ABSTRACT

Title of Dissertation:	ACTION AND PERCEPTION: NEURAL INDICES OF LEARNING IN INFANTS
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Early human development offers a unique perspective in investigating the potential cognitive and social implications of action and perception. Specifically, during infancy, action production and action perception undergo foundational developments. One essential component to examine developments in action processing is the analysis of others' actions as meaningful and goal-directed. Little research, however, has examined the underlying neural systems that may be associated with emerging action and perception abilities, and infants' learning of goal-directed actions. The current study examines the mu rhythm—a brain oscillation found in the electroencephalogram (EEG)—that has been associated with action and perception. Specifically, the present work investigates whether the mu signal is related to 9-month-olds' learning of a novel goal-directed means-end task. The findings of this study demonstrate a relation between variations in mu rhythm activity and infants'

ability to learn a novel goal-directed means-end action task (compared to a visual pattern learning task used as a comparison task). Additionally, we examined the relations between standardized assessments of early motor competence, infants' ability to learn a novel goal-directed task, and mu rhythm activity. We found that: 1a) mu rhythm activity during observation of a grasp uniquely predicted infants' learning on the cane training task, 1b) mu rhythm activity during observation and execution of a grasp did not uniquely predict infants' learning on the visual pattern learning task (comparison learning task), 2) infants' motor competence did not predict infants' learning on the cane training task, 3) mu rhythm activity during observation and execution was not related to infants' measure of motor competence, and 4) mu rhythm activity did not predict infants' learning on the cane task above and beyond infants' motor competence. The results from this study demonstrate that mu rhythm activity is a sensitive measure to detect individual differences in infants' action and perception abilities, specifically their learning of a novel goal-directed action.

ACTION AND PERCEPTION: NEURAL INDICES OF LEARNING IN INFANTS

by

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Dissertation submitted to the Faculty of the Graduate School of the
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Dedication

To my beloved husband Sean, my mother and stepfather Mira and Hyung Chun, my

brother Richard, and my grandmother Yoo.

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Growing up in a rural village in South Korea, I never imagined I would be pursuing the highest level of education that would culminate to my doctoral work. As a result of this experience, I have grown emotionally, mentally, and intellectually in ways I never thought possible. For this, I am extremely fortunate and have many wonderful people to thank.

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Chapter 1: Overview

A fundamental issue in cognitive neuroscience is how the brain encodes and understands the actions of others. One hypothesis posits that there is a coupling between action and perception, in other words, the ability to match self to others may underlie the capability to understand and process others' actions as meaningful and intentional (Rizzolatti, Fogassi, & Gallese, 2001). This link between action and perception, proposed to be supported (in part) by the mirror system, is thought to support an internal representation of others' actions. This internal representation is linked, via a common neural code, to one's own actions and also connected, by network and extension, to the goals, beliefs, and intentions associated with the action. Thus, the link between the self and other may facilitate an understanding of others' mental states through the perceived goals, beliefs, and intentions behind others' actions (Iacoboni et al., 2005; Rizzolatti & Sinigaglia, 2010).

In human development, the systems involved in action and perception are suggested to support the processing of others' actions, specifically with regards to the intentions and goals behind these actions (Woodward, 1998). Early development offers a unique perspective to investigate the potential cognitive and social implications of action and perception coupling, because during infancy, action production and action understanding undergo foundational developments (Csibra & Gergely, 2010). One essential component of assessing developments in action understanding is the analysis of others' actions as meaningful and goal-directed (Gerson & Woodward, 2012; Sommerville & Woodward, 2005b; Woodward & Sommerville, 2000). That is, infants represent the others' actions with respect to the objects and outcomes to which the actions

are directed rather than simply the perceptual properties (e.g., kinematics) of the actions (Woodward & Gerson, 2014). Further, this body of work demonstrates that there are rich connections between action processing and action experiences (Sommerville, Hildebrand, & Crane, 2008).

Recent electrophysiological work provides evidence of a neural signal associated with the coupling of action and perception. The mu rhythm is recorded in the electroencephalogram over the sensorimotor areas, and this brain oscillation is thought to reflect the involvement of the sensorimotor system, and by extension, the activity of an action-perception system (Fox et al., 2015; Marshall, Young, & Meltzoff, 2011; Pineda, 2005; Vanderwert, Fox, & Ferrari, 2013a). Further, there exists evidence to support that the mu rhythm differentially behaves to meaningful and goal-directed actions. Muthukumaraswamy and Johnson (2004) found that the mu rhythm suppressed more in amplitude (called mu rhythm event-related desynchronization or mu ERD) during perception of object-directed actions (i.e., goal oriented) compared to actions that were not goal oriented (Muthukumaraswamy, Johnson, & McNair, 2004). In infants, parallel findings were found (Southgate, Johnson, Osborne, & Csibra, 2009; Virji-Babul, Rose, Moiseeva, & Makan, 2012a). Studies with infants have also reported mu ERD during observation and execution of goal-directed (e.g., object-directed) grasps providing support for the emergence of the coupling between action and perception (Marshall, Saby, & Meltzoff, 2013b; Marshall et al., 2011). This coupling system, as assessed via the mu rhythm, is differentially responsive to meaningful and intentional actions compared to non-goal oriented actions (Muthukumaraswamy et al., 2004; Muthukumaraswamy & Johnson, 2004; Streltsova, Berchio, Gallese, & Umilta', 2010).

Until recently, electrophysiological research in the emergence and development of action and perception—and its coupling—has primarily focused on how the mu rhythm is tuned to the experiences of the infant. Specifically, studies have examined the relations between mu rhythm activity and the action or motor experiences that the infant has acquired (e.g., Cannon et al., 2015; Yoo, Cannon, Thorpe, & Fox, 2015). For example, one study investigated the relation between the amount of experience (e.g., crawling and walking) and mu rhythm activity, reporting that greater crawling and walking experience was correlated with greater mu ERD (van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). In another study, de Klerk and colleagues (2014) manipulated pre-walking infants' experience by exposing them to an infant treadmill and examining mu rhythm activity after the infants acquired this experience (de Klerk, Johnson, Heyes, & Southgate, 2014). They found that neural activity responded differentially to perception of walking actions when infants had prior walking experience on the treadmill. Together, these studies provide evidence that mu rhythm activity can be tuned to the action and motor experiences of the individual.

The past two decades have seen the culmination of infant studies that investigate whether the activity mu rhythm activity can inform us about infants' goal-directed behavior. A study by Filippi and colleagues (2016) with 7-month-old infants found that mu rhythm activity during *perception* of an experimenter's goal-directed action was observed prior to infants' reproduction of the goal of the experimenter compared to the infants' non-goal response. In addition, they found that mu rhythm activity during *execution* of infants' goal-directed action (grasping a toy) was related to the proportion of infants' goal responses (i.e., reproducing the goal of the experimenter; Filippi et al.,

2016). Another study (Southgate, Johnson, El Karoui, & Csibra, 2010) presented 9-month-old infants with part of an action (making a grasping action seemingly towards an object behind an occlusion). They found greater mu ERD during observation of actions for which the infants can infer a likely outcome or goal (grasping an object) compared to actions for which the outcome is ambiguous and not goal oriented. However, this study did not examine whether heterogeneity in mu ERD is related to infants' own actions.

All together, there exists evidence to support the relation between mu rhythm activity (during observation *and* execution of actions) and infants' goal-related behaviors. However, to date, it remains unclear whether the mu rhythm can reflect infants' readiness to learn goal-directed actions. Furthermore, it has been suggested that motor skills and competence are related to the ability to detect the goal structure of actions (e.g., means-end tool use actions), an ability that is necessary for problem solving (Keen, 2011). The current study assessed infants' motor competence using standardized assessments to examine the relation between infants' learning of a novel goal-directed action and their motor competence.

In addition, studies have demonstrated that mu rhythm is tuned to the motor experiences and skills of the individual, specifically greater mu ERD is associated with greater experience (Cannon et al., 2014, 2015; Paulus, Hunnius, van Elk, & Bekkering, 2012; van Elk et al., 2008). On the other hand, there also exists evidence to suggest greater motor experience does not result in greater mu ERD (Del Percio et al., 2010). Instead, a decrease in mu ERD is observed in line with the "neural efficiency" hypothesis, which posits that a more efficient cortical function is achieved with better performance in cognitive functions. These mixed findings may be attributed to a

methodological difference in which motor experience is measured differently across studies. Some studies examine mu activity in relation to crawling and walking (van Elk et al., 2008), to preshaping and bimanual reaches (Cannon et al., 2015), and latency to reach for an object (Yoo et al., 2015). Therefore, the inclusion of standardized assessments of motor competence also allows us to examine the relation between mu rhythm activity and infants' motor competence, which may elucidate the precise relation between mu activity and motor skills and competence.

Finally, the current study examined the relations between variations in mu rhythm activity, learning of a novel goal-directed action, and motor competence using standardized assessments of motor competence in infants. Specifically, we wanted to examine whether mu rhythm activity can detect variations in infants' learning of a novel goal-directed action and is sensitive enough to reflect this learning above and beyond behavioral assessments of infants' motor competence.

The present study had four aims: 1) examine individual differences in mu rhythm activity and infants' ability to learn a novel goal-directed means-end task compared to a non-goal-directed task, 2) investigate the relations between infants' motor competence and their learning of a novel goal-directed means-end task, 3) assess the relation between mu rhythm activity and motor competence, and 4) examine whether mu rhythm activity predicts infants' learning of a novel goal-directed means-end task above and beyond motor competence assessments. We recruited 9-month-old infants and randomly assigned them to one of two groups. The first group learned a novel means-end task, a task that was adapted from Sommerville and colleagues (Sommerville et al., 2008). The second group learned a novel statistical learning task, specifically a visual pattern learning

paradigm (i.e., comparison task) adapted from Saffran and colleagues (Saffran, Pollak, Seibel, & Shkolnik, 2007) to assess infants' learning in a task that did not involve a goal-directed component. This task was chosen, because this learning task did not have a goal component to the learning (i.e., it is a sequence learning task), and it did not require an action or motor response from the infant. Further, visual pattern learning tasks have been implemented with infants in the first year of life and indicate that infants around 9-months of age could learn to extract rules from these tasks (Fiser & Aslin, 2002; Saffran et al., 2007). To measure mu rhythm activity, infants' EEG was collected during an observation and execution paradigm for which they observed goal-directed actions performed by an experimenter, and the infants reached for objects themselves.

Next, we evaluated infants' motor competence using a battery of standardized assessments to investigate whether: a) infants' emerging motor competence can inform their learning of goal-directed means-end task, b) mu rhythm activity is related to motor competence, and c) mu rhythm activity can predict infants' learning of a goal-directed task above and beyond standardized assessments of motor competence.

We made the following hypotheses: 1a) variations in mu rhythm activity (i.e., specific to central sites) during perception and execution of a goal-directed action would be related to infants' learning of a novel goal-directed means-end task, specifically that greater mu ERD would be related to better learning, 1b) ERDs across the scalp (frontal, central, parietal, and occipital) would be related to infants' learning of a novel non-goal-directed task (our comparison task), 2) motor competence would be related to infants' learning on a novel goal-directed means-end task, i.e., greater motor competence would be related to better learning on the goal-directed means-end task, 3) mu rhythm activity

would be related to infants' motor competence, i.e., greater mu ERD during observation and execution related to greater motor competence, and 4) mu rhythm activity during perception and execution of a goal-directed action would predict infants' learning of a novel goal-directed task above and beyond motor competence assessments.

Chapter 2: Background

The coupling of action and perception is hypothesized to be an evolutionary precursor and springboard for much of higher cognition and complex social behavior fundamental and unique to humans. Many researchers posit that the ability to match self to others made possible (in part) by a mirror system may underlie the capability to understand others' actions and intentions by means of a common representation for both observation and execution (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). The general notion behind a role for mirror system in these complex social and communicative abilities rests on the position that when we perceive others' action, the mirror system supports an internal representation of this perceived action (Rizzolatti & Craighero, 2004). This internal representation is linked via a common neural code to one's own actions and also connected, by network and extension, to the goals, beliefs, and intentions associated with the action. Therefore, these links between the self and other may facilitate an understanding of other's mental states through the perceived goals, beliefs, and intentions behind others' actions.

In development, it is posited that the systems involved in action and perception support the processing and understanding of others' actions, specifically with regards to the intentions and goals behind said actions. From the perspective of investigating the potential social and cognitive implications of action and perception coupling, early development offers a unique perspective. During infancy, action production and action understanding undergo foundational developments. Specifically, an essential component of action understanding, i.e., the analysis of actions as goal-directed, emerges in the first year of life (Woodward & Gerson, 2014). Infants perceive others' actions as meaningful,

intentional, and goal-directed in that the observed actions are represented with respect to the objects and outcomes to which the actions are directed rather than just the actions' perceptual properties. It has been proposed that a mirror system may support these foundational social and cognitive functions, and this body of work also demonstrates that there are rich connections between action understanding and motor abilities (Iacoboni et al., 2005; Pineda & Hecht, 2009; Rizzolatti & Fabbri-Destro, 2008; J. A. Sommerville, Woodward, & Needham, 2005).

The aim of the current chapter is to provide a review of theoretical and empirical work on the relation between action and perception with a specific focus on developmental research. I will first discuss the behavioral work on action and perception coupling in infants, specifically infants' analysis of others' actions as goal-directed, and the link between this analysis and infants' own experience with actions. Second, I will discuss the neural evidence behind the coupling of action and perception, i.e., the mirror system, and this system's specificity to goal-directed actions. This neurophysiological evidence will be discussed in the context of the empirical work accomplished in non-human primates as well as in humans, in both adults and in infants. Third, I will present neurophysiological work investigating the relation between action and perception and the role of experience in adults. Fourth, I will present neurophysiological evidence on the relation between early motor competence, experience, and action-perception abilities in infants. And finally, the last section of this chapter concludes with a summary and the hypotheses for the current study.

2.1 Behavioral Evidence of Action and Perception Coupling in Infants

2.1.1 Infants' Analysis of Others' Actions

Behavioral research has demonstrated that the ability to encode others' actions as meaningful and goal-directed emerges during infancy. Over the first year life, infants encode certain events as goal-directed, representing actions with respect to the objects and outcomes to which they are directed rather than just the actions' perceptual properties (Phillips & Wellman, 2005; Sommerville & Woodward, 2005). Woodward (1998) used a visual habituation paradigm to examine infants' analysis of others' actions as goal-directed. In a visual habituation paradigm, infants are habituated to an event (e.g., an actor reaching for Toy A) then, they are exposed to the habituated event and a novel event. The idea behind this paradigm is that if the infants encoded the events during the habituation (e.g., the goal of the actor), then they would look longer at the novel event compared to the habituated (or familiar) event. Woodward (1998) habituated nine-month-old infants to an actor reaching for and grasping one of two toys that were sitting side by side on a curtained stage. After habituation, the toys' positions were switched and the infants saw test events during which there was change in either the path of motion taken by the actor's arm (i.e., same goal) or change in the object grasped by the actor's arm (i.e., change in goal). She found that nine-month-olds looked longer when the actor grasped a new toy than when she moved through a new path (Woodward, 1998). This result suggests that young infants distinguish in their reasoning about object motion and human action and encode others' actions in ways that are consistent with understandings of a goal-directed action.

