tray and slide the tray within the infant's reach. The infant was then given an opportunity to pick up the toy and play with it. Then, another experimenter came out from behind the stage and took the toy from the infant, so that the next toy could be presented. This was continued until all 12 toys had been presented. Infants engaged in coordinated visual and tactile contact with the toys on 94% of the familiarization trials, and on average, the mean duration of their reaches toward the toys was 1,452 ms. These trials provided an opportunity for us to assess EEG during action execution.

Following familiarization, a suspended curtain came down to hide the stage from the infant, and the presenter set up a tray with two toys in front of her. When the curtain came up, the presenter first ensured that the infant saw both toys. Then, the presenter drew the infant's attention to center by saying "Hi!" (i.e., so that the infant attended to the presenter). Next, the presenter turned her head toward one of the toys and said, "Look." After a brief pause, the presenter reached toward and grasped the toy (See Figure 4a). The presenter reached with her right hand when reaching for the toy on her right and with her left hand when reaching for the toy on her left. On average, the duration of the presenter's reach was 292 ms. After grasping the toy, the presenter released her grip, put her hands to her sides, and drew the infant's attention to center by making eye contact and again saying "Hi!" Once the infant looked at the presenter, the presenter pushed the tray of toys toward the infant so that it was within the infant's reach, and the infant was allowed to select one of the toys (See Figure 4b). That is, infant could select either the same toy that the presenter had selected (goal response) or the toy that the presenter had not selected (nongoal response). Trials on which the infant did not make a clear selection of one of the toys were excluded from subsequent analyses.

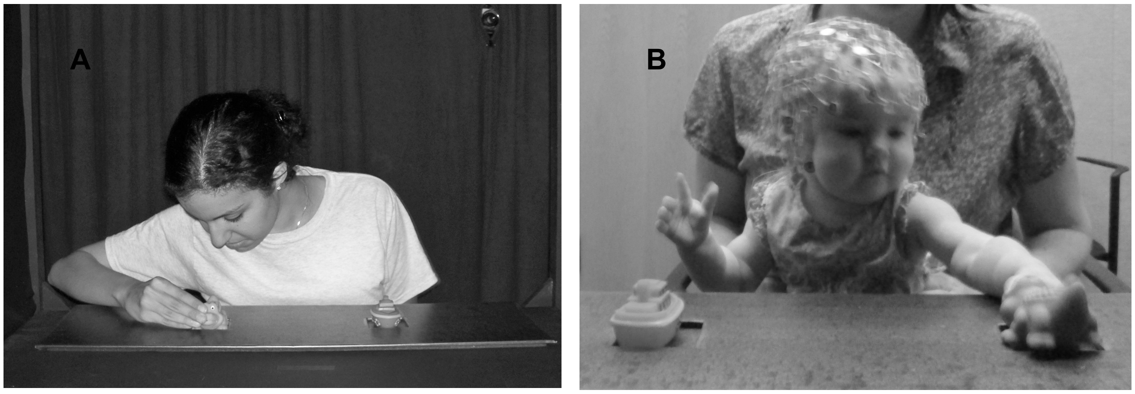

Figure 4

Depiction of the experimental setup. In the action-observation phase (a), infants observed the presenter as she selected one of two toys. Subsequently, (b), infants were given an opportunity to select one of the toys themselves.

This procedure was repeated for a total of 12 trials. The presenter alternated between reaching to the toy on the left and reaching to the toy on the right. Because there were six unique pairs of toys, after the sixth pair was presented, the presenter repeated the sequence. Each infant saw the pairs of toys presented in one of four random orders. The side that the experimenter reached to first (right or left) and which toy in each pair was the goal were counterbalanced within each random order.

Behavior Coding

I identified the first toy that an infant coordinated visual and manual contact toward on a given trial to be the infant's selection. I coded the first toy that the infant touched because infants were not always able to remove the toys from the table. Responses were coded by two independent coders. The coders agreed on 93% of the trials (k = .87). When there were disagreements, a third coder decided which toy the infant coordinated visual and manual contact toward. This coding was completed off-line by coders who were unaware of the presenter's actions. A trial on which the infant touched a toy without looking at it was marked as a mistrial and excluded from further analyses (5% of trials were excluded for this reason). To determine the proportion of goal-response trials, I divided the number of trials on which an infant produced a goal response by the total number of trials on which that infant generated a codeable response of either kind (goal or nongoal).

To ensure that infants were attending to the presenter as she chose between the toys, an independent observer**,** coded (offline) how long each infant looked at each event, using a digital coding program (Mangold International, 2010**).** A second independent observer coded the trials of 25% of infants, and the two coders were in agreement on 97% of these trials. Trials on which the infant was not attending to the presenter were excluded from analysis (3% of trials).

Motor System Activation

The measure of motor system activation was event-related desynchronization (ERD) of the mu rhythm (within the alpha frequency band, 6–9 Hz) over central sites during both action execution and action observation (Marshall & Meltzoff, 2011; Pfurtscheller & Aranibar, 1979). ERD refers to instances where there is less electroencephalography EEG power in the frequency band of interest during a test event as compared to a baseline period (Pfurtscheller & Aranibar, 1979). Prior research has demonstrated that power in the mu frequency range (i.e., 8–13 Hz for adults) is reduced over central electrode sites when adults produce actions and when they observe other people's goal-directed actions (Arnstein, Cui, Maurits, & Gazzola, 2011; Pfurtscheller & Aranibar, 1979). This pattern is similarly found in infants—although in a lower frequency range (i.e., 6–9 Hz; Cuevas, Cannon, Yoo, & Fox, 2014; Marshall & Meltzoff, 2011; Southgate et al., 2010). This reduction in power over central sites is thought to reflect sensorimotor cortical activity. Evidence in support of this claim comes from simultaneous functional MRI and EEG recordings showing that during action observation and execution, the mu rhythm is correlated with activation of several cortical areas of the mirror neuron system in adults (Arnstein et al., 2011). As has been demonstrated in adults (e.g., Cannon et al., 2014), mu desynchronization over central sites may be modulated by prior action experience (Cannon et al., 2015; Saby et al., 2012; van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). Specifically, the more experience infants have producing an action, the stronger their mu-desynchronization response when they observe someone else performing this same action (Cannon et al., 2015; van Elk et al., 2008).

EEG Collection and Processing

EEG was recorded using a 128-channel HydroCel Geodesic Sensor Net and sampled at 500 Hz via EGI software (Net Station Version 4.5.1; Electrical Geodesics, Inc., Eugene, OR). Impedance values for all EEG channels were below 100 kW at the start of data acquisition. All processing of the data was completed off-line in MATLAB (Release 2013a; The MathWorks, Natick, MA). Continuous data from the entire recording session were first baseline-corrected and forward/reverse Butterworth-filtered (pass band: 1–50 Hz; stop band: 0.1–59 Hz; 3-dB ripple; 10-dB attenuation from pass to stop band). By default, I excluded from analysis a set of 31 channels on the outermost ring of the sensor array, which lie furthest down on the head and nearest to the face and eyes, as they are heavily prone to artifact in infancy research. The continuous data were then artifact edited using a thresholding procedure that removed high-amplitude waveforms associated with egregious movement artifact. The procedure was applied as follows: First, the continuous data were broken into adjacent 250-ms epochs. Epochs for which 5 or more channels exceeded a threshold of 250 mV were removed from the record and the timestamp of all such discontinuities was recorded. Individual channels that exceeded the threshold on more than 10% of all epochs were deemed bad, and their data were interpolated (spherical spline) from the set of channels for all epochs. Data for channels not deemed bad for all epochs but which exceeded the threshold in individual epochs that had not been dropped were interpolated from the set of good subthreshold channels.

The resulting data were then average-referenced and decomposed into independent components using the fastica algorithm developed by Hyvärinen (1999). Components related to eye movement and net displacement over the front of the head were rejected using a twofold criterion. First, rejected components had to have their greatest loading magnitude at one of seven channels located over the most anterior part of the head (closest to the eyes). Second, rejected components had to have their greatest spectral power outside a band of interest from 4 through 16 Hz. This second criterion ensured that I rejected only those frontally dominant components with EEG that peaked either in the 0- to Hz delta band (e.g., components related to blink or saccade waveforms) or above 16 Hz (e.g., components related to high-frequency broadband muscle artifact). This procedure resulted in an average of 13 independent components being rejected for each subject. Artifact-cleaned EEG data were then reconstructed in channel space from the remaining set of good components.

Next, I segmented the EEG data into intervals surrounding the events of interest. Two independent coders created markers for segmentation by viewing each video off-line, frame by frame, and identifying these events. The test event in the familiarization phase was the time when the infant first touched a toy. For 87% of the trials, the two coders agreed within three frames on the time of the first touch. . EEG data were taken from the 1-s window ranging from 1,000 ms prior to the touch through the touch. The baseline event for this action-execution test event corresponded to the first movement of the tray toward the infant (i.e., ~3,000 to 2,000 ms before the infant touched the toy). For this marker, the two coders agreed within three frames on 98% of the trials. I took EEG data from a 1-s window starting at this event. The test event during the action-observation phase was when the presenter first touched the toy with her hand. For 90% of the trials, the two coders agreed on the time of the first touch. I took EEG data from the 1-s window ranging from 1-s prior to the touch through the touch. If the infant produced an overt movement during the time when the presenter was reaching, the trial was eliminated from further analyses. On average, 1.08 trials per infant were excluded for this reason. The baseline event for this action-observation test event corresponded to the lifting of the curtain that began each observation trial. I took EEG data from the 1-s window ranging from 3,000 ms to 2,000 ms prior to that event.

Any trials for which the artifact-editing routine resulted in a discontinuity in any of these intervals were excluded from analysis. For each trial, data from both the baseline and the test intervals were Fourier-transformed, and an ERD score was then computed as 10 times the log (base 10) ratio of power during the test interval to power during the baseline interval (i.e., decibel difference**).** Resultant ERD scores were averaged across the 6- to 9-Hz band. Thus, negative scores indicate desynchronization, and positive scores indicate synchronization, of band-specific EEG during the execution (or observation) of the grasp relative to baseline. Finally band-averaged ERD scores were averaged over groups corresponding to left and right central channels (C3: 93, 103, 104, 105, 111; C4: 29, 30, 36, 41, 42), parietal channels (P3: 85, 86, 91, 92, 97, 98; P4: 47, 51, 52, 53, 59, 60), frontal channels (F3: 3, 4, 117, 118, 123, 124; F4: 19, 20, 23, 24, 27, 28), and occipital channels (O1:82, 83, 84, 89, 76; O2: 66, 69, 70, 71, 74). Additionally, prior to data analysis**,** I excluded average ERD values that were more than 2.5 standard deviations above the group mean for both the action-observation phase (*n* = 2 excluded; frontal: *n*=1; parietal: *n*=1) and the action-execution phase (*n* = 3 excluded; frontal sites: *n*=1; central sites: *n*=2) data sets**.**

Results

Preliminary Analysis of Behavioral Responses

Preliminary analyses indicated that, on average, the infants in the sample selected the same object as the experimenter (i.e., generated a goal response) on 49% of the trials (*SD* = 18%). This naturally occurring variability in goal-response behavior permitted us to compare neural activity when the infants subsequently reproduced the presenter's goal-directed action and when they did not. Although the goal response rate in this study was lower than has been previously reported, this is likely due to the extended duration of the testing session, which was required to collect sufficient EEG data. (See the Supplemental Material for more details).

Neural activity as a Predictor of Goal Imitation

The focal analysis concerned relations between neural response and behavior. First, I examined whether within-subjects variation in sensorimotor activation during the action-observation phase predicted whether the subsequent response would be goal based. Next, I examined whether between-subjects variation in sensorimotor activation during action execution predicted later propensity to reproduce the observed goal-directed actions. Each of these analyses revealed that sensorimotor-system activation was related to goal imitation.

Within-subjects analyses. I first assessed whether mu desynchronization during action observation predicted infants' subsequent behavioral responses. These analyses included only trials on which the infants attended to the presenter's actions during the observation phase and then launched a clear motor response, selecting one of the two toys. On average, infants provided 10.89 artifact-free trials (*SD* = 1.43, range = 6–12; 5.28 trials followed by goal responses (*SD* = 1.88) and 5.61 trials followed by nongoal responses (*SD* = 2.32)). Infants attended to the presenter's actions an average of 97% of the time (*SD* = 5%), and attention did not differ between trials with goal and nongoal responses, $t(33) = -0.17$, $p < .864$. Preliminary analyses demonstrated that there were no effects of hemisphere on desynchronization at central sites ($p > .138$), so I collapsed across hemisphere for subsequent analyses (see the Supplemental Material for topographic maps of the EEG data).

I evaluated neural activity over central sites during the action-observation phase of each trial and binned this activity according to the infant's subsequent behavioral response on that trial (i.e., goal response vs. nongoal response). I ran a repeated measures analysis of variance (ANOVA) on mean ERD values with trial type (goal response vs. nongoal response) as a within-subjects factor. Results indicated that there was a significant main effect of trial type, $F(1, 35) = 4.54$, $p < .040$, $h_p^2 = .12$; infants showed greater mu desynchronization on trials on which they subsequently produced the goal response ($M = -0.48$, $SD = 1.04$) than on trials on which they produced a nongoal response ($M = 0.16$, $SD = 1.56$; see Figure 5). One-sample *t* tests indicated that desynchronization was significantly different from zero (suggesting significant change from a resting baseline period) prior to goal responses, $t(35) = -2.78$, $p < .009$ and was not different from zero prior to nongoal responses, $t(35) = 0.62$, $p < .539$.

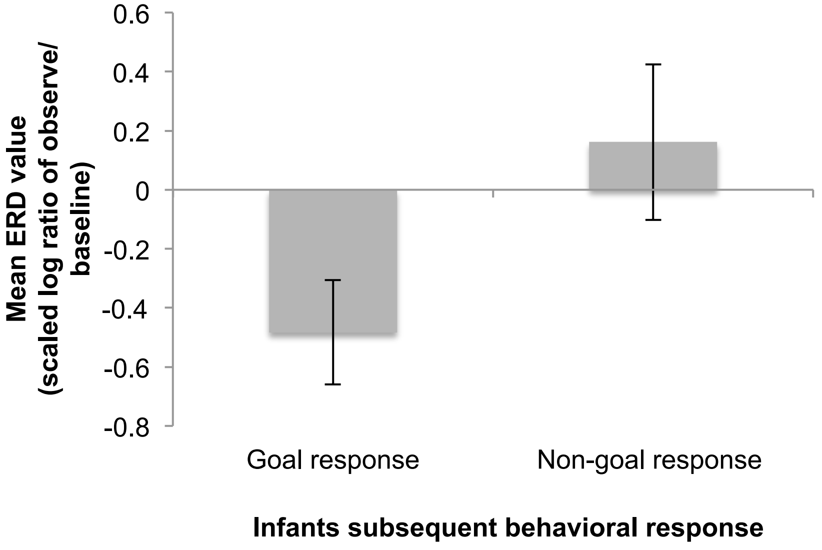

Figure 5.

Mean event-related desynchronization (ERD) scores in the mu frequency range (6–9 Hz) over central sites during action observation, for trials with goal responses and trials with nongoal responses. The ERD score for a trial was calculated as 10 times the log ratio of power during the test interval to power during the baseline interval. Errors bars indicate ±1 SE.

To determine whether this power reduction preceding a goal response was unique to central sites, I ran identical repeated measures ANOVAs on mean ERD values for frontal, parietal, and occipital sites. I found no effects at frontal sites (goal response: $M = -0.21$, $SD = 1.14$; nongoal response: $M = 0.21$, $SD = 1.58$; $ps > .21$). However, at parietal sites, there was a significant main effect of trial type, $F(1, 34) = 7.72$, $p < .009$, $h_p^2 = .19$; there was more power during action observation relative to baseline prior to a nongoal response ($M = 0.31$, $SD = .1.08$) than prior to a goal response ($M = -0.18$, $SD = 0.76$). One-sample t tests indicated that parietal desynchronization prior to goal responses was not significantly different from zero, $t(34) = -1.43$, $p < .163$. Additionally, the difference between power during the test interval and baseline power was not significantly different from zero on trials with nongoal responses, $t(35) = 1.73$, $p < .093$.

Thus, although the desynchronization scores for parietal sites differed significantly between trials with goal responses and trials with nongoal responses, power during action observation was not significantly different from baseline levels in either trial type. At occipital sites, I also found a significant main effect of trial type, $F(1, 35) = 4.87$, $p < .034$, $h_p^2 = .12$; there was significantly more desynchronization prior to goal responses ($M = -0.66$, $SD = 1.36$) compared with nongoal responses ($M = -0.03$, $SD = 1.18$). Activation of occipital regions during action observation was significantly different from baseline activation for trials with goal responses, $t(35) = -2.93$, $p < .006$, but not for trials with nongoal responses, $p < .866$. Thus, similar patterns of neural activation were found at occipital sites and central sites. This result is consistent with prior reports that mu desynchronization over central sites is accompanied by desynchronization at occipital sites during action observation (e.g., Marshall, Bouquet, Shipley, & Young, 2009). Given that sensorimotor regions and occipital regions were both recruited to a greater extent before infants generated a goal response than before they generated a nongoal response, I next evaluated whether the neural response at central sites differed from the neural response at occipital sites during action observation. I examined correlations between occipital ERD and central ERD on trials with goal responses and trials with nongoal responses. I found no relations between activity at central sites and activity at occipital sites for either trial type (goal response: $p > .235$; nongoal response: $p > .622$). To further test whether central and occipital ERD were related, I ran a between subjects test of the relationship between central site ERD and occipital site ERD: I examined whether those infants who showed stronger central site ERD responses during goal trials relative to non-goal trials, were the same infants who showed stronger occipital site ERD responses during goal trials relative to non-goal trials. To do so, I computed differences scores between ERD scores on goal trials and non-goal trials for both central sites and occipital sites. Larger difference scores indicate infants that have more negative ERD scores for goal relative to non-goal trials. By comparing difference scores for central sites to those for occipital sites, we can test whether those infants who recruit the motor system more on goal trials relative to non-goal trials are the same infants that are recruiting the occipital system more on goal trials relative to non-goal trials. I found that there was not a reliable correlation between central site difference scores and occipital site difference scores ($r = .23$, $p > .176$)—indicating that those infants who recruit the motor system more on goal trials are not the same infants who are recruiting the visual system more on goal trials.

