

MANIPULATION OF HAND MOVEMENT OBSERVATION AND EXECUTION ON
MU SUPPRESSION MEASURED BY ELECTROENCEPHALOGRAPHY

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A Thesis

Submitted in Partial Fulfillment
of the Requirements for the Degree of
Master of Arts
In Psychology

Northern Arizona University

December 2011

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ABSTRACT

MANIPULATION OF HAND MOVEMENT OBSERVATION AND EXECUTION ON
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Researchers in the field of electroencephalography have been aware of mu suppression since the 1950's, yet the specific function of the mu rhythm in the brain and what exactly its suppression is connected to is not completely clear. With the relatively recent discovery of mirror neurons in the macaque monkey as well as in humans, it has been suggested that mu suppression may in fact be related to activation of the mirror neuron system in the human motor cortex (Pineda, 2005). Because previous research in this lab examined only execution and observation of right-hand movements, the current study attempted to replicate these right-hand findings and examine how these levels of suppression change when execution and observation are switched to the left-hand. Furthermore, individual empathic levels were assessed using the Interpersonal Reactivity Index (IRI), with the expectation of finding a correlation with mu suppression of participants.

While previous research has found a lateralization effect with the right hand, the results of this study indicate that there was greater mu suppression during the left-handed execution and observation condition, and that the left-handed observation condition was correlated with the fantasy subscale of the Interpersonal Reactivity Index (IRI). The laterality effect between electrode C4 and the left handed execution as well as observation condition suggest that mu suppression does have some relationship with

mirror neuron (MN) activation because of the contralateral relationship between electrode and hand being used or observed. However, it is curious that there was no significant lateralization effect with the right hand and electrode C3, which has been found in other research. Additionally, because other researchers have voiced concerns that mu suppression during observation is simply a correlate of alpha-band suppression occurring in occipital areas, recordings from the occipital area electrodes were evaluated as well, and were found to share no relationship with the mu suppression recorded from central electrodes.

Table of Contents

CHAPTER 1: INTRODUCTION.....	6
THE MIRROR NEURON SYSTEM IN MONKEYS.....	8
TMS MEASURES OF A MNS HUMANS.....	10
FMRI AND SHARED VOXELS.....	11
INTRACRANIAL RECORDINGS IN HUMANS.....	13
ELECTROENCEPHALOGRAPHIC MEASURES OF MNS.....	14
EMPATHY.....	18
CHAPTER 2: METHODS.....	21
CHAPTER 3: RESULTS.....	29
CHAPTER 4: DISCUSSION.....	33
REFERENCES.....	42
APPENDIX: FIGURES.....	46

List of Figures:

Figure 1. Alpha-band suppression in central electrodes during left handed execution and observation hand tapping tasks.....	46
Figure 2. Alpha-band suppression in central electrodes during right handed execution and observation hand tapping tasks.....	47
Figure 3. Alpha-band suppression in occipital electrodes during left handed execution and observation hand tapping tasks.....	48
Figure 4. Alpha-band suppression in occipital electrodes during right handed execution and observation hand tapping tasks.....	49
Figure 5. Alpha-band suppression difference scores (execution – observation) in central electrodes during left and right handed tasks.....	50
Figure 6. Alpha-band suppression difference scores (execution – observation) in occipital electrodes during left and right handed tasks.....	51
Figure 7. Alpha-band suppression averaging across task (execution and observation) in central electrodes for the left and right hand.....	52

CHAPTER 1: Introduction

Though often taken for granted, the motor system is quite complex, utilizing many interconnected systems in order to accomplish a task. Connections between various specialized motor areas are so closely interrelated, that it can be difficult to distinguish the many separate components. For example, imagine the process of picking up a pen from a desk. Of the myriad objects lying there, the correct object must first be discriminated from the others, requiring one to swivel his head and eyes in order to first allow the fovea to fall on the object of interest. Once discovered, the pen's location with respect to one's body must be assessed. Only at this point can a hand be extended to grasp the object, but even then there are the additional steps that require forming the hand into the proper shape so as to grasp the pen appropriately.

The pen itself has specific geometric properties, including shape and orientation, lending itself to a certain type of prehension. While there is a plethora of ways the pen could be grasped, certain ways are more efficient than others. As the hand starts to curl in anticipation of the cylindrical form, there is already the expectation of the feeling of the plastic casing at one's fingertips as they touch the pen. Once the pen is picked up, information continues to be sent to the motor system from the hand, joints, arm, eyes and so on; allowing perfection of grasp and use of the pen with precision. This seemingly simple gesture of picking up a pen from the desk requires the necessary coordination of sight, proprioception, tactile sensation, and postural adjustment that combine harmoniously in the anticipation of the consequences of one's actions.