In a study by Behne and colleagues (2005), nine to eighteen months old infants experienced an adult handing them toys. And sometimes in these exchanges, the transaction failed, either because the adult was unwilling to give the toy (e.g., teasing the child with it or playing with the toy herself) or the adult was unable to give the toy (e.g., she accidentally dropped it). Infants as young as nine months of age reacted with more impatience (e.g., looking away, reaching for the toy that the adult had), when the adult was unwilling to give the toy compared to when she was unable to give it, demonstrating that infants begin to understand actions as goal-directed and intentional in the first year of life (Behne, Carpenter, Call, & Tomasello, 2005).

Further, Gerson and Woodward (2012) examined how the opportunity to compare a familiar action with a novel, means-end tool action enables infants to extract the goal of the means-end action. Infants were provided with the chance to compare their own goal-directed reaches (e.g., grasping for objects) with an experimenter reaching for a toy with a novel mechanical tool. They found that infants who reproduced the goal of the experimenter using a novel tool later aligned their own actions with those of the experimenter. Their results suggest that infants compare their own familiar goal-directed actions to the actions of others' goal-related action.

2.1.2 The Link between Action and Perception in Infants

Not only do infants encode others' actions as intentional and goal-directed, but there exists evidence to suggest there is a coupling between action and perception (Thelen, 1995), specifically that one's action can influence perception of others' actions. A study by Sommerville and colleagues (2005) examined how experience with a goal (e.g., picking up toys) influenced 3-month-olds' perception of others' actions in a visual

habituation paradigm. They put on mittens—which had Velcro attached to the mittens—on the infants' hands to which the toys would stick. It is important to note that at three months of age, infants have not acquired the refined ability to grasp objects themselves, however, with these 'sticky mittens,' they are able to pick up the toys. They found that infants who had the experience of retrieving toys with the 'sticky mittens' prior to the visual habituation paradigm looked longer at the new goal event (i.e., new toy) compared to the new path event (i.e., same toy in a different location). But infants who did not have this prior experience with the 'sticky mittens' did not show this difference in their looking time during the test phase (Sommerville, Woodward, & Needham, 2005).

Further, there exists evidence of a relation between infants' prior experience and the ability to anticipate containment actions (Cannon, Woodward, Gredebäck, Hofsten, & Turek, 2012). Twelve-month-old infants were given the opportunity to participate in a containment activity (e.g., placing balls into a container) before observing the experimenter engaging in the same activity. They found that when the infants were given this containment opportunity, the infants' spontaneous level of activity of containment action was related to how quickly they encoded the goal of the experimenter compared to the infants who had the simply observed the experimenter's containment activity. In another study, Myowa-Yamakoshi and colleagues (2011) examined whether infants' own visual experience affected their perception of the visual status of others engaging in goal-directed actions. In their study, 12-month-old infants viewed video clips of goal-directed actions executed by a blindfolded experimenter, and they found that infants who were previously exposed to viewing a blindfolded experimenter during object-directed actions paid more attention to the subsequent stages of the action as if the experimenter can see

compared to the infants who had no prior experience viewing the blindfolded experimenter. In addition, the experimenter performed both successful (i.e., grasped objects) and unsuccessful (i.e., failed to grasp objects) actions. Findings revealed that infants preferred to look longer at the experimenter's successful actions when they had been previously exposed to the blindfolded experimenter executing the actions. Their findings suggest that previous experience (of being blind folded) influenced the subsequent perception of others' goal-directed actions, and that this preference for successful actions (i.e., goal-directed) demonstrates the influence of perceptual experience on considering the visual status of others engaging in goal-directed actions in the first year of life (Myowa-Yamakoshi, Kawakita, Okanda, & Takeshita, 2011).

In another study, Sommerville and colleagues examined the relation between action and perception (Sommerville, Hildebrand, & Crane, 2008). In one condition, infants experienced an active training task where they were trained to use a cane to obtain an out-of-reach toy. In another condition, infants experienced an observation session where they viewed an experimenter obtain an out-of-reach toy. Findings revealed that infants who experienced active training sessions were able to encode the goal of the cane use compared to the infants who passively viewed an experimenter using the cane.

Furthermore, not only is there evidence for one's own action influencing perception of others' actions, but there also exists evidence that this phenomenon is bidirectional (i.e., perception influencing action). In a Piagetian A-not-B error, nine-month-old infants recovered a toy hidden at location A or observed an experimenter recover the toy (Longo & Bertenthal, 2006). After the toy was hidden at location B, for both conditions, the infants perseverated in reaching to location A, demonstrating that

active search by the infant is not necessary for the A-not-B error. Infants, consistent with prior research, demonstrated this ipsilateral bias when reaching for objects. A similar ipsilateral bias was observed depending on the manner in which the experimenter reached. Infants perseverated following observation of ipsi- but not contralateral reaches by the experimenter, suggesting that infants perseverated only when they observed actions they themselves were able to perform.

Taken together, this body of work demonstrates that there is indeed a relation between action and perception emerging in the first year of life, and that not only can action influence perception but also that perception can influence action. Infants not only perceive others' actions as intentional and goal-directed, but infants' own actions can influence how they perceive and process others' actions. Further, this body of work shows that there exist close relations, during early development (e.g., in the first year of life), between action and perception of others' goal-directed actions, which play an important role in the development of infants' action understanding.

2.2 Neural Bases of Action and Perception

2.2.1 Mirror Neurons in Non-human Primates

The neural representation between action and perception was first discovered in the adult Rhesus macaque through single-cell recordings. These so-called mirror neurons (MNs) were discovered in area F5 of the premotor cortex, and they discharged to observation and execution of grasping actions. A distinguishing characteristic of MNs is that this group of motor neurons (referred to as the mirror system) discharge to the observation of goal-directed (e.g., object-directed) actions, and not to the sight of the

object or to mimicked action without the object present (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese et al., 1996). Another class of neurons, called canonical neurons, was discovered in area F5, which discharged not only during execution of an object-directed action, but also during visual presentation of the object (Murata et al., 1997). It is posited that canonical neurons may play a role in the transformation of the visual properties of perceived objects to determine how to appropriately interact with the object, for example, to determine to what type of grip to use to obtain a cup (Oztop, Kawato, & Arbib, 2013). However, what distinguishes mirror neurons from canonical neurons is the importance of the observation of goal-directed motor action. Mirror neurons require the perception of such action while canonical neurons discharge at the mere sight of the object (Gallese et al., 1996).

In a study by Umiltà and colleagues, they trained a monkey to use pliers to grasp objects. The monkey was trained to use two kinds of pliers, the first one ('normal pliers') for which the monkey had to close its hand to grasp a piece of food, and the second one for which the monkey had to open its hand to grasp food. They found that during use of both of the pliers, the same set of MNs discharged suggesting that it was the goal of the action (i.e., grasping a piece of food) that the MNs were encoding and not necessarily the kinematics themselves (Umiltà et al., 2008). Subsequently, studies have demonstrated the goal-specificity of MNs in other sensory modalities such as with auditory MNs (during peanut cracking), providing evidence that it is the goal behind the action that is driving MN activity (Kohler et al., 2002). Further, similar patterns of activation to perceived goal-directed activity in the parietal areas, which make dense connections with the premotor area has resulted in the theory that MNs make up the mirror system, i.e., action-

perception system, proposed to facilitate action processing and action understanding (Vittorio Gallese & Goldman, 1998; Rizzolatti & Luppino, 2001).

2.2.2 Mu Rhythm Activity during Action and Perception in Humans

The discovery of MNs and the extended claims and implications of the function of the mirror system for cognition has led to efforts in identifying similar action-perception coupling activity in humans. However, the invasiveness of single-cell techniques has precluded its use in humans. Thus, these efforts have involved the use of non-invasive neurophysiological methods via the electroencephalogram (EEG), which has been a particularly popular tool due to its relative ease with which data can be collected across a diverse range of populations including infants and children. EEG studies investigating human action and perception activity focuses on the modulation of a frequency band that is associated with sensorimotor activity — the mu rhythm. The mu rhythm is thought to reflect sensorimotor activity in the alpha band (i.e., ~8-13 Hz in adults, ~6-9 Hz in children), and is recorded over the central scalp regions (Marshall, Bar-Haim, & Fox, 2002; Jaime Pineda, 2005).

The mu rhythm was first observed in the EEG by Gastaut and Bert (1954), and they noticed that this rhythm was blocked (i.e., decreased in amplitude) during observation of movements when the participants showed no apparent motor movements (Gastaut & Bert, 1954). Subsequently, studies reported this same phenomenon during the production of motor acts (Chatrian, Petersen, & Lazarte, 1959; Kuhlman, 1978; Pfurtscheller, Neuper, Flotzinger, & Pregenzer, 1997). The blocking of the mu rhythm, referred to as mu rhythm event-related desynchronization or mu ERD, is proposed to reflect an active state of sensorimotor system (Pineda, 2005). To calculate mu ERD, the

percentage of change in EEG power between a test event (e.g., observation or execution of action) and a baseline event is computed. This ERD during a test event from a baseline event would yield negative values or positive values (synchronization) with zero representing no changes in spectral power between the test event and the baseline event. Further, mu rhythm activity is proposed to reflect the collective activity of the neuronal networks such as the premotor, motor, and parietal areas involved in motor processing. These networks that are firing in synchrony during a baseline period begin to fire asynchronously as these they process and relay information, and this asynchronous activity of neuronal networks results in a decrease in EEG amplitude or decrease (Pineda, 2005). On the other hand, synchronization or event-related synchronization (ERS) is assumed to reflect deactivation, inhibition, or at the very least the "idling" state of the sensorimotor network (Neuper & Pfurtscheller, 2001). Studies have reported mu synchronization during perception of patterns and during visual information processing such as reading (Klimesch et al., 1996; Koshino & Niedermeyer, 1975). One interpretation of this phenomenon is that since mu rhythm reflects sensorimotor processing and is not directly involved in visual processing, the sensorimotor network becomes "idle," thus, synchronized during such tasks.

The EEG recording of mu rhythm activity, however, poses a challenge due to EEG's poor spatial resolution. Magnetoencephalogram (MEG) studies, on the other hand, have demonstrated that the likely origin of mu rhythm is the sensorimotor areas (Salmelin & Hari, 1994). With EEG, mu rhythm is typically recorded over the central and parietal scalp electrodes, which are thought to overlay the sensorimotor areas with its modulation being associated with motor tasks (Babiloni et al., 1999; Pfurtscheller et al., 1997).

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Although the mu and the occipital rhythms are observed in the same frequency band (8-13 Hz in adults), mu rhythm is thought to be distinct from occipital alpha (Kuhlman, 1978). The occipital alpha is most prominent, or displays the largest spectral power, over the posterior areas of the scalp. The challenge is that the occipital alpha rhythm also desynchronizes during visual stimulation (e.g., lights off to lights on) and during various visual attention tasks (Berger, 1929; Sauseng et al., 2005). Thus, the occipital rhythm sharing the same frequency band as the mu rhythm introduces a unique challenge for mu rhythm researchers. Indeed, some have speculated that mu desynchronization may be a result of occipital alpha desynchronization "leaking" over to the central areas from posterior areas during stimulus presentation (Pineda, 2005). As a result, studies have attempted to localize mu rhythm in various ways. In one study, Hari and colleagues (1998) localized mu rhythm activity based on the individual MRIs of their participants, and report that mu rhythm's likely source lies in the sensorimotor regions (motor and somatosensory). They recorded oscillatory activity using MEG in adult participants during rest and during participants' finger flexion movements. They observed changes in the activity of the mu rhythm, and this activity originated from the sensorimotor cortex. In fact, Hari and colleagues (1997) characterized alpha rhythms during different conditions such as the presentation of a visual stimulus and body part movements. They reported that the sources of posterior alpha rhythm (i.e., occipital alpha) clustered mainly around the parieto-occipital sulcus while the mu rhythm sources clustered around the somatosensory and the motor cortices. Specifically, the mu rhythm was not affected by opening/closing of the eyes but was desynchronized during hand movements. Indeed, accumulating evidence suggests that mu rhythm is a distinct phenomenon indicative of

sensorimotor activity—distinct from the occipital alpha rhythm—with an independent source generated by the sensorimotor areas, providing evidence of functionally distinct cortical rhythms (Hari & Salmelin 1997; Formaggio et al. 2008; Pineda 2005).

Studies have also demonstrated a correspondence between the body area movement that desynchronized mu rhythm at a given site and the body region that was affected by stimulation at the same site. Arroyo and colleagues (1993) recorded mu rhythm using subdural electrodes, and found that the presence and the desynchronization of the mu rhythm corresponded to the somatic representation of the cortex (from electrical stimulation of the body part) from which it was recorded. In another study, Pfurtscheller and colleagues (1997) reported a topographical analysis of scalp EEG data during hand and foot movements. They found that hand and foot areas have their own intrinsic rhythmic activity (mu rhythm recorded over the central electrodes), which desynchronize when the corresponding area becomes activated. In another words, the movement of the hand, for example, resulted in a desynchronization of mu rhythm that was close to the hand area. Furthermore, they observed ERD over the foot area during foot movements, but ERS over the hand area. This enhancement of mu rhythm over the hand area may be explained as an electrophysiological correlate of a temporary resting or idling hand area.

Mu rhythm studies have also explored the somatotopic characteristics of mu rhythm in development. Marshall and colleagues explored infants' somatotopic pattern of mu rhythm activity when infants acted upon objects with their own hands or feet and also observed an experimenter use her hands or feet to achieve the same goal (Marshall, Saby, & Meltzoff, 2014). Specifically, they explored ERD over sensorimotor areas that

corresponded to the hand (C3/C4 electrodes) and foot areas (Cz). They found that during infants' own production of hand acts, mu ERD over the hand areas was greater compared to mu ERD over the foot area. Further, they found that during infants' own production of foot acts, greater mu ERD was observed over the foot area compared to the hand areas. These results also extended to the observation condition during which the infant observed the experimenter performing hand and foot acts.

Other mu rhythm studies have demonstrated that early mu ERD, possibly indicative of motor preparation, is found over the contralateral central region comprising the primary motor cortex. Then, it is followed by a bilateral desynchronization occurring over the ipsilateral and contralateral central regions during the production of the motor movement (Leocani et al., 1997). These results suggest that contralateral mu ERD is associated with motor preparation while bilateral mu ERD is related to the performance of the movement.

All together, these studies provide evidence that: a) mu rhythm reflects sensori-motor activity with desynchronization of this rhythm potentially reflecting an active state of the sensorimotor system, b) mu rhythm is functionally and topographically separate from the occipital alpha rhythm, c) body part areas such as the hand and foot areas may have their own intrinsic mu rhythm activity, and d) desynchronization of mu rhythm is observed before production of actions, with contralateral mu ERD occurring during motor preparation followed by ipsilateral ERD occurring during action production.

2.2.3 Mu Rhythm Activity as a Neural Index of Action Perception Coupling

Similar to the properties of mirror neurons (i.e., discharging during both observation of execution of action) studies have demonstrated that mu rhythm exhibits

mirroring properties. That is, this rhythm not only desynchronizes during production of motor actions (as discussed above) but also during *observation* of actions. In fact, empirical interest in this phenomenon (that mu rhythm desynchronizes during observation of action) did not gain much attention between the 1950s and 1990s. However, after the discovery of MNs, this phenomenon was revisited to examine mu rhythm as a neural correlate of a coupling between action and perception. A recent meta-analysis of mu rhythm studies found moderate effect sizes of mu ERD during observation and execution of actions, suggesting that it is a robust phenomenon and that mu ERD may be used as a neural index of action perception coupling (Fox et al., 2015).

