

5-7-2016

# Effects of Active and Observational Experience on EEG Activity during Early Childhood

Lauren Bryant

University of Connecticut, [lauren.bryant@uconn.edu](mailto:lauren.bryant@uconn.edu)

---

## Recommended Citation

Bryant, Lauren, "Effects of Active and Observational Experience on EEG Activity during Early Childhood" (2016). *Master's Theses*. 888.  
[https://opencommons.uconn.edu/gs\\_theses/888](https://opencommons.uconn.edu/gs_theses/888)

This work is brought to you for free and open access by the University of Connecticut Graduate School at OpenCommons@UConn. It has been accepted for inclusion in Master's Theses by an authorized administrator of OpenCommons@UConn. For more information, please contact [opencommons@uconn.edu](mailto:opencommons@uconn.edu).

Effects of Active and Observational Experience on EEG Activity during Early Childhood

Lauren J. Bryant

B.A., B.S. Southern Connecticut State University, 2013

A Thesis

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

at the

University of Connecticut

2016

APPROVAL PAGE

Masters of Science Thesis

Effects of Active and Observational Experience on EEG Activity during Early Childhood

Presented by

Lauren J. Bryant, B.A., B.S.

Major Advisor\_\_\_\_\_

Kimberly Cuevas, Ph.D.

Associate Advisor\_\_\_\_\_

Chi-Ming Chen, Ph.D.

Associate Advisor\_\_\_\_\_

Adam Sheya, Ph.D.

University of Connecticut

2016

## Abstract

How we encode and understand others' actions is a core problem in social learning. In recent decades, the human neural mirroring system (NMS) has been implicated as a potential neural mechanism of action understanding. To investigate the effects of experience on NMS activity, we manipulated 3- to 6-year-old children's ( $N = 16$ ) active and observational experience with two tools and then examined EEG mu (7-10 Hz) and central beta rhythm (17-21 Hz) desynchronization as measures of NMS activity during observation and execution of these actions. Children exhibited neural mirroring within both individualized and standard mu bands. Although mu and beta rhythm activity at central sites did not differ as a function of training condition, desynchronization within individualized and standard mu frequency bands was greater during perception of the active training task at occipital sites. We attribute this differential activity of the occipital region to visual attention, which may mediate the association between first-hand experience and desynchronization of the occipital alpha rhythm.

*Keywords:* early childhood, neural mirroring, mu rhythm, beta rhythm, EEG, experience

## EFFECTS OF ACTIVE AND OBSERVATIONAL EXPERIENCE ON EEG ACTIVITY DURING EARLY CHILDHOOD

How we encode and understand others' actions has been widely investigated over the past several decades. This is a central problem in social learning, which is theorized to underlie various cognitive processes, including acquisition of motor and tool-use skills (Marshall & Meltzoff, 2011). Action understanding refers to the ability to recognize that an individual is performing an action and differentiate the observed action from similar movements (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Research suggests that experience performing an action plays a major role in one's understanding of the same or similar actions by others. It has been hypothesized that one's representations, and thus understanding, of an object, concept, or event involves a perceptual, motoric, and somatosensory "re-experiencing" of that stimulus (e.g., Kontra, Goldin-Meadow, & Beilock, 2012).

The topic of action understanding has also been addressed through a variety of neuroimaging techniques. For instance, the discovery of mirror neurons, found in the cortices of rhesus macaque monkeys, has served as a catalyst in the growth of the body of literature on the neural underpinnings of action understanding. Mirror neurons fire in response to both the perception and performance of goal-directed actions (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). This overlap in activation during action observation and execution has led to the hypothesis that macaque mirror neurons, as well as an analogous human neural mirroring system (NMS), serve as a crucial neural mechanism for action understanding (Gallese et al., 1996). A prominent theory regarding action understanding posits that these systems serve as a means of mapping action perception onto an internal motor representation of the observer. When an action is performed, a representation of that motor act, including knowledge of the

goals and consequences of that action, is generated. Mirroring systems serve as a mechanism by which this representation is re-activated during the observation of the same or similar actions. In other words, mirroring systems allow us to use our action experience as a frame of reference when observing the actions of others (Gallese et al., 1996; Gallese, Gernsbacher, Heyes, Hickok, & Iacoboni, 2011; Iacoboni, Molnar-Szakacs, Gallese, Buccino, & Rizzolatti, 2005; Rizzolatti & Sinigaglia, 2010).

Consistent with this hypothesis, several studies have documented that both mirror neurons (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996) and the human NMS are more reactive to the perception of actions within the observer's motor repertoire (e.g., Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005). Despite the body of research in support of neural mirroring theories of action understanding, there are arguments to the contrary. The most common argument is that individuals are generally capable of understanding actions that they cannot physically perform (e.g., Hickok, 2009). For example, individuals who have never played tennis can generally understand what tennis players are doing while they are watching a game. However, others argue that though the NMS is not necessary for basic understanding of actions, it does provide a deeper level of knowledge; in this context, a skilled tennis player may be more likely to predict the speed and direction of the ball while observing a game (Gallese et al., 2011).

Although the majority of studies have concluded that motor experience is associated with increased NMS activity, several studies have found that experience is associated with decreased NMS activity ("neural efficiency"; e.g., Del Percio et al., 2010). These conflicting findings indicate that associations between motor experience and NMS activity are complex and require further study. Additionally, although a small number of studies have found evidence of neural

mirroring during early childhood (e.g., Ruysschaert, Warreyn, Wiersema, Oostra, & Roeyers, 2014), no study has investigated the influences of motor experience on NMS activity at this stage of development. To further our understanding of these associations during early childhood, we employed an at-home training paradigm to control children's motor experience with novel actions prior to electrophysiological recording. In the following sections we discuss the human NMS, with a particular focus on electroencephalography (EEG) measures of NMS activity (i.e., mu and beta rhythms) and its associations with motor experience. Next, we describe the development of these systems during infancy and early childhood. We conclude by addressing the gaps in the current literature regarding associations between motor experience and NMS activity, particularly during early childhood.

### **The Human Neural Mirroring System**

Since the discovery of mirror neurons in 1992 (di Pellegrino et al., 1992), investigations of human brain regions with analogous properties have flourished. Research using subdural electrodes has provided initial evidence that human motor regions contain individual neurons with mirroring properties (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010); however, whether humans possess mirror neurons is widely debated<sup>1</sup> (e.g., Gallese et al., 1996; Hickok, 2009; Pineda, 2005). Like the mirror neurons found in macaque cortices, the human NMS collectively refers to brain regions that respond to both the observation and execution of actions. These regions have been widely studied; an extensive meta-analysis of 125 functional magnetic resonance imaging (fMRI) studies revealed several brain areas are reliably activated in response to both the observation and execution of actions. These “neural mirroring” regions include the inferior frontal gyrus, dorsal and ventral premotor cortex, and the inferior and superior parietal lobule (Molenberghs, Cunnington, & Mattingley, 2012). Studies using a wide variety of other

methods, including transcranial magnetic stimulation (TMS; e.g., Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995), magnetoencephalography (MEG; e.g., Hari & Salmelin, 1997), and EEG (e.g., Muthukumaraswamy & Johnson, 2004) have provided further evidence for the existence of a human NMS.

**EEG mu and beta rhythms.** Research has demonstrated that the EEG mu rhythm (adult: 8-13 Hz), a rhythm recorded over central scalp sites that overlie the sensorimotor cortex, has mirroring properties (Marshall & Meltzoff, 2011). The mu rhythm is hypothesized to originate from the primary somatosensory cortex (Tiihonen, Kajola, & Hari, 1989; but see Thorpe, Cannon, & Fox, 2016) and it desynchronizes, or decreases in power relative to a baseline resting state, during the observation and execution of goal-directed actions. For example, in adults, the mu rhythm desynchronizes during the perception and performance of an object-directed precision grip (Muthukumaraswamy & Johnson, 2004). The EEG mu rhythm is considered to be a measure of activity within the NMS; simultaneous EEG-fMRI recordings indicate that mu rhythm desynchronization during action observation and execution is correlated with BOLD activation of areas within the NMS, including the inferior parietal lobe, dorsal premotor cortex, and primary somatosensory cortex (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011). It is also hypothesized that the mu rhythm reflects the downstream modulation of the activity of mirror neurons (e.g., Pineda, 2005). Similarly, although it has not been as widely studied as the mu rhythm, there is some evidence that the central beta rhythm also exhibits neural mirroring properties (e.g., Babiloni et al., 2002; but see Nyström, 2008).

### **Influences of Motor Experience on Neural Mirroring**

Many studies suggest that the activation of the human NMS during action perception varies with the observer's prior experiences with the target action. For example, ballet dancers



exhibit greater activation of the NMS while observing dance movements with which they have motor experience than movements with which they have only visual experience (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006). This differential NMS reactivity can be achieved after a relatively short-term training period (Cross, Hamilton, & Grafton, 2006). Similarly, additional EEG research has indicated that motor experience is associated with greater mu rhythm desynchronization during action observation (e.g., Marshall, Bouquet, Shipley, & Young, 2009).

Cannon et al. (2014) investigated both mu and central beta rhythm desynchronization in adult participants with varying levels of experience using a claw-like tool to move objects into a bucket. The sample included students that had extensive motor experience with this tool after serving as experimenters on a previous protocol (“expert performers”); students that had visual experience with this tool after serving as video coders on that protocol (“expert observers”); and students that had no prior experience with this task (“novices”). Expert performers exhibited significantly greater mu rhythm desynchronization than expert observers and novices while observing another experimenter use this tool; expert observers and novices, on the other hand, did not significantly differ in ERD during action perception. These effects, however, were not found within the beta band.

On the contrary, other EEG research has found evidence that motor learning can have significant effects on beta rhythm activity. For example, greater skill in performing a novel motor action is associated with greater desynchronization of the upper beta band (18.5-21.0 Hz; Nakano, Osumi, Ueta, Kodama, & Morioka, 2013). Similarly, professional dancers, but not non-dancers, exhibit desynchronization of the lower beta (13-18 Hz) band while observing dance movements (Orgs, Dombrowski, Heil, & Jansen-Osmann, 2008). Taken together, these findings

suggest that activity within the EEG beta rhythm may function as an important neural mechanism of motor learning.

Despite a large body of evidence that increased motor experience is associated with greater NMS activation during action perception, some studies have demonstrated the opposite effect. In some instances, novel actions can elicit greater activation of the NMS (e.g., Del Percio et al., 2010; Vogt et al., 2007). These findings are consistent with the neural efficiency hypothesis, which posits that expertise with a given task results in more efficient (i.e., requires less processing) brain activity while performing that task (Vernon, 1993). These discrepancies in the literature suggest that associations between NMS activity and motor experience are complex, and thus warrant further study.

### **Development of the EEG Mu and Beta Rhythms**

Waking EEG activity undergoes an increase in frequency throughout early development (see Bell, 1998, for review). The 8- to 13-Hz frequency band is considered to be the most prominent frequency during adulthood; activity within this range desynchronizes in response to cognitive processing and exhibits the highest power during rest (e.g., sitting quietly). However, during the first years of life, the dominant frequency is considerably lower (6-9 Hz; Marshall, Bar-Haim, & Fox, 2002). Similarly, whereas adult studies have found evidence of neural mirroring within the 8- to 13-Hz band, infant researchers have found significant desynchronization within the 6- to 9-Hz band (i.e., the infant mu rhythm) during action observation and execution (e.g., Marshall, Young, & Meltzoff, 2011). Peak mu frequency increases throughout early childhood, with neural mirroring occurring over a span of frequency bands ( $M = 9 - 11$  Hz) among 4- to 11-year-olds (Lepage & Théoret, 2006) and within the “adult” 8- to 13- Hz band by middle childhood (Raymaekers, Wiersema, & Roeyers, 2009).

EEG activity at higher frequencies (e.g., beta) also exhibits age-related changes, yet these have not been as thoroughly studied as the mu rhythm (Bell, 1998). Within this limited body of research, no study has found evidence of neural mirroring properties of this rhythm during infancy (Meyer, Braukmann, Stapel, Bekkering, & Hunnius, 2015; Nyström, 2008). Further research has suggested that the beta rhythm has complex patterns of activation; for example, 4-to 11-month-olds' central beta rhythms did not significantly change from baseline while watching reaching motions, yet significantly desynchronized while watching moving objects and synchronized (i.e., increased in power relative to baseline) while observing walking (Virji-Babul, Rose, Moiseeva, & Mekan, 2012). No study has yet investigated the potential neural mirroring properties of the beta rhythm during early childhood.