Based on this model of motor function, the hands and brain implement a series of organized processes that involve integrating afferent and efferent connections to translate

sensory information into action representations. This description however, is an incredibly simplified version of what actually occurs. Beginning in the 1930s scientists like Wilder Penfield (Penfield & Boldrey, 1937) attempted to map the sensory areas of the motor cortex in humans, which resulted in a visual characterization of the sensory motor system, described as the homunculus. Maps of sensory areas were created by recording activity through macro-electrodes that were placed on the surface of the motor cortex. This technique distinguished separate areas, classified as the primary motor area and the supplementary motor area. However, these maps are not in total accord with the neuronal organization that occurs physiologically in the brain. More recently it has become apparent that, not only are motor areas connected anatomically to thought and sensation, but there are a number of functions that are incompatible with the idea of the motor area existing as simply an executive map of motor function.

Rather than the existence of only two areas within the motor system there is currently thought to be a constellation of distinct and varied systems. This conceptualization of the scope of the motor system requires more than just an identification of pieces that create the mosaic of the motor cortex. Instead of seeing motor functions housed in separate regions and limited to movement as the passive executor of commands, it is now hypothesized that motor function represents a complex web of intracortical circuits, each contributing to sensory-motor translations, and thereby allowing interaction with the environment. Additionally, this complex web interacts with certain higher-order cognitive systems. Specifically, recent research has discovered what may be pathways in the motor system, allowing the recognition of actions by others, and thereby facilitating the abilities of imitation and communication.

How have the abilities of certain motor areas and their combined function with other motor areas been discovered? A technique commonly used with non-human species to individuate the functions of neurons in specific motor areas is to preliminarily record activity of single neurons, and to correlate it with specific motor behavior of the subject. This can be accomplished by having the subject perform only specific movements for which it was trained, or by having it perform a wide range of spontaneous movements within a more natural context. While it may seem more haphazard, there are certain benefits to using the latter strategy. For example, when actions occur in a more natural context, these actions are less susceptible to preconceived notions and sometimes lead to discoveries of unexpected functions. In fact, this is how a very special property of neurons was first discovered that exist in area F5 of the macaque monkey.

Mirror Neuron System in monkeys

The concept of a mirror neuron system was first introduced after the discovery of a special type of neuron in the brain of the macaque monkey. Researchers were recording activity from individual neurons in area F5 of the ventral premotor cortex to better understand how these visuomotor neurons code for goal-directed action, as well as respond to visual stimuli. In particular, neurons in this area are known to fire for goal-directed action involving the hands and mouth. While performing these recordings a serendipitous event occurred as researchers were preparing a context situation with the macaque monkey. The researchers discovered that certain neurons in this region of the brain would fire not only when the monkey performed a specific action, but also when the monkey watched someone else perform the same goal-directed action. Previous behavioral research had shown that animal behavior is learned by simply watching

others, as when a monkey learns fear of another creature after witnessing other monkeys express fear toward it. However, it was unknown how the brain in social animals functions to perceive actions of others. The fact that these neurons fired when the monkey reached for a piece of food as well as in response to watching the reaching action of another, has earned them the name “mirror neurons.”

An early study of mirror neurons involved the measurement of 532 neurons in area F5 of two macaque monkeys (Gallese et al., 1996). Microelectrodes attached to the subject’s heads recorded neuron activity while the monkeys performed specific goal-directed actions, as well as when similar actions were observed, which were performed by the experimenter. Ninety-two percent of the measured neurons fired, both during observation and during execution of an action. Because of the similarity in neural activity, researchers hypothesized that these neurons might serve as a matching system. In other words, this system is used to match the actions of others onto one’s own motor plans, thereby aiding in understanding another’s intentions.

This finding has been both replicated and extended in a single neuron study by Umiltà et al. (2001), in which monkeys were given clues about certain goal directed actions, even though they could not always see the end result of the actions. The experiment began by having the monkey watch a fully visible hand as it reached for an object, which set the baseline for the motor action required for the study. The experiment then began with the same action, however a curtain blocked the monkey’s view of the end result of the grasping action. In one condition the monkey was allowed to see the object that would be hidden behind the curtain, the other condition involved the same stage, but with no object. The curtain was then drawn, and the monkey watched as a hand

reached behind the screen. While the action being observed was the same in both conditions, the mirror neurons would only respond when the monkey knew that there was an object that could be grasped behind the curtain. This provided strong evidence that, in monkeys at least, the MNS is primarily used as a matching system for understanding visual cues during action-observation and execution.