To further examine the relative contribution of activity at central and occipital sites, I tested whether neural activity at either site uniquely predicted imitation of goal-directed behavior. To do this, I conducted a stepwise multiple regression to determine whether ERD scores at central or occipital sites during action observation predicted the most unique variance in the proportion of goal responses generated by an infant. In the first step, the predictor with the highest predictive value was entered. This predictor was ERD at central sites, which was significantly related to goal-response behavior, $F(1, 35) = 4.17$, $p < .049$. The multiple correlation coefficient was .33, indicating that 11% of the variance in the proportion of trials on which an infant reproduced the goal of the presenter could be accounted for by ERD values at central sites. ERD values at occipital sites ($t = 0.70$, $p = .486$) did not enter into the regression equation at Step 2 because occipital ERD did not uniquely predict any of the remaining variance in the proportion of goal responses generated by an infant. Thus, sensorimotor activity predicted more unique variance in imitative behavior.

Between-subjects analyses. To further assess the relations between the sensorimotor system and goal imitation, I next examined between-subjects variation in neural activity during action execution. Previous research has demonstrated that infants exhibit substantial individual differences in the mu-ERD response during both action execution and action observation (e.g., Marshall, Saby, & Meltzoff, 2013; Marshall et al., 2011). In particular, new research suggests that differences in motor development may be linked to the variability in the mu-ERD response during the observation of action (Cannon et al., 2015). Given that variations in motor experience are related to the robustness of the neural response during action observation, it seems possible that the mu-ERD response might reflect variation in motor skill. I reasoned that early in development, variation in the mu-ERD response during action execution could reflect differences in the maturity of the motor system (See Chapter 1 for evidence supporting this claim). Thus, examining neural activity during action execution could provide further evidence that general developments in the sensorimotor system are linked to goal imitation. I therefore tested whether variation in the neural response during action execution in the familiarization phase predicted infants' subsequent propensity to reproduce the observed goal-directed actions. On average, I obtained artifact-free data for per infant (range = 5–12).

I conducted a stepwise multiple regression to determine whether ERD values at each site (frontal, central, parietal, and occipital) during action execution was necessary to predict the proportion of goal responses generated by an infant. ERD values at central sites predicted the most unique variance and were therefore entered into the regression equation in Step 1. Central ERD was significantly related to goal response behavior, $F(1, 32) = 8.12$, $p < .008$. The multiple correlation coefficient was .46, indicating that 21% of the variance in the proportion of trials that infants produced goal responses could be accounted for by action-execution ERD values at central sites. ERD values at occipital ($t = 1.61$, $p = .118$), frontal ($t = -0.76$, $p = .452$), and parietal ($t = -0.52$, $p = .605$) sites did not enter into the equation in Step 2 of the analysis because

ERD at these sites did not uniquely predict any of the remaining variance in the proportion of goal responses generated. Thus, desynchronization at central sites during action execution uniquely predicted infants' behavioral responses to observed actions (see Figure 3). (See the Supplemental Material for further analyses.)

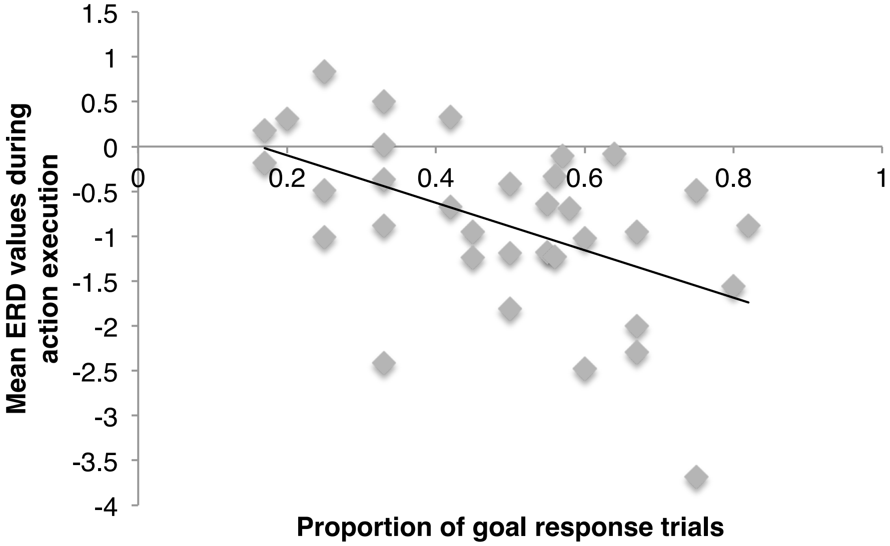

Figure 6.

Scatterplot (with best-fitting regression line) demonstrating the relation between mean event-related desynchronization (ERD) at central sites during action execution and the proportion of trials on which each infant produced goal responses.

Supplemental Analyses

In this section I provide additional supporting details for the main effects described above. These supporting details provide strong evidence about the dependent measures used in the analyses reported above, provide detail in support of the assumptions made throughout the focal analyses section, and examine the extent to which the variability I find within and across infants are reflective of the sample as a whole. In this section, I also provide supporting information about the topography of the effects.

Behavioral analyses. Infants in the main analyses reproduced the goal of the presenter on 49% of trials, a response rate lower than that reported in prior studies using this behavioral method in which infants selected the goal object on 60-66% of trials (Hamlin et al., 2008; Gerson & Woodward, 2012). I conducted follow up analyses to evaluate whether this difference in findings resulted from the longer, and potentially more tiring testing session that was required in the current study, due to the need to apply the EEG net and the extended number of testing trials. In the follow up analyses I included all infants who produced clean behavioral data (without side bias) (*n*=46), regardless of whether they produced useable EEG data. 6 additional infants were excluded due to side bias and 2 additional infants were excluded because their scores fell more than 2 standard deviations from the mean.

To examine whether imitation changed over the course of the session I conducted a one-way repeated measures ANOVA on imitation rate with time (trials 1-6 vs. trials 7-12) as a within subjects factor. I found a marginally significant main effect of time on imitation rate ($F(1,45)=16.284$, $p<.001$; See Figure 7). Furthermore, I found that if you examine only the first 6 trials of testing (i.e., a direct replication of Hamlin et al, 2008), infants were marginally more likely to reproduce the experimenters' goal ($M=.56$, $SD=.21$) than would be expected by chance ($t(45)=1.80$, $p<.078$). If at 7 months of age the propensity to reproduce the goals of others is fragile, as the data suggests that it is, then it is possible that the extended duration of the testing session may make it more difficult to replicate the original Hamlin et al (2008) finding. Nevertheless, this supplemental analysis demonstrates that overall I marginally replicate the original finding despite significant changes in the timing of behavioral testing due to the addition of EEG measurements.

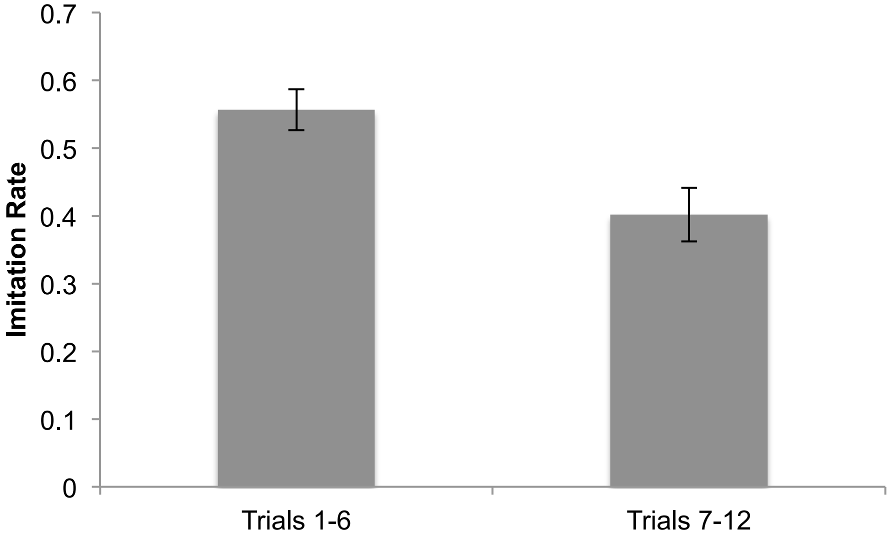

Figure 7. Average imitation rate across the first half (trials 1-6) and second half (trials 7-12) of trials.

Localization of ERD effect. In addition to examining changes in average ERD across frontal, central, parietal and occipital sites for action execution and action observation trials, I also provide topoplots of average ERD for familiarization (See Figure 8), goal (See Figure 9) and non-goal (See Figure 10) trials to provide more detail about the topography of the effect. While infant EEG data is noisy, these figures depict patterns of activation that are concordant with the primary findings.

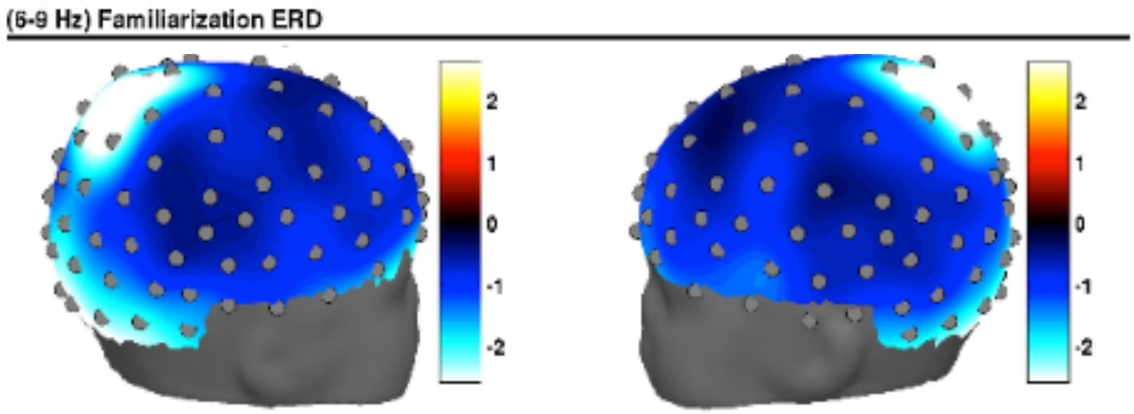

Figure 8. Topoplot of average ERD on action execution trials

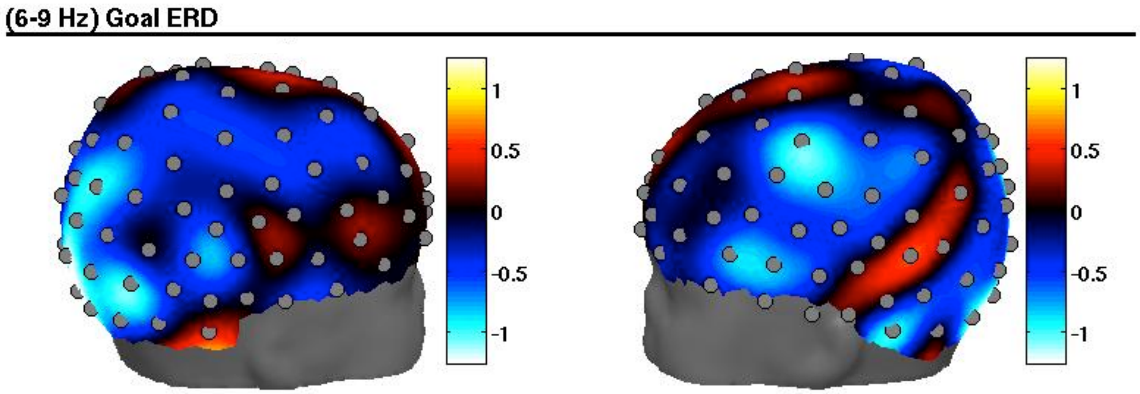

Figure 9. Topoplot of average ERD on goal response trials

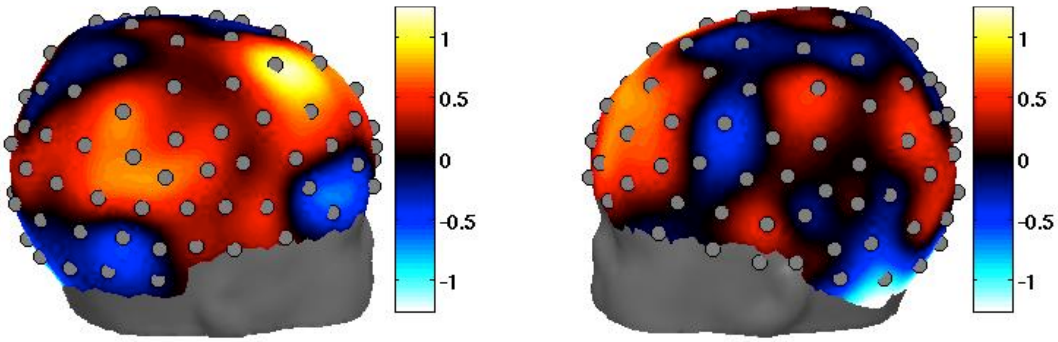

Figure 10 Topoplot of average ERD on non-goal response trials

Action execution neural response. Analyses were also run to characterize the neural response during action execution. One-sample t-tests indicated that there was significant mu desynchronization compared to zero during action execution at both central (*M*= -.85), frontal *(M*= -1.08*),* occipital sites (*M*= -1.92) and parietal sites *(M*=-.76; all *ps*<.001; See Figure 11).

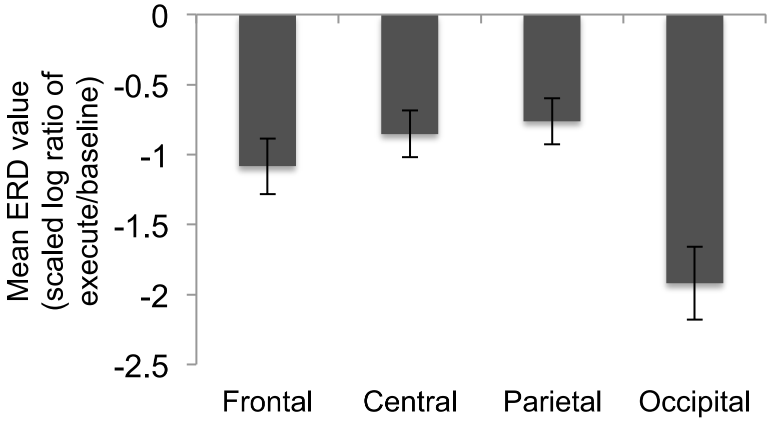

Figure 11. Action Execution Neural Response. Bars represent mean ERD scores over central sites (6-9 Hz frequency range) during action execution. Averages are plotted for four scalp sites. Errors bars indicate one standard error.

In the focal analyses, I describe individual variability both in neural activity over central sites and in goal imitation abilities and I demonstrate that greater goal imitation is linked to a stronger ERD response over central sites (See Figure 6). This correlation raises the question of whether variation in infants' behavioral responses below as well as above chance was associated with systematic differences in neural response. Infants' behavioral scores were variable, and at a group level, did not differ from chance. Some infants produced behavioral scores that fell below chance, as would be expected when group level performance is random. In a follow up analysis I tested whether these infants differed from those whose scores fell closer to chance or those whose scores fell above chance in terms of the neural response during action execution. I grouped infants that imitated the goal at above chance rates (imitation scores of .6 to .8; *n*=11), at chance rates (imitation scores of .4 to .6; *n*=14) and at less than chance rates (imitation scores of

.2 to .4; *n*=11). Following this grouping, I evaluated whether ERD scores at central sites differed significantly across groups. Infants whose imitation scores fell below chance did not differ reliably from those whose scores were close to chance ($M_{ERD\ at\ Central}$=-.32; *t*(22)= 1.52, *p*>.14). In contrast, infants whose scores fell above chance differed marginally from those at chance *t*(12.81)= 2.03, *p*<.06, and reliably from those whose scores fell below chance, (*t*(19)= 2.84, *p*<.01) (See Figure 12). Thus, the correlation shown in Figure 3 seems to be driven by infants whose imitation scores fell above chance.