**Early influences of motor experience.** As in the adult literature, developmental research has provided somewhat inconsistent evidence for the influences of motor experience on mu and beta rhythm desynchronization. One study found that differences in both mu (7-9 Hz) and beta (17-19 Hz) rhythm reactivity during the observation of videos of crawling and walking was associated with 14- to 16-month-old infants' crawling, but not walking, experience (i.e., greater crawling experience was associated with greater differences in ERD during observation of crawling as compared to walking; van Elk et al., 2008). Conversely, twelve-month-old infants exhibit less power within the mu rhythm during the observation of unusual actions (i.e., actions with which the infant has no experience) than during the perception ordinary actions (i.e., actions with which the infant likely has motor experience; Stapel, Hunnius, van Elk, & Bekkering, 2010).

Recent work has expanded on these findings by experimentally controlling infants' experience with novel actions. Gerson, Bekkering, and Hunnius (2015) manipulated infants'

experience with two novel actions by means of an at-home training paradigm. Parents of 9- to 10-month-old infants were provided with two novel toys, each of which made a distinct sound. At home, infants received active training (i.e., played with the toy) and observational training (i.e., watched their parents play with the toy) for approximately three 5-min training sessions per toy. After at-home training, infants received electrophysiological recording in the laboratory during the perception of sounds associated with each training stimulus. Infants exhibited significantly greater mu rhythm desynchronization in response to the sound associated with the toy they played with than the sound associated with the toy they had only observed. This study suggests that active experience, but not observational experience, is associated with increased mu rhythm desynchronization during infancy.

### **Limitations of the Current Literature**

These initial studies have provided valuable insight on associations between active experience and mu and beta rhythm desynchronization. However, it should be noted that the majority of the aforementioned studies did not report whether participants exhibited significant mu or beta rhythm desynchronization during action execution<sup>2</sup> (Cannon et al., 2014; Gerson et al., 2015; van Elk et al., 2008). Reporting activity during action execution is critical in research on the human NMS as it is defined as regions that activate in response to both action observation and action execution (Cuevas, Cannon, Yoo, & Fox, 2014). Additionally, most of the previous research on mu rhythm desynchronization did not experimentally manipulate participants' prior experience with the target action (e.g., Cannon et al., 2014; van Elk et al., 2008). Although Gerson et al. (2015) controlled for infants' experience with the stimuli through the use of an at-home training paradigm, instead of measuring mu rhythm desynchronization during visual action perception, as is typical in most mu rhythm research, they measured mu rhythm

desynchronization in response to sounds associated with the target action. This may have made the task more taxing on infant memory due to a lack of a visual cue and thus may have measured neural activity associated with memory, in addition to action perception.

Of course, an additional limitation of literature on mu and beta rhythm desynchronization and motor experience is the absence of studies with child participants. Although one fMRI study found that 4- to 5-year-old children who received first-hand motor experience drawing letters exhibited greater increases in activation of the visual-association cortex than children who had only received visual experience with the letters (James, 2010), no study has investigated the effects of motor experience on neural mirroring at this stage of development. Additionally, there are relatively few studies investigating neural mirroring during early childhood, especially compared to the body of literature on the infant and adult NMS. This is surprising, given that many researchers hypothesize that the NMS may play a role in a variety of cognitive functions that develop during early childhood, including imitation, theory of mind, and empathy (e.g., Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Gallese & Goldman, 1998; Oberman et al., 2005).

Given that the NMS reacts to action observation and action execution in very similar ways, it is hypothesized to play a crucial role in perceiving and understanding others' actions (e.g., Gallese et al., 2011). Research on associations between action experience and mu and beta rhythm desynchronization during early childhood could offer critical insight into potential neural mechanisms underlying how children understand others' actions. Such investigations could provide information on how children learn from practice or by watching others, and how they develop new motor skills that may provide them with opportunities to interact with their

environments in unique ways. The EEG mu and beta rhythms offer researchers valuable, developmentally appropriate tools for assessing this brain system.

### **The Current Study**

The current study investigates the influences of active and observational experience on mu and beta rhythm desynchronization in children ages 3 to 6 years. This age range was selected because it encompasses a time of rapid cognitive development and is much understudied in the NMS literature. To investigate this, we employed at-home training procedures similar to those of Gerson and colleagues (2015). Children received active (i.e., played with a toy) and observational experience (i.e., watched a video of a demonstrator playing with a similar toy) with two sets of stimuli over the course of a 4-day training period. After training, children completed in-laboratory action observation and action execution trials during electrophysiological recording. We employed a within-subjects design to control for individual differences in mu and beta rhythm activity. We hypothesized that children would exhibit significant mu rhythm desynchronization during both action observation and action execution. Based on the findings of Cannon et al. (2014) and Gerson et al. (2015), we predicted that children would demonstrate significantly greater mu rhythm desynchronization during the observation of actions with which they have existing active experience than the perception of actions with which they have only observational experience. Due to the conflicting findings regarding both the neural mirroring properties of the central beta rhythm and its associations with action experience, our analyses on this rhythm were exploratory in nature.

## Method

### Participants

The sample consisted of 16 children (10 boys, 6 girls; 3 Hispanic, 13 non-Hispanic; 11 Caucasian, 2 African American, 1 Asian American, 1 multiracial, 1 unreported race). Participants were recruited through research contact lists and by word of mouth. Children ranged in age from 38.83 – 72.72 months on the day of EEG recording ( $M = 57.37$ ,  $SD = 11.16$ ). All participants were typically developing, were born within 4 weeks of their expected due dates, and weighed at least 5.5 lbs at birth. All mothers and fathers completed a high school education (25.0% and 25.0% bachelor's degree; 62.5% and 56.3% graduate degree; respectively). For parents that reported parental age at birth (15 mothers, 14 fathers) average maternal and paternal age at birth was 30.1 and 31.8 years ( $SD = 5.8$  and  $6.3$ ), respectively. Children received a certificate of participation and a t-shirt or a small toy and parents were compensated \$20.

### Apparatus

The apparatus included “fishing hook” and “lobster” toy sets (see Figure 1). The “fishing hook” set consisted of a hook-shaped tool and container. The hook was constructed with PVC pipe and blue electrical tape. The handle of the hook was approximately 7 cm in diameter and 25.5 cm long. An additional 15 cm long pipe was connected to the handle at a right angle. A third, approximately 7 cm piece of pipe was then attached at a right angle to form a “J” shape. The container was a commercially available decorative box that opened to form a ramp leading into the box. The ramp was approximately 17.5 cm long and 9 cm high at its highest point. The open container was mounted to a thin piece of wood for stability.

The “lobster” toy set consisted of a plastic lobster tool (Melissa and Doug Louie Lobster Claw Catcher) and a blue plastic bucket. The lobster tool was 33 cm long, and the bucket was 20

cm high, with an opening that was 15 cm in diameter. The tail of the lobster contained a squeeze trigger that closed the lobster's claws to pick up a small toy. This experiment also utilized randomly assorted plastic aquatic animal toys (Melissa and Doug Seaside Sidekicks Creature Set). The aquatic animal toys ranged in width from 4 to 6 cm ( $M = 4.62$  cm). The lobster tool, bucket, and plastic animal toys were commercially available. Parents verified that the participants did not have prior experience with the lobster tool. Finally, parents were provided with a training itinerary (see Appendix), stickers, and a sticker chart.

### **Training Sessions**

Procedures for the at-home training sessions are based on Gerson et al. (2015) and adapted for young children. Parents were provided with one set of toys, a Samsung camcorder, tripod, and a DVD or electronic copy a demonstration video. All training sessions took place over the course of four subsequent days, with children participating in active and observational training sessions on alternating days.

**Active training sessions.** Parents had their children interact with the toys provided on alternate days for approximately 5 min each day (range: 3.35 – 7.65 min,  $M = 5.62$ ). During motor training, parents were asked keep the child focused on the task and were allowed to teach their child the task if necessary. Parents were instructed to present their child with one small animal toy at a time so the child could use the hook or lobster to move the toy into the respective container. Parents filmed their children throughout the duration of both motor training sessions so that the child and all toys were visible throughout the recording. Offline coding of these videos indicated that the number of trials completed per active training session did not differ between children given the fishing hook ( $M = 31.81$ ,  $SD = 16.24$ )<sup>3</sup> or lobster tools ( $M = 24.31$ ,  $SD = 8.45$ ),  $t(14) = 1.16$ ,  $p = .26$ .



**Observational training sessions.** Parents were provided with one of two videos that were filmed for this experiment. The videos showed a female demonstrator not otherwise involved in the study protocol modeling the use of either set of toys. In modeling the fishing hook task, the demonstrator used the hook to pull an animal toy up the ramp and into the box. To model the lobster task, the demonstrator used the lobster tool to pick up an animal toy and drop it into the bucket (see Figure 2). Each video consisted of 20 demonstrations. A black screen was presented for 1 s in between each trial. The fishing hook and lobster demonstration videos were 2.75 min and 2.52 min<sup>4</sup> in duration, respectively. Parents that received the fishing hook toy set were given the lobster demonstration video, and parents that received the lobster toy set were given the fishing hook demonstration video.

On alternate days (i.e., days on which the child was not participating in active training), the child watched the demonstration video. Parents were instructed to record the video training sessions so that both their child's face and the video were visible. If this was not possible, parents recorded the child's face and ensured that the camera could record the audio of the video. Offline coding of the videos indicated that the number of trials viewed per observational training session did not differ between children given the fishing hook ( $M = 19.06$ ,  $SD = 1.43$ ) or lobster ( $M = 19.06$ ,  $SD = 1.92$ ) demonstration videos,  $t(14) = 0.64$ ,  $p = .52$ . However, participants completed a significantly greater number of trials per session during active training ( $M = 28.06$ ,  $SD = 13.10$ ) than during observational training ( $M = 18.78$ ,  $SD = 1.66$ ),  $t(15) = 2.87$ ,  $p = .01$ ,  $d = 1.50$ .

The order in which these tasks were presented was counterbalanced, with some children playing with the toys and other children watching the video on the first day of training. Parents were encouraged to give their child a sticker as a reward halfway through and at the conclusion

of each training session. Additionally, parents were instructed to have their child perform each task in the same room and at approximately the same time ( $\pm 2$  hours) throughout the 4 days of training.

### **Post-training Session**

Post-training sessions occurred the day immediately after the final at-home training session. One child's post-training session was postponed an additional day (i.e., 2 days after the final at-home training session) due to illness. After becoming familiarized with the experimenters and the room, children were fitted with an EEG cap.

**Initial baseline.** EEG recording began with a 2.82 min initial baseline in which children were instructed to sit quietly and observe moving images on a computer or television screen approximately 1.3 m from the participant. The initial baseline depicted alternating videos of moving bubbles (20 s) and abstract shapes (10 s; see Figure 3). This provided a measure of resting EEG activity for later comparisons.

**Action observation.** Participants sat quietly and watched as a live demonstrator modeled either the lobster or fishing hook task for one block of approximately 20 trials (fishing hook:  $M = 20.31$ ,  $SD = 0.95$ ; lobster:  $M = 20.38$ ,  $SD = 1.54$ ). Whether children observed the fishing hook or lobster task during the first observation block was counterbalanced based on age, sex, and the toy they had received for home motor training.

**Action execution.** After the first block of action observation trials, children performed approximately 20 trials of the task they had just observed in the previous block of trials (fishing hook:  $M = 18.75$ ,  $SD = 3.28$ ; lobster:  $M = 18.94$ ,  $SD = 3.80$ ). After the first set of observation and execution trials were completed, children participated in an additional block of observation trials, followed by another block of action execution trials, with the remaining toy. Action

execution blocks were always preceded by action observation blocks using the same toy. (See Figure 4 for a flowchart summary of the action observation and action execution protocol.)

### **EEG Recording and Processing**

EEG recordings were made from 26 left, right, and central scalp sites and left and right mastoids. All electrode sites were referenced to Cz during recording. EEG was recorded using a stretch cap (Electro-Cap, Inc.; Eaton, OH; E1 series) with tin electrodes in the 10/20 system pattern. A small amount of abrasive gel was placed into each recording site and the scalp was gently rubbed. Conductive gel was then added to the recording sites. Electrode impedances were measured and accepted if they were below 10 k $\Omega$ . The electrical activity from each lead was amplified using separate BioAmps instruments (James Long Company, Caroga Lake, NY). During data collection, the high-pass filter was a single pole RC filter with a 0.1 Hz cut-off (3 dB or half-power point) and 6 dB per octave roll-off. The low-pass filter was a two-pole Butterworth type with a 100 Hz cut-off (3 dB or half-power point) and 12 dB octave roll-off. Activity for each lead was displayed on the monitor of the acquisition computer. The EEG was digitized online at 512 samples per second for each channel to eliminate the effects of aliasing. The acquisition software was Snap-Master (HEM Data Corp., Southfield, MI), and the raw data were stored for later analyses. The day of the recording of each subject, a 10 Hz, 50  $\mu$ V, peak-to-peak sine wave was input through each amplifier. This calibration signal was digitized for 30 s and stored for subsequent analyses.