It appears that this system is stimulated in response to auditory cues as well. Kohler et al. (2002) examined the firing of neurons in monkeys, both while performing a specific action, as well as while hearing its corresponding sound. As expected, sounds that were not action-related (i.e. white noise) did not evoke any excitatory response. However in the area examined, about 13% of the neurons responded both to witnessing the experimenter tear a piece of paper, as well as to only hearing the sound. This same effect was found with the firing of specific neurons when the monkey observed the opening of a peanut shell, and when just the sound was heard as the peanut shell was broken. This suggests mirror neurons in monkeys appear to be activated visually as well as auditorily. While the existence of mirror neurons in monkeys has been well studied and verified using electrodes recording activity of individual neurons in the brain, techniques that measure potential mirror neuron activity in humans tend to be less direct.

TMS measures of mirror neurons in humans

Using transcranial magnetic stimulation (TMS), Fadiga et al. (1995) demonstrated evidence for an action-observation and execution matching system in humans. TMS is a non-invasive tool that enhances electrical stimulation in the nervous system. If TMS is applied to the appropriate area, motor evoked potentials (MEPs) can be recorded from contralateral extremity muscles. Since mirror neurons are defined as neurons that fire

both during action-observation as well as during action-execution, it would be expected that they produce some sub-threshold muscle activity when stimulated. Assuming that action observation involves sub-threshold activation of the premotor cortex in humans, magnetic stimulation of the motor cortex should increase MEPs in those anatomical pathways, leading to stronger activation of the same muscles being observed in another. Results from this study demonstrated the motor system does indeed reflect activation during the observation of an action performed by another. The muscle excitation pattern evoked during TMS was similar to the muscle contraction seen during the condition of execution. The act of observing an action recruited neurons in the motor area, and using TMS converted this activation into measurable muscle contraction that was recorded through EMG. This suggests there is a mirror neuron system in humans, and that simply watching another person performing a task activates sub-threshold motor activity. If TMS can enhance the motor activation that occurs while watching someone else perform an action, the same activation should also be apparent in recordings of motor areas of the brain.

fMRI and shared voxels

The cortical mechanisms behind human observation and imitation have been investigated using fMRI scans of participants during various activities. The direct matching hypothesis, which describes the neural mechanism that directly matches an observed action onto an internal motor representation of that action, was examined in a study conducted by Iacoboni et al. (1999). The study used three imitative conditions and three non-imitative conditions. In the imitative execution condition, participants observed and then executed a finger movement. In the non-imitative condition, participants

received symbolic or spatial cues, and then executed the requested finger movement. The imitative condition reliably produced larger signal intensity than either the spatial or symbolic cue execution tasks. Specifically, activation was observed in the left frontal operculum, the right anterior parietal region, and the right parietal operculum. The authors' results indicate that the left frontal operculum and the right anterior parietal cortex (PE/PC) have what appears to be an imitation mechanism, previously postulated by the direct matching hypothesis. The authors explain that the left frontal operculum contains Brodman's area 44, and has been thought to be homologous with area F5 in the monkey.

Activation of area F5 in monkeys is related to the elaboration of proprioceptive movement and was one of the first areas in which MNs were discovered, providing strength to the finding that this study may indeed have measured MN activity in participants. While this study did not measure single neuron recordings in the human brain, the pattern of activation does suggest that a similar phenomenon to what had been discovered in studies that had used monkeys. The fact that these finger movements were not goal directed also indicates that there are distinctions between how the mirror neuron system activates in humans versus monkeys. Apparently goal directed tasks are not necessary for activation in humans, which underscores the importance of exploring how the brain expresses this activity under a variety of conditions, and how it might relate to other aspects of cognitive function.

Another fMRI study by Gazzola and Keysers (2009) investigated somatosensory areas in the brain that activate both during observation of an action as well as during execution. In this study participants viewed static images, viewed movies of action

scenes, or engaged in motor tasks that were similar to the movies they had viewed. In describing areas of brain activation, the authors use the term “shared voxels” to describe areas where the blood oxygen level dependent (BOLD) signal is augmented both during observation and during execution of a given task. The reason for this is because there may be processes involved other than true mirror neurons propagating an effect. For example, it may be that separate but spatially overlapping sets of neurons are firing during periods of observation and execution. Therefore any one specific process cannot be assumed to be hard evidence of individual mirror neurons in humans. Nevertheless, shared voxels that showed increased activation during both observation as well as execution were most prominent in the somatosensory, parietal and premotor area, especially on the left side. While the authors admit that a weakness of this study is that each voxel contains an untold number of neurons, it has still provided strength to the evidence of a similar mirror neuron system in humans.