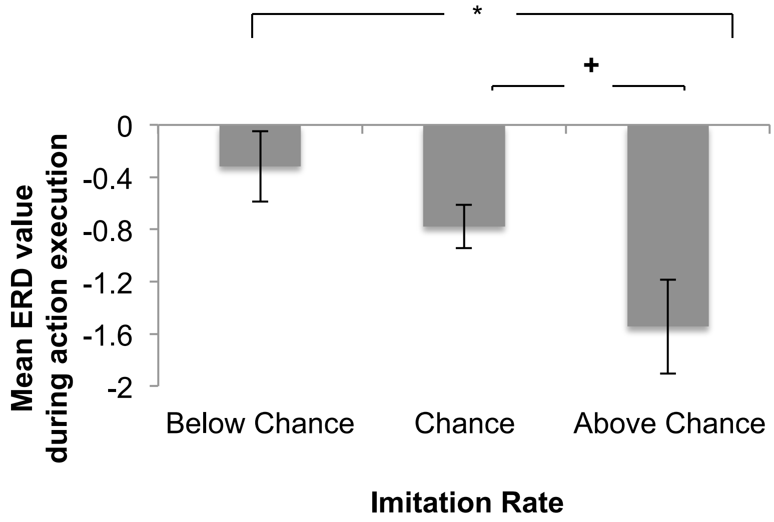

***Figure 12.** Action execution neural response examined as a function of imitation rate (below chance= 20-40% imitation; chance= 40-60% imitation; above chance= 60-80% imitation). Bars represent mean ERD scores (6-9 Hz frequency range over central sites) during action execution. Errors bars indicate one standard error.*

In the between subjects analyses, I describe the action execution effects in terms of infants' propensity to reproduce the goal of the experimenter. This interpretation relies on the assumption that propensity to reproduce the experimenters' action should be viewed as a continuous spectrum (with some infants being more likely to reproduce the goal than others). This raises the question of whether variation above or below chance levels may indicate systematic patterns of behavior to imitate or "counter-imitate" the observed action goals. The data from the current study do not provide sufficient power to address this issue. Infants' imitation scores were, at a group level, not different from chance, and, as shown in the histogram below (See Figure 13), there was no indication of a bimodal distribution with groups of infants systematically below and above chance. The question of whether some infants may, in fact, systematically avoid reproducing an observed goal is an issue that requires further research.

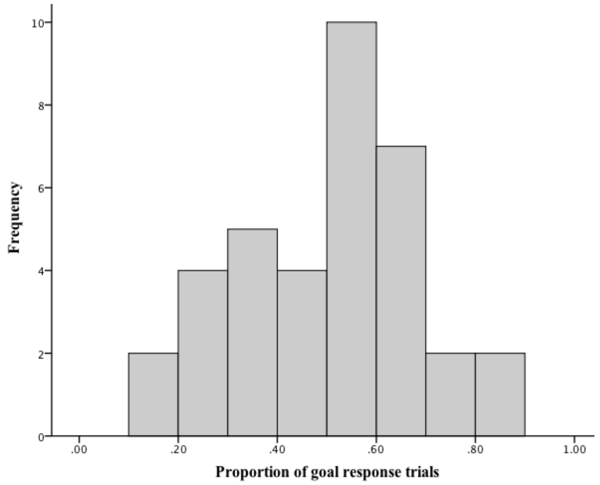

Figure 13. Histogram of the average proportion of goal response trials (i.e., trials imitated). This histogram demonstrates that there is no indication of a bimodal distribution in the imitation data.

Maturity as a driver of the correlations. One possibility is that the relationship between the neural response and imitative behavior is driven by general developmental maturation. To further explore this possibility, I ran follow up correlational analyses to examine whether age correlated with infants' propensity to imitate, the neural response at any site (i.e., action observation and action execution) or attention to the action events. There was no correlation between age and imitation (*p*>.483), neural activity at any site (all *p*s>.095) or total attention (*p*>.187). This suggests that general developmental maturity may not explain the findings.

Comparing neural response during action observation and action execution. While previous studies with adults have demonstrated that the motor system activation response during action observation is comparable to the neural response during action execution, relatively few infant studies have examined neural activity during both action execution and action observation (Cuevas et al., 2014). Given that the current study sought to examine motor system activation in one of the youngest populations studied to date and that young infants' motor repertoires develop rapidly, it was important to evaluate whether the neural response I observed during action observation reflected motor system activity. As has been found in other studies (Marshall et al., 2013), ERD across the scalp was greater during action execution than during observation (Central: $t(33)=1.94$, $p<.06$; Frontal: $t(34)=3.00$, $p<.005$; Occipital: $t(35)=3.65$, $p<.001$; Parietal: $t(33)=3.65$, $p<.003$). Thus, there was a similar, though greater in magnitude and more diffuse, pattern of suppression during action execution as compared to observation. This result is consistent with prior observations in infants (Marshall et al., 2013).

Because both motor skill and goal perception show developmental variation at 7 months, I next asked whether the neural responses during action execution and action observation were related. Specifically, since I hypothesized that neural activity that preceded goal responses would be linked to goal perception, I examined neural activity during action observation and binned the neural response based on infants' subsequent behavioral response (i.e., goal response trials vs. non-goal response trials). I first ran correlations on the mean action execution ERD scores and mean ERD scores for goal response trials during the action observation phase. I found that infants who showed greater mu desynchronization at central sites during action execution also showed greater mu desynchronization at central sites during action observation prior to generating a goal response ($r= .40$, $p<.02$). There were not reliable correlations between action execution ERD and action observation ERD at occipital, frontal or parietal sites (ps>.52). Importantly, no correlations were found between ERD scores during action execution and ERD scores for non-goal responses at any scalp site (*p*s> .24). These results indicate that the neural response at central sites during action execution was related to the neural response associated with responding to the goal-structure during action observation.

Discussion

Responding selectively to other people's goal-directed actions is central to social interaction. In the current study, I made use of spontaneous variation in infants' abilities as a natural case for exploring contingent relations between neural activity and social behavior. By integrating a behavioral measure of goal sensitivity with EEG, I was able to test whether infants' motor system activation as they observed an action was selectively linked to their goal-based behavioral responses. On each trial, infants observed (and were attentive to) an adult who performed a well-formed goal-directed action. On each trial, they also generated a behavioral response to that action, choosing either the goal or the nongoal object. Nevertheless, I found that activation of the motor system during observation was selective to trials on which the infants reproduced the observed action. That is, motor system activation (and visual system activity) during infants' observation of a goal-directed action predicted whether they subsequently chose the presenter's prior goal rather than the non-goal toy.

Because I included only those trials on which infants attended to the actions of the presenter and then produced a clear behavioral response, I conclude that this differential neural activity reflected variations in infants' sensitivity to the presenter's goal during observation rather than variations in attentiveness, engagement, or motor preparation. Furthermore, ERD over central sites during action execution predicted infants' later behavioral propensity to produce goal-based behavioral responses. The findings provide evidence that the neural response during action observation is linked to the neural systems recruited for producing goal-directed actions. These findings demonstrate a link between the motor system and social behavior at the level of individual trials and at the level of variation across infants. Thus, these findings provide novel evidence that motor system activation predicts goal-based behavioral responses during infancy.

These results with infants are consonant with findings from adults in indicating that certain social-cognitive functions are contingent on motor-system activation. In adults, aspects of social perception, including visual anticipation of actions (Stadler et al., 2012) and inference of actions from context (Michael et al., 2014), are reduced, but not eliminated, by TMS to the motor cortex. In the task, infants were not required to anticipate the outcome of an action nor to make an inference about an action from context. Nevertheless, performance in the task, as in the tasks used with adults, depended on infants' ability to respond to other people's goal-directed actions. Furthermore, these findings with infants suggest a starker contrast than has been observed in adults, in that there was no detectable mu-desynchronization on trials on which infants attended to the presenter's actions but chose the nongoal toy. In adults, mu-desynchronization occurs robustly during the observation of goal-directed actions. The variation in this response in infants is consistent with the variation that typically occurs when skills are new in development (e.g., Siegler & Shipley, 1995)**,** and with behavioral findings showing that variability in behavioral measures of goal perception correlates with motor expertise during periods of developmental change (e.g., Sommerville & Woodward, 2005). Together, these findings indicate that studying early development provides a unique lens for characterizing processes that in adulthood may show little variability.

Findings from adult neuroimaging studies have shown that mature action understanding involves a network of regions (Arnstein et al., 2011; de Lange, Spronk, Willems, Toni, &

Bekkering, 2008), and this raises questions about the extent to which broader neural networks are involved in infants' responses to other people's actions. The finding of significant desynchronization over occipital regions before goal responses, but not before nongoal responses, is in line with the idea that a network of regions is activated during action processing. Given that the mu frequency band overlaps with the alpha frequency band and occipital alpha is linked to visual attention (Pfurtscheller, 2003), it is possible that these findings reflect engagement of visual processing or selective attention in perceiving and responding to the presenter's actions. To examine this possibility, I assessed infants' visual attention behavior and their neural response over visual attention regions. I found that the link between sensorimotor system response and their goal imitation behavior holds independent of variations in global attention. I also found that occipital ERD scores were not correlated with central ERD scores and that central ERD scores during action observation accounted for the most variance in goal-response behavior. Furthermore, results in the between-subjects analyses demonstrated that sensorimotor activity during action execution uniquely predicted infants' tendency to imitate goal-directed behavior, with no evident relation between imitation behavior and occipital ERD**.** Thus, there is converging evidence that visual processing cannot solely account for the findings.

Even so, the attention network may interact with the motor system in functionally interesting ways during the perception of other individuals' actions. In adults, the motor system response is modulated by changes in attention (Johansen-Berg & Matthews, 2002). Indeed, action observation likely involves specialized, fine-grained patterns of visual attention. For example, skilled action production requires tightly coordinated shifts in visual attention, and adults (Flanagan & Johansson, 2003) and infants (Rosander & von Hofsten, 2011) both exhibit similar patterns of attention when observing others' actions and when acting themselves. Future research is needed to determine how attention may modulate changes in the motor system response in infancy.

In adults, activation of the parietal cortex has been associated with goal processing, particularly for events involving animated stimuli (e.g., Hamilton & Grafton, 2006; see Southgate, Begus, Lloyd-Fox, di Gangi, & Hamilton, 2014, for similar findings in infants). Although I did not find desynchronization at parietal sites, I cannot conclude from this that the parietal attention network plays an insignificant role in infants' action processing. Although there is suggestive evidence that mu desynchronization over central sites reflects motor system activity in infants (see Marshall & Meltzoff, 2011), little is known about how activity across different brain regions relates to scalp EEG in infants. Further work is needed, at both the behavioral and neural levels, to understand relations among different behavioral indicators of goal perception and the neural networks that support them during early development.

I found that the strength of the ERD in mu rhythm as infants reached for objects predicted their propensity to act selectively with respect to another person's goals. Other studies have shown that the magnitude of the ERD when infants observe actions correlates with their motor skill and experience (Cannon et al., 2015; de Klerk, Johnson, Heyes, & Southgate, 2014; Marshall et al., 2013; van Elk et al., 2008). Thus, foundational developments in motor skill during infancy may have cascading effects on social behavior. Understanding the neural bases that underlie the development of skilled, attention-driven motor control will be critical for understanding social behavior during typical development and may shed new light on developmental impairments in social cognition.

In summary, the current study provides novel evidence that motor system activation is selectively associated with infants' responses to others' goal-directed actions. In addition, these findings demonstrate that a developmental perspective offers insight into the functional role that the motor system plays in this foundational social-cognitive ability. This work raises new questions about the development of the neural systems that underlie skilled action production and action perception, and it provides a methodological approach—using naturally occurring variability during early development—to address these questions.

CHAPTER 3: Action and the development of theory of mind

Understanding others' mental states is critical to social development. When the ability to infer others' mental states is disrupted, as is the case in autism, social interaction is difficult. Despite considerable interest in mental state inference abilities (i.e., *theory of mind, ToM*) in both typical and atypical populations, we still know relatively little about the mechanisms that support the development of this social capacity. In part, this gap in the literature is related to controversy over how theory of mind develops. Many different developmental stories about the trajectory of theory of mind development seem plausible given the research has demonstrated robust links between theory of mind performance and general cognitive developments (e.g., executive functioning, language; Astington, J. W., & Jenkins, 1999; Carlson & Moses, 2001; Carlson, Moses & Breton, 2002; Carlson, Moses & Claxton, 2004; Müller, Zelazo & Imrisek, 2005; Perner & Lang, 1999) and links between infant social cognition to theory of mind development. Indeed, while researchers generally agree that infant social cognition develops continuously into mature social cognition, the mechanisms that support this link in the case of theory of mind are largely underspecified.

One possibility is that the system that supports mature mental state representation develops in part from social interaction early in life (Watson, Nixon, Wilson, Capage, 1999; Charman et al, 2000). In infancy, the motor system facilitates engagement with social partners (e.g., Reid, Striano, Iacoboni, 2011; Saby, Marshall, Meltzoff, 2012) and social perception (e.g., Filippi et al, 2016; Marshall & Meltzoff, 2011; Southgate et al., 2010; Southgate et al, 2009). It could be that these are the kinds of inputs that may be important for developing theory of mind later in life. Recent research provides initial support for this hypothesis. For instances, Lloyd-Fox and colleagues (2015) show that those infants who have better fine-motor abilities also show a stronger recruitment of the STS and TPJ during social perception tasks. These regions of the brain are often described as relevant for mature theory of mind processing (Gweon & Saxe, 2013; Saxe & Kanwisher, 2003; Saxe, Whitfield-Gabrieli, Scholz, Pelphrey, 2009) and have been linked to infant social perception (e.g., Lloyd-Fox, Blasi, Volein, Everdell, Elwell, & Johnson, 2009). Providing at least initial evidence that the motor system might be functionally linked to recruitment of the regions of the brain that, later in life, go onto specialize in social reasoning (including theory of mind).

Still other research suggests that the action perception system might have a unique link to theory of mind development. To illustrate, Wellman and colleagues (2004) found that faster habituation to intentional actions (not novelty preference) in infancy predicted better theory of mind abilities later in development. This finding (and others like it; Aschersleben, Hofer & Jovanovic, 2008; Sodian et al, 2016; Wellman et al, 2008) hold when controlling for general cognitive abilities (e.g., language, IQ, executive functioning)--suggesting that some aspects of action understanding early in life may be linked to theory of mind development above and beyond general cognitive abilities. While this provides initial evidence that action encoding is linked to theory of mind, it is puzzling that the relation between infant attention and theory of mind only holds for habituation rate, not novelty preference. Previous research has shown that habituation rate correlates strongly IQ later in life (Bornstein & Tamis-LeMonda, 1994; McCall & Carriger, 1993; Rose, Slater, Perry, 1986) thereby making it difficult to interpret these findings as independent of general cognitive development. Indeed, this correlational finding could still be, in part, related to general cognitive development. Only one study, to date, has found evidence that the relation between infant social attention and theory of mind development might be related to developments specifically in social cognition: Yamaguchi and colleagues (2009) compared attention to social and non-social events and found that only attention to social events predicted better theory of mind at five years. However, it is difficult to compare this study to the rest of the literature because the nonsocial task is not a visual task (unlike the rest of the literature)—leaving open the possibility that infants recruit an entirely different mechanism to interpret the nonsocial task. Furthermore, even in this study the type of processing that infants are engaging in during action observation remains underspecified.

To date, infant action encoding abilities have largely been measured using their visual attention response—leaving open the question of whether visual attention processing alone could also account for these effects or whether the motor system (the system that supports the development of action encoding) is specifically linked to theory of mind. The current study uses EEG measures to directly investigate whether the sensorimotor system, the visual attention system or both systems are selectively linked to the development of theory of mind. To do so, I followed up with the 7-month-old infants described in chapters 1 and 2 by asking parents to fill out a series of questionnaires about their child's development (including the child's mental state understanding, language development and general cognitive development and temperament) at age 3. Just as 7-months is one of the earliest developmental time points for assessing action encoding in infancy, three years is also a transitional point in theory of mind development. Behavioral variability, both between children and across time, is inherent to developmental change and can be harnessed to understand developmental mechanisms (Siegler & Shipley, 1995; Smith & Thelen, 2003). Thus, I reasoned that if the action system provides the input for the system that later goes on to support ToM, then variability in sensorimotor system response (early in development) could be linked to variability in early theory of mind.

To determine if the action system is selectively linked to the development of theory of mind, I examined the infant sensorimotor system response at 7 months. In chapter 2 I demonstrate that (in this sample) variability in the sensorimotor system response is linked to variability in action encoding both during action execution and during action observation. As such, I reasoned that these phases of the experiment would provide us sufficient variability to see a relation between the neural system that supports action in infancy and that this variability is highly likely to be meaningful linked to behavior. If the sensorimotor system is selectively linked to theory of mind, then we would expect to find that variability in the sensorimotor system response, not the visual system response, would predict theory of mind abilities.

To examine theory of mind development I collected the Children's Social Understanding Scale, a parental report measure developed by Tahiroglu and colleagues (2014). I chose this measure because it has been used with children as young as three, provided an inexpensive measure that would give us a descriptive report of children's mental state reasoning across a variety of domains and that would be easy to distribute so as to minimize attrition rates that are common with longitudinal studies. I chose to examine mental state inference abilities across a variety of mental states (i.e., desire, belief, intention, perception, knowledge, emotion) because, to date, the literature examining the longitudinal relation between infant social cognition and theory of mind has considerable heterogeneity in the measures used to assess theory of mind. Generally speaking, having some heterogeneity in a measure but consistent conclusions across a variety of studies indicates that the relation between early and later developing social cognition are robust because they holds independent of precisely how theory of mind is indexed (e.g., Wellman et al, 2004; Wellman et al, 2008; Yamaguchi et al, 2009). However, in this particular case, research examining the specific types of mental states that link to theory of mind in early childhood suggests that some types of mental state inferences (e.g., inferences about perception) are related to infant action understanding—while others are not (Colonnesi et al, 2008) and some types of theory of mind tasks (e.g., false belief tasks) relate to action understanding better than general theory of mind composites[1] (See Aschersleben, Hofer, Jovanovic, 2008). This heterogeneity makes it difficult to determine whether or not all aspects of theory of mind are related to infants action encoding. Thus, the primary goal of the current study is to provide a descriptive account of exactly which aspects of theory of mind correlate with neural correlates of infant action encoding and neural indices of motor maturity. As such, I report these effects using both a general theory of mind composite and across each individual subscale.