**EEG analysis.** Spectral analysis of the calibration signal and computation of power at the 7- to 13-Hz frequency band was accomplished. The power figures were used to calibrate the power derived from the subsequent spectral analysis of the EEG. Next, EEG data were examined and analyzed using EEG Analysis software developed by James Long Company. Data

were re-referenced via software to an average reference. The re-referenced EEG data were artifact scored for eye movements using an artifact detection algorithm; this algorithm identified and scored epochs in which Fp1 had a pulse height of 43.75 uV or greater<sup>5</sup>. Artifact associated with gross motor movements over 200 uV peak-to-peak was also scored. These artifact-scored epochs were eliminated from all subsequent analyses. No artifact correction procedures were used.

The data were then analyzed with a discrete Fourier transform (DFT) using a Hanning window of 1-s width and 50% overlap. In order to be included in the final sample, children had to provide a minimum of 3 artifact-free DFT windows for the observation and execution of both the active and observational tasks, as well as baseline and tool grasping (Marshall et al., 2011). Sufficient artifact-free EEG data was collected from all children in the current sample. Across children, the mean number of artifact-free DFT windows during observation of the active training task (i.e., the task with which children received at-home motor experience) and the observational training task (i.e., the task with which children received at-home visual experience) was 9.38 ( $SD = 3.88$ ) and 10.06 ( $SD = 4.75$ ) DFT windows, respectively; children did not significantly differ in the number of DFT windows during observation of these two tasks,  $t(15) = 0.55, p = .59$ . Children also did not differ in the mean number of artifact-free DFT windows during execution of the active ( $M = 10.31, SD = 4.28$ ) and observational ( $M = 10.94, SD = 5.45$ ) tasks,  $t(15) = 0.63, p = .54$ . The mean the mean number of artifact-free DFT windows during tool grasping, which was used to determine individualized frequency bands (see below), and baseline was 15.69 ( $SD = 7.43$ ) and 147.56 ( $SD = 47.19$ ), respectively.

## **Video Analysis**

The post-training session was video recorded with a vertical interval time code (VITC) being placed on the video signal to ensure that video and EEG signals were synchronized. Video coding procedures were based on those of Cannon et al. (2014) and adapted for the stimuli used in this study. One individual coded all videos offline for event marks for onset and offset of baseline epochs and the frame in which the experimenter or child used the tool to pick up a toy. These frames were defined as the frame in which the fishing hook first touched the toy or in which the lobster claws reached their most-closed point around a toy (see Figure 5). Only instances in which the tool was successfully used to pick up a toy were marked. Videos were also coded to mark the frame in which the child first touched the lobster or fishing hook tools to grasp them, as these marks were later used to identify individualized frequency bands for each child. An additional independent coder event marked 19% of the video recorded sessions to determine inter-rater reliability, which was accomplished within three frames (approximately 100 ms) for 100% of observation trials, 82% of execution trials, and 89% of tool grasping trials. When the two scores differed, the primary coder's event mark was used for analysis. Additionally, epochs in which the child was talking, not attending to the experimenter or the apparatus, or making movements that resembled reaching, pointing, or use of either toy were marked and excluded from subsequent analyses.

## **ERD Computation**

Computation of event-related desynchronization (ERD) was time-locked to the frame in which the child or experimenter used the fishing hook or lobster tool (i.e., used the tool to pick up the toy) with the epoch extending 500 ms before and after the event mark (Cannon et al., 2014). To determine individualized mu frequency bands, ERD was time-locked in the same

manner to the frame in which the child first grasped the tool. ERD was calculated using the formula  $\log_{10}(A/R)$  in which A is the band power during task (i.e., tool grasping; observation of tool use; or tool use execution) and R is band power during baseline (Bernier, Dawson, Webb, & Murias, 2007). Negative ERD scores reflect desynchronization (i.e., a decrease in power relative to baseline) and positive scores reflect synchronization (i.e., an increase in power relative to baseline).

ERD was calculated in this manner for the mu (7-10 Hz) and beta (17-21 Hz) bands. Based on the procedures of Meyer and colleagues, we expected these frequencies to most closely reflect activity within the mu and beta rhythms of our sample (Meyer, Hunnius, van Elk, van Ede, & Bekkering, 2011). To account for age-related and individual differences in EEG activity, we also determined individualized mu frequency bands for each participant. ERD during tool grasping was calculated for a series of 4-Hz-wide frequency bands ranging from 6-9 Hz to 10-13 Hz for frontal (F7/F3/Fz/F4/F8), central (C3/C4), parietal (P7/P3/Pz/P4/P8), and occipital (O1/O2) regions (Marshall et al., 2011). This range was selected because it encompasses the lower end of the infant and child mu range and the upper portion of the adult mu range (Southgate, Johnson, Karoui, & Csibra, 2010). Each child's maximally attenuated band during the grasping phase was identified and used for all analyses for action observation and action execution with individualized bands (i.e., if a child's maximally attenuated band during grasping was 9-12 Hz, data within that range was selected for analysis). Participants' mean individualized mu frequency band was 8.31-11.31 Hz.<sup>6</sup> To our knowledge, there is no precedent in the literature for use of similar procedures in determining individualized bands for the beta rhythm, therefore, we only examined the 17-21 Hz beta band.

## Analyses

Our analyses examined effects of observational and active experience on ERD scores. Our analyses consisted of separate multivariate analyses of variance (MANOVAs) on ERD scores for action observation and action execution, with region and training condition as within-subjects variables. To examine interactions, follow-up MANOVAs were also performed; a multivariate approach for assessing interaction effects has been suggested by Keselman (1998). To determine the magnitude of ERD at central sites, we then performed a series of directional one-sample *t*-tests comparing ERD scores to zero (i.e., non-zero differences scores indicate a significant change in power from baseline; Marshall et al., 2011). We hypothesized that significant mu rhythm desynchronization would occur at central sites. Although our hypotheses were specific to central sites, we also completed one-sample *t*-tests for ERD scores at frontal, parietal, and occipital regions; inclusion of non-central sites enables analyses to confirm that activity measured at central sites has not been influenced by activity from neighboring regions (e.g., the occipital alpha rhythm; Muthukumaraswamy & Johnson, 2004). Analysis of non-central sites can also account for potential age-related changes in spatial localization of mu rhythm desynchronization. Two-tailed *p*-values were used for all analyses with non-central regions. As recommended in Cuevas et al. (2014), these analyses were performed within both individualized and standard (7-10 Hz) mu bands, as well as the beta (17-21 Hz) band.

Additional analyses were performed to confirm that any observed effects of training condition on ERD scores were not the result of differences in the number of at-home active and observational training trials. Difference scores between ERD values during the active and observational training tasks were computed for all regions (i.e., frontal, central, parietal, and occipital) and frequency bands of interest (i.e., standard mu, individualized mu, and beta bands)

during both action observation and execution (e.g., ERD during observation of the active training task minus ERD during perception of the observational training task). Difference scores were also calculated for the number of active and observational training trials participants completed prior to electrophysiological recording; these scores were then correlated with all ERD difference scores.

## Results

### Preliminary Analyses

**Number of training trials.** Preliminary Pearson correlations confirmed that, during both action observation and action execution, there were no significant correlations among difference scores between the number of active and observational training trials and ERD difference scores within all regions and frequency bands ( $ps > .06$ ).

**Sex differences.** During action observation, preliminary MANOVAs on ERD scores within all frequency bands of interest confirmed that there were no significant main effects of sex ( $F_s < 1$ ), or interactions of sex and region ( $F_s < 1$ ), or training condition [Individualized mu band:  $F(3, 13) = 2.03, p = .18$ ; Standard mu band:  $F(3, 13) = 4.40, p = .06$ ; Beta band:  $F < 1$ ].

During action execution, MANOVAs found no significant main effects of sex or Sex  $\times$  Region interactions ( $F_s < 1$ ) among all three frequency bands. There was a significant Sex  $\times$  Training Condition interaction within the beta band,  $F(3, 13) = 4.97, p = .04, \eta_p^2 = .26$ , though follow-up analyses were not significant ( $ps > .06$ ). Sex  $\times$  Training Condition interactions within the mu bands were non-significant [Individualized mu band:  $F(3, 13) = 1.34, p = .27$ ; Standard mu band:  $F < 1$ ].



### EEG Mu Rhythm

**Tool grasping: Individualized frequency bands.** A MANOVA was completed on ERD scores within participants' individualized mu frequency bands during grasping at frontal, central, parietal, and occipital regions. There was a main effect of region,  $F(3, 13) = 17.90, p < .001, \eta_p^2 = .80$ . Follow-up contrasts revealed that ERD scores were greater at central sites ( $M = -0.27, SD = 0.27$ ) than frontal ( $M = -0.14, SD = 0.20, p = .01$ ) and occipital sites ( $M = -0.08, SD = 0.35, p < .001$ ), but not parietal sites ( $M = -0.22, SD = 0.22, p = .50$ ). Planned  $t$ -tests revealed that ERD scores were significantly less than zero at frontal,  $t(15) = -2.78, p = .01, d = .070$ , central,  $t(15) = -3.98, p < .001, d = 0.99$ , and parietal sites,  $t(15) = -3.87, p = .002, d = 0.97$ , but not at occipital sites ( $p = .36$ ; see Figure 6).

**Action execution: Individualized frequency bands.** A MANOVA was completed on execution ERD scores within participants' individualized mu frequency bands. The within-subjects factors were training condition (i.e., active or observational) and region (i.e., frontal, central, parietal, or occipital). There was a main effect of region,  $F(3, 13) = 11.67, p = .001, \eta_p^2 = .73$ . There were no significant effects of training condition (i.e., no main effect or interaction involving training condition,  $F_s < 1$ ), thus execution ERD scores were collapsed across conditions. Follow-up contrasts revealed significantly greater ERD over central sites ( $M = -0.43, SD = 0.30$ ) than frontal ( $M = -0.15, SD = 0.16, p = .001$ ), parietal ( $M = -0.22, SD = 0.23, p = .004$ ), and occipital ( $M = -0.12, SD = 0.28, p < .001$ ) sites. Planned  $t$ -tests revealed that ERD scores were significantly less than zero at frontal,  $t(15) = -3.91, p = .001, d = 0.94$ , central,  $t(15) = -5.61, p < .001, d = 1.43$ , and parietal sites,  $t(15) = -4.12, p = .001, d = 0.96$ , but not occipital sites,  $t(15) = -1.74, p = .10$  (see Figure 7a).

**Action execution: 7- to 10-Hz band.** As recommended in Cuevas et al. (2014), we investigated mu rhythm ERD within a standardized frequency band in addition to individualized frequency bands. As hypothesized, results within the 7- to 10-Hz band were analogous to those found within participants' individualized frequency bands. A MANOVA on execution ERD scores within the 7- to 10-Hz band revealed a significant main effect of region,  $F(3, 13) = 10.59$ ,  $p = .001$ ,  $\eta_p^2 = .71$ , with no significant effects of condition ( $F_s < 1$ ). Follow-up contrasts revealed significantly greater ERD over central sites ( $M = -0.35$ ,  $SD = 0.27$ ) than frontal ( $M = -0.13$ ,  $SD = 0.16$ ,  $p = .003$ ) and occipital ( $M = -0.15$ ,  $SD = 0.28$ ,  $p = .003$ ) sites. Planned  $t$ -tests revealed that ERD scores were significantly less than zero at frontal,  $t(15) = -3.26$ ,  $p = .005$ ,  $d = 0.81$ , central,  $t(15) = -5.22$ ,  $p < .001$ ,  $d = 1.29$ , and parietal sites,  $t(15) = -5.18$ ,  $p < .001$ ,  $d = 1.30$ , and marginally less than zero at occipital sites,  $t(15) = -2.06$ ,  $p = .057$ ,  $d = 0.54$  (see Figure 8a).

**Action observation: Individualized frequency bands.** A MANOVA on observation ERD scores within participants' individualized frequency bands revealed a significant main effect of region,  $F(3, 13) = 14.72$ ,  $p < .001$ ,  $\eta_p^2 = .77$ . Although there was no significant main effect of training condition ( $F < 1$ ), there was a significant Region  $\times$  Training Condition interaction,  $F(3, 13) = 4.62$ ,  $p = .02$ ,  $\eta_p^2 = .52$ . Follow-up paired  $t$ -tests demonstrated significantly greater ERD at occipital sites during perception of the active training task ( $M = -0.09$ ,  $SD = 0.23$ ) than the observational training task ( $M = 0.00$ ,  $SD = 0.22$ ),  $t(15) = -2.44$ ,  $p = .03$ ,  $d = 1.04$ . There were no significant differences in ERD during perception of the active and observational tasks at frontal, central, or parietal regions ( $ps > .10$ ).