Importantly, similar to the characteristics of MNs in the monkey, studies in both adult and infant/children populations have demonstrated that mu rhythm desynchronizes during observation of object-directed or goal-directed actions such as grasping and communicative gestures (Muthukumaraswamy, Johnson, & McNair, 2004; Southgate, Johnson, El Karoui, & Csibra, 2010; Streltsova, Berchio, Gallese, & Umilta, 2010). For example, Avanzini and colleagues examined mu rhythm activity during perception of different types of hand movements. They found that these movements induced mu ERD during observation of these movements analogous to that occurring during execution of these movements providing evidence of a neural mechanism that matches observed action to executed action (Avanzini et al., 2012). Therefore, it is suggested that the functional characteristics of mu rhythm may parallel those of MNs in the monkey, i.e., that mu rhythm may also be modulated by the goal-specificity of actions and that mu ERD desynchronizes during meaningful actions. In sum, mu rhythm activity may also reflect higher cognitive functions associated with motor actions such as the goal of the

action (Jaime Pineda, 2005). Mu rhythm, which is suggested to reflect an activity of the sensorimotor system, 'translates' what we see and perceive into our own actions.

2.2.4 Action Perception Coupling in Adult Populations

Studies have demonstrated mu ERD during action perception (and execution) of motor actions in adult populations. From these observations, mu ERD during observation and execution of motor actions is used to suggest an activity of an action-perception link, and that mu ERD may be sensitive to goal-directed actions (Avanzini et al., 2012; Marshall, Young, & Meltzoff, 2010).

Muthukumaraswamy and colleagues recorded mu rhythm in healthy adults while the participants observed either a precision grip of a manipulation (object or goal-directed) or an empty grip using the same hand position (non-goal directed). They found that the magnitude of mu ERD was significantly higher for the object grip condition compared to the empty grip condition, providing support that mu ERD is tuned to whether perceived actions are goal-directed or not goal-directed (Muthukumaraswamy et al., 2004).

Additional studies have demonstrated mu ERD during observation and execution of goal-directed and meaningful actions such as gripping a wooden board, observing meaningful actions, and during observation of communicative gestures (Calmels et al., 2006; Muthukumaraswamy & Johnson, 2004; Streltsova et al., 2010). For example, point-light display of meaningful motion (a person doing jumping jacks) desynchronizes the mu rhythm during observation of this motion. In contrast, observation of non-meaningful motion (scrambled meaningless point-light motion) did not result in mu rhythm desynchronization (Ulloa & Pineda, 2007). Together, these studies provide

evidence for mu rhythm as a neural correlate of both action and perception, and not only this, but that the activity of mu rhythm may be similar to the functional characteristics of MNs in that meaningful and goal-directed actions modulate this brain rhythm.

2.2.5 Action Perception Coupling in Infant Populations

Infant studies of mu rhythm have also demonstrated parallel findings to the adult literature (Cuevas, Cannon, Yoo, & Fox, 2014; Marshall et al., 2010; Saby, Marshall, & Meltzoff, 2012; Stapel, Hunnius, van Elk, & Bekkering, 2010; Virji-Babul, Rose, Moiseeva, & Makan, 2012b). Southgate and colleagues examined mu rhythm desynchronization during perception and execution of object-directed grasps in 9-month-old infants. They found that mu ERD during action perception directly matched the magnitude of mu ERD during infants' action production (Southgate et al., 2009). In another study, Marshall and colleagues explored mu rhythm activity during observation and infants' own execution of object-directed action, a button-pressing action (Marshall et al., 2010). They also found that during perception and execution of the goal-directed action, significant mu rhythm desynchronization was observed over central sites, providing evidence for mu rhythm as a neural correlate of action and perception coupling.

In addition, another study assessed the recruitment of the sensorimotor system during perception of actions. Southgate and colleagues examined mu rhythm activity during observation of goal-directed action (grasping hand) and found mu ERD during perception of goal-directed hand actions but during perception of mimed hand actions with no object present in 9-month-old infants (Southgate et al., 2010). These findings suggest that mu rhythm is a viable neural index of action perception coupling in infants. Although infants' motor repertoire is still developing, studies have used reaching

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behaviors to examine mirror activity. In fact, mu desynchronization is reported during observation and execution of object-directed action (Marshall et al., 2011; Nyström, Ljunghammar, Rosander, & Von Hofsten, 2010). Greater mu ERD has been reported during observation of object-directed grasps compared to mimicked grasps. In addition to object reaches, goal-directed actions such as button presses and meaningful actions such as observation of walking and crawling have also been reported to induce mu ERD in infants (Saby et al., 2012; van Elk et al., 2008).

A recent study also found that mu ERD was specific to goal-directed actions. Filippi and colleagues (2016) recorded mu rhythm while 7-month-old infants' observed and responded to actions of an experimenter (grasping objects). They found that greater mu ERD during observation of the experimenter's action was observed prior to the infants reproducing the experimenter's goal compared to when infants acted on the object that was not the experimenter's target object (i.e., goal object; Filippi et al., 2016). In addition, they found that mu ERD during execution was related to the infants' later propensity to reproduce the experimenter's goal-directed action. In sum, their findings suggest that mu ERD is sensitive and differentially responds to the goal aspects of an action, and this phenomenon can be observed early on in life.

The studies outlined in this section demonstrate that mu ERD may indeed be a sensitive index to the goal properties of actions. Actions that are goal-directed (in these studies, object-directed) and meaningful are related to greater magnitude of mu ERD, and this is observed in the first year of life. The findings in infant mu rhythm research parallel those that are reported in the adult mu rhythm literature—that mu rhythm may index not

just the activity of action and perception coupling but that this brain oscillation may be functionally characteristic to actions that are goal-directed, intentional, and meaningful.

2.3 Activity of the Mu Rhythm and Action Experience in Adults

One central question regarding mu rhythm and action-perception coupling processes concern how motor experiences (e.g., dancing) may influence mu rhythm activity and possibly even its developmental trajectory. Further, it is suggested that experience with or the acquisition of particular motor actions may influence the perception of these actions since active motor experience of the action may facilitate the recognition or understanding of the perceived action. Adult studies of mu rhythm have demonstrated the relation between motor skills and mu rhythm activity. For example, individuals with acquired motor skills such as dancing show greater mu ERD during perception of the motor actions in their domain of expertise (i.e., greater activity of the action-perception system) compared to individuals without such abilities (Behmer & Jantzen, 2011; Orgs, Dombrowski, Heil, & Jansen-Osmann, 2008). Another study examining how tool use experience affects mu rhythm recruited three groups of adults: novices, observers, and performers. The novices had no experience with the tool (a mechanical claw to grasp objects). The adults in the observers group only had visual experience of watching an experimenter pick up objects with the tool, and the participants in the performers group had active motor experience with the tool (Cannon et al., 2014). They found that the performers who had the active motor experience with the tool had greater mu ERD compared to the novices and the observers groups. Thus, motor experiences may lead to the formation of a motor representation of these skills (Rizzolatti

et al., 2001), which influences the coupling of action and perception as measured via mu rhythm activity.

2.4 Activity of the Mu Rhythm and Action Experience in Infants

Recent studies of infants with mu rhythm have also demonstrated that mu rhythm activity may be experience-dependent. Specifically, not only has mu rhythm activity been demonstrated to reflect the activity of an action perception coupling in infants, specifically in relation to goal-directed actions, but there also exists evidence that suggests this neural signal may be tuned to infants' motor experiences. For example, one study has shown that 14- to 16-month old infants' mu ERD during perception of an infant crawling and walking was related to their amount of crawling and walking experience (in months) as reported by the caregiver (van Elk et al., 2008). Specifically, greater mu ERD was observed in infants who had greater experience crawling and walking, suggesting that mu rhythm may be experience-dependent and this phenomenon emerges in infancy.

As well, mu ERD has also been demonstrated with object weight in which infants' own experience with objects was reported to influence their perception of others' actions on the objects. Marshall and colleagues examined whether mu rhythm shows differential response to actions that shared similar goals but had different sensory or motor requirements (Marshall, Saby, & Meltzoff, 2013a). They varied the object weight to control for the abstract goal (e.g., grasp, reach, and lift the object) while enabling other aspects of the action to vary. They found that during observation of the experimenter's acting on the objects, infants' prior experience with the objects (e.g., light versus heavy objects) was related to the infants' mu activity during observation of the action. Specifically, differential mu activity was observed between observation of actions on

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heavy and light objects, i.e., the goal of the actions was the same but the object property (weight) was different, suggesting that prior experience contributes to the activity of mu rhythm.

In another study, Virji-Babul and colleagues (2012) exposed infants in the first year of life to goal-directed actions that were within their motor repertoire such as reaching for objects and found mu ERD during perception of these actions (Virji-Babul et al., 2012b). In a study with pre-walking infants, de Klerk and colleagues (2015) examined how experience influenced infants' perception of others' actions. They manipulated 7- to 9-month-old infants' opportunities to associate the visual and motor representation of a novel action, and investigated mu rhythm activity when the infants observed this action that was performed by others (de Klerk et al., 2014). The infants performed stepping movements in an infant treadmill while they either observed their own real-time leg movements or previously recorded leg movements of another infant (only visual experience). At post-test (after experience), they found that greater mu ERD during observation was associated with greater experience, providing evidence for the emergence of action and perception coupling that is related to infants' own experience.

Infant mu rhythm studies have also investigated how infants' emerging reach-grasp competence is related to mu ERD (beyond crawling and walking experiences). In a recent study, 9-month-old infants' grasping competence was quantified (e.g., latency to grasp toys), and this grasping skill was found to be associated with mu ERD during execution of grasps. In other words, infants who were more competent at reaching compared to less competent infants, showed greater mu ERD while observing an experimenter reach and grasp for objects (Cannon et al., 2015). A follow up study with

nine to twelve month old infants also found that infants' grasping competence was related to greater mu ERD during observation of a means-end action (e.g., an experimenter grasping for an object with a mechanical claw; Yoo, Cannon, Thorpe, & Fox, 2015). Together, infant mu rhythm studies demonstrate that the action-perception system is sensitive to the experiences of the infant and this phenomenon is reflected at neural level through mu rhythm activity.

Further, previous research has found that cortical activation during action perception was related to action production abilities in infants (Lloyd-Fox, Wu, Richards, Elwell, & Johnson, 2013). Specifically, Lloyd-Fox and colleagues found that neural activity over the sensorimotor areas was related to infants' motor competence measured by a standardized assessment. They measured neural activity in 4- to 6-month-old infants during perception of manual actions and administered a standardized assessment (e.g., Mullen Scales of Early Learning). They found that greater motor competence, specifically manual dexterity skills (i.e., fine motor skills), was associated with greater neural activity over the sensorimotor areas during perception of manual actions. Although they did not measure mu rhythm activity via EEG but rather used functional near-infrared spectroscopy (fNIRS) to measure sensorimotor activity, their results provide evidence of the relation between neural activity over the sensorimotor regions during action perception and infants' own motor competence and experience.

Although studies have demonstrated that mu rhythm is tuned to the motor experiences and skills of the individual, specifically greater mu ERD being associated with greater experience (Cannon et al., 2014, 2015; Paulus et al., 2012; van Elk et al., 2008), there also exists evidence to suggest greater motor experience is not associated

with greater mu ERD (Del Percio et al., 2010). Instead, a decrease in mu ERD is observed in line with the "neural efficiency" hypothesis, which posits that a more efficient cortical function is achieved with better performance in cognitive functions.

These mixed findings outlined above may be attributed to a methodological difference in which motor experience is measured differently across studies. Some studies examine mu activity in relation to crawling and walking (van Elk et al., 2008), to preshaping and bimanual reaches (Cannon et al., 2015), and latency to reach for an object (Yoo et al., 2015). Therefore, the inclusion of standardized assessments of motor competence allows us to standardize the method with which we measure motor competence, which may help clarify the mixed findings that report a relation between mu activity and motor skills and competence.

2.5 Summary and Hypotheses

Behavioral studies in developmental research demonstrate that action and perception are intimately linked and that this relation between action and perception emerges early in life. Further, this coupling appears to be related to infants' analysis of others' actions as goal-directed. Studies have demonstrated that infants' experience with goal-directed actions facilitates their analysis of others' actions as meaningful, intentional, and goal-directed. As well, a growing body of work demonstrates that this phenomenon can be observed on a neural level with mu rhythm activity. These mu rhythm studies in both adults and in infants document that this rhythm responds differentially to goal-directed motor actions compared to meaningless non-goal-directed actions. In addition, both behavioral and electrophysiological work demonstrates that the action-perception system is modulated by one's own prior action experiences.

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However, existing infant work on action-perception coupling and its neural bases (via mu rhythm activity) has so far examined mu rhythm modulation after infants have acquired action experiences. If mu rhythm activity is tuned to one's action experiences, then it is plausible that mu rhythm may indicate one's readiness to learn novel actions, specifically goal-directed actions. However, no known studies have investigated how individual differences in mu rhythm activity are related to infants' learning of novel goal-directed actions. Thus, it remains unclear to what extent the state of one's action-perception abilities, i.e., one's readiness to learn, can elucidate one's learning of goal-directed actions. Elucidating these relations in development may provide further support for the specificity of mu rhythm to meaningful goal-directed actions, which is an important step in understanding the social and cognitive processes in infancy.

In addition, as mentioned previously, there are mixed findings regarding the relation between mu rhythm activity and motor experiences and competence of the individual. These mixed findings may be due to a methodological difference between the mu rhythm studies. Specifically, mu studies that examine the relation between motor experience/competence and mu rhythm activity measure motor competence using behavioral coding of various skills (e.g., reaching, grasping, and crawling), and parent report of motor competence. Therefore, the inclusion of standardized assessments of motor competence allows us to standardize the method with which we measure motor competence, which may help clarify the mixed findings that report relations between mu activity and motor skills and competence.

Finally, the current study examines the relations between mu rhythm activity, learning of a novel goal-directed action, and motor competence using standardized

assessments of motor competence in infants. Specifically, the present study investigates whether mu rhythm activity reflects infants' learning of a novel goal-directed action above and beyond behavioral assessments of infants' motor competence.

The present study had four aims: 1) examine individual differences in mu rhythm activity and infants' ability to learn a novel goal-directed means-end task compared to a non-goal-directed task, 2) investigate the relations between infants' motor competence and their learning of a novel goal-directed means-end task, 3) assess the relation between mu rhythm activity and motor competence, and 4) examine whether mu rhythm activity predicts infants' learning of a novel goal-directed means-end task above and beyond motor competence assessments.

We recruited 9-month-old infants and randomly assigned them to one of two groups. The first group learned a novel means-end task, a task that was adapted from Sommerville and colleagues (Sommerville et al., 2008). The second group learned a novel statistical learning task, specifically a visual pattern learning paradigm (i.e., comparison task) adapted from Saffran and colleagues (Saffran et al., 2007) to assess infants' learning in a task that did not involve a goal-directed component. This task was chosen, because this learning task did not have a goal component to the learning (i.e., it is a sequence learning task), and it did not require an action or motor response from the infant. Further, visual pattern learning tasks have been implemented with infants in the first year of life and indicate that infants around 9-months of age could learn to extract rules from these tasks (Fiser & Aslin, 2002; Saffran et al., 2007). To measure mu rhythm activity, infants' EEG was collected during an observation and execution paradigm for which they observed goal-directed actions performed by an experimenter, and the infants

reached for objects themselves.