To test the general hypothesis that the sensorimotor system is linked to theory of mind abilities in early childhood I conducted two sets of focal analyses. In the first set of focal analyses, I examine the relation between infants' neural response during action encoding and their theory of mind development. I hypothesized that greater recruitment of the sensorimotor system during action observation (not recruitment of visual attention regions) would predict performance on theory of mind tasks. To examine this effect I take two analytic approaches: first, I examine whether there is a correlation between infants' sensorimotor system response (or their visual system response; i.e., using ERD in the alpha/mu frequency band as the index) and theory of mind.

In the second set of focal analyses, I examine the sensorimotor system response during action execution. I do so because previous research suggests that motor development is linked to developments in theory of mind and social perception parts of the brain (Lloyd-Fox, Wu, Richards, Elwell, & Johnson, 2015) and to other advancements in social competence (Clearfield,

---

[1] Composites typically consist of generating one score that indicates *how many* mental states children correctly attribute (independent of the type of mental state).

Osborne, Mullen, 2008; Karasik, Tamis-LeMonda, & Adolph, 2011; 2014; Libertus & Needham, 2011). In chapter 1, I demonstrate that the strength of the mu-ERD response is linked to motor maturity in young infants—providing initial evidence that the mu-ERD response during action execution could be a particularly robust index of infants' sensorimotor system development[2]. I hypothesize that if the motor maturity provides input for theory of mind development, then we might find that a greater mu-ERD response during action execution predicts better theory of mind at age three. For both sets of focal analyses I report individual differences in children's composite theory of mind scores and also individual differences on each subscale. Thus, the current study provides an initial report of the descriptive relations between theory of mind, motor maturity and infants neural encoding of others' actions.

Methods

Participants

Sixty-three full-term 7-month-old infants from a metropolitan area (15 female, mean age = 7 months 8 days, range = 6 months 17 days–8 months 5 days) participated in an EEG study at 7 months of age (See Filippi et al, 2016). These infants are the same infants that were reported in Chapter 2. Of these 63 infants, 36 met inclusion criteria for this past study (*See Chapter 2 Participants section for more details).* When these 36 children reached three years of age, their parents were contacted to be a part of a longitudinal follow-up study. The parents of 30 children consented to participate and completed all of the surveys before their child's turned three years and 3 months of age.

---

[2] Also, the sensorimotor system response during action execution seems to be related to some aspects of motor development (See study 1). Thus, it could be that this response indexes motor development which could be related to theory of mind behavior (See Lloyd-Fox et al, 2015 for initial evidence).

Infant Task

At 7-months of age, infants participated in an EEG study investigating the neural correlates of early imitation behavior. Infants were first fitted with a 128-sensor Geodesic sensor net (EGI) before engaging in the experimental paradigm. Testing began with a familiarization phase whereby infants got an opportunity to engage one at a time with each of the toys that they would see during the subsequent imitation phase of the experiment. Following familiarization, a curtain came down to hide the stage and allow an experimenter could set up two toys on the table. When these objects were set up, the curtain was raised and infant observed the experimenter grasp one of the two toys (Action Observation Phase). The experimenter then released her grip, looked up, and pushed the tray of toys to the infant (*For more details see Study 2 Methods Section*). At this point the infant could select between the toys (Choice Phase). Infants could either act on the same toy as the experimenter (goal response) or select the previously untouched toy (non-goal response).

Preschool Follow-up

When infants turned three years old, parents were sent a series of online questionnaires to assess both general cognitive development and developments in social cognition specifically. The surveys included: the Children's social understanding scale (CSUS; Tahiroglu et al, 2014), developmental vocabulary assessment for parents (DVAP; Libertus et al, 2015) and the Child Behavior Questionnaire (CBQ; Rothbart et al, 1994; 2001). Parents received a $20 Amazon gift card in exchange for completing all three surveys.

Specific Measures

Infant neural measures. To investigate the neural processing that underlies action encoding, I conducted a series of exploratory analyses that were guided by the findings in Study

2. To begin, I examine neural activity during action observation because this is an index of neural processing during action encoding. Then, I investigate infants' neural response during action execution.

Action encoding. To provide a detailed account of infants' neural activity during action encoding I examined two action observation neural measures. The first measure is of infants' neural activity when they observe an action (AO-all trials). I chose this neural index because it mirrors measures used widely in the literature and it reflects spontaneous differences in processing of actions. The second measure I used is an index that could reasonably map onto infants' successful coding of another's goal. Indeed, in Chapter 2, I report that there is considerable variability in whether infants' recruit their sensorimotor system and this variability maps onto their goal imitation behavior (one index of action encoding). The second measure examines only neural activity when infants' observed an actor produce and action and they subsequently imitated the actor's goal (i.e., AO-goal)

Neural response during all action observation trials (AO-all trials). While I suspected that the action observation response for goal imitation trials would be the strongest indicator of infants' successful action encoding, it could also be a noisy measure because so few trials are included in the average—thereby making it difficult to detect a longitudinal relation. As such, I also computed an average neural response for all action observation trials—regardless of the infants' subsequent behavior. This average provides an estimate of infants' action observation response and aligns closely with the infant EEG literature on action understanding. While this neural response might not be as strong of an index of infants' successful action encoding response, it is an estimate that takes advantage of all the action observation data. Indeed, the fact that I found variability in the mu-ERD response at the trial level (in Study 2) suggests that the average response may provide similar index of infants' action encoding response. To test whether this is the case, I report (in preliminary analyses) how this neural response is related to the AO-goal response.

Neural response during action observation preceding goal imitation response (AO-goal). I reasoned that while the average ERD response during action observation does provide a robust estimate in terms of the spontaneous neural activity during action observation, it might not provide a robust estimate of the neural processing involved in successfully encoding other people's goals. To get an estimate of the neural response involved in successful action encoding I examined infants' neural response during action observation on trials where the infant subsequently imitated the experimenter's goal (AO-goal). In Study 2, I demonstrated that infants' showed a stronger mu-ERD response over sensorimotor and visual attention regions prior to generating a goal response. The strength of this response also predicted infants' imitation rate. Further, recent research suggests that there is a relation between goal prediction and imitation in infancy (Gampe, Prinz, Daum, 2015; Thoermer et al, 2013)—suggesting that this behavioral response is meaningfully linked to action encoding. Thus, the neural response during AO-goal trial provides an estimate of infants' successful action encoding.

Neural response during action execution. The final neural measure I recruited was the action execution neural response. The Chapter 2 results demonstrated a selective link between the sensorimotor system response during action execution and infants' goal imitation behavior (See Figure 6). Thus, I reasoned that this neural measure might be a robust estimate of infants' motor system maturity (See Chapter 1).

Preschooler survey measures. The CSUS asks parents to report on a Likert scale of 1-4 (i.e., definitely untrue to definitely true[3]) the things their kids have said, done and understand about others' behavior and the motivations (or intentions) behind others' behavior. The 42 questions on this survey comprise six subscales (i.e., belief, knowledge, perception, desire, intention and emotion). In the analyses to follow I focus specifically on the perception, intention and belief subscales because these aspects of theory of mind represent two early developing aspects of theory of mind (i.e., perception and intention) and one aspect of later developing theory of mind (i.e., belief). The DVAP asks parents to report their children's productive vocabulary—this measure acted as a control for general cognitive development. The CBQ asks parents to report their children's behavior across a number of everyday situations and consists of several subscales involved in general cognitive development (e.g., attention focusing, inhibitory control) and provides a composite including all of these subscales (i.e., effortful control which I gloss here as executive functioning)). I use these subscales to control for specific developments in general cognitive development that could facilitate the development of theory of mind.

Results

Preliminary Analyses

In Study 2, I demonstrated that on average infants show event-related desynchronization in the mu/alpha frequency band over all sites during action execution and that infants show selective recruitment of the motor and visual systems during successful action encoding (i.e., when infants subsequently imitate the experimenter's goal). Preliminary analyses indicated that

---

[3] All questionnaires required that parents answer every question so there was also a "Don't know" option. Prior to computing averages for the CSUS subscales I excluded all "don't know" answers.

the 30 infants in this subsample showed patterns consistent with the group data reported in Chapter 2[4].

Theory of mind data. Preliminary analyses indicated strong correlations among subscale measures (see analyses reported below) so in addition to reporting the subscale measures individually, I computed a ToM composite score that consisted of mean performance across all questions for all subscales. I found that the composite score correlated significantly with all of the subscale measures (ps<.0001) except perception (p>.412). The composite score (as is true of all subscales except perception) is also strongly correlated with productive vocabulary as assessed with the DVAP (r=.620, p<.001) and executive functioning as assessed by the effortful control subscale of the CBQ (r=.489, p<.006) at three years.

Correlations among subscale measures. Preliminary analyses examined the relation between the theory of mind subscale measures. Previous studies have reported that these subscales are highly correlated with each other but show this effect across a much larger age range (26 to 76 months). While these studies report correlations that hold even after statistically controlling for age, it remains possible that some of these effects are age related. Indeed, very few children in previous reports (approximately 16% of the largest sample using the CSUS) fell within my sample's age range. Thus, for replication purposes, I examined the correlation between all the subscales for children in the sample (See Table 1). In Table 2, I show that all

---

[13] Specifically I found greater mu-ERD prior to goal response relative to nongoal response t(30)=-1.994, p<.055. I also found that the mu-ERD response was significantly greater than baseline for goal responses (t(30)=-2.936, p<.006). There was no significant difference from baseline for nongoal responses (t(30)=.405, p<.688). When averaged across all trials (AO-all trials), I found that on average infants in the current study subsample also did not show a significant central site mu-ERD response compared to baseline (t(29)=-1.678, p<.104) and this did not differ from the sample reported in Chapter 2. I also examined neural activity during action execution. I found that the mu-ERD response during action execution was significantly different from baseline across all four scalp sites (i.e., frontal, central, parietal, occipital; all ps<.001).

subscales (except perception) are highly correlated with executive functioning and vocabulary development--as we would expect from prior literature. Interestingly, all significant correlations in Table 1 held when controlling for executive functioning (all *p*s< .012) at three years and when controlling for productive vocabulary at three years (all *p*s<.037).

Table 4.

Depicts correlations between each subscale of the CSUS.

	Perception	Intention	Belief	Emotion	Desire	Knowledge
Perception						
Intention	.034					
Belief	-.086	.800***				
Emotion	.180	.616***	.573***			
Desire	.186	.758***	.762***	.799***		
Knowledge	.092	.776***	.771***	.699***	.835***	

Note ***p<.001

Table 5.
Depicts correlations between each subscale and general cognitive development measures (i.e., executive functioning and productive vocabulary).

	Perception	Intention	Belief	Emotion	Desire	Knowledge
Executive Functioning (3 years)	.160	.421*	.385*	.632***	.353 $^+$	.371*
Productive Vocabulary (3 years)	.016	.553**	.551**	.545**	.534**	.569***

Note: $^+$p<.06, *p<.05, **p<.002, ***p<.001

Focal Analyses

Focal analyses examined the relation between neural activity at 7-months and preschool theory of mind. First I examine whether there is a link between individual variability in the motor system response during action encoding and theory of mind development. I hypothesized that if the motor system supports the development of social cognition beyond infancy, we may find that individual variability in the motor system response during action observation predicts developments in theory of mind. Alternatively, I could find that variability in the visual system response predicts early developing aspects of theory of mind or that activity at neither site is predictive of theory of mind. Second, I examined the relation between neural activity during action execution (an index of motor maturity; See Chapter 1) and theory of mind development.

Action encoding. To investigate the mechanisms during action encoding that support social development later in life, I first asked whether theory of mind ability was related to engagement of the motor system or visual attention system during any trial where the infant observed an action (M_{trials}=10.77). To do so, I investigated whether mu-ERD predicted theory of mind above and beyond executive functioning at three years. Hierarchical regression modeling indicated that while executive functioning at three was highly predictive of theory of mind (r^2=.239; β=.339, p<.006)—neither the mu-ERD response over central sites (r^2_{change}=.000, F(1,27)=.0001, p<.993) or occipital sites (r^2_{change}=.029, F(1,27)=1.066, p<.311) predicted remaining variance. These results suggest that there is not a strong relationship between the neural response during all instances of action observation and theory of mind at three years[5].

Next, I assessed neural activity on trials where there is good reason to suspect that the infant had encoded the goal of the actor (i.e., because the infant subsequently reproduced the

---

[5] There were no significant correlations between any of the subscales on the CSUS and mu-ERD at central or occipital sites.

actor's goal; i.e., AO-goal; See Figure 14). To do so, I investigated whether there was a relation between theory of mind and the neural responses during successful goal encoding (M_{trials}=5.29, SD_{trials}=1.97). Results indicated that (relative to a model with only executive function as a predictor) there was a significant effect of adding occipital sites (β=.097, p<.026) to the model (r^2_{change}=.369, F(1,27)=5.530, p<.026)—suggesting that less desynchronization (or more synchronization) of occipital sites was correlated with better theory of mind at age 3. There was no effect of central sites (p>.355)—suggesting that even during successful action encoding there is not an effect of central sites. These findings suggest that less recruitment of the visual system during action encoding is predictive of better theory of mind development at age three[6].

Table 6.

Depicts correlations between neural activity during action observation –goal response and Subscales of CSUS controlling for executive function. Parenthesis show correlation when controlling for productive language.

	Perception	Intention	Belief	Emotion	Desire	Knowledge
Central Site Mu-ERD for goal response trials	-.129	.204	.251	.026	.140	.091
Occipital Site Mu-ERD for goal response trials	-.224	**.438 *** **(.388 *)**	**.404 *** **(.349 $^+$)**	.271	.243	**.417 *** **(.360 $^+$)**

Note +p<.06, *p<.05

---

[6] Further analyses examined whether there was an interaction between the occipital site response and the central site response. To do so, we compared a model with only executive functioning as a predictor of theory of mind (model 1) to a model with executive functioning, the central site response, occipital site response and the interaction as predictors of theory of mind (model 2). Results indicated that model 2 did not predict any better than model 1 (F(3,28)=2.246, p<.107). In model 2 executive functioning was the only significant predictor of theory of mind (p<.012); the occipital site response only marginally predicted theory of mind (p<.107). These results indicated that neither the central site response nor the interaction term were significantly related to theory of mind (ps>.280). Nevertheless, it could be that the relation between theory of mind and the occipital response is fragile—indeed, this analysis demonstrates that adding more variables into the model changed the significance of our effect.

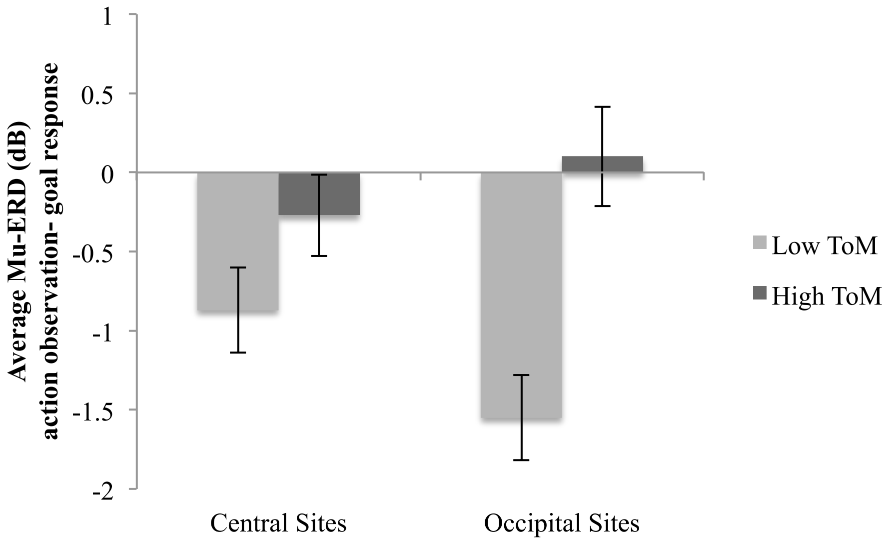

Figure 14. Mean ERD response during successful action encoding (i.e., neural response during action observation followed by a goal response).