To fully probe the Region  $\times$  Training Condition interaction, separate follow-up MANOVAs confirmed significant main effects of region during the perception of both the active,  $F(3, 13) = 9.06$ ,  $p = .002$ ,  $\eta_p^2 = .68$ , and observational training tasks,  $F(3, 13) = 10.42$ ,  $p =$

.001,  $\eta_p^2 = .71$ . Follow-up contrasts revealed significantly less ERD during perception of the active training task at frontal sites ( $M = 0.22$ ,  $SD = .010$ ) than central ( $M = -0.11$ ,  $SD = 0.20$ ,  $p = .01$ ) and parietal ( $M = -0.07$ ,  $SD = 0.13$ ,  $p = .001$ ) sites. During perception of the observational training task, parietal sites ( $M = -0.10$ ,  $SD = 0.12$ ) had significantly greater ERD scores than frontal sites ( $M = -0.01$ ,  $SD = 0.09$ ,  $p = .01$ ).

ERD scores were only significant at central sites during perception of the active training task,  $t(15) = -2.19$ ,  $p = .002$ ,  $d = 0.55$ , though they had a non-significant negative trend during perception of the observational training task,  $t(15) = -1.62$ ,  $p = .063$ . Planned  $t$ -tests revealed that ERD scores were significantly less than zero at parietal sites during observation of both the active,  $t(15) = -2.21$ ,  $p = .04$ ,  $d = 0.54$ , and observational,  $t(15) = -3.37$ ,  $p = .004$ ,  $d = 0.83$ , training tasks. Frontal and occipital sites did not have significant ERD during either condition ( $ps > .10$ ; see Figure 7b).

**Action observation: 7- to 10-Hz band.** A MANOVA on observation ERD scores within the 7- to 10-Hz band revealed a significant main effect of Region,  $F(3, 13) = 19.62$ ,  $p < .001$ ,  $\eta_p^2 = .82$ , and a significant Region  $\times$  Training Condition interaction,  $F(3, 13) = 4.86$ ,  $p = .02$ ,  $\eta_p^2 = .53$ . There was no significant main effect of condition ( $F < 1$ ). Once again, results obtained from the standard mu band paralleled those found with individualized frequency bands. Follow-up paired  $t$ -tests revealed significantly greater ERD scores at occipital sites during observation of the active training task ( $M = -0.10$ ,  $SD = .22$ ) than the observational training task ( $M = -0.01$ ,  $SD = .23$ ),  $t(15) = -2.67$ ,  $p = .02$ ,  $d = 0.64$ . There were no significant differences in ERD during perception of the active and observational tasks at frontal, central, or parietal regions ( $ps > .10$ ).

Separate MANOVAs confirmed a significant main effect of region during perception of the active,  $F(3, 13) = 9.72$ ,  $p = .001$ ,  $\eta_p^2 = .69$ , and observational,  $F(3, 13) = 9.00$ ,  $p = .002$ ,  $\eta_p^2 =$

.67, training tasks. For both the active and observational training tasks, follow-up contrasts revealed significantly greater ERD at parietal (active:  $M = -0.12$ ,  $SD = 0.11$ ; observational:  $M = -0.14$ ,  $SD = 0.13$ ) than frontal sites (active:  $M = -0.03$ ,  $SD = 0.11$ ,  $p = .001$ ; observational:  $M = -0.04$ ,  $SD = 0.10$ ,  $p = .001$ ).

ERD scores were only significant at central sites during the active training task ( $M = -0.13$ ,  $SD = 0.20$ ),  $t(15) = -2.54$ ,  $p = .01$ ,  $d = 0.65$ , and had a non-significant negative trend during the observational training task ( $M = -0.09$ ,  $SD = .23$ ),  $t(15) = -1.60$ ,  $p = .07$ . Planned  $t$ -tests revealed that ERD scores were significantly less than zero at parietal sites during observation of both the active,  $t(15) = -4.38$ ,  $p = .001$ ,  $d = 1.09$ , and observational,  $t(15) = -4.91$ ,  $p = .001$ ,  $d = 1.08$ , training tasks. Frontal and occipital sites did not have significant ERD during either condition ( $ps > .10$ ; see Figure 8b).

### EEG Beta Rhythm

**Action execution.** A MANOVA was also completed on ERD scores within the beta band (17-21 Hz) during action execution. There was a significant main effect of region,  $F(3, 13) = 48.67$ ,  $p < .001$ ,  $\eta_p^2 = .92$ , and no significant effects of training condition ( $Fs < 1$ ). Follow-up contrasts revealed significantly greater ERD over central sites ( $M = -0.09$ ,  $SD = 0.21$ ) than parietal ( $M = 0.05$ ,  $SD = 0.17$ ,  $p = .03$ ) and occipital ( $M = 0.17$ ,  $SD = 0.18$ ,  $p < .001$ ) sites; frontal sites ( $M = -0.24$ ,  $SD = 0.18$ ) also had greater ERD scores than parietal and occipital sites ( $ps < .001$ ). Additionally, occipital sites had significantly greater event-related synchronization (ERS) than parietal sites ( $p = .04$ ). ERD scores at central sites were marginally less than zero,  $t(15) = -1.72$ ,  $p = .054$ ,  $d = 0.43$ . Planned  $t$ -tests revealed that ERD scores at frontal sites were significantly less than zero,  $t(15) = -5.14$ ,  $p < .001$ ,  $d = 1.41$ , and that ERD scores at occipital

sites were significantly greater than zero,  $t(15) = 3.84$ ,  $p = .002$ ,  $d = 0.94$ . Parietal ERD scores did not significantly differ from zero ( $p > .10$ ; see Figure 9a).

**Action observation.** A MANOVA was also completed on action observation ERD scores within the beta band (17-21 Hz). There was no significant main effect of region,  $F(3, 13) = 2.82$ ,  $p = .08$ , or training condition ( $F < 1$ ), and no significant Region  $\times$  Condition interaction,  $F(3, 13) = 1.45$ ,  $p = .27$ . Planned  $t$ -tests revealed that ERD scores at frontal sites were significantly less than zero,  $t(15) = -2.46$ ,  $p = .03$ ,  $d = 0.65$ . ERD scores at central, parietal, and occipital regions did not significantly differ from zero ( $ps > .06$ ; see Figure 9b).

## Discussion

In the current study, we provided 3- to 6-year-old children with at-home active (i.e., children played with a novel toy) and observational (i.e., children watched a video of a demonstrator using a similar toy) training prior to laboratory electrophysiological recording. As expected, children exhibited neural mirroring within both individualized and standard (7-10 Hz) mu bands. Although mu and beta activity at central sites did not differ as a function of training condition, occipital ERD scores within both individualized and standard mu frequency bands were significantly greater during the perception of the active training task than the observational training task, suggesting that active training may influence visual attention during later observation of the task. To our knowledge, this is the first study to investigate the effects of action experience on EEG mu and beta rhythms during early childhood.

## EEG Mu Rhythm

**Neural mirroring.** As hypothesized, children exhibited significant desynchronization of the EEG mu rhythm within both individualized and standard (7-10 Hz) frequency bands during action execution and observation of the active training task. A similar trend was found during

perception of the observational training task ( $p < .07$ ), suggesting that increased statistical power (i.e., larger sample size) could reveal significant ERD during observation of this task. Thus, the current study offers evidence of neural mirroring during early childhood. Our findings are consistent with the small number of studies investigating the mu rhythm during early childhood (e.g., Lepage & Théoret, 2006; Warreyn et al., 2013) as well as the broader infant (e.g., Marshall et al., 2011; Southgate et al., 2009) and adult (e.g., Muthukumaraswamy & Johnson, 2004) mu rhythm literature.

This is the first demonstration of mu rhythm desynchronization during the observation and execution of tool use during early childhood. These findings are similar to those of EEG research on the infant (Southgate & Begus, 2013) and adult (Cannon et al., 2014) mu rhythms, as well as single-cell recording studies on macaque mirror neuron activity (Ferrari, Rozzi, & Fogassi, 2005), during perception of tool use. In this context, Ferrari et al. suggest that tools are represented as a prolongation of the arm, and thus activity that is normally generated in response to the perception simple manual actions (e.g., grasping) generalizes to the perception of a similar action by a tool. As the current study demonstrated neural mirroring during the observation and execution of an action with a tool, our findings suggest that this mapping of tool use to motor representations of manual actions also occurs in humans during early childhood.

This study is also the first to report mu rhythm desynchronization within both standard (i.e., 7-10 Hz) and individualized frequency bands during early childhood. Throughout infancy and early childhood, EEG signals increase in frequency (see Saby & Marshall, 2012, for review). As these signals mature at varying rates across children, the use of individualized frequency bands controls for these individual differences by selecting the frequency band that is maximally attenuated during movement (i.e., tool grasping). Controlling for individual differences in peak

frequency of mu rhythm activity was especially critical in the current study, given the relatively wide age range of the sample. However, use of individualized frequency bands can mask potentially meaningful individual differences in the EEG signal and complicate cross-study comparisons, as the selected frequency bands vary between participants (Cuevas et al., 2014). Given the benefits and drawbacks of either method, it is thus encouraged that researchers report findings generated from both individualized and standard frequency bands (Cuevas et al., 2014). Although studies on mu rhythm desynchronization during early childhood have used either individualized (e.g., Berchicci et al., 2011; Lepage & Théoret, 2006; Ruysschaert, Warreyn, Wiersema, Oostra, & Roeyers, 2014; Warreyn et al., 2013) or standard bands (e.g., Liao et al., 2015; Martineau, Cochin, Magne, & Barthelemy, 2008; Meyer et al., 2011), none have reported findings using both methods.

**Effects of active and observational training.** Although children in the present study exhibited neural mirroring within the EEG mu rhythm, there were no effects of training condition on central mu rhythm ERD. These findings are inconsistent with existing research comparing NMS activity during perception of tasks with which the subject has active and observational experience (e.g., Calvo-Merino et al., 2006; Cannon et al., 2014; Gerson et al., 2014). One potential explanation for these null findings is that active and observational training either have no influence mu rhythm desynchronization or modulate it in similar ways during early childhood. However, given that research has demonstrated differential influences of active and observational training on mu rhythm ERD during both infancy (Gerson et al., 2015) and adulthood (Cannon et al., 2014), alternative explanations should also be considered.

The inclusion of action execution trials may have also contributed to these null findings. The majority of research that has found that active experience was associated with increased

NMS activity did not include an action execution phase (e.g., Cannon et al., 2014; Calvo-Merino et al., 2005, 2006). However, studies that have found the opposite association (i.e., active experience associated with decreased NMS activity) required participants to perform a task after the observation phase, including executing the same action (Vogt et al., 2007) or making a judgment about the difficulty of that action (Babiloni et al., 2010). Vogt and colleagues hypothesize that these inconsistent findings are the result of different aims of the observation phases across studies. As execution of a novel action is generally more difficult than performance of an action with which one has experience, observation of a novel action prior to imitation may require increased cognitive processing. Vogt and colleagues suggest that the effects of later action execution on NMS activity may reflect modulatory input from prefrontal areas during action perception.

Based on the findings of Vogt et al. (2007), we suggest that the inclusion of execution trials in the current study may have differentially influenced mu rhythm ERD during perception of the active and observational training tasks. Children may have found the active training task easier to perform, as they had practiced this action multiple times at home prior to EEG recording. Therefore, perception of the observational training task may have required additional cognitive resources as children prepared to perform a relatively novel task. However, whereas Vogt et al. (2007) found significantly greater NMS activation during perception of a novel task, we found no significant difference in mu rhythm ERD during the perception of the active and observational training tasks. There are many methodological differences between Vogt et al. (2007) and the current study, including duration of training and the difficulty of the tasks, which may have varied the level of modulation by subsequent execution trials. We hypothesize that, in the current study, this modulation was sufficient to shift the direction of associations between



action experience in the direction opposite what we had expected, but not strong enough to demonstrate significantly greater mu rhythm ERD during perception of the observational training task than the active training task. To eliminate this potential confound, researchers could instead inform participants that they will be asked to perform the target action after all observation trials are complete. However, this may pose a challenge in developmental studies, as children have limited inhibitory capacity, especially when presented with a desirable object.

Another contributing factor to the observed null associations between mu ERD and training condition may be the influence of tasks that are motorically similar to the target actions. Although children had no prior experience with the study apparatus, the actions on which participants received training were motorically similar to a variety of other actions within participants' motor repertoires. Southgate and Begus (2013) suggest that, while observing an action, if a direct motor representation of that action is not available, representations of similar actions are then recruited. Given the flexibility of the NMS, similarities between the target actions and actions already within participants' motor repertoires may have interfered with the effects of at-home training on mu rhythm desynchronization. For example, use of the hook may have recruited motor representations of simple manual reaching, and the lobster task, which is performed by squeezing a trigger in the lobster's tail, may recruit representations of similar actions such as squeezing a stress ball. Though Cannon et al. (2014) used a similar claw-like tool in their study and demonstrated a significant effect of active experience on mu rhythm ERD, participants had extensive motor experience with that tool, having completed an average of 225 trials. In the current study, on average, participants completed approximately 54 active training trials, which may not have been sufficient to overcome the effects of motor experience with similar tasks. Future work that varies the number of training trials participants complete prior to

EEG recording is needed to address potential limitations of brief motor training. Additionally, research that trains participants on novel tasks that have minimal overlap with actions already in their motor repertoires could provide more insight on the flexibility of NMS activation; however, given the level of motor skill and experience achieved by early childhood, conceiving a truly novel action may pose a considerable challenge at this stage of development.