Next, we evaluated infants' motor competence using a battery of standardized assessments to investigate whether: a) infants' emerging motor competence can inform their learning of goal-directed means-end task, and b) mu rhythm activity can predict infants' learning of a goal-directed task above and beyond standardized assessments of motor competence.

We made the following hypotheses: 1a) variations in mu rhythm activity (i.e., specific to central sites) during perception and execution of a goal-directed action would be related to infants' learning of a novel goal-directed means-end task, specifically that greater mu ERD would be related to better learning, 1b) ERDs across the scalp (frontal, central, parietal, and occipital) would be related to infants' learning of a novel non-goal-directed task (comparison task), 2) motor competence would be related to infants' learning on the goal-directed means-end task, i.e., greater motor competence would be related to better learning on the goal-directed means-end task, and 3) mu rhythm activity during observation and execution of a goal-directed action would be related to infants' early motor competence, i.e., greater mu ERD related to greater motor competence, and 4) mu rhythm activity during observation and execution of a goal-directed action would predict infants' learning of a novel goal-directed task above and beyond motor competence assessments.

Chapter 3: Methods

3.1 Participants

Sixty full-term 9-month-old infants (*M* = 9.07, *SD* = 0.42; 34 females, 26 males) participated in this study. We selected nine month-old infants because around this age, infants begin to recognize the goal component of actions and recognize as well as engage in means-end actions (Behne et al., 2005; Johnson-Frey, 2004; McCall & Clifton, 1999). Infants were recruited from the Infant and Child Studies Database (ICSD) around the Washington D.C. region. The ICSD is managed by the Infant and Child Studies Consortium, which are led by developmental researchers at the University of Maryland, College Park. All infants were typically developing with no known or suspected neurodevelopmental or medical diagnoses. Prior to infants' participation in the study, informed consent—approved by the University of Maryland Institutional Review Board—was obtained from the infants' parents. At the end of the visit, we gave $20 as compensation to the parent/caregiver and a toy to the infant. For the Cane Task, 32 infants were recruited, however, 2 infants were excluded from the final sample due to technical difficulties, and 3 infants excluded due to excessive fussiness. For the Visual Pattern Learning Group, 28 infants were recruited, however, 3 infants were excluded in the final sample due to technical difficulties, and 6 infants excluded due to excessive fussiness.

3.2 Observation and Execution Task

The infants, fitted with an EEG cap (see below for EEG acquisition and processing), sat on their caregiver's lap approximately 40 cm away from the front of a

black puppet stage (99 cm [W] x 61 cm [L] x 84 cm [H]) placed on a tabletop covered with a black cloth. Black panel curtains covered the areas surrounding the stage to hide the two experimenters (all females) and the equipment from infants' view. Two video cameras were used to record events of interest during the testing session: 1) The first video camera was placed behind the experimenter focused on the infant, and 2) the second video camera was placed behind the infant and the caregiver focused on the experimenter. Caregivers were instructed to remain as observers and not to display any behaviors (e.g., pointing at the toy or at the experimenter) that may shift the infants' attention.

The task consisted of the following events: 1) Baseline event during which infants observed Experimenter 1 moving a geometric shape on a flashcard that was attached to a wooden handle, 2) Observation event during which infants observed Experimenter 1 grasping a toy, and 3) Execution event during which infants were provided the opportunity to grasp for the toy themselves. During these three events—baseline, observation, and execution—a taupe curtain operated by Experimenter 2 was raised and lowered at the start and end of each of these events. To begin the baseline event, the curtain was raised, which revealed Experimenter 1, sitting across from the infant but with her head down, shaking the flashcard attached to the wooden handle side to side. After three seconds, the curtain as lowered to mark the end of the baseline event. To begin the observation event, the curtain was raised, revealing Experimenter 1 (still sitting across from the infant). Then, Experimenter 1 made eye contact with the infant while saying "Hi baby!" in order to capture the infant's attention. Next, Experimenter 1 shifted her gaze towards a toy that was placed at the center of the stage, but not within the infant's grasp.

Then, Experimenter 1 reached for the toy with her right hand, picked up the toy, brought the toy to herself, and gave the toy a brief shake. The curtain was then lowered to mark the end of the observation event, which lasted approximately 4 seconds.

During the execution event, a toy was placed on the tabletop, and the experimenter (with her head down to avoid eye contact), pushed the tabletop towards the infant within reaching distance as the curtain was being raised. Infants were given approximately 60 seconds to reach for the toy, and if not, the event ended by lowering the curtain and the procedure continued on to the next event. After the infants obtained the toy, the tabletop was retracted, and the curtain was lowered to mark the end of this event, and the toy was retrieved from the infant (See Figure 3-1 for an example of a trial).

Infants completed up to 12 trials ($M_{trials\_completed} = 10.54$, $SD_{trials\_completed} = 2.58$, minimum = 4, maximum = 12). One trial consisted of baseline, observation, baseline, and execution with the order in which the observation or the execution event was presented first was pseudo-randomized. Six unique toys were used, with the same toy used within one trial for observation and execution. The same toys were reused for the second set of 6 trials, and the observation and execution task lasted approximately twenty minutes.

| **Baseline** | **Observation** | **Baseline** | **Execution** |
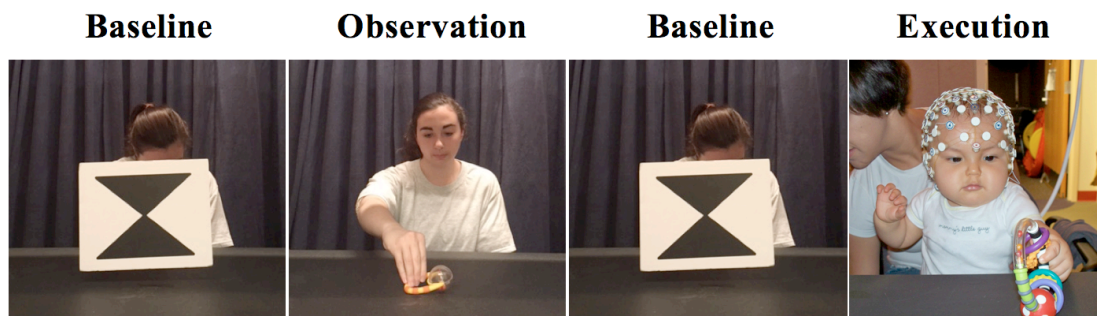
Figure 3-1 An example of one trial for the Observation and Execution Task.

Electroencephalogram was recorded using a 128-channel HydroCel Geodesic Sensor Net and sampled at 500 Hz via EGI software (Net Station v4.5.4; Electrical Geodesics, Inc., Eugene, OR). The eye lead channels 125 through 128 (above and below the eyes) were removed from the net, thus, EEG data were collected from 124 channels referenced online to the vertex. Impedance values for all channels measured less than 100 kΩ at the start of EEG acquisition.

The pre-processing and computation of desynchronization were carried out using MATLAB (R2015a; Mathworks, USA). Continuous EEG data were baseline corrected and forward/reverse Butterworth filtered (1-50 Hz pass band, 0.1-59 stop band, 10 dB attenuation, and 3 dB maximum ripple) and re-referenced to the average of 115 electrodes, because we excluded from this reference channels (17, 38, 43, 44, 48, 49, 113, 114, 119, 120, 121, 125, 126, 127, 128, 129), which lie about the sides of the face and at the nape of the neck, and as such are heavily prone to net displacement artifact. A threshold of ± 150 μV was used for artifact editing to remove excessive movements and spurious noise. Continuous EEG data were sectioned into 125 ms epochs and epochs in which more than 10% of all good channels exceeded this threshold were rejected (the sample numbers of all such discontinuities were recorded for purposes of identifying bad trials after segmentation). The resulting data were then decomposed into Independent Components using the FastICA algorithm developed by Hyvärinen & Hurri (2004) and Hyvärinen (1999). The implementation of an ICA converts the EEG data into a matrix that contains spatially fixed and temporally independent components in which the number of EEG channels matches the number of components (Lee, Girolami, & Sejnowski, 1999). Components related to eye movement and net displacement over the

front of the head were identified for rejection using a two-fold criterion. First, rejected components had to have greatest loading magnitude at one of the designated set of channels located over the most anterior part of the head positioned closest to the eyes (specifically channels 1, 2, 8, 9, 14, 15, 21, 25, 26, 32, 122). Second, rejected components had to have peak spectral power outside a band of interest chosen as 4-16 Hz. This second criterion ensured we only reject frontally dominant components with EEG peaked in either the 0-4 Hz delta band (such as the components related to blink/saccade/net-displacement waveforms) or >16 Hz (such as components related to high frequency broadband muscle artifact). We utilized this method of artifact rejection based on previous infant EEG studies (Cannon et al., 2015; Thorpe, Cannon, & Fox, 2015; Yoo et al., 2015).

For the observation and execution events, a 1,000 ms window was used to segment the EEG. For both events, the segmentation window was -1,000 to 0 ms *prior* to the touch that resulted in the grasp and pick up of the toy by the infant (for execution) or by the experimenter (for observation). If there was no toy pick up (as was the case for some infants), we considered the time when when multiple fingers were wrapped around the toy. This segmentation window was chosen based on evidence indicating that mu rhythm starts to desynchronize before action completion (Neuper & Pfurtscheller, 2001; Southgate et al., 2009; Yoo, Cannon, Thorpe, & Fox, 2015). As well, the segmentation for these two events (observation and execution) were based on previous research on mu rhythm research that uses live presentations rather than recorded/video presentations (Cannon et al., 2014; Thorpe et al., 2015; Yoo et al., 2015). For both conditions, the segmentation windows involve the period of time that surrounds the grasping of the

object for both the presenter and the infant. For the baseline event (flashcard presentation), the middle 1-second time window was segmented, i.e., -2,000 ms to -1,000 ms from the *end* of the baseline event. Importantly, any trials for which the earlier artifact thresholding procedure resulted in a discontinuity occurring anywhere in the window of analysis for either the baseline or observation/execution event segment was excluded from analysis.

Event-related de/synchronization (ERD/ERS) across scalp locations was computed in the 6-9 Hz band *a priori* for each observation and execution trial and channel. Previous infant studies of mu rhythm activity have demonstrated that infant mu rhythm is found in this frequency band (Marshall, Bar-Haim, Fox, 2002; Saby, Marshall, & Meltzoff, 2012). The primary channels of interest for mu rhythm activity were clusters of electrodes over the central sites according to the 10/20 system (C3: 29, 30, 36, 41, 42; C4: 93, 103, 104, 105, 111). To explore event-related de/synchronization (ERD/ERS) of EEG power in the same frequency band as mu rhythm and for comparison during analysis, frontal, parietal, and occipital electrode clusters were also analyzed (F3: 19, 20, 23, 24, 27, 28; F4: 3, 4, 117, 118, 123, 124; P3; 47, 51, 52, 53, 59, 60; P4: 85, 86, 91, 92, 97, 98; O3: 66, 69, 70, 71, 74; O4: 76, 82, 83, 84, 89; See Figure 3-2). The ERD/ERS compared spectral power of observation and execution trials to baseline segments that preceded each of the observation and execution trials. EEG power over the one-second segment window for observation and execution was averaged to compute a value for ERD/ERS, and this methodology was based on existing research on how to compute ERD/ERS (see Pfurtscheller & Lopes da Silva, 1999).
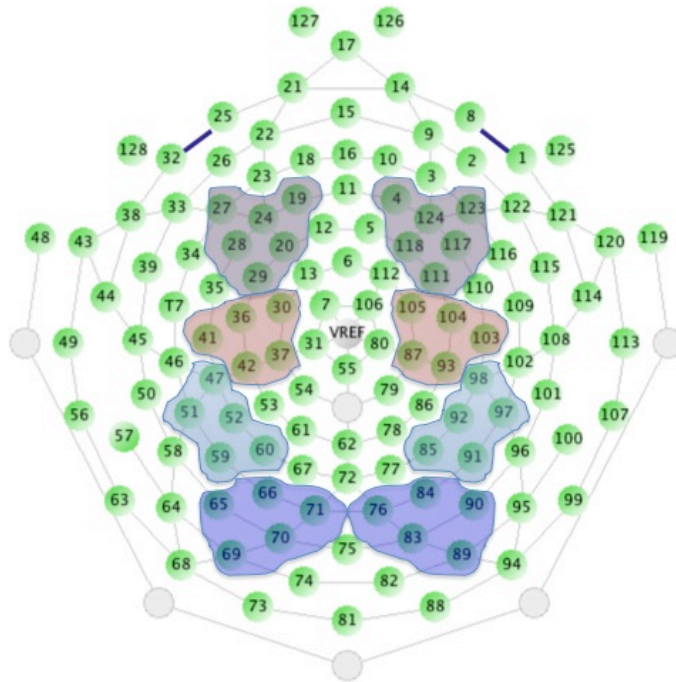
Figure 3-2 Electrode clusters, from top to bottom, for Frontal, Central, Parietal, and Occipital scalp locations.

Fourier coefficients for each segment were obtained via Fast Fourier transform (FFT). ERD/ERS at the 6-9 Hz band was computed in dB units (i.e., ten times the log (base 10) ratio of power in the observation (or execution) and power in the baseline segment). Negative values indicate desynchronization with respect to baseline whereas positive values indicate synchronization. This computation was performed for each of the channels of interest. After ERD was computed for each observation and execution trial and for each channel, ERDs for observation trials were averaged over frequency bins (6-9 Hz; 1 Hz bins) and subsequently over the electrode clusters to derive ERD values over frontal, central, parietal, and occipital sites. An identical process was implemented for the execution trials to yield an average ERD for the execution condition for frontal, central, parietal, and occipital sites.

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3.3 Cane Training Task

As the novel motor task, a cane training task adapted from Sommerville, Woodward, & Needham (2005) was used. For this task, infants were seated on the caregiver's lap at the same black puppet stage used in the Observation and Execution Task. An experimenter (different from the experimenters for the Observation and Execution Task) sat to the left of the infant. The cane to use as a tool to obtain out-of-reach toys was placed in front of the infant. To begin the trial, the experimenter placed a toy approximately 20 inches away from the infant at the rook of the cane (see Figure 3-3 for set up of the task). The first trial was a pre-test trial, followed by 9 training trials, and 1 post-test trial. During the pre-test and post-test trials, the experimenter did not provide any assistance or cues to the infant on how to obtain the toy that was out of reach. Each trial ended after a) the infant pulled the cane and touched or grasped the toy, or b) 30 seconds have elapsed. During the training trials, the experimenter used a variety of methods to enhance the infant's ability to learn to use the cane to retrieve the toys. These cues provided by the experimenter involved tapping on the toy, tapping on the cane, helping the infant pull the cane, modeling cane pulling, and providing praise after the infants obtained the toy. Specifically, if the infant was attending to the apparatus but not being physically engaged with the apparatus (e.g., touching the cane, or staring at the apparatus), then the experimenter encouraged the infant to touch the cane by touching the infant's hand and then the cane. If the infant was not attending to the cane apparatus (e.g., looking elsewhere), then the experimenter tapped his/her fingers under the rook of the cane to draw the infant's attention to the apparatus. If the infant was holding onto the cane but was not moving it, the experimenter pointed between the cane and the toy. If the

infant kept pulling the cane back and forth, the experimenter re-oriented the infant's attention to the toy by tapping her fingers by the toy. Also, if the infant did not pick up the toy after raking the toy in, the experimenter squeezed the toy to draw the infant's attention to the toy. These behavioral cues have been adapted from Sommerville et al. (2005) to facilitate infants' learning of the cane task. The cane training task lasted approximately 10 minutes.