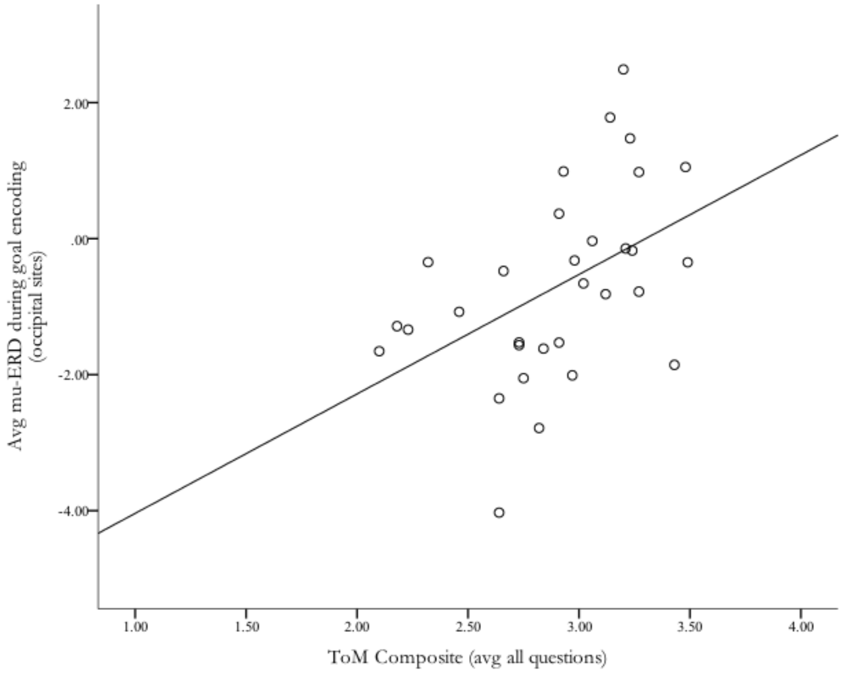

Figure 15. Scatterplot demonstrating the relation between mean occipital ERD response during successful action encoding and theory of mind (i.e., prior to controlling for executive function).

Motor system maturity and theory of mind. Next to investigate whether recruitment of the maturity of the sensorimotor system predicts theory of mind development, I examined whether central site activity during action execution predicts theory of mind independent of executive function. Results indicated that sensorimotor system response during action execution did not predict theory of mind on the composite measure. Supplemental analyses examining the correlation between central site activity and each theory of mind subscale demonstrated that there was a correlation between perception understanding and the sensorimotor system response that remained significant after controlling for executive functioning (r=-.383, p<.044) and after controlling for productive vocabulary (r=.410, p<.030) at three years.

Table 7.

Depicts correlations between central site activity during action execution and Subscales of CSUS.

	Perception	Intention	Belief	Emotion	Desire	Knowledge
Central Site Mu-ERD (action execution)	**-.383***	-.125	.167	-.180	.020	-.112

Note *p<.05

Supplemental Analyses

In addition to assessing whether the early mechanism that supports the development of theory of mind using neural measures, I also examined whether an early behavioral marker of action encoding predicted theory of mind development. Research suggests that imitation behavior correlates well with infants' ability to predict other's action in tests of social perception (Gampe, Prinz, Daum, 2015) and with responses to goal-directed actions in a visual habituation paradigm (Thoermer et al, 2013). As such, I tested whether imitation rate (i.e., the proportion of trials that infants imitated over the total number of codeable trials) in infancy predicted theory of mind at age 3. Regressions controlling for executive function and productive language indicated that imitation rate at 7 months did not predict theory of mind as a composite score or any of the individual subscales (*ps*>.17). These null findings indicate that (using these measures) there is no detectable relation between infant imitation and theory of mind at three years.

Discussion

Interpreting the goals and intentions of others is foundational to later developing social cognition. Yet, to date, we know relatively little about the mechanisms that support the development of early social cognition. The current study is the first to investigate whether there are longitudinal links between the neural systems involved in action perception and execution and later developing theory of mind. To do so, I took a focused, exploratory approach to investigating the link between neural activity during action encoding (and action execution) and theory of mind. I focus on two systems that research suggests could be critical to action encoding: the sensorimotor system and visual attention system (See Chapter 2 results). Results indicated that the visual attention system response during successful action encoding predicts theory of mind development. Those infants who engaged their visual attention system less during successful action encoding had better theory of mind scores at age three.

This effect is consistent with other studies of the early precursors of theory of mind (e.g., Aschersleben, Hofer & Jovanovic, 2008; Colonnesi, Rieffe, Koops, Perucchini, 2010; Welch-Ross & Miller, 2000; Sodian et al, 2016; Wellman et al, 2004; Wellman et al, 2008; Yamaguchi, Kuhlmeier, Wynn, VanMarle, 2009). To date, one of the most reliable findings reported in the literature is that habituation speed is linked to theory of mind (e.g., Aschersleben, Hofer &

Jovanovic, 2008; Wellman et al, 2004; Wellman et al, 2008). The faster infants stop attending to a repeated action—the better developed their theory of mind at age four. This finding provides novel neural evidence that fits with this claim: during action encoding, the smaller the magnitude of the visual attention processing response, the better children's theory of mind. One possibility is that habituation measures and the neural index of visual attention are capturing the same behavioral phenomenon—those infants who show a less robust visual attention response (as indicated in our neural measures) may process encode action events faster; although additional longitudinal studies are necessary to directly test this claim. This work suggests that further investigation of the role of visual attention regions during action encoding could provide insight into the development of social reasoning from early infancy to preschool.

Another possibility is that what we're capturing is a between subjects shift in patterns of neural recruitment over much broader networks. It could be that those infants who are faster at processing actions show less recruitment of the visual attention system during action encoding and more recruitment of another (potentially more mature) social cognition brain system (e.g., STS or rTPJ). In other words, it could be that recruiting the low-level visual attention system during action encoding is actually a less mature pattern of activity—insofar as this pattern is linked to lower ToM performance at age three. Leading to the question: is it better to activate another neural system or network? Future work should investigate how this relative decrease in visual attention processing is linked to the recruitment of other social brain networks in infancy. While EEG cannot provide adequate spatial resolution about patterns of neural activity in subcortical regions critical for mature theory of mind reasoning (e.g., mPFC, STS, rTPJ), this data provides a foundation for neuroimaging research investigating the neural correlates of early developing theory of mind.

Interestingly, I found that the magnitude of the sensorimotor system mu-ERD response was not linked to the composite index of theory of mind development in early childhood. Although, a break down of each subscale demonstrated that there was a correlation between the magnitude of the sensorimotor system response and children's understanding of perception—such that better perception understanding was correlated with a larger mu-ERD response. These findings could suggest that the link between the action system and social cognition is largely situated in the domain of perception. Alternatively, it could be that this result is spurious. Indeed, the perception subscales was the only subscale that did not show a strong correlation with the other subscales, did not correlate with the composite measure, and did not show a significant relation with productive language or executive function. This could indicate that, for this younger sample, the perception subscale is a less reliable subscale. While this is a possibility, it seems plausible that the perception subscale is capturing variability that is meaningfully linked to the action system. Considerable research suggests that the action system is linked to social perception early in life (Woodward et al, 2009). These results may provide novel evidence that the motor system is also linked to perception understanding at three years.

There are also many possible reasons why there was not a relation between recruitment of the motor system during action encoding and the theory of mind composite. It could be that abstract mental state reasoning does not emerge from the development of the action system. Alternatively, it could be that the sensorimotor system response that was indexed is too noisy to detect a pattern. I suspect that this alternative, while possible, is unlikely because I did not find a relation between the action execution response and theory of mind. The action execution response is robust and has been linked to infant social behavior (See Chapter 2). In some ways, it is surprising that the sensorimotor system response during action execution did not relate to preschool theory of mind. A large body of converging research suggests that in infancy, developments in infant motor skill are linked action encoding (Woodward et al, 2009). Thus, these findings raise new questions about the boundary conditions of the motor systems involvement in early social cognition.

New research also suggests that motor development is linked to the development of regions of the brain that support mature theory of mind processing (e.g., STS, TPJ; Lloyd-Fox et al, 2015). To illustrate, Lloyd-Fox and colleagues found that infants whose motor skills were more developed (as indexed by the Mullen Scales of Early Learning) showed stronger cortical activation[7] over the STS/TPJ region of the brain. It could be that while motor development is linked to developments in these regions of the brain, these neural developments do not yet have effects on behavior. Another possibility is that motor development shows this link to parts of the brain involved in social reasoning because advancements in motor development facilitate different types of interactions with their caregivers (e.g., Watson, Nixon, Wilson, Capage, 1999). These social interactions might be key to the development of mental state inference, more so than the maturity of the sensorimotor system. Indeed some research suggests that in early childhood the relationship between mu-ERD, motor skill, action processing, and theory of mind might not be direct (Bowman, Thorpe, Cannon & Fox, in press). Future research is needed to understand how motor development is linked to social reasoning.

Interestingly, I did not find that the neural response averaged across all action observation trials was linked to preschool theory of mind—indicating that the neural responses averaged across all action observation events and the neural response preceding goal response behavior might capture different variability. Indeed, it could be that the neural response when action

---

[7] In this study, cortical activation was measured via fNIRS hemodynamic response—particularly changes in oxygenated hemoglobin (HbO_2).

encoding is successful (i.e., AO-goal response) is a more robust index of *successful* action encoding than infants' action observation response generally. One reason for this finding could be that the action observation response across all trials is a more noisy measure. Indeed, I did not find that infants' neural response to all action observation events was correlated with imitation rate[8]. Nevertheless, this raises the question of what this neural response reflects in terms of infants' social capacities. Future work should investigate whether this pattern holds for other samples.

It is also important to keep in mind that the index of childhood theory of mind that I used was a parental report measure. While parental report measures are limited by parents knowledge of their child and might be subject to response bias (e.g., demand characteristics), these measures allowed us to rapidly assess social reasoning in children. These measures, in addition to being validated with in-lab testing, are highly reliable and show many of the relations that one would expect from laboratory-based theory of mind assessments. For instance, in the current study there are strong correlations to measures of general cognitive development (e.g., executive functioning and language) and strong correlations between the unique subscales of theory of mind. However, since all of these measures are parental report measures, the possibility of parental bias can't be eliminated.

To conclude, these results provide initial evidence that neural processing during action encoding is linked to the development of theory of mind. These findings demonstrate that those infants who recruit their visual processing regions less during action encoding show more advanced theory of mind abilities at age three. These results also showed that the magnitude of the sensorimotor system response was largely not linked to theory of mind—raising new

---

[8] This is different from the finding in Chapter 2 showing that there is a strong relation between the neural response during successful action encoding (AO-goal) and action imitation.

questions about the role that the sensorimotor system plays in the development of social reasoning in early childhood.

GENERAL DISCUSSION

Considerable research suggests that action experience shapes cognition across the lifespan (e.g., Kontra, Goldin-Meadow, Beilock, 2012; Woodward et al, 2009). However, to date, the mechanism that translates experiences into changes in perception is underspecified. Action experience involves both changes in motor representations and changes in fine-grained attention (e.g., adults: Flanagan & Johansson, 2003; infants: Rosander & von Hofsten, 2011). Nevertheless, to date, there is limited discussion of the role that the development of attention could play in early experience. In part, there is limited discussion because the behavioral literature consistently fails to show gross differences in visual attention as a function of action training (e.g., Cannon et al, 2011; Gerson & Woodward, 2012, 2014a). While there are not gross differences in visual attention as a function of experience, it is possible that there are more fine-grained shifts in visual attention. In fact, we know that both adults (Flanagan & Johansson, 2003) and infants (Rosander & von Hofsten, 2011) show similar patterns of visual attention during action execution and action observation—providing initial evidence that the attention system is shaped by motor experience.

In this dissertation, I propose that one method of investigating whether fine-grained differences in visual attention influence cognition is to use a more sensitive measure of visual attention processing—such as EEG. Across three studies, I assess the possibility that action processing (as indexed in the mu-ERD response) involves both relevant activity in the motor system and in regions associated with visual processing. Event-related changes in EEG power have been used extensively both to measure changes in visual attention and sensorimotor system processing (e.g., Klimesch, Doppelmayr, Russegger, Pachinger, Schwaiger, 1998; for review see: Pfurtscheller, 2003 Pineda, 2005). In adults, the relation between EEG power over occipital sites and visual attention is clear—greater alpha desynchronization over occipital cortex predicts voluntary shifts in visual attention (e.g., Sauseng et al, 2005; Thut Nietzel, Brandt, Pascual-Leone, 2006). Despite their being less evidence in infants, some research suggests that the infant occipital alpha rhythm responds comparably to the adult occipital alpha activity (e.g., Stroganova & Orekhova, 2007; Stroganova, Orekhova, Posikera, 1999; Marshall, Bar-Haim, Fox, 2002 for review). While both the sensorimotor mu-rhythm and the occipital alpha rhythm respond to sustained visual attention, there are a number of functional distinctions between the two. For instance, just as is in adults, infants' occipital alpha response is most prominent over posterior sites and when there is visual input (Stroganova & Orekhova, 2007), shows a posterior to anterior gradient (Gasser, Jennen-Steinmetz, Sroka, Verleger & Mocks, 1988). This evidence from infants suggests that the occipital alpha response is functionally distinct from the mu-ERD response.

Throughout this dissertation, I recruit the functional differences between these two systems to ask how action experience might shape the sensorimotor mu-ERD response relative to the occipital alpha response. In chapter 1, I compare various aspects of motor development to the sensorimotor mu-ERD response and the occipital alpha response to demonstrate functional specificity in the link between the sensorimotor mu-ERD response and motor development. Results indicated that the sensorimotor mu-ERD response was uniquely correlated with motor planning behavior and this relationship was particularly robust early in development (i.e., at 7-months). In a series of exploratory supplemental analyses, I uncovered that some aspects of motor behavior, particularly those aspects that involve efficiently coordinating the visual and manual modalities, may be best predicted by occipital mu-ERD. This provides converging evidence that occipital mu-ERD may play a role in aspects of skilled behavior that involved focused visual attention. Overall, these results evidence are consistent with the idea that action experience shapes a network of regions of the brain.

In chapter 2, I find that the infant sensorimotor mu-ERD response and occipital mu-ERD response are both selectively present during goal encoding. This provides some evidence that the occipital and sensorimotor systems may interact during goal encoding. However, I did not find a correlation between occipital mu-ERD and sensorimotor mu-ERD response—suggesting that those infants showing both a robust sensorimotor mu-ERD response and a robust occipital mu-ERD response during action encoding may not be the same infants. Nevertheless, we cannot rule out the possibility that visual attention may modulate the sensorimotor system response (Johansen-Berg, Matthews, 2002) in functionally interesting ways. It is, however, important to note that the sensorimotor mu-ERD response during action (a response that seems to be indicative of infants' own motor planning abilities—See Chapter 1) predicts the most unique variance in overall goal encoding abilities.

In chapter 3, I again use the sensorimotor mu-ERD response and the occipital mu-ERD response to distinguish between visual attention processing and sensorimotor system engagement. Here one open question in the behavioral literature is whether the system that supports action understanding (i.e., the sensorimotor system) or the system that supports rapid visual processing of events (i.e., the visual system), or both systems are selectively linked to the development of theory of mind. In this section I use EEG measures to distinguish between these systems by assessing neural processing during action encoding (and action execution) to see whether variability in one system uniquely predicts theory of mind development. These findings suggest that during action encoding, less recruitment of the visual attention system is linked to better preschool theory of mind. There were no significant differences in motor system activity as a function of theory of mind development at either the group or individual subject level. However, I did find that when infants engage in action, the strength of their sensorimotor mu-ERD response predicted one aspect of theory of mind, that is, perception understanding. This provides initial evidence that variability in the sensorimotor mu-ERD response might be most strongly tied to tasks involved in perception.

While further work is needed to fully understand the behavioral correlates of this this popular index of sensorimotor system activity, the work described in this dissertation, sheds light on the relation between the infant sensorimotor mu-ERD response and motor planning, action perception. Specifically, I show that the sensorimotor mu-ERD response is selectively linked to action encoding (as indexed by infants propensity to imitate others' goals) and to motor planning behavior. This work suggests that the infant sensorimotor mu-ERD response does not relate to theory of mind—but does provide initial evidence that the development of the attention system may relate to theory of mind development. This finding could suggest that there may be limits in the extent to which the action system could support abstract mental state reasoning. It also raises new questions about how this finding may fit in with previous research showing correlations between infant action understanding tasks and preschool theory of mind (e.g., Aschersleben, Hofer, Jovanovic, 2008; Colonnesi, Rieffe, Koops, Perucchini, 2010; Welch-Ross & Miller, 2000; Wellman et al, 2004; Wellman et al, 2008; Yamaguchi, Kuhlmeier, Wynn, VanMarle, 2009). Future research should continue to investigate longitudinal links between social behavior and mu-ERD response in the first year of life.

This work also raises new directions for future directions for research. For one, these findings suggest that considering the action system as a network might provide additional insight links between brain and behavior in infancy. A growing body of work has shown the infant mu-

ERD response differs as a function of experience (e.g., Cannon et al, 2015; de Klerk et al, 2015; Saby et al, 2012; Upshaw, Bernier, Sommerville, 2015; van Elk et al, 2008) and differs as a function of task (e.g., Southgate et al, 2009, 2010, Southgate & Begus, 2013; Warreyn et al, 2013) However, the majority of this work reports the mu-ERD response exclusively over sensorimotor regions. In this dissertation, I report mu-ERD across all scalp sites to provide detailed analysis of how selective the mu-ERD response is in infancy. To illustrate, in chapter 1, I show that while unimanual reaching shows robust links to central mu-ERD, there are relations between motor behavior and the mu-ERD response at other scalp sites. For instance, at 7 months hand pre-shaping is correlated with frontal mu-ERD and the occipital mu-ERD response links strongly with speed and rate of trajectory changes—two aspects of motor behavior that involve efficient coordination of the visual and manual modalities. In chapter 2, I also suggest that one interpretation of these results could involve the functional integration of the sensorimotor and visual attention systems. Overall, this work is consistent with the claim that the neural system that supports action functions as a network. Future research should implement analytic methods (e.g., coherence or neural network analyses) to further investigate network dynamics in infant EEG activity.