Gerson et al. (2015) is the first study to investigate effects of active and observational training on mu rhythm ERD within a developmental population. Though our findings are inconsistent with those of Gerson and colleagues, there are some methodological differences between these experiments that make cross-study comparisons more difficult. For example, Gerson et al. (2015) measured differences in mu ERD during perception of sounds that were associated with stimuli on which infants received active and observational training. Had the current study measured ERD during audition, as compared to visual perception, we may have also revealed significant differences in mu ERD based on training condition. Additionally, the use of different baselines across experiments pose further challenges in drawing cross-study comparisons. Whereas the current study recorded resting-state EEG as baseline, Gerson and colleagues used activity during perception of a novel sound and did not collect EEG activity during rest. Based on their figures (p. 1212) it appears that there was no significant difference in central mu rhythm reactivity during perception of the novel or observational sound, however we cannot determine if mu ERD desynchronized from rest during perception of either sound.

Though the current study provides evidence that observational and active training have similar effects on mu rhythm ERD during early childhood, additional research is needed to determine whether either training, regardless of type, elicits change in the strength of mu rhythm activity at this age. To investigate these effects, it is necessary to include an additional condition

in which participants observe a task with which they had no previous active or observational experience. The current study could have achieved this by adding this third condition to our within-subjects design; however, this would pose a challenge in data collection due to the resulting increased protocol duration and children's limited attentional capacity. Instead, future analyses will incorporate data collected from participants who had neither active nor observational training on these tasks for additional between-subjects comparisons. Inclusion of this group may uncover a significant influence of training during early childhood, as both Cannon et al. (2014) and Gerson et al. (2014) both revealed significant differences in mu rhythm ERD during observation of active and novel tasks. Cannon et al. (2014) measured mu ERD during observation of a novel task by including a group that had no prior experience with the target action; although they did not report effect sizes or mean group differences, visual inspection of their figures (p. 5) suggests that the significant group differences were greater between the expert performers group and the novice group than between the expert performers and the expert observers.

As discussed, there are significant inconsistencies in the current literature on mu rhythm ERD and action experience, in terms of both methodology and the directions of studies' findings. Given that some studies have found that active experience is associated with increased mu ERD, while others have found the opposite association, it is highly likely that others have found null associations. Although we are not aware of any null associations between mu rhythm ERD and action experience in the literature, this is likely because these null results are not often published.

**The occipital alpha rhythm.** One interesting, and unexpected, finding of the current study was differential reactivity at occipital sites as a function of training condition; effects of training condition on ERD at occipital sites were significant within the frequency ranges of both

individualized and standard mu bands. It is possible that these findings reflect activity of the occipital alpha rhythm, an EEG rhythm recorded over posterior regions that occupies the same frequency band as the mu rhythm during infancy and adulthood (Stroganova, Orekhova, & Posikera, 1999). The occipital alpha rhythm has a high amplitude during exposure to a homogeneous visual field (e.g., eyes closed) and desynchronizes during visual processing (Lehtonen & Lehtinen, 1971). Suppression of the occipital alpha rhythm is also considered to be an indicator of visual attention; for example, occipital alpha rhythm desynchronizes in the hemisphere contralateral to an attended object's location within the visual field (Sauseng et al., 2005).

In the current study, activity at occipital sites (within the frequency ranges of both individualized and standard mu bands) was significantly greater during perception of the task on which participants had active, rather than observational, training. We interpret our findings to indicate that short-term active experience with an action increases visual attention during subsequent observation of that task; this enhanced visual attention is associated with greater occipital alpha desynchronization. Our findings within occipital regions most closely mirror those of James (2010), an fMRI study that found that 4- to 5-year-olds exhibited increased activation of the visual association cortex after first-hand motor training drawing letters, but not after only receiving visual training on letter recognition. James hypothesizes that these findings indicate the development of functional specialization for drawing letters as a result of sensori-motor experience, rather than increased visual attention, as participants in this study did not exhibit a significant advantage in letter recognition as result of motor experience. However, performance on this task was greater after motor training than after visual training, though this difference was not statistically significant ( $p < .07$ ). We therefore conclude that attention-based

explanations for differential influences of active and observational training on occipital activity warrant further consideration.

Some adult research on the effects of active experience on cortical activity has also noted associations between experience and occipital alpha activity. Cannon et al. (2014) found a significant effect of group at occipital sites, though follow-up tests were not significant after multiple comparison (Bonferroni) corrections. However, based on their figures (p. 5), it appears that expert observers exhibited greater occipital alpha ERD than the expert performer and novice groups. Similarly, other adult EEG studies have also indicated that action experience is associated with decreased activation of occipital regions (e.g., Haufler et al., 2000; Loze, Collins, & Holmes, 2001). These studies indicate that greater performance or expertise with an action is associated with more efficient (i.e., decreased) cortical processing and are thus consistent with the neural efficiency hypothesis. Taken together, the findings of both the current study and previous literature indicate that motor experience influences activation within occipital regions, though the direction of this association may vary depending on a variety of factors.

### **EEG Beta Rhythm**

**Neural mirroring.** Whereas there is little research on the mu rhythm during early childhood, research on the central beta rhythm during early childhood is even less common. To our knowledge, Meyer and colleagues' investigations with 3-year-olds is the only examination of the central beta rhythm during early childhood (Meyer et al., 2011); however, this study has several significant limitations including a small sample size ( $N = 7$ ), insufficient artifact-free execution trials for subsequent analysis, and absence of a baseline condition. In contrast, the current study included baseline and execution conditions, which made it possible to determine whether the beta rhythm exhibits significant desynchronization during both action observation

and execution. These characteristics of the current protocol thus made it possible to determine whether the beta rhythm exhibits mirroring properties during early childhood, which not have been ascertained from Meyer et al. (2011) alone. Additionally, the current study has a considerably larger sample size than that of Meyer and colleagues and investigates central beta rhythm activity within a broader age range (3 – 6 years, as compared to only 3 years).

Current research on the neural mirroring properties of the adult EEG beta rhythm has mixed findings. For example, while Babiloni et al. (2002) found evidence of neural mirroring within the beta band, Nyström (2008) found that the beta rhythm did not significantly change from zero during either action observation or action execution. There is currently no evidence of neural mirroring properties of the beta rhythm during infancy (Meyer, Braukmann, Stapel, Bakkering, & Hunnius, 2015; Nyström, 2008; Virji-Babul et al., 2012). These discrepant findings may reflect developmental differences in central beta rhythm activity, or may be the result variation of the motor properties of the tasks used across studies (Avanzini et al., 2012).

One challenge in interpreting and comparing findings on the beta rhythm is the variability in the frequency bands used across studies. Whereas within infant studies, the mu frequency range has been somewhat consistently defined as approximately 6-9 Hz, the frequency bands used to investigate beta rhythm activity widely vary. For example, infant studies have defined the beta band as 7-12 Hz (van Elk et al., 2008) or 15-35 Hz (Virji-Babul et al., 2012) and these variations do not appear to be associated with age-related changes in EEG frequency. Adult studies on the beta rhythm exhibit similar variability, with some defining beta as 13-25 Hz (Orgs et al., 2008), 15-25 Hz (Cannon et al., 2014), or 18 – 22 Hz (Haufler, Spalding, Santa Maria, & Hatfield, 2000). This variability, paired with the scarcity of studies on the beta rhythm during early childhood, makes it difficult to ascertain which “beta” rhythm to analyze and may

contribute to the inconsistencies in the current beta literature. It is therefore recommended that studies investigating neural mirroring properties of the mu band also report data from the central beta rhythm (Cuevas et al., 2014); this will allow researchers to determine patterns across studies and may assist in the development of more standard practices in this area of research.

**Effects of active and observational training.** The current study did not reveal a significant influence of training condition on central beta rhythm ERD during early childhood. Current findings on associations between central beta rhythm ERD and action experience are mixed. For example, Orgs et al. (2008) found significant influences of dance experience on beta ERD while observing dance movements, while Cannon et al. (2014) did not find significant differences in central beta ERD as a function of experience. In addition to the previously discussed challenges and inconsistencies in beta rhythm research, there are several alternative explanations for these discrepancies. Cannon and colleagues suggest that the beta rhythm may be particularly sensitive to the duration of prior action experience; whereas professional dancers had approximately 15 years or greater experience with the target dance movements (Orgs et al., 2008), expert performers in Cannon et al. (2014) had approximately 9 months experience with the target action. In the current study, participants received brief active and observational training over the course of a 4 day training period. If duration of training moderates associations between central beta rhythm ERD and action experience, this could potentially account for the null influences of training condition observed in the current study.

It is possible that active and observational training on relatively simple actions such as reaching with a tool, as in the present study, may not evoke differential reactivity of the central beta rhythm. This rhythm may be sensitive to the physical nature of the perceived task, including action complexity, speed, and object weight (Cannon et al., 2014). For example, Orgs

et al. (2008) found effects of action experience on beta ERD while presenting participants with sequences of dance movements, which are more complex than reaching actions. Additional studies found that beta rhythm ERD is modulated by velocity profiles of repeated actions during perception (Avanzini et al., 2012) and object weight (Quandt, Marshall, Shipley, Beilock, & Goldin-Meadow, 2012).

### **Limitations and Future Directions**

Strengths of the current study include experimental manipulation of both children's active and observational experience with the study stimuli, use of a within-subjects design, analyses determining the magnitude of mu and beta rhythm desynchronization, and the inclusion of action execution trials. Whereas many prior studies on the effects of action experience on NMS activity did not report or collect data during action execution (e.g., Cannon et al., 2014; van Elk et al., 2008), inclusion of this phase is essential in NMS research (Cuevas et al., 2014). However, the current study had little control over the number of active training trials completed prior to EEG recording. Children completed a significantly greater number of active training trials than observational training trials. Although analyses confirmed that differences in the number of active and observational trials were not correlated with differences in subsequent ERD scores, future investigations on the effects of experience should have participants perform a set number of trials prior to EEG recording.

As demonstrated in the current study and previous literature, associations between active experience and cortical activity are complex and may be influenced by a variety of factors. Methodological inconsistencies within the relevant literature provide an incomplete understanding on the effects of experience on EEG activity. Additional research is needed to investigate factors that may moderate associations between active and observational experience



and cortical activity (e.g., duration of motor training). Potential moderating effects of motor skill on the associations between active experience and mu and central beta rhythm desynchronization is also of interest; in the current study, we also administered the fine motor scale of the Mullen Scales of Early Learning (Mullen, 1995) and these potential associations are being investigated.

### **Conclusion**

This study is the first to investigate influences of active and observational experience on central mu and beta rhythm desynchronization during early childhood. Although there were no significant effects of training condition on central mu and beta rhythm ERD, our findings suggest that action experience may influence desynchronization of the occipital alpha rhythm. ERD was greater during perception of the task on which participants had active, rather than observational, training. Thus, our findings conflict with the majority of literature on action experience and mu rhythm desynchronization during infancy and adulthood; these studies have provided evidence that the NMS serves as a mechanism of action understanding by mapping action perception onto an internal motor representation. In contrast, our findings suggest that, in some contexts, the NMS may not be necessary for action understanding. In sum, associations between action experience and EEG activity are complex and may be influenced by a wide variety of factors.