Figure 3-3 Set up of the Cane Training Task.

3.4 Visual Pattern Learning Task

A visual pattern learning task adapted from Saffran, Pollak, Seibel, & Shkolnik (2007) was used to assess infants' learning in a task that did not involve a goal-directed component (our comparison learning task). Visual pattern learning tasks have been implemented with infants in the first year of life and indicate that infants around 9-months of age could learn to extract rules from these tasks (Fiser & Aslin, 2002; Saffran et al., 2007). Infants were seated on their caregiver's lap, and exposed to triads of color photographs of dogs taken from the breed standard of the American Kennel Club[SM] (AKC) as shown on the AKC website. Dogs were chosen as stimuli, because young

infants treat pictures of dogs as members of the same category despite considerable perceptual diversity across the examples (Quinn, Eimas, & Rosenkrantz, 1993). Thus, pictures of dogs and other animals are the most frequently used stimuli in habituation-based studies of infant visual categorization.

Infants were familized with the stimuli with either an ABA sequence or ABB sequence (half of the infants in the ABA group and half in the ABB group). Thus, ABB
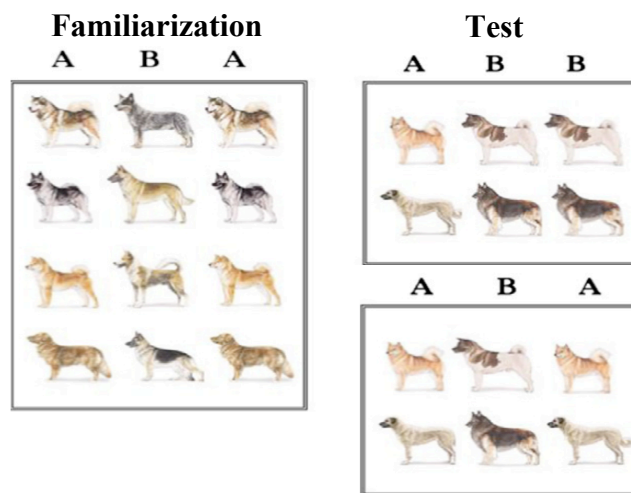
Figure 3-4 Example of the familiarization phase for an ABA sequence (left). Four test items (novel and familiar) for the test phase. Each triad of dogs indicates a single test event (Image adapted from Saffran et al., 2007).

sequences were novel to the infants in the ABA group, and vice versa. Four pictures were assigned to the A group and four to the B group. Then, the A and B pictures were combined to generate 16 different ABA and 16 different ABB sequence triads. Previous research has demonstrated that visual pattern learning is influenced by the use of sequential stimulus presentation compared to simultaneous stimulus presentation (e.g., Saffran, 2002). Furthermore, visual categorization in infancy is facilitated by simultaneous presentation of the stimulus (Oakes & Ribar, 2005). Thus, both structures (sequential and simultaneous) were implemented in the presentation of the dog triads to

increase the likelihood of successful visual categorization for the infants. The first picture was displayed for .33 s towards the left edge of the screen, then the second picture was added to the right of the first picture; we presented this two-dog display for .33 s. After the third picture was added to the right of the second picture, the full sequence triad (ABA or ABB) was displayed for .83 s. Thus, each sequence triad was displayed for a total of 1.5 s. A blank screen (.5 s) separated each sequence triad. Then, an experimenter re-oriented the infant to the location whether the next triad conforming to the ABA or the ABB sequence triad was presented using short animations with sound (e.g., a ball bouncing up and down). The familiarization phase terminated after 25 trials (adapted from Saffran et al., 2007). After the familiarization phase, infants received 4 test trials in random order, repeated twice totaling 8 test trials. Each test trial consisted of repetitions of the triads made up of 4 novel dog species (different dog pictures from the familiarization phase). Half of the test trials followed the pattern seen during familizarization and half followed the novel pattern (ABB for infants in the ABA group and ABA for infants in the ABB group). The task lasted approximately 10 minutes. Example triads for familiarization and test phases for ABA group are presented in Figure 3-4.

3.5 Motor Competence Assessments

3.5.1 Caregiver Report of Motor Competence

The Early Motor Questionnaire (EMQ; Libertus & Landa, 2013) is a parent-report (or primary caregiver such as a nanny or a grandparent) measure of motor competence that is organized around various 'contexts' that an infant or child encounters in everyday

situations. The EMQ utilizes a 5-point scale (-2 to +2) to quantify the parents' certainty. A behavior is rated -2 if the parent (or caregiver) is sure the infant does not exhibit the behavior yet, and +2 if the parent is certain or remembers a particular instance where the infant showed the behavior in question. Further, the EMQ is composed of three sections of Fine Motor (FM: 48 items), Gross Motor (GM: 49 items), and Perception-Action section (PA: 31 items). Figure 3-5 provides sample items from the EMQ for the three sections.

For the current study, we shifted the scale from 1 through 5 (not -2 to +2). This does not affect the scoring of the EMQ as it is a linear transformation. With the scale of -2 to +2, it is expected that around nine months of age, infants score around zero (personal

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Gross Motor Scale

When placed into a sitting position on the floor, your child is able to…

A   … sit independently without support (hands lifted up).

B   … use hands and legs to scoot forward on his/her bottom?

C   … maintain a stable sitting position while turning head and torso to look around?

Fine Motor Scale

When sitting on your lap or in a high chair while playing with toys, you notice your child is able to…

A   … successfully hold on to a small object such as a ring or stick?

B   … reach for a toy with one hand by extending the arm and fingers?

C   … successfully grasp a toy with one hand following a reach?

Perception-Action Scale

While lying on his/her back in a crib, baby gym, or on the floor, your child sometimes will…

A   … turn the head all the way to one side (90°) to follow your face?

B   … notice his/her own hands and look at them for some time?

C   … swat at toys hanging from a baby gym or car seat?

Figure 3-5 Sample items from the Early Motor Questionnaire (EMQ) for Gross Motor, Fine Motor, and Perception-Action scales (Figure from Libertus & Landa, 2013).

communication with Klaus Libertus, December 2014). With our shifted scale, we would expect the infants who are around nine months of age to score around 147 for GM, 144 for FM, and 93 for PA. The means and SDs for the EMQ are presented in Table 1.

3.5.2 Standardized Assessments of Motor Competence Performed in the Laboratory

<u>Mullen Scales of Early Learning</u> (Mullen, 1995):

The Mullen is administered to infants and children up to sixty-eight months of age. This assessment has been widely used to measure motor competence in both typical and non-typical populations (Akshoomoff, 2006; Landa & Garrett-Mayer, 2006; Zwaigenbaum et al., 2005). For the five scales of assessment—gross motor, fine motor, visual reception, receptive and expressive language—separate T scores, percentile ranks, and age equivalents can be computed. For the purpose of the current study, the subscales of gross and fine motor tasks were used to assess infants' early motor competence and T-scores corresponding to scale raw scores were calculated by age.

Early Motor Questionnaire (EMQ)		
Gross Motor Score *M (SD)*	Fine Motor Score *M (SD)*	Action Perception *M (SD)*
Cane Training Group 132.64(17.10)	128.76(15.61)	90.85(13.27)
Visual Pattern Group 139.64(15.84)	127.55(7.04)	89.22(9.37)

Table 1 Means and SDs for EMQ scores by subscales (GM, FM, and AP) by group assignment.

<u>Alberta Infant Motor Scale</u> (AIMS; Piper & Darrah, 1994):

The AIMS is administered to infants from birth to eighteen-months of age. This assessment has been widely used to measure gross motor competence in both typical and non-typically developing infants, and has been demonstrated to be a reliable and valid

measure of gross motor competence (Jeng, Tsou Yau, Chen, & Hsiao, 2000). To test gross motor skills, infants are examined as they are moved into and out of 4 positions: prone, supine, sitting, and standing. The AIMS' items focus on variables such as weight bearing and postural alignment that contribute to motor skills. All the items on the Alberta are scored as observed (O) or not observed (NO). Subscale scores for the 4 positions, total score, and percentile rankings were calculated following the scoring guidelines in Piper & Darrah (1994).

The mean scores and their standard deviations as well as the percentile ranks for the Mullen GM, Mullen FM, and the Alberta are presented in Table 2. The percentile ranks indicated that the infants in both groups ranged from below average to above average.

	Mullen Gross Motor		Mullen Fine Motor		Alberta	
	T score M (SD)	Percentile M (SD)	T score M (SD)	Percentile M (SD)	Score M (SD)	Percentile M (SD)
Cane Training Group	39.54(14.04)	26.96(31.34)	46.13(46.79)	40.73(43.24)	41.31(3.81)	52.88(14.71)
Visual Pattern Group	39.84(11.49)	26.20(26.03)	44.32(11.77)	34.33(29.62)	45.02(6.07)	62.4(23.94)

Table 2 Means and SDs for Mullen Early Scales of Learning (GM and FM) and the Alberta by Group.

3.6 Procedure

Infants were randomly assigned to one of two groups: cane training or visual pattern learning group. Within the visual pattern group, infants were randomly assigned to either ABA or ABB condition. Families were invited for a single visit to the Child Development, and prior to coming into the laboratory, parents/caregivers completed questionnaires online regarding demographics and motor competence (EMQ). After

consent, the infant and the caregiver were escorted into a room for the Observation and Execution Task (during which EEG was recorded; see above for details on this task).

After the observation/execution task, half of the infants completed the cane training task and the other half completed the visual pattern learning task (see above for details of these two tasks). Afterwards, the caregiver and the infant were escorted into another room. Then, the Mullen and the Alberta were administered. For the Fine Motor Scale of the Mullen, the infant sat on the caregiver. Afterwards, the Gross Motor scale of the Mullen and the Alberta were administered on the floor so that the infant could freely move around the room. The infant was video recorded throughout the visit, which lasted approximately 1-1.5 hour.

3.7 Behavioral Coding and Reliability

3.7.1 Observation and Execution Task Coding

Recorded video was synchronized to the EEG at a resolution of 320 x 240 pixels and at a frame rate of 30 Hz, enabling the coding accuracy to be within approximately 33 ms for the infant behaviors in which we were interested. Datavyu (v:1.2.2), a video coding tool, was used to code the videos. Two independent coders viewed each video offline (100% of the videos) frame-by-frame and identified the following events: a) frame in which the presenter first made contact with the toy with her hand that resulted in grasp completion of the toy (observation condition), and b) frame in which the infant first made contact with the toy that resulted in grasp completion of the toy (execution condition). The segmentation for these two events (observation and execution) were based on previous research on mu rhythm research that involves live presentations rather than

recorded/video presentations (Cannon et al., 2014; Thorpe et al., 2015; Yoo et al., 2015). For both conditions, the segmentation windows involve the period of time that surrounds the grasping of the object. The inter-rater agreement within three frames was achieved on 100% of the trials for observation and on 100% of the trials for execution. The EEG data were segmented around these observation and execution events. In addition, trials in which infants were not attending to or reaching/grasping during the observation event were coded and excluded.

3.7.2 Cane Training Task Coding

Infants were recorded on video during the task and their behaviors were coded off-line to assess their training success. The outcome of each trial was coded for all trials. To be considered a successful trial, the infant had to pull the cane (raking the toy in) and touches/grasps/picks up the toy within 3 seconds. The 3-second criterion was used, because the infant would pull the cane and rake the toy in, however, sometimes would disengage his/her attention from the apparatus. Thus, executing a continuous flow of action (pulling the cane and touching/grasping the toy) would demonstrate that the infant learned the outcome of pulling the cane (i.e., getting the toy within reach). In order to establish inter-coder reliability, two independent coders coded twenty percent of the videos. The inter-coder reliability was 100%.

3.7.3 Visual Pattern Learning Task Coding

Infants were recorded on video to assess looking time, which was coded off-line. At the beginning of the task, we calibrated infants' gaze by shaking the toy outside of the edges of the monitor (top, bottom, left, and right) and in front of where the sequence triad

of dogs would appear (left, middle, right). As the experimenter was shaking the toy, she made sure that the infant was following the experimenter's toy shakes. We used this gaze information to discern whether the infant was looking at the stimuli (i.e., the pictures of dogs) and when they looked away from the stimuli. Datavyu (v: 1.2.2) was used to code the videos. The duration of the infants' looking time in ms (i.e., from the time the infant looked at the monitor to when the infant looked away from the monitor) was coded for each trial. Two independent coders coded twenty percent of the videos, and inter-rater reliability of infants' looking time (within plus or minus 500 ms) was 100%.

3.8 Preliminary Results and Data Analysis

3.8.1 Preliminary results—ERDs across the scalp

To examine differences in ERDs between conditions, hemispheres, and regions, we ran a repeated-measures Analysis of Covariance (ANCOVA) with Condition (Observation and Execution), Region (Frontal, Central, Parietal, and Occipital), and Hemisphere (Left and Right) as within-subjects factors, Group (Cane Task and Visual Task) as the between-subjects factor, and Age as a covariate. Greenhouse-Geisser correction for degrees of freedom was used for violations of sphericity. Post-hoc paired t-tests were used to follow up on any significant main effects of interactions and all p-values were Bonferroni corrected for multiple comparisons. In addition, to identify significant ERDs from zero, we employed one-sample t-tests against zero.

Our preliminary results revealed no main effects or interactions demonstrating that there are no differences in ERDs across conditions, regions, hemispheres, or between groups. Because we did not find any group or hemisphere differences, we collapsed the

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ERDs across the two groups (Cane Task and Visual Pattern Task) and the two hemispheres (left and right) to examine whether there are significant desynchronizations from zero in each condition (Observation and Execution). Our one-sample t-tests against zero revealed the following significant ERDs for Observation: Frontal ($t(45) = -3.12$, $p = .003$), and Central ($t(45) = -2.82$, $p = .007$). For the Execution Condition, the following significant ERDs were revealed: Central ($t(41) = 2.16$, $p = .04$), and Occipital ($t(41) = -2.27$, $p = .03$; see Figure 3-6). No other ERDs were significantly different from zero ($ps > .09$).
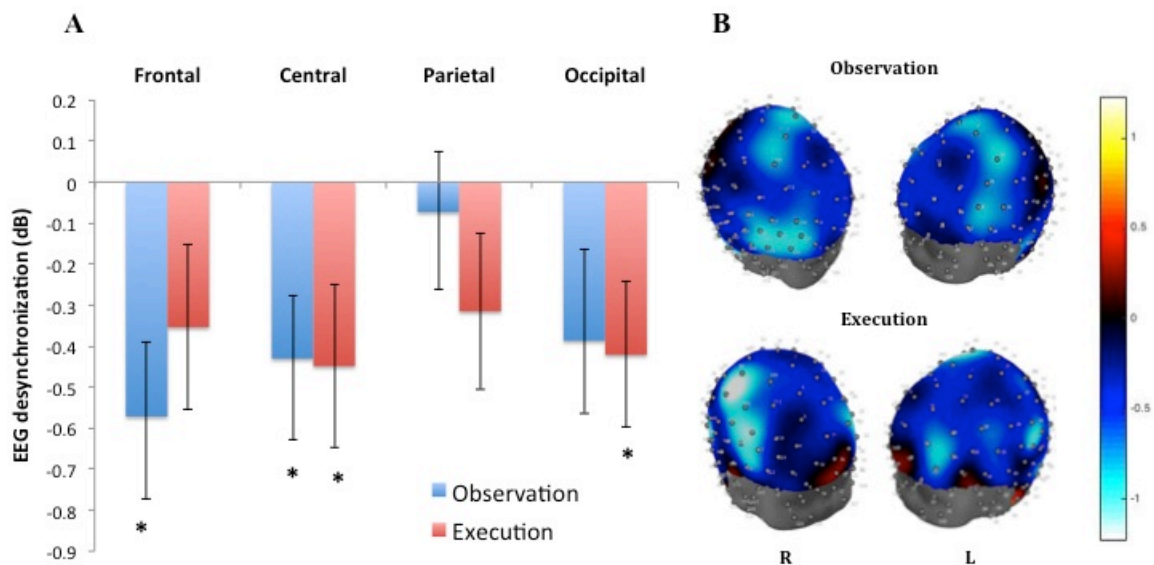
Figure 3-6 Panel A shows the means for ERDs by Condition (Observation and Execution) and Region (Frontal, Central, Parietal, and Occipital). Asterisks indicate significant ERD from zero at p-value of 0.05. Panel B shows the scalp topographies by Condition. Cooler colors indicate greater ERD.