The findings reported in this dissertation also raise questions about whether my findings (reported exclusively from the mu/alpha band) would generalize to the beta band (15-25 Hz in adults). In studies with adults, power in the beta band has also been implicated as an index of motor cortex activity. This work suggests that beta activity and alpha/mu activity may emerge from unique sources in the brain and index activation of distinct cortical networks (e.g., Hari, 2006; Hari, 2002; Hari et al, 1998). For example, research investigating the role of the beta-desynchronization suggests that, in adults, beta activity reflects evaluation processes (e.g., uncertainty or correctness) involved in motor planning (e.g., Kowlewijn et al, 2008; Tzagarakis, Ince, Leuthold, Pellizzer, 2010) and maps onto kinematic properties of reaching actions (e.g., Meirovitch et al, 2015). In infants, the role of the beta band remains unclear, while some researchers report differences in beta power as a function of experience (e.g., van Elk et al, 2008) and task type (e.g., Meyer et al, 2011), there are still many open questions about the functional relation between beta activity and behavior. Indeed, some research suggests that there is little power in the beta band in infancy (Thorpe et al, 2015). Nevertheless, it remains an open question in the literature whether there are similar parallels between infant beta-desynchronization, motor behavior, and cognition. Future research should examine the behavioral correlates of the beta activity.

Taken together, the research described in this dissertation suggests that there are clear links between action, mu-ERD and perception and provides evidence that integrating behavioral and neural measures can provide enormous insight into the functional significance of the mu-ERD response. This work converges with a body of work (e.g., Cannon et al, 2015; de Klerk et al, 2015; Saby et al, 2012; Upshaw, Bernier, Sommerville, 2015; van Elk et al, 2008) that suggests that the mu-ERD response recorded over sensorimotor regions reflects developments in infants' motor skills. This work also provides initial evidence that the neural system that supports infant motor development is also recruited during action perception.

REFERENCES

Adolph, K.E., Avolio, A.M. (2000). Walking infants adapt locomotion to changing body dimensions. *Journal of Experimental Psychology: Human Perception and Performance.* 26(3), 1148-1166.

Adolph, K. E., Cole, W. G., Komati, M., Garciaguirre, J. S., Badaly, D., Lingeman, J. M., Chan, G. L. Y. , & Sotsky, R. B. (2012). How do you learn to walk? Thousands of steps and dozens of falls per day. *Psychological Science*, 23, 1387-1394

Adolph, K. E., Cole, W. G., & Vereijken, B. (2015). Intra-individual variability in the development of motor skills in childhood. In M. Diehl, K. Hooker, & M. Sliwinski (Eds.), *Handbook of Intra-individual Variability Across the Lifespan*. New York: Routledge/Taylor & Francis Group, pp. 59-83.

Adolph, K.E., Robinson, S.R. (2015). Motor development. In Handbook of Child Psychology and Developmental Science. 2:4:1–45.

Ambrosini, E., Reddy, V., de Looper, A., Costantini, M., Lopez, B., Sinigaglia, C. (2013). Looking Ahead: Anticipatory gaze and motor ability in infancy. PLOS ONE, **8** e67916. (doi: 10.1371/journal.pone.0067916)

Arnstein, D., Cui, F., Maurits, N. M., & Gazzola, V. (2011). m-suppression during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal and SI cortices. *Journal of Neuroscience, 31*, 14243–14249. doi:10.1523/JNEUROSCI.0963-11.2011

Aschersleben, G., Hofer, T., Jovanovic, B. (2008). The link between infant attention to goal-directed action and later theory of mind abilities. *Developmental Science, 11*(6), 862-868. (doi: 10.1111/j.1467-7687.2008.00736.x)

Astington, J. W., & Jenkins, J. M. (1999). A longitudinal study of the relation between language and theory-of-mind development. Developmental Psychology, 35, 1311–1320. (doi: 10.1037/0012-1649.35.5.1311)

Baillargeon, R., Scott, R.M., He, Z. (2010). False-belief understanding in infants. *Trends in Cognitive Science.* 14(3), 110-118. (doi: 10.1016/j.tics.2009.12.006)

Babiloni, C., Carducci, F., Cincotti, F., Rosini, P.M., Neuper, C., Pfurtscheller, G., et al. (1999). Human movement-related potentials vs desynchronization of EEG alpha rhythm: A high-resolution EEG study. *NeuroImage,* 17, 559-72.

Barral, J., De Pretto, M., Debû, B., & Hauert C.A. (2010). Activation and inhibition of bimanual movements in school-aged children. *Fiziologiia Cheloveka*, 36 (1) (2010), pp. 56–66

Beilock, S., T. Carr, MacMahon, C., Starkes, J. (2002). When paying attention becomes counterproductive: Impact of divided versus skill-focused attention on novice and experienced performance of sensorimotor skills. Journal of Experimental Psychology: Applied, 8(1), 6-16. (doi: 10.1037//1076-898X.8.1.6)

Beilock, S. L., & Goldin-Meadow, S. (2010). Gesture changes thought by grounding it in action.*Psychological Science, 21,* 1605-1611.(doi: 10.1177/0956797610385353)

Beilock, S. Gray, R. (2012). From attentional control to attentional spillover: A skill-level investigation of attention, movement and performance outcomes. Human Movement Science, 31, 1473-1499. (doi:10.1016/j.humov.2012.02.014)

Beilock, S. L., Lyons, I. M., Mattarella-Micke, A., Nusbaum, H. C., & Small, S. L. (2008). Sports experience changes the neural processing of action language. *Proceedings of the National Academy of Sciences*, *USA*, *105*, 13269–13273. (doi: 10.1073/pnas.0803424105).

Bornstein, M.H. Tamis-LeMonda, C.S. (1994). Antecedents of information-processing skills in infants: Habituation, novelty responsiveness, and cross-modal transfer. *Infant behavior and development,* 17, 371-380.

Biringen, Z., Emde, R.N., Campos, J.J., Appelbaum, M.I. (1995). Affective reorganization in the infant, the mother, and the dyad: The role of upright locomotion and its timing. *Child Development, 66*(2), 499-514. (doi: http://doi.org/10.2307/1131593)

Behmer, Jr., L.R., Jantzen, K.J. (2011). Reading sheet music facilitates sensorimotor mu-desynchronization in musicians. Clinical Nuerophysiology, 122,(7) 1342-7. (doi: 10.1016/j.clinph.2010.12.035.)

Benson, J.E., Sabbagh, M.A., Carlson, S.M., Zelazo, P.D. (2013). Individual differences in executive functioning predict preschoolers' improvement from theory of mind training. *Developmental Psychology, 49*(9),1615-1627. (doi: 10.1037/a0031056)

Bowman, L.C., Thorpe, S.G., Cannon, E.N., Fox, N.A. (in press). Action mechanisms for social cognition: Behavioral and neural correlates of developing Theory of Mind. *Developmental Science.*

Brune, C.W., Woodward, A.L. (2007). Social cognition and social responsiveness in 10-month-old infants. *Journal of Cognition and Development, 8*(2), 133-158. (doi: 10.1080/15248370701202331)

Calvo-Merino, B., Glaser, D.E., Grezes, J., Passingham, R.E., Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex, 15*, 1243-1249. (doi: :10.1093/cercor/bhi007)

Calvo-Merino, B., Grezes, J., Glaser, D.E., Passingham, R.E., Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology, 16,* 1905-1910. (doi: 10.1016/j.cub.2006.07.065).

Campos, J.J., Anderson, D.I., Barbu-Roth, M.A., Hubbard, E.M., Hertenstein, M.J., Witherington, D. (2000). Travel broadens the mind. *Infancy, 1*(2), 149-219. (doi: 10.1207/S15327078IN0102_1)

Cannon, E. N., Simpson, E. A., Fox, N. A., Vanderwert, R. E., Woodward, A. L., & Ferrari, P. F. (2015). Relations between infants' emerging reach-grasp competence and event-related desynchronization in EEG. *Developmental Science,19*, 50–62.

Cannon, E. N., Yoo, K. H., Vanderwert, R. E., Ferrari, P. F., Woodward, A. L., & Fox, N. A. (2014). Action experience, more than observation, influences mu rhythm desynchronization. *PLoS ONE, 9*(3), Article e92002. doi:10.1371/journal.pone.0092002

Cannon, E.N., Woodward, A.L. (2012). Infants generate goal-based action predictions. *Developmental Science, 15*(2), 292-298. (doi: 10.1111/j.1467-7687.2011.01127.x)

Cannon, E.N., Woodward, A.L., Gredeback, G., von Hofsten, C., Turek, C. (2011). Action production influences 12-month-old infants' attention to others' actions. *Developmental Science, 15*(1), 35-42. (doi: 10.1111/j.1467-7687.2011.01095.x)

Carlson, S.M., Moses, L.J. (2001). Individual differences in inhibitory control and children's theory of mind. *Child development, 72*(4), 1032-1053. (doi: 10.1111/1467-8624.00333)

Carlson, S.M., Moses, L.J. & Brenton, C. (2002). How specific is the relation between executive function and theory of mind? Contributions of inhibitory control and working memory. Infant and Child Development, 11(2), 73-92. (doi:10.1002/icd.298)

Carlson, S.M., Moses, L.J., Claxton L.J. (2004). Individual differences in executive functioning and theory of mind: An investigation of inhibitory control and planning ability. *Journal of Experimental Child Psychology, 87,* 299-319. (doi: 10.1016/j.jecp.2004.01.002)

Casasanto, D. (2011). Different bodies, different minds The body-specificity of language and thought. *Current Directions in Psychological Science,* 20(6), 378-383. Doi: 10.1177/0963721411422058

Casasanto, D., & Chrysikou, E.G. (2011). When left is "right": Motor fluency shapes abstract concepts. *Psychological Science, 22*(4), 419-422. (doi: 10.1177/0956797611401755)

Casasanto, D., & Dijkstra, K. (2010). Motor action and emotional memory. *Cognition, 115*(1), 179-185. (doi: 10.1016/j.cognition.2009.11.002)

Charman, T., Baron-Cohen, S., Swettenham, J., Baird, G., Cox, A., Drew, A. (2000). Testing joint attention, imitation and play as infancy precursors to language and theory of mind. *Cognitive development, 15*(4), 481-498. (doi: 10.1016/S0885-2014(01)00037-5)

Claxton, L. J., Keen, R., and McCarty, M. E. (2003). Evidence of motor planning in infant reaching behavior. *Psychol. Sci.* 14, 354–356. doi: 10.1111/1467-9280.244

Clearfield, M.W. (2004). The role of crawling and walking experience in infant spatial memory. *Journal of Experimental Child Psychology, 89,* 214-241. (doi: 10.1016/j.jecp.2004.07.003)

Clearfield, M.W., Osborne, C.N., Mullen, M. (2008). Learning by looking: Infants' social looking behavior across the transition from crawling to walking. *Journal of Experimental Child Psychology, 100*(4), 297-307. (doi: 10.1016/j.jecp.2008.03.005)

Colonnesi, C., Rieffe, C., Koops, W., Perucchini, P. (2010). Precursors of a theory of mind: A longitudinal study. *British Journal of Developmental Psychology, 26*(4), 561-577. doi: 10.1348/026151008X285660

Csibra, G. (2008). Action mirroring and action understanding: An alternative account, in *Sensorimotor Foundations of Higher Cognition. Attention and Performance* (Oxford University Press), *vol. 22*, pp. 435-459.

Cook G., Bird., Catmur, C., Press, C., Heyes, C. (2014). Mirror neurons: From origin to function. *Behavioral and Brain Sciences,* **37**, 177-241. (doi: 10.1017/S0140525X13000903)

Csibra, G. (2008). Action mirroring and action understanding: An alternative account. In P. Haggard, Y. Rossetti, & M. Kawato (Eds.), *Attention and performance XXII: Sensorimotor foundations of higher cognition* (pp. 435–459). Oxford, England: Oxford University Press.

Cuevas, K., Cannon, E. N., Yoo, K., & Fox, N. A. (2014). The infant EEG mu rhythm: Methodological considerations and best practices. *Developmental Review, 34*, 26–43. doi:10.1016/j.dr.2013.12.001

de Klerk, C. C. J. M., Johnson, M. H., Heyes, C. M., & Southgate, V. (2014). Baby steps: Investigating the development of perceptual–motor couplings in infancy. *Developmental Science, 18*, 270–280. doi:10.1111/desc.12226

de Klerk, C.C.J.M. Johnson, M.H., Southgate, V. (2015). An EEG study on the somatotopic organization of sensorimotor cortex activation during action execution and observation in infancy. *Developmental Cognitive Neuroscience, 15,* 1-10. (doi: 10.1016/j.dcn.2015.08.004) de Lange, F. P., Spronk, M., Willems, R. M., Toni, I., & Bekkering, H. (2008). Complementary systems for understanding action intentions. *Current Biology, 18*, 454–457. doi:10.1016/j.cub.2008.02.057

Desmurget, M., Reilly, K.T., Richard, N., Szathmari, A., Mottolese, C., Sirigu, A. (2009). Movement intention after parietal cortex stimulation in humans. *Science,* 324, 811. doi: 10.1126/science.1169896

Evarts, E.V. (1968). Relation of pyramidal tract activity to force exerted during voluntary movement. *Journal of neurophysiology,*

Ferrari, P., Tramacere, A., Simpson, E. A., & Iriki, A. (2013). Mirror neurons through the lens of epigenetics. *Trends in Cognitive Sciences, 17*, 450–457. doi:10.1016/j.tics.2013.07.003

Fetters, L., & Todd, J. (1987). Quantitative assessment of infant reaching movements. *Journal of Motor behavior,* 19, 147-166.

Filippi, C., Cannon, E. N., Fox, N. Thorpe, S., Ferrari, P.F., Woodward, A. (2016). Motor system activation predicts goal imitation in 7-month-old infants.

Filippi, C., & Woodward, A.L. (2016). Action experience changes attention to kinematic cues. *Frontiers in Developmental Psychology.*

Fitts, P.M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, *47*, 381-391.

Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Letters to Nature, 630*, 1–3. doi:10.1038/nature01861

Fox, N.A., Bakermans-Kranenburg, M.J., Yoo, K.H., Bowman, L.C., Cannon, E.N., Vanderwert, R.E., Ferrari, P.F., & van Ijzendoorn, M.H. (2015). Assessing human mirror activity with EEG mu rhythm: A meta-analysis. *Psychological Bulletin,* (doi:10.1037/bul0000031)

Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G. (1996). Action recognition in premotor cortex. *Brain.* **119**, 593-609. (doi: http://dx.doi.org/10.1093/brain/119.2.593*)*

Gampe, A., Prinz, W., Daum, M. (2015). Measuring action understanding: Relations between goal prediction and imitation. *British Journal of Developmental Psychology.* :10.1111/bjdp.12125

Georgopoulos, A.P., Kalaska, J.F., Caminiti, R., Massey, J.T. (1982). On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *Journal of Neuroscience, 2*(11), 1527-37.

Gerson, S.A., Woodward, A. (2012). A claw is like my hand: Comparison supports goal analysis in infants. *Cognition*, **122**, 181-192. (doi: 10.1016/j.cognition.2011.10.014)

Gerson, S., & Woodward, A. (2013). The goal trumps the means: Highlighting goals is more beneficial than highlighting means in means-end training. *Infancy*, 18(2), 289-302. doi: 10.111/j.1532-7078.2012.00112.x

Gerson, S.A., Woodward, A.L. (2014a). The joint role of trained, untrained, and observed actions at the origins of goal recognition. *Infant Behavior & Development, 37*, 94-104. (doi: 10.1016/j.infbeh.2013.12.013)

Gerson, S.A., Woodward, A.L. (2014b). Labels facilitate infants' comparison of action goals. *Journal of Cognition and Development, 15*(2), 197-212. (doi:10.1080/15248372.2013.777842).

Gonzalez, S.L., Reeb-Sutherland, B.C., Nelson, E.L. (2016). Quantifying motor experience in the infant brain: EEG Power, Coherence, and mu desynchronization. *Frontiers in Psychology.* doi: http://dx.doi.org/10.3389/fpsyg.2016.00216

Grafton, S. T., Hazeltine, E., and Ivry, R. B. (2002). Motor sequence learning with the nondominant left hand. A PET functional imaging study. Exp. Brain Res. 146, 369–378. (doi: 10.1007/s00221-002-1181-y)

Gweon, H., Saxe, R. (2013). Developmental cognitive neuroscience of Theory of Mind. *Neural Circuit Development and Function in the Brain: Comprehensive Developmental Neuroscience. Elsevier.* Ed: J. Rubenstein & P. Rakic

Hamilton, A., Grafton, S.T. (2006). Goal representation in human anterior intraparietal sulcus. *Journal of Neuroscience,* **26,** 1133-1137. (doi: 10.1523/JNEUROSCI.4551-05.2006)

Hamlin, K., Hallinan, E., Woodward, A. (2008). Do as I do: 7-month-old infants selectively reproduce others' goals. *Developmental Science*. **11**, 487-494. (doi: 10.1111/j.1467-7687.2008.00694.x)

Hamlin, K., Wynn, K. (2011). Infants prefer prosocial to antisocial others. *Cognitive Development* 26(1), 30-39. (doi: 10.1016/j.cogdev.2010.09.001)

Hari, R. (2002). Brain rhythms and reactivity of the human motor cortex. *International Congress Series,* 1226, 87-95. (doi: 10.1016/S0531-5131(01)00499-X)

Hari, R. (2006). Action-perception connection and the cortical mu rhythm. *Progress in Brain Research,* 159, 253-260. (doi: 10.1016/S0079-6123(06)59017-X)

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: A neuromagnetic study. *PNAS,* 95, 15061-5.