## References

- Arnstein, D., Cui, F., Keysers, C., Maurits, N. M., & Gazzola, V. (2011).  $\mu$ -suppression during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal, and SI cortices. *The Journal of Neuroscience*, *31*, 14243–14249. doi:10.1523/JNEUROSCI.0963-11.2011
- Avanzini, P., Fabbri-Destro, M., Dolla Volta, R., Daprati, E., Rizzolatti, G., & Cantalupo, G. (2012). The dynamics of sensorimotor cortical oscillations during the observation of hand movements: An EEG study. *PLoS ONE*, *7*(55): e37534. doi:10.1371/journal.pone.0037534
- Babiloni, C., Babiloni, F., Carducci, F., Cinotti, F., Coccozza, G.,... Rossini, P.M. (2002). Human cortical electroencephalography (EEG) rhythms during the observation of simple aimless movements: A high-resolution EEG study. *NeuroImage*, *17*, 559-572. doi:10.1006/nimg.2002.1192
- Babiloni, C., Marzano, N., Infarinato, F., Iacoboni, M., Rizza, G.,... Del Percio, C. (2010). “Neural efficiency” of experts’ brain during judgment of actions: A high-resolution EEG study in elite and amateur karate athletes. *Behavioral Brain Research*, *207*, 466-475. doi:10.1016/j.bbr.2009.10.034
- Bell, M. A. (1998). The ontogeny of the EEG during infancy and childhood: Implications for cognitive development. In B. Garreau (Ed.), *Neuroimaging in child neuropsychiatric disorders* (pp. 97-111). Berlin: Springer-Verlag.
- Berchicci, M., Zhang, T., Romero, L., Peters, A., Annett, R.,... Comani, S. (2011). Development of mu rhythm in infants and preschool children. *Developmental Neuroscience*, *33*, 130-143. doi: 10.1159/000329095
- Bernier, R., Dawson, G., Webb, S., & Murias, M. (2007). EEG mu rhythm and imitation impairments in individuals with autism spectrum disorder. *Brain and Cognition*, *64*, 228-237. doi: 10.1016/j.bandc.2007.03.004
- Calvo-Merino, B., Glaser, D.E., Grèzes, J., Passingham, R.E., & Haggard, P. (2005). Action observation and acquired motor skills: An fMRI with expert dancers. *Cerebral Cortex*, *15*, 1243-1249. doi: 10.1093/cercor/bhi007
- Calvo-Merino, B., Grèzes, J., Glaser, D.E., Passingham, R.E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology*, *16*, 1905-1910. doi: 10.1016/j.cub.2006.07.065
- Cannon, E.N., Yoo, K.H., Vanderwert, R.E., Ferrari, P.F., Woodward, A.L., & Fox, N.A. (2014). Action experience, more than observation, influences mu rhythm desynchronization. *PLoS ONE*, *9*(3): e92002. doi: 10.1371/journal.pone.0092002
- Carr, L., Iacoboni, M., Dubeau, M., Mazziotta, J.C., & Lenzi, G.L. (2003). Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic studies. *Proceedings of the National Academy of Sciences USA*, *100*, 5497-5502. doi: 10.1073/pnas.0935845100
- Cross, E.S., Hamilton, A., & Grafton, S.T. (2006) Building a motor simulation de novo: Observation of dance by dancers. *NeuroImage*, *31*, 1257-1267. doi: 10.1073/pnas.0935845100
- Cuevas, K., Cannon, E.N., Yoo, K., & Fox, N.A. (2014). The EEG mu rhythm: Methodological considerations and best practices. *Developmental Review*, *34*, 26-43. doi: 10.1016/j.dr.2013.12.001

- Del Percio, C., Infarinato, F., Iacoboni, M., Marzano, N., Soricelli, A.,... Babiloni, C. (2010). Movement-related desynchronization of alpha rhythms is lower in athletes than non-athletes: A high-resolution EEG study. *Clinical Neurophysiology*, 121, 482-491. doi: 10.1016/j.clinph.2009.12.004
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, 91, 176-180. doi: 10.1007/BF00230027
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, 73, 2608-2611.
- Ferrari, P.F., Rozzi, S., & Fogassi, L. (2005). Mirror neurons responding to observation of actions made with tools in monkey ventral premotor cortex. *Journal of Cognitive Neuroscience*, 7, 212-226. doi: 10.1162/0898929053124910
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, 119, 593-609. doi: 10.1016/0926-6410(95)00038-0
- Gallese, V., Gernsbacher, M. A., Heyes, C., Hickok, G., & Iacoboni, M. (2011). Mirror neuron forum. *Perspectives on Psychological Science*, 6, 369-407. doi: 10.1177/1745691611413392
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Neuroscience*, 2, 493-501. doi: 10.1016/S1364-6613(98)01262-5
- Gerson, S.A., Bekkering, H., & Hunnius, S. (2015). Short-term motor training, but not observational training, alters neurocognitive mechanisms of action processing in infancy. *Journal of Cognitive Neuroscience*, 27, 1207-1214. doi:10.1162/jocn\_a\_00774
- Hari, R., & Salmelin, R. (1997). Human cortical oscillations: A neuromagnetic view through the skull. *Trends in Neurosciences*, 77, 3401-3405. doi:10.1016/S0166-2236(96)10065-5
- Haufler, A.J., Spalding, T.W., Santa Maria, D.L., & Hatfield, B.D. (2000). Neuro-cognitive activity during a self-paced visuospatial task: Comparative EEG profiles in marksmen and novice shooters. *Biological Psychology*, 53, 131-160.
- Hickok, G. (2009). Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *Journal of Cognitive Neuroscience*, 21, 1229-1243. doi:10.1162/jocn.2009.21189
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS ONE*, 3(3): e79. doi:10.1371/journal.pbio.0030079
- James, K. (2010). Sensori-motor experience leads to changes in visual processing in the developing brain. *Developmental Science*, 13, 279-288. doi:10.1111/j.1467-7687.2009.00883.x.
- Keselman, H.J. (1998). Testing treatment effects in repeated measures designs: An update for psychophysiological researchers. *Psychophysiology*, 35, 470-478. doi: 10.1111/1469-8986.3540470
- Kontra, C., Goldin-Meadow, S., & Beilock, S.L. (2012). Embodied learning across the life span. *Topics in Cognitive Science*, 4, 731-739. doi: 10.1111/j.1756-8765.2012.01221.x
- Lehtonen, J.B. & Lehtinen, I. (1972). Alpha rhythm and the uniform visual field in man. *Electroencephalography and Clinical Neurophysiology*, 32, 139-147. doi:10.1016/0013-4694(72)90136-8

- Lepage, J. & Théoret, H. (2006). EEG evidence for the presence of an action observation-execution matching system in children. *European Journal of Neuroscience*, 23, 2505-2510. doi:10.1111/j.1460-9568.2006.04769.x
- Liao, Y., Acar, Z., Makeig, S., & Deak, G. (2015). EEG imaging of toddlers during dyadic turn-taking: Mu-rhythm modulation while producing or observing social actions. *NeuroImage*, 122, 52-60. doi:10.1016/j.neuroimage.2015.02.055
- Loze, G.M., Collins, D., & Holmes, P.S. (2001). Pre-shot EEG alpha-power reactivity during expert air-pistol shooting: A comparison of best and worst shots. *Journal of Sports Sciences*, 19, 727-733. doi: 10.1080/02640410152475856
- Marshall, P.J., Bar-Haim, Y., & Fox, N.A. (2002). Development of EEG from 5 months to 4 years. *Clinical Neurophysiology*, 113, 1199-1208. doi:10.1016/S1388-2457(02)00163-3
- Marshall, P.J., Bouquet, C.A., Shipley, T.F., & Young, T. (2009). Effects of imitative experience on EEG desynchronization during action observation. *Neuropsychologia*, 47, 2100-2106. doi: 10.1016/j.neuropsychologia.2009.03.022
- Marshall, P. J., & Meltzoff, A. N. (2011). Neural mirroring systems: Exploring the EEG mu rhythm in human infancy. *Developmental Cognitive Neuroscience*, 1, 110-123. doi: 10.1016/j.dcn.2010.09.001
- Marshall, P. J., Young, T., & Meltzoff, A. N. (2011). Neural correlates of action observation and execution in 14-month-old infants: an event-related EEG desynchronization study. *Developmental Science*, 14, 474-480. doi: 10.1111/j.1467-7687.2010.00991.x
- Martineau, J., Cochin, S., Magne, R., & Barthelemy, C. (2008). Impaired cortical activation in autistic children: Is the mirror neuron system involved? *International Journal of Psychophysiology*, 68, 35-40. doi:10.1016/j.ijpsycho.2008.01.002
- Meyer, M., Braukmann, R., Stapel, J.C., Bekkering, H., & Hunnius, S. (2015). Monitoring others' errors: The role of the motor system in early childhood and adulthood. *Developmental Psychology*, 34, 66-85. doi: 10.1111/bjdp.12101
- Meyer, M., Hunnius, S., van Elk, M., van Ede, F., & Bekkering, H. (2011). Joint action modulates motor system involvement during action observation in 3-year-olds. *Experimental Brain Research*, 211, 581-592. doi: 10.1007/s00221-011-2658-3
- Molenberghs, P., Cunnington, R., & Mattingley, J.B. (2012). Brain regions with mirror properties: A meta-analysis of 125 human fMRI studies. *Neuroscience & Biobehavioral Reviews*, 36, 341-349. doi:10.1016/j.neubiorev.2011.07.004
- Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-neuron responses in humans during execution and observation of actions. *Current Biology*, 20, 750-756. doi:10.1016/j.cub.2010.02.045
- Mullen, E.M. (1995). Mullen Scales of Early Learning. Circle Pines, MN: American Guidance Service.
- Muthukumaraswamy, S. D., & Johnson, B. W. (2004). Changes in rolandic mu rhythm during observation of a precision grip. *Psychophysiology*, 41, 152-156. doi: 10.1016/j.cogbrainres.2003.12.001
- Nakano, H., Osumi, M., Ueta, K., Takayuki, K., & Morioka, S. (2013). Changes in electroencephalographic activity during observation, preparation, and execution of a motor learning task. *International Journal of Neuroscience*, 123, 866-875. doi: 10.3109/00207454.2013.813509
- Nyström, P. (2008). The infant mirror neuron system studied with high density EEG. *Social Neuroscience*, 3, 334-347. doi: 10.1080/17470910701563665

- Oberman, L.M., Ramachandran, V.S., & Pineda, J.A. (2008). Modulation of mu suppression in children with autism spectrum disorders in response to familiar and unfamiliar stimuli: The mirror neuron hypothesis. *Neuropsychologia*, 46, 1558-1565. doi: 10.1016/j.neuropsychologia.2008.01.010
- Orgs, G., Dombrowski, J.-H., Heil, M., & Jansen-Osmann, P. (2008). Expertise in dance modulates alpha/beta event-related desynchronization during action observation. *European Journal of Neuroscience*, 27, 3380–3384. doi:10.1111/j.1460-9568.2008.06271.x
- Pineda, J. A. (2005). The functional significance of my rhythms: Translating “seeing” and “hearing” into “doing”. *Brain Research Reviews*, 50, 57-68.
- Quandt, L.C., Marshall, P.J., Shipley, T.F., Beilock, S.L., & Goldin-Meadow, S. (2012). Sensitivity of alpha and beta oscillations to sensorimotor characteristics of action: An EEG study of action production and gesture observation. *Neuropsychologia*, 50, 2745-2751. doi:10.1016/j.neuropsychologia.2012.08.005
- Raymaekers, R., Wiersema, J.R., & Roeyers, H. (2009). EEG study of the mirror neuron system in children with high functioning autism. *Brain Research*, 1304, 113-121. doi: 10.1016/j.brainres.2009.09.068
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, 3, 131-141. doi:10.1016/0926-6410(95)00038-0
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*, 11, 264-274. doi: 10.1038/nrn2805
- Ruysschaert, L., Warreyn, P., Wiersema, J., Oostra, A., & Roeyers, H. (2014). Exploring the role of neural mirroring in children with autism spectrum disorder. *Autism Research*, 7, 197-206. doi: 10.1002/aur.1339
- Saby, J.N. & Marshall, P.J. (2012). The utility of EEG band power analysis in the study of infancy and early childhood. *Developmental Neuropsychology*, 37, 253-273. doi: 10.1080/87565641.2011.614663
- Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S.,... Birbaumer, N. (2005). A shift of visual spatial attention is selectively associated with human EEG alpha activity. *European Journal of Neuroscience*, 22, 2917-2926. doi: 10.1111/j.1460-9568.2005.04482.x
- Southgate, V., & Begus, K. (2013). Motor activation during prediction of nonexecutable actions in infants. *Psychological Science*, 24, 828-835. doi: 10.1177/0956797612459766
- Southgate, V., Johnson, M. H., Karoui, I. E., & Csibra, G. (2010). Motor system activation reveals infants' on-line prediction of others' goals. *Psychological Science*, 21, 355-359. doi: 10.1177/0956797610362058
- Southgate, V., Johnson, M. H., Osborne, T., & Csibra, G. (2009). Predictive motor activation during action observation in human infants. *Biology Letters*, 5, 769-772. doi: 10.1098/rsbl.2009.0474
- Stapel, J.C., Hunnius, S., van Elk, M., & Bekkering, H. (2010). Motor activation during observation of unusual versus ordinary actions in infancy. *Social Neuroscience*, 5, 451-460. doi: 10.1080/17470919.2010.490667
- Stroganova, T. A., Orekhova, E. V., & Posikera, I. N., (1999). EEG alpha rhythm in infants. *Clinical Neurophysiology*, 110, 997-1012. doi:10.1016/S1388-2457(98)00009-1

- Thorpe, S.G., Cannon, E.N., & Fox, N.A. (2016). Spectral and source development of mu and alpha rhythms from infancy through adulthood. *Clinical Neurophysiology*, 26, 254-265. doi: 10.1016/j.clinph.2015.03.004
- Tiihonen, J., Kajola, M., & Hari, R. (1989). Magnetic mu rhythm in man. *Neuroscience*, 32, 793-800. doi:10.1016/0306-4522(89)90299-6
- van Elk, M., van Schie, H. T., Hunnius, S., Vesper, C., & Bekkering, H. (2008). You'll never crawl alone: Neurophysiological evidence for experience-dependent motor resonance in infancy. *NeuroImage*, 43, 808–814. doi:10.1016/j.neuroimage.2008.07.057
- Vernon, P.A. (1993). Intelligence and neural efficiency. In D.K. Detterman (Ed.), *Current Topics in human intelligence* (pp. 171-187), Norwood, NJ: Ablex Publishing.
- Virji-Babul, N., Rose, A., Moiseeva, N., & Makan, N. (2012). Neural correlates of action understanding in infants: influence of motor experience. *Brain and Behavior*, 2, 237–242. doi: 10.1002/brb3.50
- Vogt, S., Buccino, G., Wohlschläger, A.M., Canessa, N., Shah, N.J., Zilles, K., Eickhoff, S.B.,... Fink, G. (2007). Prefrontal involvement in imitation learning of hand actions: Effects of practice and expertise. *NeuroImage*, 37, 1371-1383. doi: 10.1016/j.neuroimage.2007.07.005
- Warreyn, P., Ruyschaert, L., Wiersema, J. R., Handl, A., Pattyn, G., & Roeyers, H. (2013). Infants' mu suppression during the observation of real and mimicked goal-directed actions. *Developmental Science*, 16, 173–185. doi: 10.1111/desc.12014

## Footnotes

<sup>1</sup>As this debate is not the focus of this thesis, we use the term “neural mirroring system” (NMS) to refer brain regions that exhibit neural mirroring properties. Use of this terminology is a conservative approach to acknowledge brain regions that exhibit similar reactivity during action observation and execution without making distinct claims regarding the presence or absence of mirror neurons in humans (Marshall & Meltzoff, 2011).