In addition, we ran a partial correlation (controlling for age) between ERDs for observation and ERDs for execution. However, we did not find any relations between ERDs during observation over the four regions (frontal, central, parietal, and occipital)

and ERDs during execution over the four regions (frontal, central, parietal, and occipital; *ps* > .16).

3.8.2 Preliminary results—Relations between motor competence assessments

We examined the relations between the three motor competence measures used in the current study (Mullen, Alberta, and EMQ). First, we examined whether there was a significant difference between the two groups (Cane or Visual task) on the three motor competence measures of the Mullen, Alberta, or the EMQ. However, we did not find a significant relation between the two groups, thus, we collapsed across the two groups to look at the relations between the Mullen, Alberta, and the EMQ (Mullen (*t*(39) = -1.09, *p* = .28); Alberta (*t*(38) = -1.84, *p* = .17); EMQ (*t*(40) = -.62, *p* = .54)).

Next, we examined the relations between the three motor competence assessments (collapsed across the two groups as mentioned above). We ran a partial correlation (controlling for age) between each of the subscales of the three motor competence measures (2 subscales for Mullen, 4 subscales for Alberta, and 3 subscales for EMQ). To correct for multiple comparisons (9 comparisons), Bonferroni correction was applied (.05/9). Table 3 presents the correlation coefficients for the relations between the subscales of the Mullen, Alberta, and the EMQ. Significant correlations, which have p values of .005 or less, are marked with an asterisk.

Additionally, we ran a partial correlation (controlling for age) between the Mullen (GM and FM) and the EMQ, the Alberta and the EMQ (GM), and the Alberta and the Mullen (GM). To note, because the Alberta only assesses gross motor competence, we examined the correlation between the Alberta scores and the *gross motor* measures of the EMQ and the Mullen. We found a significant correlation between the Mullen and the

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Motor measures	Mullen (GM)	Mullen (FM)	Alberta (Prone)	Alberta (Supine)	Alberta (Sit)	Alberta (Stand)	EMQ (GM)	EMQ (FM)	EMQ (AP)
Mullen (GM)	1.00	.49*	.34	.27	.40	.36	.53*	.32	.42
Mullen (FM)	.49*	1.00	.04	.10	.42	.27	.37	.24	.37
Alberta (Prone)	.34	.04	1.00	.63*	.44	.61*	.24	-.04	.05
Alberta (Supine)	.27	.10	.63*	1.00	.31	.50*	.28	.07	.14
Alberta (Sit)	.40	.42	.44	.31	1.00	.47*	.23	.19	.22
Alberta (Stand)	.36	.27	.61*	.50*	.47*	1.00	.35	.08	.32
EMQ (GM)	.53*	.37	.24	.28	.23	.35	1.00	.53*	.50*
EMQ (FM)	.32	.24	-.04	.07	.19	.08	.53*	1.00	.66*
EMQ (AP)	.42	.37	.05	.14	.22	.32	.50*	.66*	1.00

*$p < .005$

Table 3 Correlation coefficients between the subscales of the motor competence measures (Mullen, Alberta, and EMQ). GM = Gross motor; FM = Fine motor; AP = Action perception. Significant correlations are marked with asterisks, Bonferroni corrected at p value of .005.

EMQ ($r(34) = .54$ $p = .001$), a significant relation between the Alberta and the EMQ ($r(33) = .331$, $p = .05$), and a significant relation between the Alberta and the Mullen ($r(37) = .49$, $p = .002$). Figure 3-7 shows the scatter plots of these three relations between the motor competence measures.
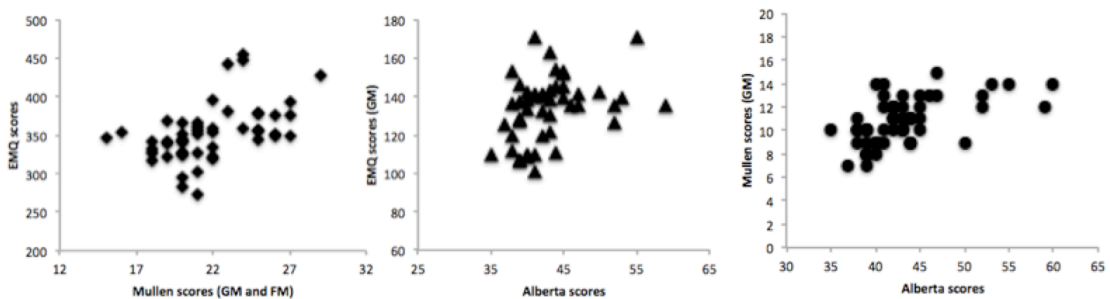

Figure 3-7 Scatterplots of the relations between the three motor measures of the Mullen, Alberta, and EMQ scores. EMQ and Mullen scores (left), EMQ (GM) and Alberta scores (middle), and Mullen (GM) and Alberta scores (right).

3.8.3 Data analysis

First, to examine the relations between mu rhythm activity and infants' learning on the two learning tasks (Cane Task and Visual Pattern Task), we computed learning indices for the Cane Task and determined whether infants learned the visual pattern task. To compute the learning index for the Cane Task, we fit a linear function (using the "least squares" method) across trials to calculate a straight line that best fitted the data, which yielded a learning slope (higher slope being equivalent to better learning) with an intercept for each infant. Next, we examined whether the infants learned the visual pattern task. We implemented an independent samples t-test to examine whether there were condition differences (i.e., looking time for the ABA group versus the ABB group). Then, we employed a paired t-test to examine whether infants looked longer at the novel sequence compared to the familiar sequence.

We then investigated the relations between ERDs across the four scalp regions (Frontal, Central, Parietal, and Occipital) and infants' learning on the cane task and on the visual pattern learning task. We employed a stepwise multiple regression analysis to determine how much of the variance in infants' learning on both the cane task and the visual pattern task is predicted by ERDs across the four scalp regions (i.e., which of the ERDs uniquely predicted the variance in infants' learning on both of the tasks). Separate stepwise regression analyses were run for ERDs during observation and execution conditions.

Second, we examined whether infants' motor competence (Mullen, Alberta, and EMQ) predicted infants' learning on the cane task. We employed a stepwise multiple

regression analysis to determine how much of the variance in infants' learning on the cane task was predicted by the infants' scores on the three assessments.

Third, we investigated the relations between ERDs across the four scalp regions (Frontal, Central, Parietal, and Occipital) and infants' motor competence measures. We employed a partial correlation (controlling for age) between ERDs across the scalp regions for each condition (Observation and Execution) and infants' scores on the Mullen, Alberta, and the EMQ.

Fourth, we examined whether variations in mu ERD (for Observation and Execution) predict infants' learning of a novel goal-directed action (Cane Task) above and beyond assessments of motor competence (Mullen, Alberta, EMQ). We employed a hierarchical regression analysis for which motor competence assessments were entered into the first model, and mu ERD was entered into the second model to determine whether mu ERD predicted infants' learning above and beyond motor competence measures.

Chapter 4: Results

4.1 The Relations between Infant Learning on the Cane Task and ERDs

<u>Hypothesis 1a:</u> Mu rhythm activity during perception and execution of a goal-directed action is related to infants' learning of a novel goal-directed task (Cane task), specifically, greater mu ERD is related better learning.

We first calculated the learning indices for the Cane Task. Figure 4-1 shows the learning slopes for each infant for the Cane Training Task where steeper slopes are equivalent to better learning ($M_{cane\ slope}$ = 0.47, $SD_{cane\ slope}$ = 0.35, minimum = 0.00, maximum = 1.00). Five of the twenty-seven infants, however, did not learn the task (i.e., had a slope of zero). We observed considerable variability in infants' learning on the cane task as shown in Figure 4-1.
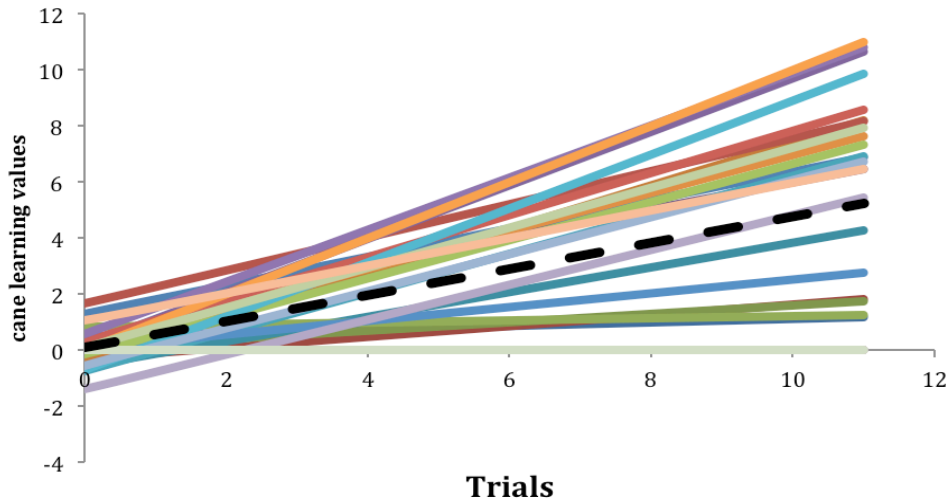

Figure 4-1 Learning slopes for the Cane Training Task where higher slope equals better learning. Trial 0 is equivalent to trial

We examined whether variations in infants' learning on the cane task were linked to the variability in ERDs across the scalp (frontal, central, parietal, occipital) during Observation and Execution, specifically whether ERDs during observation and execution of a grasp could be used to predict infants' learning slope on the cane task. We employed a stepwise multiple regression analysis (one for observation and one for execution following the analyses from Filippi et al. (2016)) to examine the relative contribution of activity at frontal, central (mu), parietal, and occipital sites to test if ERD at one site uniquely predicted infants' learning slope on the cane task. In the model, we included frontal ERD, central or mu ERD, parietal ERD, and occipital ERD during *observation* of a grasp to determine whether ERD activity at a particular scalp region during action observation was necessary to predict infants' learning slope on the cane task. The model began by entering in the predictor with the highest predictive value first and showed us that central ERD was entered into the regression equation. Central ERD was significantly related to infants' learning slope on the cane task ($F(1,25) = 4.65$, $p = .04$). The multiple correlation coefficient was .40, indicating that 16% of the variance in the learning slope could be accounted for by ERD over central sites. ERDs over frontal ($t = 0.14$, $p = .89$), parietal ($t = 1.24$, $p = .23$), and occipital ($t = 0.19$, $p = .85$) did not enter into the equation at step 2 of the analysis, because these ERDs did not uniquely predict any of the remaining variance in infants' learning on the cane task. Therefore, central ERD (i.e., mu ERD) during observation of a grasp uniquely predicted infants' learning of the cane task (see Figure 4-2). For ERDs during *execution* of a grasp, no predictors (frontal, central, parietal, and occipital) were entered into the regression equation, which demonstrated that the ERDs over the four regions did not predict infants' learning of the cane task.

Figure 4-2 Scatter plot demonstrating the relation between ERD over central sites (mu ERD) during action observation and cane learning slope for each infant.

4.2 The Relations between Infant Learning on the Visual Pattern Task and ERDs

Hypothesis 1b: ERDs across the scalp (frontal, central, parietal, and occipital) during observation and execution are related to infants' learning on a novel non-goal-directed comparison task (Visual Pattern task).

For the visual pattern task, we first compared the results from the ABA and ABB conditions. We ran an independent samples t-test to look at differences in looking time between the two groups. This analysis revealed no significant differences between the

2 conditions (t(17) = 1.11, p = .28), so results from the ABA and ABB conditions were combined in the following analysis. Infants looked significantly longer at the novel sequence (3.52 s, SE = 0.39) compared to the familiar sequence (2.81 s, SE = 0.33); t(18) = 3.00, p = .008 (see Figure 4-3). Sixteen of the nineteen infants showed this preference. These results, which are consistent with those reported in Saffran et al. (2007), indicate that the infants learned the dog sequence presented during familiarization and transferred this knowledge to include the new dog exemplars presented during the test phase.
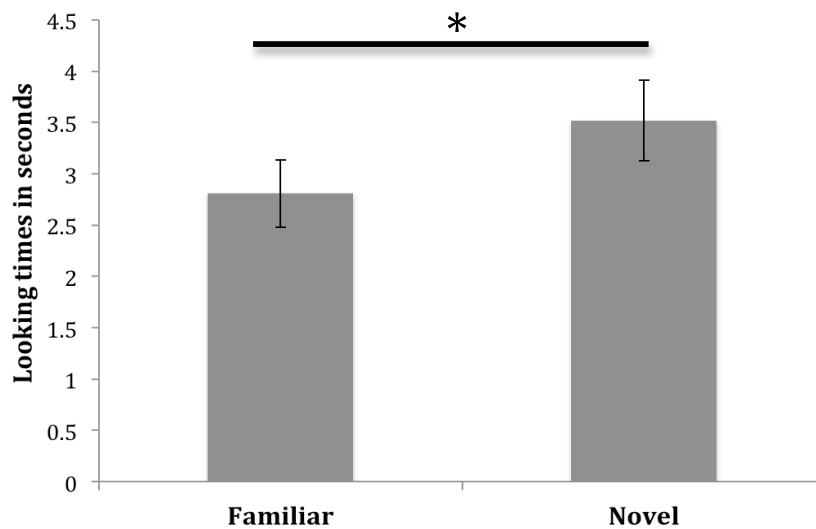
Figure 4-3 Looking times (sec) to familiar and novel test sequences, collapsed across conditions ABA and ABB.