Intracranial recordings in humans

Until recently, the only evidence we have had of mirror neurons in humans has been during the recording of brain activity using fMRI, PET, MEG and EEG type technologies, lacking the spatial resolution that would enable us to say that the same neurons indeed fire both during observation and during execution of biological movement. However, in a recent study by Mukamel et al. (2010), 1177 single-neuron responses were intracranially recorded in humans during both action observation and execution. The motor neurons of patients in this study responded to specific stimuli. Neurons included action-observation only, execution only, observation and execution matched, and observation-execution non-matched cells. Interestingly, the non-matched

cells would fire more during action-execution and would be inhibited during observation. While the largest quantity was of the action-execution-only cells, there were significant numbers of execution-observation matched cells, particularly in the medial frontal lobe and medial temporal lobe.

These intracranial recordings provide strong evidence that the same kind of mirror neurons that exist in monkeys also exist in humans. The authors have suggested that the non-matched cells may even work as a buffer system to inhibit muscles from making overt movements when the MNS is activated. Through the use of this direct method, these researchers have verified the existence of an MNS in humans and important distinctions in this system and its various pathways toward activation. Between individual participants, there are subtle differences in how this system processes information, as there are within any function, thus making it important for future research to examine the degree of activation in this system and how it might relate to other cognitive processes taking place in the brain.

EEG measures of MNS

Mu rhythm desynchronization during both the observation and during execution of actions was first recognized in experiments reported by Gastaut and Cohen-Seat in the 1950's (in Rizzolatti et al., 2001) and it has only recently been linked to a potential MNS existing in humans. This is because it was originally thought to occur infrequently and only in a small percentage of the population. More recently, new techniques including independent component analysis have demonstrated that mu rhythms occur along the scalp of most healthy adults (Pineda, 2005). Despite a significant amount of work conducted in various academic fields regarding mu rhythm, their functional/behavioral

significance remains unclear. The mu rhythm typically occurs in the alpha range of 8-13 Hz in the absence of movement. While this EEG synchronization occurs when no movement is present, it is generally accepted that any desynchronization results from thalamocortical stimulation and is a reliable correlate of activated neural networks. Essentially, certain sensorimotor neurons fire synchronously in the absence of motor activity, creating large amplitude oscillations known as the rolandic mu rhythm. These oscillations occur close to the scalp and are thus relatively simple to measure using EEG. However, motor activity is not the only known factor to cause a desynchronization of mu. While many studies have examined the neural basis for mu in terms of motor preparation and execution, some have pointed to a role beyond motor control. REM sleep for example is characterized by periods where motor activity is inhibited, yet the characteristics of mu blocked by contralateral body movement or contralateral stimuli still occur (Pineda, 2005). It has also been noted that mu rhythm occurs in the absence of any preparation for motor activity, such as when watching someone else perform a motor movement.

Some researchers report that not only mu, but also occipital alpha rhythm, contribute to the recording of EEG signals in the scalp of central regions of the brain. Because both of these areas are affected by visual stimulation, it has been suggested that mu suppression seen in central motor areas is more accurately correlated to occipital alpha band suppression. However, a study that used MEG recordings to assess the distribution of occipital alpha and mu rhythms during sleep spindles, concluded that each came from distinct source locations (Manshanden et al., 2002). Nevertheless, because occipital and central areas both reflect a distinct, synchronized alpha-band rhythm in the

absence of neural activation, it is important to compare differences in alpha-band suppression in each of these areas. This will allow researchers to verify that these areas are displaying activity that is unrelated.

A connection between mu rhythms and possible mirror neuron activity was first offered by Altshuler et al. (1997) and has since been investigated by several other researchers. According to Pineda (2005), mu rhythms reflect a modulation of motor neurons by the premotor cortex, some of the cells therein potentially being mirror neurons. In this model, the point at which perception of a viewed or audible activity transitions to a motor plan for an action is when mu rhythm desynchronization reflects the modulation of mirror neurons. This link has been established through several important properties of mu suppression. The most important of these aspects is that mu power recorded with electrodes on the scalp over the sensorimotor cortex is reduced not only by self-initiated movement, but also by imagined and observed movement. In summary, the process through which suppression of mu rhythm occurs is similar to the function of mirror neurons in monkeys. Since both are sensitive to movement and each have overlapping neural sources to support the activity, mu suppression appears to be a correlate of motor preparation, connecting perception to action.