<sup>2</sup>Although Gerson et al. (2014) did not explicitly report event-desynchronization values during action execution, this activity was recorded. The authors indicated that participants exhibited a decrease in 6-9 Hz power relative to baseline during action execution, but do not specify whether this decrease was significant or specific to central sites.

<sup>3</sup>One motor training session with the fishing hook tool was not recorded, and thus that session was not included in corresponding calculations.

<sup>4</sup>Based on pilot testing, children took longer to complete tasks than the adult experimenter. Thus it was anticipated that, despite the different durations of the active and observational training tasks, participants would complete a similar number of trials across tasks.

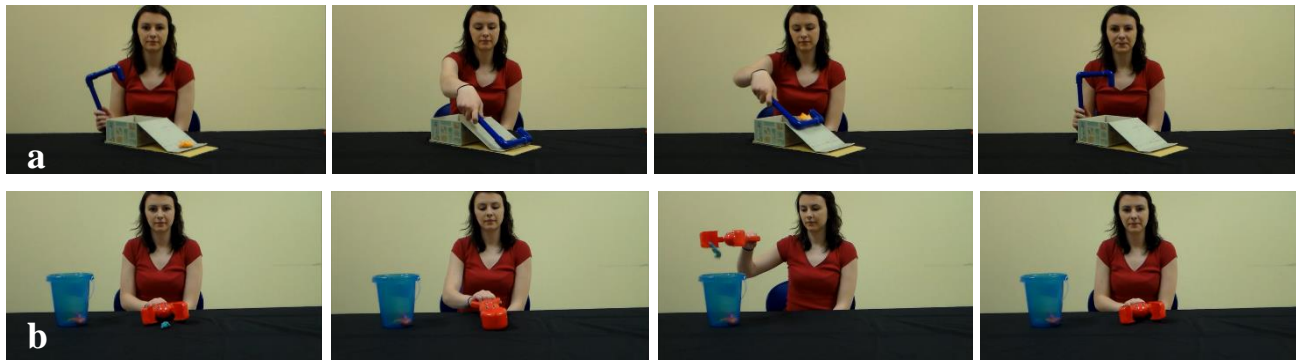
<sup>5</sup>For six participants (2 girls), the criterion of 43.75 uV did not reflect artifact due to eye movements, and thus a 50.00 uV threshold was used. These participants did not significantly differ in age from the rest of the sample,  $t(14) = 0.93$ ,  $p = .37$ .

<sup>6</sup>Participants' individualized frequency bands were 6-9 Hz ( $n = 2$ ), 7-10 Hz ( $n = 2$ ), 8-11 Hz ( $n = 2$ ), 9-12 Hz ( $n = 9$ ) and 10-13 Hz ( $n = 1$ ).

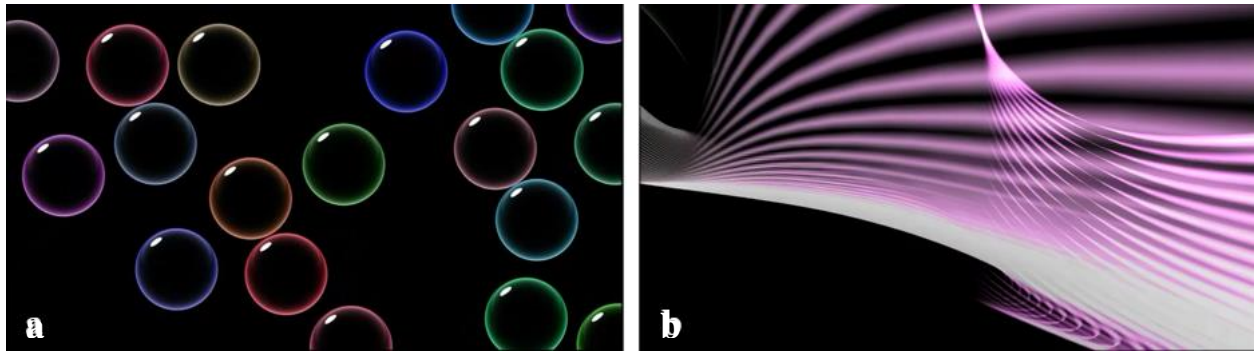


*Figure 1.* The toys and tools used in at-home motor training: (a) The fishing hook toy set, (b) the lobster toy set, and (c) assorted plastic aquatic animal toys (quarter included for scale).

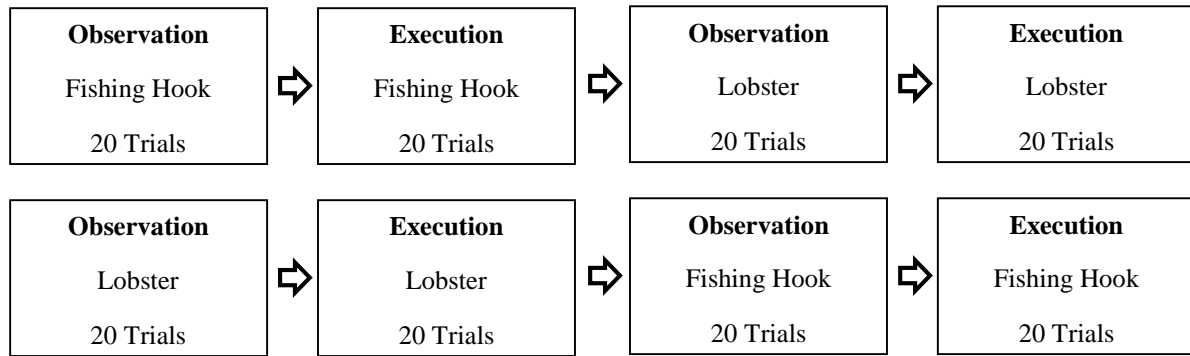




*Figure 2.* Images taken from the (a) fishing hook demonstration video and (b) the lobster demonstration video.



*Figure 3.* Images of the (a) bubbles and (b) abstract shapes presented during baseline.



*Figure 4.* Flowchart summarizing action observation and action execution tasks during the lab protocol. Participants either started the protocol with the fishing hook tool (top) or the lobster tool (bottom).



*Figure 5.* Example of frames selected for analysis of the fishing hook (top) and lobster (bottom) tasks. From left to right: Action observation, tool grasping, action execution.

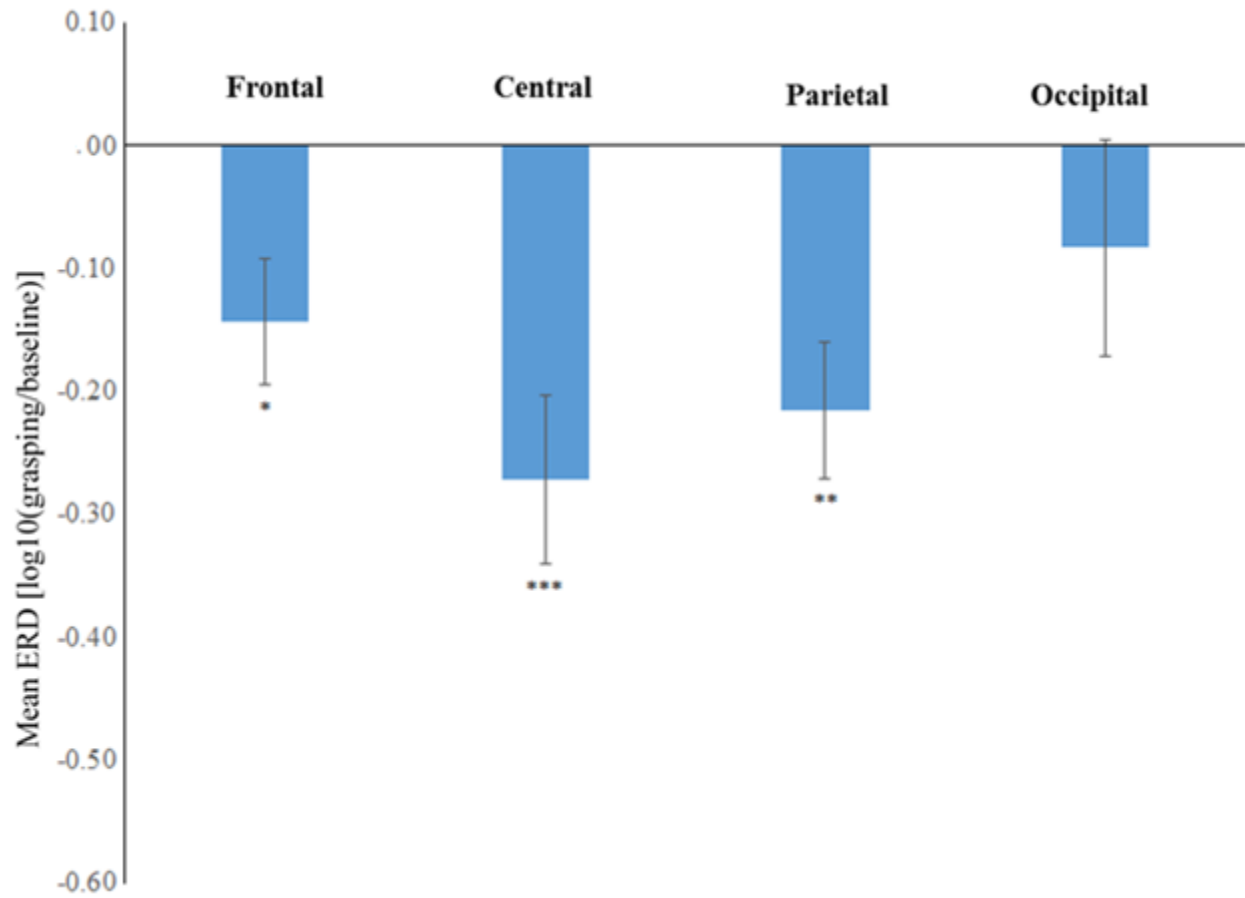


Figure 6. Mean log of the task-to-baseline ratio scores by region (frontal, central, parietal, occipital) during tool grasping within individualized mu frequency bands. Error bars show  $\pm 1$  standard error. Significant differences from zero are indicated. \*\*\*  $p \leq .001$ ; \*\*  $p \leq .01$ ; \*  $p \leq .05$ .