Next, we examined whether ERDs during observation of a grasp could be used to predict variations in infants' learning on the visual pattern task. We employed a stepwise multiple regression analysis (one for observation and one for execution) to examine the relative contribution of activity at frontal, central (mu), parietal, and occipital sites to test if ERD at one site uniquely predicted infants' looking time on the visual pattern task. In the model, we included frontal ERD, central or mu ERD, parietal ERD, and occipital

ERD during observation of a grasp to determine whether ERD activity at a particular scalp region during action observation was necessary to predict infants' looking time. However, no predictors (frontal ERD, central ERD, parietal ERD, and occipital ERD) were entered into the regression equation, which demonstrated that the ERDs over the four regions did not predict infants' learning of the visual pattern task. This same analysis was employed for ERDs during execution of a grasp, however, none of the predictors were entered into the regression equation. Most importantly, these results demonstrated
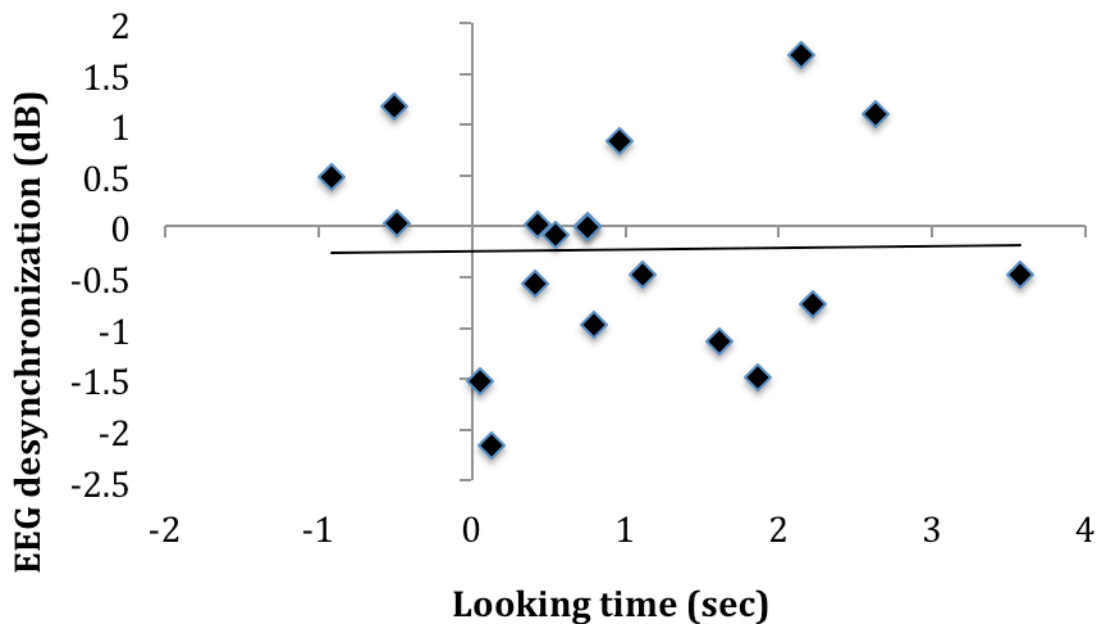
Figure 4-4 Scatter plot of the relation between ERD over central sites during action observation and looking time on the visual pattern learning task for each infant. In contrast to central ERD during observation predicting cane learning slope, central ERD during observation does not predict infants' learning of the visual pattern task.

that ERD over central sites (mu ERD) during observation did not uniquely predict infants' learning on the visual pattern learning task (see Figure 4-4). The same analyses (as observation) were conducted for ERDs during execution, however, none of the ERDs across the scalp were entered into the regression equation. These results suggest that mu

ERD does not uniquely predict infants' learning on the visual pattern learning task in contrast to infants' learning on the cane task.

4.3 The Relations between Motor Competence and Infants' Learning on the Cane Training Task

Hypothesis 2: Motor competence is related to infants' learning on a novel goal-directed task (Cane task), i.e., greater scores on motor competence assessments are related to better learning on a novel goal-directed.

We examined whether the subscales of the EMQ (GM, FM and PA), the subscales of the Mullen (GM and FM), and the subscales of the Alberta (supine, prone, sitting, standing) could be used to predict variations in infants' learning on the cane training task. Specifically, we wanted to see if one or more of these subscales from the three motor competence assessments uniquely predicted infants' ability to learn the cane task. We employed a stepwise multiple regression analysis—specifically, three stepwise regression analyses (one for each motor competence measure)—to examine the relative contribution of each of the subscales of the EMQ, Mullen, and the Alberta to test if a subscale (or combination) of the subscales of the EMQ, Mullen, or the Alberta uniquely predicted infants' learning slope on the cane task. However, no predictors were entered into the regression equation for all three motor competence assessments, which demonstrated that none of the subscales of the motor competence measures predicted infants' learning slope on the cane task. For mu ERD during execution, the same analyses as observation were employed, however, results revealed that none of the subscales of the motor competence measures of Mullen, Alberta, and EMQ were entered into the regression equation.

4.4 The Relations between ERDs and Motor Competence

<u>Hypothesis 3:</u> Mu rhythm activity is related to infants' motor competence, i.e., greater mu ERD during observation and execution related to greater motor competence.

We examined the relations between ERDs across the scalp for both observation and execution and motor competence measures used in the current study. We ran a partial correlation (controlling for age) between ERDs across the scalp (frontal, central, parietal, and occipital) and scores on the Mullen assessment, the Alberta, and the EMQ. However, for both observation and execution, we did not find any significant correlations between any of the ERDs (frontal, central (mu), parietal, and occipital) and motor competence measures ($ps > .11$).

Next, we examined whether grouping the infants based on their motor competence scores would be related to ERDs across the scalp for both observation and execution. For each assessment (e.g., EMQ, Mullen, Alberta), we binned the infants into 'high motor competence' and 'low motor competence' groups based around the mean, i.e., top 50% and bottom 50%, respectively. Then, we ran three independent samples t-tests (one for each assessment) to examine whether there were differences in ERDs between 'high motor competence' and 'low motor competence' groups. However, we did not find any group differences in ERDs (including mu rhythm during observation or execution) for any of the three assessments (EMQ, $ps > .16$; Mullen, $ps > .20$; Alberta, $ps > .14$).

4.5 The Relations between ERDs, Motor Competence, and Learning on the Cane Task

Hypothesis 4: Mu rhythm activity predicts infants' learning of a novel goal-directed task above and beyond motor competence assessments.

We investigated whether mu ERD during observation (and execution) predicted infants' learning on the Cane task above and beyond motor competence assessments. Specifically, we employed a hierarchical multiple regression to examine whether mu ERD during observation predicted infants' learning slope on the Cane task above and beyond the three standardized measures of motor competence (Mullen, Alberta, and EMQ). Because the scores of the Mullen, Alberta, and the EMQ were correlated ($ps <$ .03), we standardized the scores to address the issue of multicollinearity.

We entered into our first model, the motor competence assessments (Mullen, Alberta, and the EMQ). Then, to determine if mu ERD during observation predicted infants' learning slope on the Cane task, we entered mu ERD into our second model. However, neither the first nor the second model was significant ($ps >$ .58). We also employed the same analyses with mu ERD during execution entered into the second model, however, neither the first nor the second model was significant ($ps >$ .53), suggesting that mu rhythm activity did not predict infants' learning above and beyond motor assessments.

4.6 Summary of Results

We found that: 1a) mu ERD during observation of a grasp uniquely predicted infants' learning on the cane training task, 1b) mu ERD during observation and execution of a grasp did not uniquely predict infants' learning on the visual pattern learning task

(comparison learning task), 2) infants' motor competence did not predict infants' learning on the cane training task, 3) mu ERD during observation and execution was not related to infants' measure of motor competence (Mullen, Alberta, and EMQ), and 4) mu ERD did not predict infants' learning on the cane task above and beyond infants' motor competence assessments. Together, these results suggest that neural activity during observation of an action (i.e., mu rhythm) is related to infants' learning, and that mu rhythm is functionally related to goal-directed actions and reflects the neural activity associated with goal-directed actions.

Chapter 5: Discussion

The goal of the study was to investigate the relations between EEG activity, learning, and motor competence in 9-month-old infants. Specifically, the current study investigated: a) whether variations in mu rhythm activity were related to infants' ability to learn a novel goal-directed means-end motor task, b) whether variations in mu rhythm activity were related to infants' ability to learn a novel comparison task (visual pattern learning task) that did not have a goal-oriented component, c) whether infants' motor competence assessed through standardized measures was related to infants' learning of a novel goal-directed means-end task, d) whether mu rhythm activity was related to infants' motor competence, and e) whether mu rhythm predicted infants' learning of a novel goal-directed task above and beyond motor competence measures. To address these aims, infants' EEG was collected during an observation and execution paradigm for which they observed goal-directed actions performed by an experimenter, and when the infants reached for objects themselves. In addition, three measures of early motor competence (Mullen, Alberta, and EMQ) were collected to investigate whether infant motor competence can inform their learning of a novel goal-directed means-end task, and to examine how these motor competence measures, mu rhythm activity, and infants' learning are related.

In line with what we predicted, findings from the current study revealed that mu rhythm activity was indeed related to infants' learning of a novel goal-directed means-end task and not to infants' learning on the visual pattern learning task (comparison learning task). Specifically, greater mu ERD during *observation* of a grasp was related to

better performance on the means-end task. However, we did not find a relation between mu ERD during *execution* of infants' grasp and their performance on the goal-directed means-end task. Further, we initially hypothesized that infants' motor competence would be related to their performance on the means-end task. Contrary to this prediction, we did not find a relation between infants' behavioral measure of motor competence and infants' variations in their learning on the means-end task. We also predicted that mu rhythm activity would be related to motor competence assessments, however, we did not find this relation. Finally, we hypothesized that mu rhythm activity would predict infants' learning on the means-end task above and beyond motor competence assessments, however, we did not find this relation. A more detailed discussion of the current findings and their implications is presented below.

5.1 The Relations between EEG activity and Infant Learning on the Cane Task and the Visual Learning Task

5.1.1 EEG Activity during Action Observation and Infant Learning

The current study found a relation between infants' EEG activity and their performance in a novel goal-directed means-end motor task. Specifically, we found that infants' EEG activity over central sites (i.e., mu ERD) during observation of a grasp was specifically associated with infants' learning on the cane training task. Infants who exhibited greater mu ERD performed better on the cane training task. This result demonstrated that not only does mu ERD (in comparison to non-central ERDs) respond differentially to actions that are goal-oriented, but also that mu ERD may reflect the action-perception system's readiness to learn meaningful actions. To note, although we

found significant ERD in non-central sites during observation (frontal), we found the relation between infants' performance on the cane training task to be specific to central sites (i.e., to mu ERD). Our results are in line with findings from a previous study (Filippi et al., 2016) showing that mu ERD during observation of a grasp is greater in magnitude prior to infants reproducing the observed goal compared to infants' non-goal response, i.e., mu ERD during action observation differentially reflects infants' goal vs. non-goal-directed behaviors. Thus, our current finding is promising, adding to the developmental literature of investigating mu rhythm as a neural index of action-perception system and suggesting that this system emerges early in development and is associated with infants' emerging behavioral—specifically, goal-directed—capabilities.

Further, we also administered a visual pattern learning task (our comparison task) to a second group of infants to examine whether mu ERD during observation of a grasp was functionally specific to infants' learning of a novel goal-directed task. We predicted that ERDs across the scalp would be related to infants' performance on the visual pattern task. Contrary to our prediction, we did not find any relation between ERDs during observation and execution and infants' performance on the visual pattern task, which did not contain a clear goal-directed component, i.e., mu ERD is not specific to infants' performance on the visual pattern task. Our findings, thus, provided evidence that mu ERD during observation of a goal-directed action was functionally related to infants' goal-directed behavior.

It is important to note, however, that there also exists evidence demonstrating a relation between mu ERD during observation of actions that are not goal-directed (i.e., object-directed) and infants' own behavior. Van Elk and colleagues examined the relation

between mu ERD during observation of walking and crawling behaviors (not object-directed) and infants' own walking and crawling behaviors (van Elk et al., 2008). They found that greater mu ERD was associated with greater experience (in months) of crawling and walking. Thus, their results did not clarify whether the emerging action-perception system in infancy assessed via mu rhythm activity was necessarily functional to goal-directed actions, which was one of the aims of our current study. A recent meta-analysis (Fox et al., 2015) and an empirical study (Hobson & Bishop, 2016) report that mu ERD during observation was not specific to object-directed actions (compared to non-object-directed actions). Nonetheless, it is evident from their conclusions that there are motor contributions to mu rhythm activity during observation of action, thus, both object and not object-directed actions, which contain motor components, are related to one's own behavior. In other words, mu rhythm activity may not necessarily—or *exclusively*—reflect the object (i.e., goal) component of an action, but the entirety of the action itself including its motor components.

Our study is the first known study to examine whether mu rhythm activity can inform learning on novel tasks in infants. For our novel goal-directed task, the infants had to learn how to use a novel apparatus to achieve a goal (obtain an out-of-reach toy). For this novel task, infants had to string together motor abilities in their repertoire (e.g., pulling, grasping) to achieve a goal. Further, heterogeneity in mu ERD predicted infants' learning of this goal-directed means-end task. Although there are a few studies examining the relation between mu rhythm activity and goal-directed behavior (Cannon et al., 2014; Filippi et al., 2016; Yoo et al., 2015), our study is the first to examine, in infants, the

relation between sensorimotor activity via mu rhythm and learning of a novel goal-directed action.

5.1.2 EEG Activity during Action Execution and Infant Learning

Existing research suggests that mu rhythm activity—specifically, desynchronization of this rhythm during action perception *and* production—reflects the activity of a coupling between action and perception (Hari, 2006; Jaime Pineda, 2005; Vanderwert, Fox, & Ferrari, 2013b). We predicted that mu ERD during *execution* of a grasp (as well as during observation) would be related to infants' learning on a novel goal-directed means-end task. Contrary to our hypothesis, we did not find this relation between mu ERD and infants' learning. Further, this is in contrast to an existing published study examining the relation between mu ERD during execution and infants' goal-directed behavior. Filippi and colleagues found that mu ERD during execution of infants' grasp predicted the amount of infants' subsequent goal responses (Filippi et al., 2016). That is, greater mu ERD during execution of a grasp was related to higher proportion of goal response trials.

One reason for the difference between our results and Filippi and colleagues' (2016) results may be due to the fact that in our study, infants had to learn a new goal-directed action whereas the infants in the study by Filippi and colleagues (2016) did not. The infants in their study made their goal responses with hand grasping actions, whereas the infants in the present study had to learn a more complicated action sequence to obtain the object (i.e., achieve the goal). Both of our studies recorded mu rhythm activity during infants' execution of a grasp, however for the infant behavior, we examined how mu rhythm activity during action execution can inform our understanding of learning novel

goal-directed actions. On the other hand, Filippi and colleagues' (2016) examined how mu ERD during action execution is related to infants' goal-directed responses that are already in their action repertoire (grasping a toy with their hand). Thus, there is a closer match (compared to our study) between infant action during mu rhythm recording and subsequent infant object-directed behavior reported by Filippi and colleagues.

In addition, we found that mu ERD during production of a grasp did not uniquely predict infants' learning on a comparison learning task (visual pattern learning task). This task was chosen, because it did not have a goal component to its learning. As discussed previously, mu rhythm reflects motor and action processes (Fox et al., 2015; Muthukumaraswamy & Johnson, 2004), thus this finding is consistent with existing work that examines the relations between mu rhythm activity and motor processes.