Changes in the mu rhythm in response to motor movement have been observed in research performed by Muthukumaraswamy, Johnson and McNair (2004). This study examined differences between movements with no certain goal as well as when gripping a manipulanda, essentially a wooden block attached to a board. Recordings of both EEG and EMG were taken while the participant watched the experimenter put his hand out flat, watched the experimenter perform a grip on a manipulanda, and when the participant

formed the same grip on the manipulanda. Suppression of the mu rhythm occurred when observing and executing a precision grip with the hand, however suppression was more profound when the grip was in relation to an object. If mu suppression is indeed an indicator of mirror neuron activity, then it would seem that in humans the mirror neuron system has lost some degree of dependence on the behavior being goal-directed, reflected in previously mentioned fMRI studies as well as this EEG study. While suppression of the mu rhythm is greater when the act is goal-directed, the data from this experiment show that it is not necessary.

Disorder of the MNS and Social Understanding

Some research in mu rhythms has suggested that a lack of this rhythm suppression might be related to a neurological disorder. Autism Spectrum Disorder (ASD) is characterized by symptoms such as having greater challenges with social interactions, showing little or no eye contact, and frequently preferring to be alone. Because these behaviors exist on a spectrum potentially related to the MNS, it follows that ASD might be related to a dysfunction of the MNS. Following this line of reasoning, Oberman et al. (2005) examined mu suppression in neurotypical subjects and those with ASD. To do this, they had participants watch videos of a moving hand, a bouncing ball, and visual white noise, which were then compared with recordings from the subjects moving their own hands. They found that while neurotypical individuals exhibited mu suppression during both observation and execution of a task, those with ASD exhibited mu suppression only during the execution of a task. This supports the hypothesis that there may be some dysfunction in the MNS related to ASD. This study also suggests that there

may be other interpersonal qualities that are related to activation of the MNS in humans, such as empathy; a trait that has a significant impact on social interaction.

Despite research that has been conducted with humans, a true understanding of the functions of the MNS is still far from complete. It has been hypothesized that the MNS is related to action understanding and imitation, as well as to cognitive social skills such as empathy. As intuitive as these types of relationships may be, research is needed in this area to determine what sort of relationship exists between the MNS and these other cognitive skills, as well as understanding what type of behavior activates it.

Empathy

Empathy is characterized by a cognitive understanding within oneself of a circumstance being experienced by another. It doesn't mean that one will act or even feel compelled to act supportive or sympathetic, but rather is the capacity to understand someone else's situation (Decety & Jackson, 2004). Empathy is then used to be able to evaluate the motivations and intentions of others and to respond appropriately. While empathic concern is primarily associated with prosocial behavior, empathy in general is essential to understand any behavior of another individual. Decety and Jackson (2004) describe the three essential components of empathy as awareness of the separation between self and other, the mental flexibility to adopt the subjective perspective of another, and perception-action coupling that leads to shared representations. These three components are intertwined and essential to produce the quality known as empathy. In relation to the current study, the component of perception-action coupling is particularly important. Based on previous research, Decety and Jackson point toward four specific areas of the brain that show overlap between action execution and observation: the

premotor cortex, the parietal lobule, the supplementary motor area and the cerebellum.

These areas have been found to activate differently for those who score higher on empathy measures as well.

Current Study

A primary purpose of this study was to investigate the question of whether a lateralization effect occurs with mu suppression, based on whether the right or left hand is involved in a specific task. EEG recordings were taken while participants observed and executed a hand-tapping task similar to that used by Oberman et al. (2005). Because previous research has only examined mu suppression in observation and execution using the right hand, the current study investigated changes in alpha-band suppression between observation and execution using both the right and left hand. The purpose was to determine whether activation reflects a laterality change across the motor cortex for action-execution and action-observation when the left hand is used. It was hypothesized that the size of the difference between execution and observation would be dependent on whether the subject is engaged in right- or left-hand execution/observation. Specifically, we expected the size of the difference to be greater in electrode C3 in the right-hand condition and greater in electrode C4 in the left-hand condition. This hypothesis is based on previous findings (Woodruff, Martin & Bilyk, 2011) of a laterality effect of electrode C3 during a right-hand condition only experiment. For this reason we expected the same effect to be obtained for the right-hand condition in this experiment, and that the laterality effect would shift to electrode C4 for the left-hand condition.