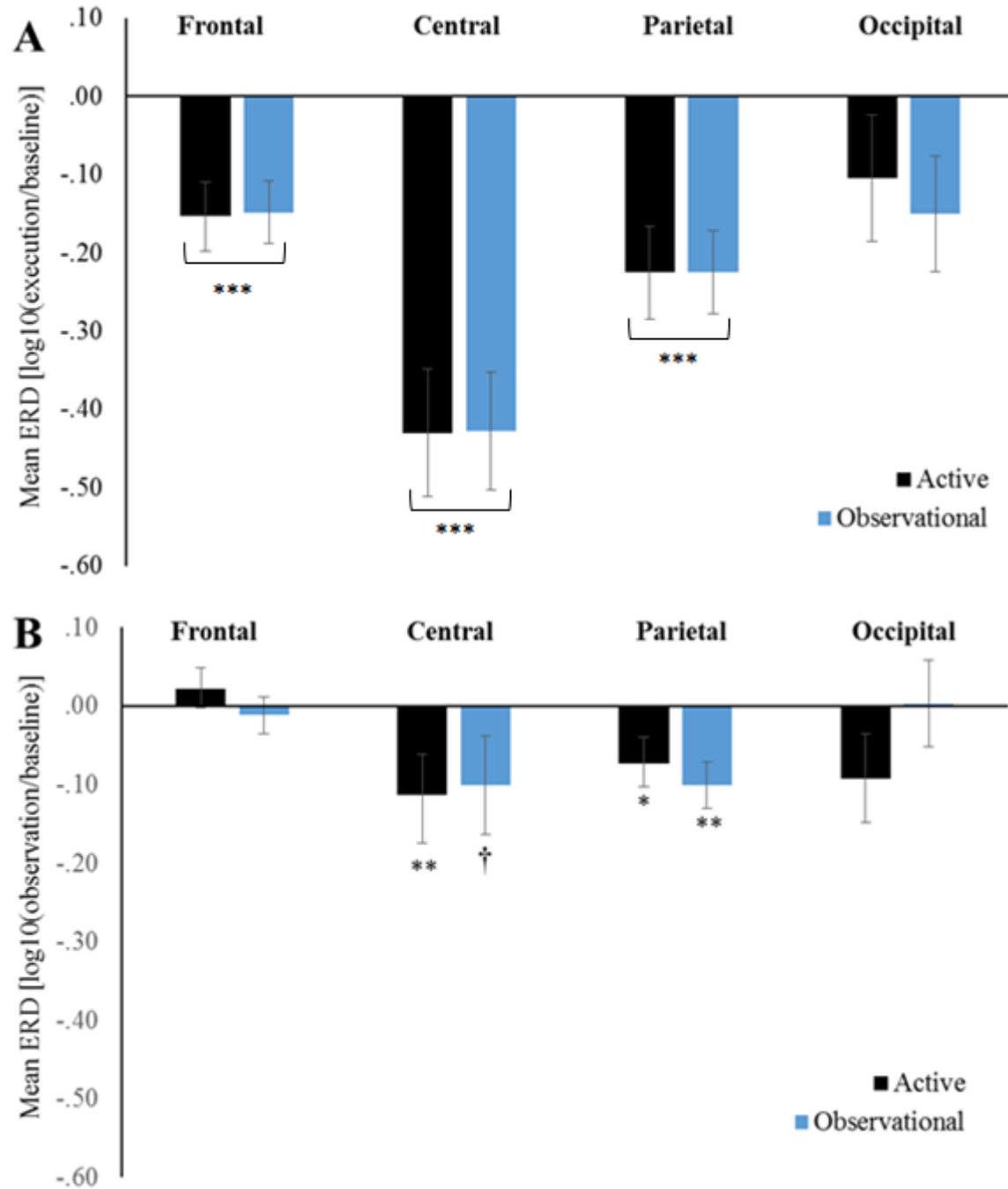
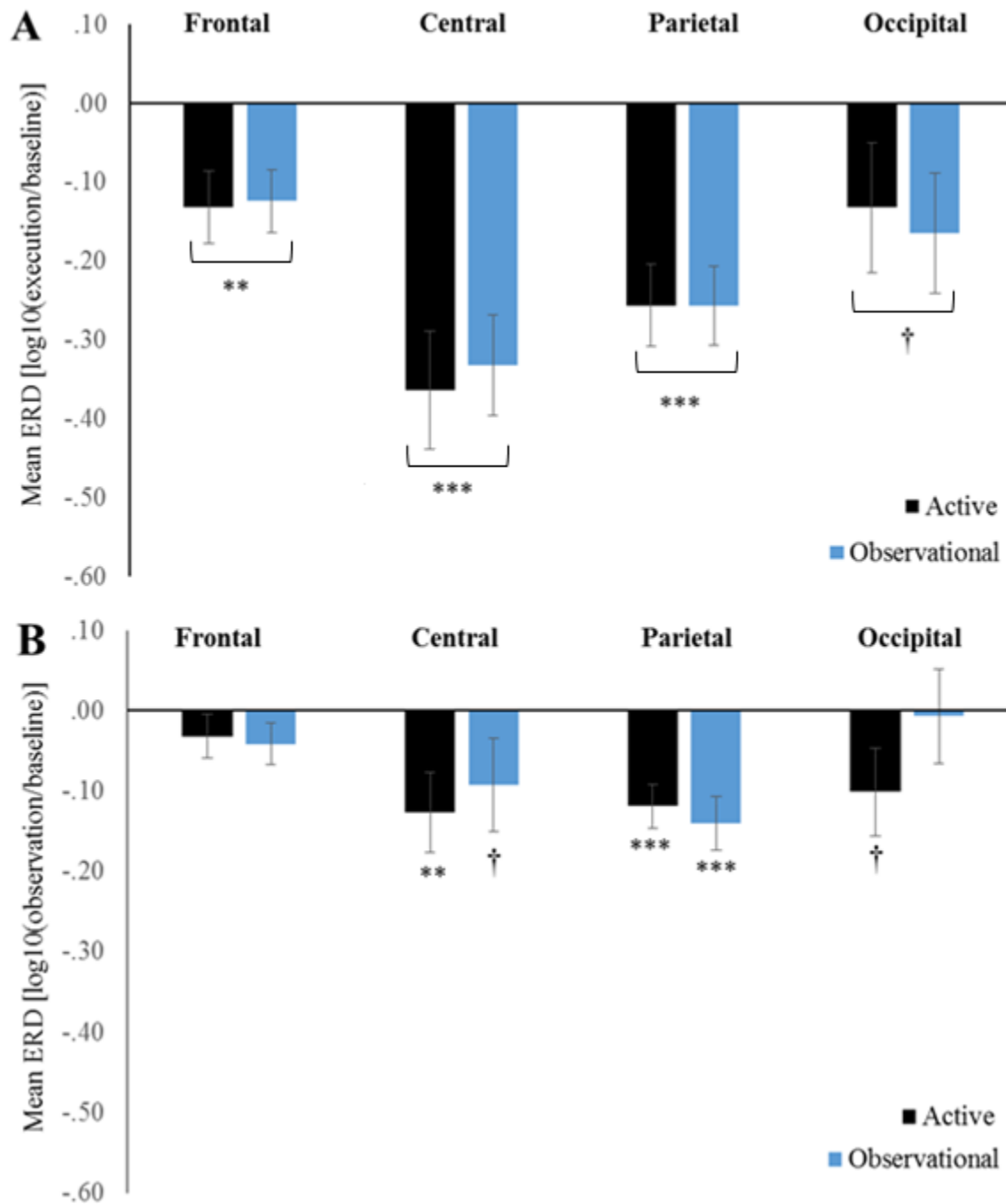


Figure 7. Mean log of the task-to-baseline ratio scores by region (frontal, central, parietal, occipital) and condition (active and observational tasks) during (a) action execution and (b) action observation within individualized mu frequency bands. Both training conditions are plotted for informational purposes. Error bars show  $\pm 1$  standard error. Significant differences from zero are indicated. \*\*\*  $p \leq .001$ ; \*\*  $p \leq .01$ ; \*  $p \leq .05$ ; †  $p < .10$ .



*Figure 8.* Mean log of the task-to-baseline ratio scores by region (frontal, central, parietal, occipital) and condition (active and observational tasks) during (a) action execution and (b) action observation within the 7- to 10-Hz frequency band. Both training conditions are plotted for informational purposes. Error bars show  $\pm 1$  standard error. Significant differences from zero are indicated. \*\*\*  $p \leq .001$ ; \*\*  $p \leq .01$ ; †  $p < .10$ .

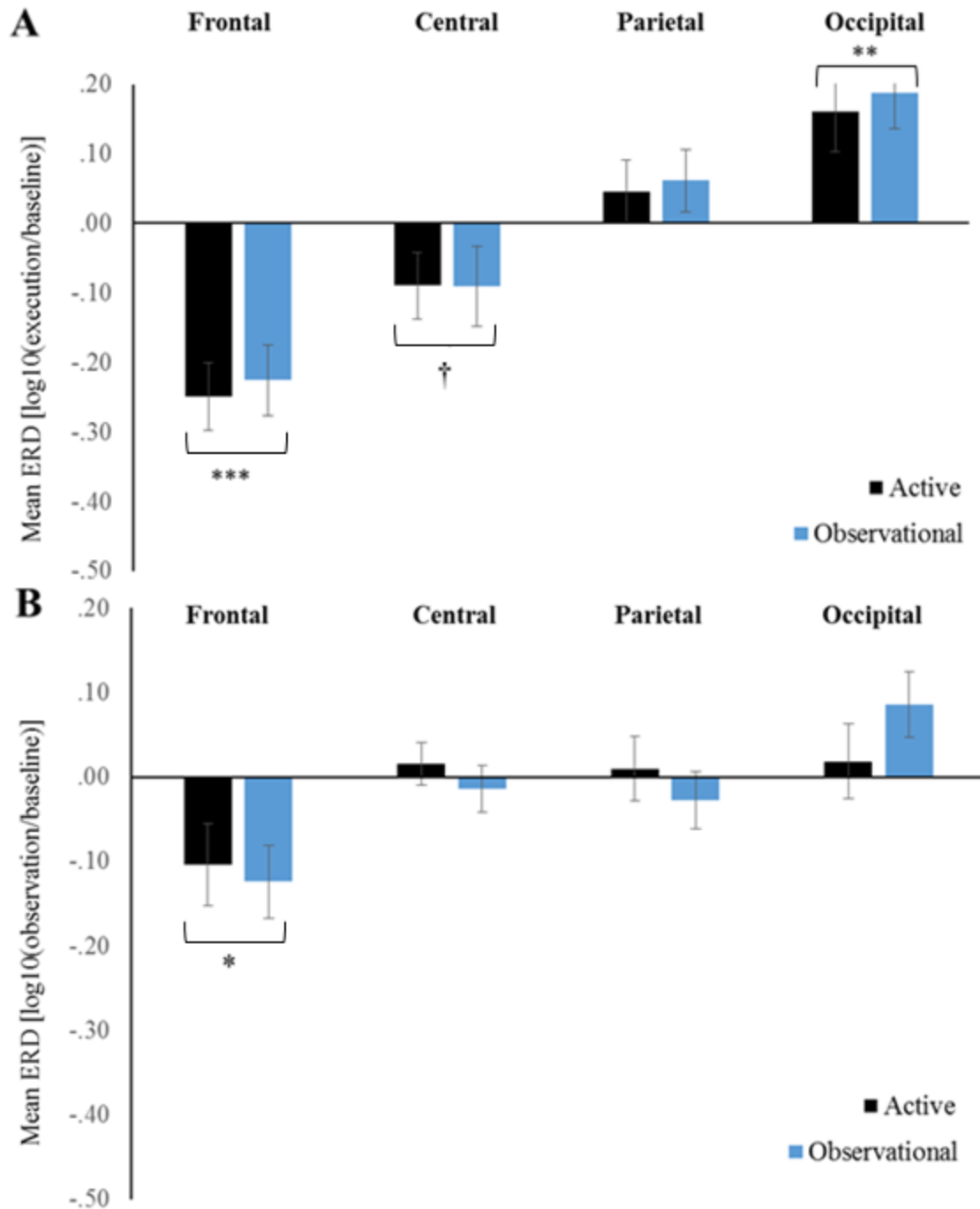


Figure 9. Mean log of the task-to-baseline ratio scores by region (frontal, central, parietal, occipital) and condition (active and observational tasks) during (a) action execution and (b) action observation within the beta band (17-21 Hz). Both training conditions are plotted for informational purposes. Error bars show  $\pm 1$  standard error. Significant differences from zero are indicated. \*\*\*  $p \leq .001$ ; \*\*  $p \leq .01$ ; \*  $p \leq .05$ ; †  $p < .10$ .



**APPENDIX**  
**Home Training Itinerary**

| Date | Time | Today's Activity<br>(Toy or video) | For how many minutes was your child<br>doing this? |
|------|------|------------------------------------|--|
|      |      |                                    |  |
|      |      |                                    |  |
|      |      |                                    |  |
|      |      |                                    |  |
|      |      |                                    |  |
|      |      |                                    |  |
|      |      |                                    |  |

**Reminders:**

- ***Please have your child play these games at about the same time each day ( $\pm$  2 hours).***
  - *Also try to have your child do these tasks in the same room every day.*
  - *Please have your child perform these tasks for five minutes each.*
- ***While your child is watching the video, angle the camera so it can see both your child's face and the TV screen (e.g., at a right angle).***
- ***While your child is playing with the toy, angle the camera so it can see your child's face and hands (filming your child "straight on" is recommended).***
- ***Please try to keep your child "on task!"***

***Have any questions? Don't hesitate to call or text Lauren at [REDACTED] or e-mail her at [REDACTED].***