Although we did not find that mu ERD during execution was related to infants' learning on a novel goal-directed means-end task, our present study nonetheless adds to the growing body of research on mu rhythm activity and infant behavior. To fully understand the role of mu rhythm, not only during action observation but also during action execution, more research is needed to disentangle what mu rhythm reflects during action and perception and its relation to infant behavior.

5.1.3 Action Observation, Action Execution, and Goal-directed Learning

Contrary to what we predicted, we did not find a relation between mu rhythm during action execution and infants' learning on a novel goal-directed task (i.e., cane task). We found a relation between mu rhythm during action observation and infants' learning on the cane task. Specifically, greater mu ERD during infants' perception of others' goal-directed action (e.g., grasping of an object) was related to better learning on

the cane task. These results may be attributed to two differences that existed between the action observation and the action execution condition.

First, during action observation, the experimenter was trained to reach and grasp in the same manner during the task (e.g., the duration of each trial was approximately four seconds, and the reaching and grasping were consistent for every trial). However, during action execution, infants were more variable in their reaching and grasping between trials, i.e., babies were not precise reachers and sometimes did not grasp and/or pick up toys. Thus, there was more variability in the action execution condition compared to the action observation condition, which may have contributed to our findings for the relations between cane learning, action observation, and action execution.

Second, during observation of the experimenter's grasping action, the infant saw the experimenter that also included her face (compared to, for example, seeing only her hand). Thus, there existed a socially contingent component during action observation compared to action execution (infants grasping the toy themselves). Before each action observation trial started, the experimenter made eye contact with the infant, and made a verbalization ("Hi baby") to draw attention to what the experimenter was about to do (grasping a toy). However, during action execution, this socially contingent aspect did not exist. Instead, the infants primarily saw their hands reaching for toys. Thus, it is possible that a social component may have driven the results we found (i.e., mu rhythm during observation, not during execution, related to learning).

In fact, research has demonstrated that mu rhythm is sensitive to social contexts and interactions (Gallese, Keysers, & Rizzolatti, 2004). Reid and colleagues recorded mu rhythm activity during face-to-face dyadic interactions in 14-month-old infants (Reid,

Striano, & Iacoboni, 2011). Specifically, the adult and infant engaged in copying each other's facial and hand actions. They found that during these dyadic interactions greater mu ERD was observed compared to a non-dyadic baseline condition, suggesting that mu rhythm during perception of others' actions may be sensitive to social contexts and interactions. In addition, the cane training task also had a socially contingent component. During the cane task, the experimenter sat next to the infant, showing the infant how to use the cane to obtain toys that were out of reach and providing verbal praise throughout the task. Thus, it is possible that the relation between mu rhythm during action observation and learning on the cane task may be attributed to the fact that both scenarios had a social component, whereas during action execution, this social aspect did not exist.

5.2 The Relation between Motor Competence and Infants' Learning on the Cane Training Task

The present study also examined the relations between infants' learning on a novel goal-directed means-end task and motor competence measures. As previously discussed, we found a relation between infants' performance on the cane training task and mu ERD, specifically, that mu ERD during perception of a goal-directed action predicted infants' ability to learn on the cane training task. It was possible that the infants who performed or learned better on the cane training task were more motorically advanced, which might have been sufficient to predict their learning on this task. However, contrary to what we predicted, we did not find a relation between infants' behavioral measure of early motor competence and infants' learning ability on the cane training task, specifically infants' Mullen, Alberta, and EMQ scores did not predict the infants' ability to learn the cane training task. Our initial hypothesis was based on a previous study with

infants using functional near-infrared spectroscopy (fNIRS), Lloyd-Fox and colleagues examined the relation between infants' perceptual processing abilities with infants' own action skills (Lloyd-Fox et al., 2013). They found that neural activity over the sensorimotor areas during infants' perception of others' manual hand actions was related to infants' fine motor skills (but not to gross motor skills). However, they did not examine the relation between infants' perception of *goal-directed* (i.e., object-directed) behaviors and infants' motor skills.

One possibility for our finding may be that our assessments of motor competence were not fine-grained or sensitive enough to detect individual differences in infants' motor competence. Although the EMQ (compared to the Mullen and the Alberta) was designed to extract individual differences (Libertus & Landa, 2013), it still used a 5-point Likert scale, which might not be sufficient to detect subtle variability in infants' motor competence. In addition, our three motor competence assessments are designed to indicate whether infants are 'lagging' behind in their motor skills, and are not necessarily used to predict whether infants' will learn novel motor skills. Our study was the first to use a neural measure to relate to infants' learning of a novel action. Thus, our results provide evidence that mu rhythm activity is: a sensitive measure of infants' action-perception abilities; and can be used as a sensitive neural measure to predict infants' ability to learn a novel action.

5.3 The Relations between ERDs and Motor Competence

We also wanted to examine the relations between ERDs (specifically mu rhythm activity) and infants' early motor competence using standardized assessments. Currently, no known studies examine the relation between mu rhythm—a motor signal that reflects

action and perception abilities—and standardized assessments of motor competence. In an fNIRS study, Lloyd-Fox and colleagues (2013) found a relation between neural activity over the sensorimotor regions during action perception (an experimenter opening and closing her fist) and infants' fine motor scores on the Mullen. However, we did not find a relation between ERDs (specifically, mu ERD) and motor competence assessments (Mullen, Alberta, and EMQ). To note, however, we recorded mu rhythm during perception of only one type of action, a grasping action. For our motor competence assessments, on the other hand, we assessed a broad range of motor skills from fine motor to gross motor skills (e.g., crawling, pincer grasps, and standing). Thus, we related mu activity during perception and execution of a grasping action and related this activity to general motor competence in infants. Future studies should record mu rhythm activity under a variety of action conditions, and examine whether the skills that the motor competence assessments measure are related to mu activity during production or perception of these various actions.

5.4 The Relations between ERDs, Motor Competence, and Learning on the Cane Task

Finally, we examined the relation between mu rhythm activity, infants' motor competence, and their learning on a novel goal-directed motor task. Specifically, we wanted to determine whether variations in mu ERD during observation and execution predicted infants' learning on the Cane task above and beyond behavioral assessments of motor competence. First, we did not find a relation between motor competence and infants' learning on the cane task. Second, the addition of mu ERD during observation (or execution) did not make any unique or significant contribution to the model. However,

this finding may be attributed to the fact that we did not observe any relation between mu ERDs (during observation or execution) and infants' motor competence, and between motor competence and infants' learning on the cane task. Thus, it is not surprising that the r-square changes in our hierarchical regression models were not significant. As mentioned above, future studies can examine motor competence using other assessments and relate this to mu rhythm activity. For example, future work can assess infants' grasping skill using the Grasping subscale of the Peabody Developmental Motor Scales and relate this to mu rhythm activity during observation and execution of a grasp.

5.5 Limitations and Additional Considerations

The current results should be interpreted in the context of the following limitations. First, the aim of the current study was to investigate how mu rhythm activity during action and perception of a goal-directed action (grasping a toy) informed infants' subsequent learning of novel goal-directed action (means-end task). We did not, however, include a condition in which infants observed the novel goal-directed action such as the cane task (and record EEG), and use this measure to examine whether mu rhythm activity during perception of novel goal-directed acts could predict subsequent learning of novel actions. Previous studies have reported mu rhythm modulation during perception of means-end actions in both adult and infant populations (Cannon et al., 2014; Yoo et al., 2015). Further, there exists evidence that mu rhythm activity during perception of means-end actions is tuned to the experiences of the individual. That is, adults who had prior experience with a means-end action (e.g., retrieving an object with a manually operated mechanical tool) showed greater mu desynchronization during perception of the same action performed by an experimenter (Cannon et al., 2014). Future studies can examine

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how perception of novel actions is related to infants' learning of the same novel actions. Nonetheless, our present study elucidates the relation between infants' mu rhythm activity and their subsequent learning of novel actions.

Second, we used a visual pattern task as our comparison task, because this task did not have a goal-directed component. Our results revealed that mu rhythm activity during action and perception of a grasp did not relate to infants' learning of the visual pattern learning task whereas mu rhythm activity was related to infants' learning on the cane training task. However, one reason that we did not find a relation between mu activity and visual learning may not necessarily be attributed to the fact that the visual learning task did not have a goal-directed component. The infants in the cane training task may have been more engaged in the task as this task was interactive, thus, we saw greater attrition in the visual pattern learning group (n=19) compared to the cane training group (n=27). In the cane training group, the experimenter demonstrated how to use the cane training apparatus, providing behavioral cues and positive verbal feedback (at the end of each trial), making it more engaging and interactive. For the visual pattern learning task, the infants sat on their caregiver's lap and watched repeated sequences of dog pictures on a computer monitor. Nonetheless, our study was the first to elucidate the relation between mu rhythm activity and infants' learning of a novel goal-directed task and inform our understanding of the neural indices of higher cognitive and motor processes.

Third, the study did not include a group that received training on the cane task without the object present, which would control for the goal component of the task. Infants could be trained to pull the cane but not obtain a toy, and the only difference

between the two groups of infants would be the presence of an object, i.e., the goal. Instead, we used the visual pattern task as a comparison task that did not have a goal component (i.e., obtaining a toy). For the current study, we examined the relation between mu rhythm and two types of learning: a learning of a novel goal-directed action, and learning of a non-goal-directed task. We chose a statistical pattern learning task, because this learning task did not have a goal component to its learning (i.e., it is a sequence learning task), and it did not require a motor or motor response component from the infant, which was important as the mu signal is suggested to be a sensorimotor response. Further, visual pattern learning tasks have been implemented with infants in the first year of life and indicate that infants around 9-months of age could learn to extract rules from these tasks (Fiser & Aslin, 2002; Saffran et al., 2007). Future studies can examine the mu signal in relation to other tasks that does not include a goal component. Nonetheless, our findings add to the literature on the link between mu rhythm and goal-directed actions, specifically the learning of a goal-directed action.

Fourth, as our measures of infants' early motor competence, we included three assessments. These assessments were the Mullen, the Alberta, and the Early Motor Questionnaire. The Mullen and the Alberta are laboratory assessments, and the EMQ is a parent-report of infants' motor competence. The EMQ is designed to reveal individual differences in early motor competence (by using a 5-point Likert scale), however, this questionnaire may not have been sensitive enough to detect heterogeneity in infants' learning on the cane training task (compared to mu rhythm activity). In general, the motor competence measures are used to assess whether infants are lagging behind certain motor milestones. In addition, the fact that infants do not display a certain motor skill in the

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laboratory does not necessarily suggest that they are unable (i.e., infant may be tired, not necessarily unable to execute a specific motor skill).

In addition, the current study did not gather data regarding infants' experience with means-end actions. There exists evidence to suggest that one's own experience can guide the perception of others' actions (Cannon et al., 2014; Sommerville et al., 2005; Southgate, Begus, Lloyd-Fox, di Gangi, & Hamilton, 2014). For the cane training task, the experimenter sat next to the infant and demonstrated how to use the cane to obtain the out-of-reach toy. Thus, infants' perception and processing abilities of the experimenter's action may be facilitated by the infants' own experience with means-end actions. Indeed, beginning at 5-6 months of age, infants begin to display sophisticated reaching ability. Infants become sensitive to the goal structure of reaching acts and by the first year of life, they demonstrate the ability to detect the relational goals of means-end actions (Sommerville & Woodward, 2005a; Sommerville & Woodward, 2014; Woodward, 1998). Our study included 9-month-old infants, which is a developmental time point during which infants are beginning to be acquainted with the relational goals associated with means-end and tool use actions. Therefore, there may exist variability in infants' means-end action experience that may elucidate their learning of novel goal-directed means-end actions. Future studies should examine how infants' own experience with means-end actions (for example, as reported by their caregiver) is related to infants' learning of novel means-end actions.

Our findings provide evidence that the neural response observed during action action observation is related to infants' learning novel goal-directed actions. This neural response is suggested to reflect the activity of the sensorimotor system, which may play a

role in goal analysis and understanding (Rizzolatti et al., 2001; Van Overwalle & Baetens, 2009). On the other hand, differences in attention during the EEG paradigm between the cane learning group and the visual task group may have driven the results we found. However, it is difficult to disentangle attention processes from action (Hobson & Bishop, 2016) as they are not mutually exclusive (i.e., one needs to attend to perceived action to decipher its goals, intentions, and meaning). To note, however, we did not find any differences in ERDs (particularly over central or occipital) between the two groups of infants, suggesting that there were no differences in neural activity that may have confounded our results.

5.6 Conclusions and Future Directions

The present study provided evidence of a neural index of learning, particularly the learning of a novel goal-directed action in infants. This neural index, the mu rhythm, is reflective of an activity of a neural system for action and perception coupling, which is integral in the processing of others' actions as meaningful and goal-directed, as well as coupling others' actions with one's own actions. In fact, both adult and infant studies have demonstrated this intimate link between action experience/behavior and perception via the mu rhythm index (Cannon et al., 2014; de Klerk, Johnson, Heyes, & Southgate, 2015; van Elk et al., 2008; Yoo et al., 2015). The foundational ability to detect the goal structures of actions and translate this knowledge to learning new goals may have cascading effects on social and cognitive behavior such as imitation and problem solving. For example, means-end actions, specifically tool use actions are proposed to be one way to examine problem solving in children under three years of age, because overt manual action can inform us of how the child plans to achieve a goal (Keen, 2011). Elucidating

the neural basis that underlie the acquisition and learning of novel actions will be pivotal to the understanding of social, cognitive, and motor behavior in typical development. Further, understanding the neural basis of action learning may elucidate our understanding of neurodevelopmental disorders characterized with impairments in social, cognitive, and motor domains (e.g., autism spectrum disorders), and possibly provide diagnostic tools for identifying candidates likely to benefit from early intervention.

There is a growing body of work investigating the neural basis of action-perception coupling and its development. Future work should focus on how the neural network involved in action understanding and processing develops over time, as well as how this network changes as a function of one's experience. Furthermore, future studies should examine how the activity action-perception system extends to goal-oriented actions such as communicative gestures. In fact, there exists evidence that the neural system for action-perception coupling may extend to meaningful actions that are acquired throughout one's life such as communicative gestures (Streltsova et al., 2010). Elucidating the extent to which the action-perception system (via the sensorimotor network) plays a role—by itself and/or in parallel with other networks—in communicative actions will be crucial for understanding the extent to which this system plays a role in social contexts.

In sum, the current study demonstrated that perception of others' goal-directed actions is related to learning of a novel goal-directed action in infants. Mu rhythm activity in nine-month-old infants during action perception predicted infants' learning of a novel means-end action. Further, mu rhythm activity did not predict learning in a novel visual pattern learning task, suggesting that action-perception activity, assessed via the

mu rhythm, was selectively related to a goal-directed action. The present study did not find relations between mu rhythm activity and a) infants' learning on a novel goal-directed task, and b) standardized measures of motor competence. Taken together, these results suggest that mu rhythm reflects action-perception processes (beyond motor abilities) and that this rhythm can detect variability in infants' readiness to learn novel actions. The current findings, taken with the above discussion, highlight the need for continued investigation of the underlying neural basis of action and perception and its relation to emerging behavior in development. Results from our study suggest that there is a relation between action and perception—measured through the mu rhythm activity—and infants' readiness to learn a novel meaningful action. To better understand these relations, future work should focus on: how early in development this relation emerges; and whether this relation extends or generalizes to other types of meaningful actions such as communicative gestures. Elucidating this neural basis of action understanding and learning will be crucial for understanding social and cognitive processes in development.

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