He, M., Walle, E.A., Campos, J.J. (2015). A cross-national investigation of the relationship between walking and language development. *Infancy, 20*(3), 283-305. (doi: 10.1111/infa.12071)

Hickok, G. (2014). *The myth of mirror neurons: The real neuroscience of communication and cognition*. New York, NY: W.W. Norton & Company, Inc.

Howard, L., Riggins, T., & Woodward, A. (under review). Priming action improves children's memory for sequences.

Hummel, F., Kirsammer, R., Gerloff, C. (2003). Ipsilateral cortical activation during finger sequences of increasing complexity: representation of movement difficulty or memory load? *Clinical Neurophysiology,114*, 605-613. (doi: 10.1016/S1388-2457(02)00417-0)

Hunnius, S. & Bekkering, H. (2014). What are you doing? How active and observational experience shape infants' action understanding. *Philosophical transaction of the royal Society B.* 369:20130490. (doi: 10.1098/rstb.2013.0490.)

Hyvärinen, A. (1999). Fast and robust fixed-point algorithms for independent component analysis. *IEEE Trans. Neural Networks.* **10**, 626–34. (doi: 10.1109/72.761722)

Iverson, J.M. (2010). Developing language in a developing body: the relationship between motor development and language development. *Journal of Child Language, 37*(2), 229-261. (doi: 10.1017/S0305000909990432)

Johansen-Berg, H., Matthews, P.M. (2002). Attention to movement modulates activity in sensori-motor areas including primary motor cortex. *Experimental Brain Research,* 142: 13-24. (doi: 10.1007/s00221-001-0905-8)

Jones, S.R., Kerr, C.E., Wan, Q., Pritchett, D.L., Hamalainen, M., Moore, C.I. (2010). Cued spatial attention drives functionally relevant modulation of the mu rhythm in primary somatosensory cortex. *Journal of Neuroscience, 30*(41), 13760-13765. (doi: 10.1523/JNEUROSCI.2969-10.2010).

Kanakogi, Y., Itakura, S. (2011). Developmental correspondence between action prediction and motor ability in early infancy. *Nature communications, 2,* 341. (doi: 10.1038/ncomms1342)

Karasik, L. B., Tamis-LeMonda, C. S., & Adolph, K. E. (2014). Crawling and walking infants elicit different verbal responses from mothers. *Developmental Science,* 17, 388-395. doi: 10.1111/desc.12129

Karasik, L.B., Tamis-LeMonda, C.S., Adolph, K.E. (2011). Transition from crawling to walking and infants' actions with objects and people. *Child Development, 82*(4), 1199-1209. (doi: 10.1111/j.1467-8624.2011.01595.x)

Kilner, J.M., Friston, K.J., Frith, C.D. (2007). Predictive coding: an account of the mirror neuron system. *Cognitive Processing, 8*(3), 159-166. (doi: 10.1007/s10339-007-0170-2)

Kilner, J.M., Marchant, J.L., Frith, C.D. (2009). Relationship between activity in human primary motor cortex during action observation and the mirror neuron system. *PLoS One,* 4(3), doi:10.1371/journal.pone.0004925

Kilner, J.M., Vargas, C., Duval, S., Blakemore, S.J. (2004). Motor activation prior to observation of a predicted movement. *Nature Neuroscience,* 7, 1299-1301. doi: 10.1038/nn1355

Kim, Y.K., Shin, S.H. (2014). Comparison of effects of transcranial magnetic stimulation on primary motor cortex and supplementary motor areas on motor learning (randomized, cross over study). *Frontiers in Human Neuroscience,* doi: http://dx.doi.org/10.3389/fnhum.2014.00937)

Klimesch, W., Doppelmayr, M., Russegger, H., Pachinger, T., Schwaiger, J. (1998). Induced alpha band power changes in the human EEG and attention. *Neuroscience Letters,* 224, 73-76. doi: 10.1016/S0304-3940(98)00122-0

Koelewijn, T., van Schie, H.T., Bekkering, H., Oostenveld, R., Jensen, O. (2008). Motor-cortical beta oscillations are modulated by correctness of observed action. *NeuroImage,* 40, 767-775. (doi: 10.1016/j.neuroimage.2007.12.018).

Kontra, C., Goldin-Meadow, S., Beilock, S.L. (2012). Embodied learning across the life span. *Topics in cognitive science,* 1-9. doi: 10.1111/j.1756-8765.2012.01221.x

Kontra, C., Lyons, D.J., Fischer, S.M., Beilock, S.L. (2015). Physical experience enhances science learning. *Psychological Science,* (doi: 10.1177/0956797615569355)

Kovacs, A.M., Teglas, E., Endress, A.D. (2010). The social sense: susceptibility to others' beliefs in human infants and adults. *Science,330* (6012), 1830-1834. (doi: 10.1126/science.1190792)

Kretch, K.S., Franchak, J.M., Adolph, K.E. (2014). Crawling and walking infants see the world differently. *Child Development*, 85 (4), 1503-1518. (doi: 10.1111/cdev.12206).

Krogh-Jespersen, S., & Woodward, A.L. (2014). Making smart social judgments takes time: Infants' recruitment of goal information when generating action predictions. *PLoSONE 9*(5): e98085. doi:10.1371/journal.pone. 009085

Krogh-Jespersen, S. & Woodward, A. L. (in preparation). *What happens next: Action experience influences 8-month-old infants' on-line action predictions*.

LeBarton, E.S., Iverson, J.M. (2013). Fine motor skill predicts expressive language in infant siblings of children with autism. *Developmental Science, 16*(6), 815-27. (doi: 10.1111/desc.12069)

Libertus, K., Needham, A. (2011). Reaching experience increases face preference in 3-month-old infants. *Developmental Science, 14*(6), 1355-1364. (doi: 1 0.1111/j.1467-7687.2011.01084.x)

Libertus, K., Joh, A.S., Needham, A. (in press). Motor training at three months affects object exploration 12 months later. *Developmental Science,* (doi: 10.1111/desc.12370)

Libertus, K., Needham, A. (2010). Teach to reach: the effects of active vs. passive reaching experiences on action and perception. *Vision Research, 50*(24), 2750-7. (doi: 10.1016/j.visres.2010.09.001)

Libertus, K., Needham, A. (2011). Reaching experience increases face preference in 3-month-old infants. *Developmental Science,* 14(6) 1355-1364. (doi: 10.1111/j.1467-7687.2011.01084.x)

Libertus, M.E., Odic, D., Feigenson, L, Halberda, J. (2015). A Developmental Vocabulary Assessment for Parents (DVAP): Validating Parental Report of Vocabulary Size in 2- to 7- Year-Old Children. *Journal of Cognition and Development.* (doi: 10.1080/15248372.2013.835312)

Liuzzi, G., Horniss, V., Zimerman, M., Gerloff, C., Hummel, F.C. (2011). Coordination of uncoupled bimanual movements by strictly timed interhemispher connectivity. *Journal of Neuroscience,* 31 (25), 9111-9117. doi:

Lloyd-Fox, S., Blasi, A., Volein, A., Everdell, N., Elwell, C.E., Johnson, M.H. (2009). Social perception in infancy: A near infrared spectroscopy study. *Child Development,* 80(4), 986-999. doi:1 0.1111/j.1467-8624.2009.01312.x

Lloyd-Fox, S., Wu, R. Richards, J.E., Elwell, C.E., Johnson, M.H. (2015). Cortical activation to action perception is associated with action production abilities in young infants. *Cerebral Cortex, 25*, 289-297. (doi:10.1093/cercor/bht207)

Lockman, J. J., Ashmead, D. H., and Bushnell, E. W. (1984). The development of anticipatory hand orientation during infancy. *J. Exp. Child Psychol.* 37, 176–186. doi: 10.1016/0022-0965(84)90065-1

Lou, Y., Baillargeon, R. (2010). Toward a mentalistic account of early psychological reasoning. *Current directions in psychological science.* 19(5), 301-307. (doi: 10.1177/0963721410386679)

Loucks, J., Sommerville, J.A. (2012). Developmental changes in the discrimination of dynamic human actions in infancy. *Developmental Science, 15*(1), 123-130. (doi: 10.1111/j.1467-7687.2011.01099.x)

Mahajan, N., & Woodward, A. L. (2009). Seven-month-old infants selectively reproduce the goals of animate but not inanimate agents. *Infancy, 14*, 667–679. doi:10.1080/15250000903265184

Manganotti, P., Gerloff, C., Toro, C., Katsuta, H., Sadato, N., Zhuang, P., Leocani, L., Hallett, M. (1998). Task-related coherence and task-related spectral power changes during sequential finger movements. *Electroencephalography Clinical Neurophysiology, 109*(1), 50-62. (doi: 10.1016/S0924-980X(97)00074-X)

Mangold P. (2010). *INTERACT Quick Start Manual V2.4.* Arnstorf: Mangold International GmbH. Available at: http://www.mangold-international.com/footermenu/references/citation-references.html

Manshanden, I., De Munck, J.C., Simon, N.R., Lopes da Silva, F.H. (2002). Source localization of MEG sleep spindles and the relation to sources of alpha band rhythms. *Clincial Neurophysiology, 113*(12), 1937-1947. (doi: 10.1016/S1388-2457(02)00304-8)

Marshall, P.J., Bar-Haim, Y., Fox, N.A. (2002). Development of the EEG from 5 months to 4 years of age. *Clinical Neurophysiology, 113*(8), 1199-208. (doi: 10.1016/S1388-2457(02)00163-3)

Marshall, P. J., Bouquet, C. A., Shipley, T. F., & Young, T. (2009). Effects of brief imitative experience on EEG desynchronization during action observation. *Neuropsychologia, 47*, 2100–2106. doi:10.1016/j.neuropsychologia.2009.03.022

Marshall, P. J., & Meltzoff, A. N. (2011). Motor system activation systems: Exploring the EEG mu rhythm in human infancy. *Developmental Cognitive Neuroscience, 1*, 110–123. doi:10.1016/j.dcn.2010.09.001

Marshall, P. J., Saby, J. N., & Meltzoff, A. N. (2013). Infant brain responses to object weight: Exploring goal-directed actions and self-experience. *Infancy, 18*, 942–960. doi:10.1111/infa.12012

Marshall, P. Young, T., Meltzoff, A.N. (2011). Neural correlates of action observation and execution in 14-month-old infants: an event-related EEG desynchronization study. *Developmental science*, 14(3), 474-480. (doi: 10.1111/j.1467-7687.2010.00991.x)

McCall, R.B., Carriger, M.S. (1993). A meta-analysis of infant habituation and recognition memory performance as predictors of later IQ. *Child Development, 641)*, 57-79. doi: 10.2307/1131437

McDonnell, P.M. (1975). The development of visually guided reaching. *Perception & Psychophysics,* 18 (3), 181-185. doi: 10.3758/BF03205963.

Meltzoff , A. N. (1995). Understanding the intentions of others: Re-enactment of intentional acts by 18-month-old children. *Developmental Psychology, 31*, 838–850. doi:10.1037/0012-1649.31.5.838

Meyer, M., Hunnius, S., van Elk, M., van Ede, F., Bekkering, H. (2011). Joint action modulates motor system involvement during action observation in 3-year-olds. *Experimental Brain Research,* 211(3), 581-592. (doi: 10.1007/s00221-011-2658-3)

Michael, J., Sandberg, K., Skewes, J., Wolf, T., Blicher, J., Overgaard, M., & Frith, C. D. (2014). Continuous theta-burst stimulation demonstrates a causal role of premotor homunculus in action understanding. *Psychological Science, 25*, 963–972. doi:10.1177/0956797613520608

Meirovitch, Y., Harris, H., Dayan, E., Arieli, A., Flash, T. (2015). Alpha and Beta band event-related desynchronization reflect kinematic regularities. *Journal of Neuroscience,* 35(4), 1627-1637. (doi: 10.1523/JNEUROSCI.5371-13.2015)

Meltzoff, A.N. (1995). Understanding the intentions of others: Re-enactment of intentional acts by 18-month-old children. *Developmental Psychology.* **31**, 838-850. (doi: http://dx.doi.org/10.1037/0012-1649.31.5.838)

Michael, J., Sandberg, K., Skewes, J., Wolf, T., Blicher, J., Overgaard, M., Frith, C.D. (2014). Continuous theta-burst stimulation demonstrates a causal role of premotor homunculus in action understanding. *Psychological Science.* (doi: 10.1177/0956797613520608)

Milligan, K., Astington, J.W., Dack, L.A. (2007). Language and theory of mind: Met_Analysis of the relation between language ability and false-belief understanding. *Child Development, 78*(2), 622-646. (doi: 10.1111/j.1467-8624.2007.01018.x)

Moran, D.W., Schwartz, A.B. (1999). Motor cortical activity during drawing movements: population representation during spiral tracing. *Journal of Neurophysiology, 82*(5), 2693-704.

Morrongiello, B., and Rocca, P. (1989). Visual feedback and anticipatory hand orientation during infants' reaching. *Percep. Mot. Skills* 69, 787–802. doi: 10.2466/pms.1989.69.3.787

Müller, U., Zelazo, P. D., & Imrisek, S. (2005). Executive function and children's understanding of false belief: How specific is the relation? Cognitive Development, 20(2), 173-189. (doi:10.1016/j.cogdev.2004.12.004)

Neuper, C., Wortz, M., Pfurtscheller, G. (2006). ERD/ERS patterns reflecting sensorimotor activation and deactivation. *Progress in Brain research, 159,* 211-222. (doi: 10.1016/S0079-6123(06)59014-4)

Novack, M., Congdon, E., Hemani, N. & Goldin-Meadow, S. (2014). From action to abstraction: Using the hands to learn math. *Psychological Science, 25*(4)*,* 903-910. (doi: 10.1177/0956797613518351).

Onishi KH, & Baillargeon R. (2005). Do 15-month-old infants understand false beliefs? *Science,* 308:255–258.(doi: 10.1126/science.1107621)

Paulus, M., Hunnius, S., van Elk, M., Bekkering, H. (2012). How learning to shake a rattle affects 8-month-old infants' perception of the rattle's sound: electrophysiological evidence for action-effect binding in infancy. *Developmental Cognitive Neuroscience, 2*(1), 90-96. (doi: 10.1016/j.dcn.2011.05.006)

Paz, R., Boraud, T., Natan, C., Bergman, Vaadia, E. (2003). Preparatory activity in motor cortex reflects learning of local visomotor skills. *Nature Neuroscience,* 6, 882-890. doi:10.1038/nn1097

Perner, J., Lang, B. (1999). The development of theory of mind and executive control. Trends in Cognitive Science, 3(9), 337-344. (doi: 10.1016/S1364-6613(99)01362-5)

Perner, J., Ruffman, T. (2005). Infants' insight into the mind: How deep? *Science,* 308(5719), 214-216. (doi: 10.1126/science.1111656)

Peterson, C.C., Siegal, M. (1999). Representing inner worlds: Theory of mind in autistic, deaf and normal hearing children. *Psychological Science, 10*(2), 126-129. (doi: 10.1111/1467-9280.00119)

Peterson, C.C., Wellman, H.M., Liu, D. (2005). Steps in theory-of-mind development for children with deafness or autism. *Child development, 76*(2), 502-517. (doi: 10.1111/j.1467-8624.2005.00859.x)

Pfurtscheller, G. (2003). Induced oscillations in the alpha band: Functional meaning. *Epilepsia,* **44**, 2-8. (doi: 10.1111/j.0013-9580.2003.12001.x)

Pfurscheller, G. Aranibar, A. (1979). Evaluation of event-related desynchronization (ERD) preceding and following voluntary self-paced movement. *Electroencephalography Clinical Neurophysiology.* **46,** 138-146. (doi: 10.1016/0013-4694(79)90063-4)

Piaget, J. & Inhlder, B. (1962). *The psychology of the child.* New York: Basic Books.

Pineda, J.A. (2005). The functional significance of mu rhythms: Translating "seeing" and "hearing" into "doing." *Brain Research Reviews,* 50, 57-68.

Pollok, B., Latz, D., Krause. V., Butz, M., Schnitzler, A. (2014). Changes of motor-cortical oscillations associated with motor learning. *Neuroscience,* 275, 47-53. (doi: doi:10.1016/j.neuroscience.2014.06.008)

Prinz, W. (2006). What re-enactment earns us. *Cortex,* 42(4), 515-517.. doi: 10.1016/S0010-9452(08)70389-7

Quandt, L.C., Marshall, P.J. (2014). The effect of action experience on sensorimotor EEG rhythms during action observation. *Neuropsychologia,* 56, 401-408, doi: 10.1016/j.neuropsychologia.2014.02.015.

Quandt, L.C., Marshall, P.J., Bouquet, C.A., Young T., & Shipley, T.F. (2011). Experience with novel actions modulates frontal alpha EEG desynchronization. *Neuroscience letters,* 499, 37-41.

Quandt, L.C., Marshall, P.J., Shipley, T.F., Beilock. S.L., Goldin-Meadow, S. (2012). Sensitivity of alpha and beta oscillations to sensorimotor characteristics of action: An EEG study of action production and gesture observation. *Neuropsychologia,* 50, 2745-2751. doi: 10.1016/j.neuropsychologia.2012.08.005.