A secondary purpose of the current study was to determine whether the level of mu suppression that occurs during action-observation and execution shows a relationship

with the level of empathy an individual has. Since empathy is defined as the ability to take the perspective of someone else, there is a potential relationship between individual levels of empathy and activation in motor areas elicited by the observation of another's movement. Previous research by Woodruff, Martin & Bilyk (2011) has found correlations between empathy measures and levels of mu suppression. Using the Interpersonal Reactivity Index (IRI), it was expected that empathy measures would reflect an inverse correlation with the amplitude of event related desynchronization in the motor area of participants, as seen in previous research (Woodruff, Martin & Bilyk, 2011). The reason why this correlation is inverse is due to the nature of mu suppression values. A more negative value represents higher level of suppression, resulting in an inverse correlation with the empathy scale. The IRI measures certain key aspects of the disposition of empathy and consists of four seven-item subscales, each of which taps a certain facet of empathy and are described in the materials section.

In addition to these measures, EMG data was concurrently recorded, though it is not reported in fulfillment of this degree requirement. It was originally hypothesized that it might be possible to obtain recordings of sub-threshold motor activity, which would then be compared with recorded mu suppression. Unfortunately, this additional measure led to many practical issues with recording, including additional set up time, difficulty with adhesion of EMG electrodes, and the fact that having yet an additional apparatus recording on the computer caused occasional freezing of software for both EEG and EMG.

This study was designed to test several hypotheses. The first hypothesis was that mu suppression would be greater during execution than observation. The second

hypothesis was that the study would reveal a laterality effect between hand and electrode, such that C3 would show greater activation during right-handed tasks, and electrode C4 would reflect greater activation during left-handed tasks. It was hypothesized that recordings taken from occipital electrodes would share no significance with action-observation and execution conditions, or with the empathy questionnaire. Lastly, difference scores based on subtracting the observation from execution condition for each hand were created, with the hypothesis that there would be a correlation with empathy measures collected from the IRI.

CHAPTER 2: Methods

Participants

Demographic Information

All participants were screened and met the qualifications of being right-handed, free from diagnosis of any mental illness or neurological disorders, with either normal or corrected to normal vision. Additionally, all participants were current NAU students between the ages of 18 and 30. The average age of participants was $M = 19.2$ (range 18-28). The participants were 24 females (81.1%) and 6 males (18.9%). All participants gave informed consent before commencement of the study. This research was reviewed and approved by the Northern Arizona University Institutional Review Board.

Materials:

Videos: Eighty-second video clips were displayed with Direct RT Research Software version 2008.1.0.13 (Empirisoft Corporation). Video observation and hand execution tasks were pseudorandomized in blocks, in order to avoid a specific task following the same task again (for example right hand execution of the hand-tapping task

followed by the next block once again asking them to complete the hand-tapping task with their right hand). By using a video setting designed to “mirror” the original videos, it was possible to create duplicate left hand videos from the right-handed ones. Having duplicate left-hand versions created from the original right-handed ones was expected to reduce potential confounds between conditions. The films showed only the actor’s hand and forearm and all videos were displayed in grey scale. Blocks were presented with rest-observation occurring twice for each hand, action-observation occurring three times for each hand, and a blank screen during which the participant engaged in action-execution occurring three times for each hand. Every participant began by watching a 20-second clip of the action-observation sample condition, to ensure that participants saw the action to be completed later and that participants understood what was expected of them.

Action-Observation Sample

Prior to recorded experimental conditions, subjects first watched the observation sample video. During this time participants viewed a 20-second long grey scale video of an actor’s right hand bringing the forefinger and thumb together to touch and then opening to form a ninety degree angle between the thumb and forefinger at approximately 1 Hz (action observation block), before closing again. This was used to demonstrate to the participant the behavior that would be executed or observed in later blocks. The same video was used again during the recorded action observation condition, but was 80 seconds long, rather than 20 seconds.

Task Execution

During the task execution condition the participants received instructions explaining that they would engage in the same task initially viewed during the 20-second

practice session at the beginning, with specifically either their right or left hand. The instructions then asked the participant to press the space bar to begin the hand-tapping task. Immediately after pressing the space bar, the screen on the computer would become black and the participant completed the action, holding the hand at a comfortable viewing distance while imitating the action.

Rest Observation Task

In order to establish a base mu rhythm from which suppression would occur, participants also watched two separate videos of a hand (one right and one left) at rest, randomly placed as video blocks in the experiment. Participants were not asked to imitate this movement, but to simply observe the hand lying flat out. Alpha-band suppression values were obtained by dividing the action observation as well as execution scores by the value obtained during this rest condition, which was used as the base alpha-band rhythm.

Survey: After completing the EEG measures of the study, participants were then asked to fill out the Interpersonal Reactivity Index. This instrument measures dispositional empathy through a set of separate but related constructs. There are four seven-item subscales that each relate to a different facet of empathy. The perspective taking scale measures the tendency to adopt another's point of view. The empathic concern scale evaluates the extent to which one experiences the feelings of sympathy and compassion for another. The personal distress scale assesses how one experiences distress or discomfort as a response to the distress of someone else. Lastly, the fantasy scale measures the tendency to transpose oneself into a fictional situation (Davis, 1983).

Procedure:

EEG Recording: After completing informed consent, the foreheads of participants were cleaned using alcohol swabs and facial wash in order to ensure a clean surface. Participants' heads were then measured for proper cap size to optimize impedance. After the proper EEG cap size was chosen, participants were seated at a comfortable distance (approximately 100 centimeters) in front of a Dell Latitude Laptop with a 14.1-inch screen, on which the series of videos were played. The scalp of the subject was then abraded and electrogel was injected into the electrode wells in the cap to ensure optimal impedance. Reference electrodes were placed on each earlobe using Ten 20 Conductive gel and medical tape. EEG recordings were taken (Mitsar 202) simultaneously from 32 channels (EasyCap, Electro-Cap International Inc., 2009), with all electrode impedances less than 5k Ω . Electrodes were placed according to the International 10-20 electroencephalography system. Data were low-pass-filtered offline at 30 Hz and high-pass-filtered at 0.1 Hz (WinEEG 2.80.32, St. Petersburg, Russia).

The alpha wave, or the brain frequency at rest, is the frequency of interest. In particular, mu rhythm, which is located at the alpha frequency of 8-13 Hz, can be differentiated from other alpha waves like occipital alpha because occipital alpha should be blocked when the eyes are open (Pineda et al., 2005). This experiment used visual stimuli that should block occipital alpha rhythm even during the baseline condition, so the baseline should be appropriate for assessing mu. While observing the baseline condition, or the hand at rest task, mu rhythm was expected to be highest in amplitude and synchronized, reflecting greater amplitude and uniformity of neuronal firing.

Normally other alpha rhythms like occipital alpha are highest in amplitude when an individual is at rest with his or her eyes closed, meaning that other alpha rhythms should not have the same pattern, due to the fact that the participant is attending to a visual stimulus. However, it was expected that while observing or executing the hand tapping task, mu rhythms would become desynchronized, particularly on the contralateral side of the brain in reference to the side of the body performing that task.

Data was collected over a total of 16 blocks, which involved six separate conditions. These included right-hand observation, right-hand execution, right-hand-at-rest observation, left-hand observation, left-hand execution, and left-hand-at-rest observation. The observation of movement and execution blocks were repeated three times each. The hand-at-rest observation videos were shown twice for each hand, randomly placed between the other conditions. Each condition lasted 80 seconds, with the order being pseudorandomly assigned. This was necessary so that participants did not complete a block, only to have it followed by the exact same condition a second time.

Electroencephalography analysis:

Principal components analysis was used to remove eye-blink artifacts and exclude any epochs with signal deviation greater than 100 μ V. Because mu suppression is generally most identifiable in the central electrodes above the premotor cortex, mean spectral power values that range from 8-13 Hz specifically from electrodes C3, Cz, and C4 for each participant during each block were analyzed and then averaged across all three blocks. The action-observation and execution mu suppression values for each hand were then calculated by dividing each action condition by the rest observation condition for the respective hand. These values were next log-transformed, to correct for the likely

violations of distribution normality. Afterward, log values were subjected to statistical analysis.

A 2 x 2 x 3 (task execution versus observation; right versus left hand; and electrode C3, Cz and C4) repeated measures analysis of variance (ANOVA) was used to identify any main effects. We predicted this analysis would yield a main effect of task, with execution generating significantly more mu suppression than observation. A main effect of hand (left, right) was also expected, with greater mu suppression for right-hand observation and execution due to the fact that participants were right-handed. We predicted an interaction of electrode and hand, whereby electrode C3 would record greatest mu suppression for right-hand execution and observation while C4 mu suppression would be greatest in response to left-hand execution and observation.