Rachwani, J., Santamaria, V., Saavedra, S.L., Woollacott, M.H. (2015). The development of trunk control and its relation to reaching in infancy: a longitudinal study. *Frontiers in human neuroscience,* 9(94). doi: 10.3389/fnhum.2015.00094

Reid, V.M., Striano, T., Iacoboni, M. (2011). Neural correlates of dyadic interaction during infancy. *Developmental Cognitive Neuroscience, 1,* 124-130. (doi: 10.1016/j.dcn.2011.01.001)

Rioult-Pedotti, M-S. Friedman, D. Hess, G., Donoghue, J.P. (1998). Strengthening of horizontal cortical connections following skill learning. *Nature Neuroscience, 1* 230-234. (doi:10.1038/678)

Robinson, F.R. (1995). Role of the cerebellum in movement control and adaptation. *Current Opinion in Neurobiology,* 5(6), 755-762.

Roland, P.E., Larsen, B., Lassen, N.A., Skinhoj. (1980). Supplementary motor area and other cortical areas in organizing voluntary movements in man. *Journal of Neurophysiology,* 43(1), 118-136.

Rosander, K., von Hofsten, C. (2011). Predictive gaze shifts elicited during observed and performed actions in 10-month-old infants and adults. *Neuropsychologia*, **49**, 2911-2917. (doi: 10.1016/j.neuropsychologia.2011.06.018)

Rose, D.H., Slater, A., Perry, H. (1986). Prediction of childhood intelligence from habituation in early infancy. *Intelligence,* 10(3), 251-263. doi: 10.1016/0160-2896(86)90019-X

Rotem-Kohavi, N. Hilderman, C.G.E., Liu, A., Makan, N., Wang, J.Z., Virji=Babul, N. (2014). Network analysis of perception-action coupling in infants. *Frontiers in Human Neuroscience, 8*(209), 1-7. (doi: 10.3389/fnhum.2014.00209)

Rothbart, M. K., Ahadi, S. A., & Hershey, K. L. (1994). Temperament and social behavior in childhood. Merrill-Palmer Quarterly, 40, 21-39.

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

Rothbart, M.K., Ellis, L.K., Rueda, M.R., Posner, M.I. (2003). Developing mechanisms of temperamental effortful control. *Journal of Personality, 71*(6), 1113-1143. (doi: 10.1111/1467-6494.7106009)

Ruffman, T., Slade, L., & Crowe, E. (2002). The relation between children's and mothers' mental state language and theory-of-mind understanding. Child Development, 73, 734–751. (doi: 10.1111/1467-8624.00435)

Sabbagh, M.A., Bowman, L.C., Evraire, L.E., Ito, J.M.B. (2009). Neurodevelopmental correlates of theory of mind in preschool children. *Child development, 80*(4), 1147-1162. (doi: 10.1111/j.1467-8624.2009.01322.x)

Saby, J.N., Marshall, P.J., Meltzoff, A.N. (2012). Neural correlates of being imitated: An EEG study in preverbal infants. *Social Neuroscience,* **6**, 650-661. (doi: 10.1080/17470919.2012.691429)

Sadato, N., Yonekura, Y., Waki, A., Yamada, H., Ishii, Y. (1997). Role of the supplementary motor area and the right premotor cortex in the coordination of bimanual finger movements. *Journal of Neuroscience,* 17(24), 9667-9674.

Saleh, M., Takahashi, K., Hatsopoulos, N.G. (2012). Encoding of coordinated reach and grasp trajectories in primary motor cortex. *Journal of Neuroscience, 32*(4), 1220-32. (doi: 10.1523/JNEUROSCI.2438-11.2012).

Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., Gruber, W.R., Birbaumer, N. (2005). A shift of visual spatial attention is selectively association with human EEG alpha activity. *European Journal of Neuroscience,* 22 (11), 2917-2926. doi: 10.1111/j.1460-9568.2005.04482.x

Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people: The role of the temporo-parietal junction in "theory of mind". *NeuroImage, 19*, 1835-1842. (doi: 10.1016/S1053-8119(03)00230-1)

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

Siegler, R.S., Shipley, C. (1995). Variation, selection and cognitive change. In T. Simon and G. Halford (Eds.). Developing cognitive competence: New approaches to process modeling. Hillsdale, NJ: Erlbaum, pp. 31-76.

Smith, L.B., Thelen, E. (2003). Development as a dynamic system. *TRENDS in Cognitive Science, 7*(8), 343-348. (doi: 10.1016/S1364-6613(03)00156-6)

Sodian, B., Licata, M., Kristen-Antonow, S., Paulus, M., Killen, M., Woodward, A. (2016). Understanding of goals, beliefs and desires predicts morally relevant theory of mind: A longitudinal investigation. *Child Development.*

Sommerville, J.A., Woodward, A.L. (2005). Pulling out the intentional structure of human action: The relation between action production and processing in infancy. *Cognition*, **95**, 1-30. (doi: 10.1016/j.cognition.2003.12.004)

Sommerville, J.A., Woodward, A.L., Needham, A. (2005). Action experience alters 3-month-old infants' perception of others' actions. *Cognition, 96,* B1-B11. (doi: :10.1016/j.cognition.2004.07.004)

Sommerville, J.A., Hildebrand, E.A., Crane, C.C. (2008). Experience matters: The impact of doing versus watching on infants' subsequent perception of tool use events. *Developmental Psychology, 44* (5), 1249-1256. (doi: 10.1037/a0012296).

Soska, K.C., Adolph, K.E., Johnson, S.P. (2009). Systems in development: Motor skill acquisition facilitates three-dimensional object completion. *Developmental Psychology, 46(1),*129-38. (doi: 10.1037/a0014618)

Southgate, V., Begus, K. (2013). Motor activation during prediction of nonexecutable action in infants. *Psychological Science.* **24**, 828-835. (doi: 10.1177/0956797612459766)

Southgate, V., Begus, K., Lloyd-Fox, S., di Gangi, V., Hamilton, A. (2014). Goal representation in the infant brain. *NeuroImage,* **85,** 294-301. (doi: 10.1016/j.neuroimage.2013.08.043)

Southgate, V., Johnson, M.H., Karoui, I.E., Csibra, G. (2010). Motor system activation reveals infants' on-line prediction of others' goals. *Psychological Science* **21**, 355-359. (doi: 10.1177/0956797610362058)

Southgate, V., Johnson, M.H., Osborne, T., Csibra, G. (2009). Predictive motor activation during action observation in human infants. *Biology Letters.* (doi: 10.1098/rsbl.2009.0474).

Southgate, V., Senju, A., Csibra, G. (2007). Action anticipation thorough attribution of false belief by two-year-olds. *Psychological Science, 18*(7), 587-592. (doi: 10.1111/j.1467-9280.2007.01944.x)

Spunt, R.P., Lieberman, M.D. (2013). The busy social brain: Evidence for automaticity and control in the neural systems supporting social cognition and action understanding. *Psychological Science.* **24,** 80-86. (doi: 10.1177/0956797612450884)

Stadler, W., Ott, D.V.M., Springer, A., Schubotz, R.I., Schutz-Bosbach, S., Prinz, W. (2012). Repetitive TMS suggests a role of the human dorsal premotor cortex in action prediction. *Frontiers Human Neuroscience*. **6**, 1-11. (doi: 10.3389/fnhum.2012.00020)

Stancak, Jr., A., & Pfurtscheller, G. (1996). Mu-rhythm changes in brisk and slow self-paced finger movements. *NeuroReport, 7*(6)*,* 1161-1164. (doi: 10.1097/00001756-199604260-00013)

Stapel, J. C., Hunnius, S., van Elk, M., & Bekkering, H. (2010). Motor activation during observation of unusual versus ordinary actions in infancy. *Social Neuroscience*, *5*(5-6), 451–60. (doi: 10.1080/17470919.2010.490667)

Stroganova, T.A., Orekhova, E.V. (2007). EEG and infant states. In M. de Haan (Eds.), *Infant EEG and Event-related potentials* (pp.251-288). New York, NY: Psychology Press.

Stroganova, T.A., Orekhova, E.V., Posikera, I.N. (1999). EEG alpha rhythm in infants. *Clincical neurophysiology, 110*(6), 997-1012. (doi: 10.1016/S1388-2457(98)00009-1)

Stuss, D.T., Gallup Jr, G.G., Alexander, M.P. (2001). The frontal lobes are necessary for 'theory of mind'. *Brain, 124*, 279-286. (doi: http://dx.doi.org/10.1093/brain/124.2.279)

Surian, L., Caldi, S., Sperber, D. (2007). Attribution of beliefs by 13-month-old infants. *Psychological Science, 18*(7), 580-586. (doi: 10.1111/j.1467-9280.2007.01943.x)

Tahiroglu, D., Moses L.J., Carlson, S.M., Mahy, C.E.V., Olofson, E.L., Sabbah, M.A. (2014). The children's social understanding scale: Construction and validation of a parent-report measure for assessing individual differences in children's theories of mind. *Developmental Psychology.* (doi: 10.1037/a0037914).

Tanji, J. (2001). Sequential organization of multiple movements: involvement of cortical motor areas. *Annu. Rev. Neurosci*. 24, 631–651. (doi: 10.1146/annurev. neuro.24.1.631)

Thelen, E., Corbetta, D., Spencer, J.P. (1996). Development of reaching during the first year: role of movement speed. *Journal of experimental psychology: Human perception and performance,* 22(5), 1059-1076.

Thelen, E., Fisher, D.M., Ridley-Johnson, R. (2002). The relationship between physical growth and a newborn reflex. *Infant behavior and development,* 25(1), 72-85.

Thelen, E., Spencer, J.P. (1998). Postural control during reaching in young infants: A dynamic systems approach. *Neuroscience and Biobehavioral reviews,* 22(4), 507-514. doi: 10.1016/S0149-7634(97)00037-7 .

Thoermer, C., Woodward, A., Eisenbeis, H., Kristen, S., & Sodian, B. (2013). To get the grasp: Seven-month-olds encode and reproduce goal-directed grasping. *Journal of Experimental Child Psychology,* 116, 499-509.

Thorpe, S.G., Cannon, E.N., Fox, N.A. (2015). Spectral and source structural development of mu and alpha rhythms from infancy through adulthood. *Clinical Neurophysiology, 127*, 254-269. (doi: 10.1016/j.clinph.2015.03.004).

Thut, G., Nietzel, A., Brandt, S.A., Pascual-Leone, A. (2006). Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience,* 26(37), 9494-502. doi: 10.1523/JNEUROSCI.0875-06.2006

Toni, I., Krams, M., Turner, R., Passingham, R.E. (1998). The time course of changes during motor sequence learning: A whole-brain fMRI study. *NeuroImage,* 8(1), 50-61. doi: 10.1006/nimg.1998.0349

Trofatter, C., Kontra, C., Beilock, S, Goldin-Meadow, S. (2014). Gesturing has a larger impact on problem-solving than action, even when action is accompanied by words. *Language, Cognition and Neuroscience, 9*(21), 1-10. (doi: 10.1080/23273798.2014.905692)

Tzagarakis, C., Ince, N.F., Leuthold, A.C., Pellizzer, G. (2010). Beta-band activity during motor planning reflect response uncertainty. *Journal of Neuroscience,* 30(34), 11270-11277. (doi: 10.1523/JNEUROSCI.6026-09.2010)

Uehara, K., Morishita, T., Kubota, S., Hirano, M., Funase, K. (2014). Functional differenece in short- and long-latency interhemispheric inhibitions from active to resting hemisphere during a unilateral muscle contraction. *Journal of Neurophyiology, 111(1),* 17-25. doi: 10.1152/jn.00494.2013

Upshaw, M.B., Bernier, R.A., Sommerville, J.A. (2015). Infants' grip strength predicts mu rhythm attenuation during observation of lifting actions with weighted blocks. *Developmental Science,* (doi: 10.1111/desc.12308)

Van Cutsem, M., Duchateau, J., Hainaut, K. (1998). Changes in single motor unit behavior contribute to the increase in contraction speed after dynamic training in humans. *Journal of Phsyiology,* 315 (1), 295-305.

van Elk, M., van Schie, H.T., Hunnius, S., Vesper, C., Bekkering, H. (2008). You'll never crawl alone: Neurophysiological evidence for experience-dependent motor resonance in infancy. *NeuroImage,* **43**, 808-814. (doi: 10.1016/j.neuroimage.2008.07.057)

Vickers, J.N. (1992). Gaze control in putting. *Perceptio*n, (doi: 10.1068/p210117)

Vickers, J.N. (2006). Gaze of Olympic speedskaters skating at full speed on a regulation oval: Percetion-action coupling in a dynamic performance environment. *Cognitive Processing,* (doi: 10.1007/s10339-006-0087-1)

Vickers, J.N. & Adolphe, R.M. (1997). Gaze behavior during a ball tracking and aiming skill. *International Journal of Sports Vision, 4*(1), 18-27.

von Hofsten, C. (1979). Development of visually directed reaching: The approach phase. *Journal of Human Movement Studies, 5*, 160-178.

von Hofsten, C. (1980). Predictive reaching for moving objects by human infants. *Journal of Experimental Child Psychology.* 30(3), 369-82.

von Hofsten, C. (1982). Eye-hand coordination in the newborn. *Developmental Psychology,* 18(3), 450-461.

von Hofsten, C. (1991). Structuring of early reaching moveents: A longitudinal study. *Journal of Motor Behavior, 23*(4), 280-292.

von Hofsten, C. (1993). Prospective control: A basic aspect of action development. *Human Development,* 36, 253-270. doi: 10.1159/000278212

von Hofsten, C., and Fazel-Zandy, S. (1984). Development of visually guided hand orientation in reaching. *J. Exp. Child Psychol.* 38, 208–219. doi: 10.1016/0022-0965(84)90122-X

von Hofsten, C., and Ronnqvist, L. (1988). Preparation for grasping an object: a developmental study. *J. Exp. Psychol. Hum. Percept. Perform.* 14, 610–621. doi: 10.1037/0096-1523.14.4.610

Walle, E., Campos, J.J. (2014). Infant language development is related to the acquisition of walking. *Developmental psychology, 50*(2), 336-348. (doi: 10.1037/a0033238).

Wang, M. V., Lekhal, R., Aaro, L. E., & Schjolberg, S. (2014). Co-occurring development of early childhood communication and motor skills: Results from a population-based longitudinal study. Child: Care, Health and Development, 40(1), 77-84. doi: 10.1111/cch.12003

Warreyn, P. Ruysschaert, L., Wiersema, J.R., Handl, A., Pattyn, G. Roeyers, H. (2013). Infnats' mu suppression during the observation of real and mimicked goal-directed actions. *Developmental Science, 16*(2), 173-85. (doi: 10.1111/desc.12014)

Watson, A.C., Nixon, C.L., Wilson, A., Capage, L (1999). Social interaction skills and theory of mind in young children. *Developmental Psychology, 35*(2), 386-391. (doi: 10.1037/0012-1649.35.2.386)

Welch-Ross, M.K., Miller, P.H. (2000). Relations between children's theory of mind and a selective attention strategy. *Journal of cognition and development, 1*(3), 281-303. (doi: 10.1207/S15327647JCD0103_2)

Wellman, H.M., Cross, D. Watson, J. (2001). Meta-Analysis of theory-of-mind development: The truth about false belief. *Child Development,* 72(3), 655-684. (doi: 10.1111/1467-8624.00304)

Wellman, H.M., Lopez-Duran, S., LaBounty, J., Hamilton, B. (2008). Infant attention to intentional action predicts preschool theory of mind. *Developmental Psychology, 44*(2), 618-23. (doi: 10.1037/0012-1649.44.2.618)

Wellman, H.M., Phillips, A.T., Dunphy-Lelii, S., LaLonde, N. (2004). Infant social attention predicts preschool social cognition. *Developmental Science.* **7**, 283–288. (doi: 10.1111/j.1467-7687.2004.00347.x)

Woodward, A. L. (1998). Infants selectively encode the goal of an actor's reach. *Cognition, 69*, 1–34. doi:10.1016/S0010-0277(98)00058-4

Woodward, A.L., Gerson, S.A. (2014). Mirroring and the development of action understanding. *Philosophical Transactions Royal Society B*. **369**. (doi: 10.1098/rstb.2013.0181)

Woodward, A. L., Sommerville, J.A., Gerson, S., Henderson, A. M. E., & Buresh, J. S. (2009). The emergence of intention attribution in infancy. In B. Ross (Ed.) *The Psychology of Learning and Motivation*, Vol. 51 (pp.187-222). Waltham,MA: Academic Press. (doi: 10.1016/S0079-7421(09)51006-7)

Yamaguchi, M., Kuhlmeier, V.A., Wynn, K., VanMarle, K. (2009). Continuity in social cognition from infancy to childhood. *Developmental Science,* 12(5), 746-752. doi: 10.1111/j.1467-7687.2008.00813.x

Yoo, K.H., Cannon, E.N., Thorpe, S.G., Fox, N.A. (2015). Desynchronizatoin in EEG during perception of means-end actions and relations with infants' grasping skill. *British Journal of Developmental Psychology,* 1-14. (doi: 10.1111/bjdp.12115).

Yoo, K.H., Fox, N.A. (2015). The mirror neuron system and the mu rhythm. In P.F. Ferrari & G. Rizzolatti (Ed.) *New Frontiers in Mirror Neuron Research,* (pp. 256-273). New York, NY: Oxford University Press.