Difference scores were then calculated by subtracting observation mu suppression from execution for each hand and each electrode, yielding six difference scores. These difference scores were submitted to six one-sample t-tests, with a Bonferroni correction applied to reduce chances of a Type I error. We predicted that difference scores from right-hand execution/observation would be significant in C3 but not C4, while difference scores would be significant for the left-hand condition in C4 but not C3. This prediction is based on the fact that Woodruff, Martin & Bilyk (2011) found significant difference scores for C3 but not for C4 in a task that used the right-hand only.

Alpha-band suppression scores, as well as difference scores, were assessed for correlations with the overall IRI and its subscales. Based on the results of Woodruff, Martin and Bilyk (2011) it was predicted that mu suppression in one or more of the three electrodes (C3, Cz, C4) would be correlated with empathy, as measured by the IRI.

Woodruff, Martin and Bilyk (2011) found negative correlations, and hence positive relationships between mu suppression difference scores and the perspective taking subscale of the IRI, however all subscales were evaluated in regard to a relationship with mu suppression during the separate conditions involved in this study.

It should be noted that while only electrodes C3, Cz and C4 as well as O1, Oz and O2 were analyzed, data from the other 26 electrodes were still collected for possible use in future post hoc analyses. All statistical analyses were conducted using SPSS version 19. Greenhouse-Geisser values are reported in the analysis of variance tests, as sphericity was not assumed.

Main Effects

Main Effect of Task

It was hypothesized that a main effect of task would reflect differences in mu suppression between observation versus execution involving the hand-tapping task, such that mu suppression would be greater during the execution task. Mu suppression values for this analysis were derived by using the execution as well as the observation condition and dividing this score by the rest-observation condition, based on hand.

Main Effect of Electrode

It was hypothesized that there would be a main effect across electrode sites. Previous research conducted by Oberman et al. (2005) did not report significant differences in regard to mu suppression between electrodes C3, Cz and C4 across the motor area.

Main Effect of Hand

A main effect of hand was expected to occur, such that greater mu suppression would occur in electrode C3, expressing a laterality preference for the right hand. Greater suppression was also expected to occur during observation and execution of actions of the left hand in electrode C4. A planned paired-samples t-test was used to evaluate differences due to the laterality effect from the hand used.

Electrode by Task Interaction

Based on previous research, mu suppression values should be higher during execution as compared to observation of the task (Muthukumaraswamy et al., 2004; Pineda, 2005; Oberman et al., 2005). This makes sense, given that mu suppression would be expected to be higher during overt movement as compared to observation of another's movement.

Electrode by Hand Interaction

It was hypothesized that there would be a laterality effect of hand by electrode, such that greater mu suppression would occur during right-hand observation and execution than in the left-hand condition. While a laterality effect was predicted, mu suppression was expected to occur across C3, Cz and C4 during all action-observation and execution tasks. Using an ANOVA, any interaction effects will be examined.

Task by Hand Interaction

No interaction of task by hand was expected. Regardless of whether the task is to observe or to execute an action, both hands were expected to elicit mu suppression during each of the conditions.

3-Way Interaction between Hand, Task & Electrode

An interaction between hand, task and electrode was not expected in the current experiment, because mu suppression should not be differing significantly between each of the electrode sites. However using ANOVA, any such interaction will be examined.

IRI and Mu Suppression Correlation

Based on previous research (Woodruff, Martin & Bilyk, 2011), an inverse correlation between IRI scores and mu suppression was expected. It was hypothesized that empathy measures, and specifically those of perspective taking in the IRI, would show a significant correlation with mu suppression. Correlations between IRI data were compared with levels of mu suppression for all participants to explore any relationship between empathy and desynchronization of alpha-band rhythms.

CHAPTER 3: Results

Of the original 48 subjects, 18 were removed for the following reasons: data were too noisy to be used accurately for 8 subjects, an undergraduate assistant failed to press the record button on the EEG for 2 of the participants, 5 subjects experienced a glitch or freeze in the EEG software leaving an inadequate amount of data for analysis, and there were mistakes in the data written down for 3 of the participants, making it impossible to accurately analyze. This resulted in a total sample of 30 participants.

Initial tests

Alpha-band suppression values were derived by dividing the action-observation condition by the rest-observation condition as well as the action-execution condition by the rest-observation condition. In this way, the rest observation values served as a baseline with which to conduct future analysis. This score was then log transformed in

order to correct for non-normal distributions. These log ratios were then submitted to a 2 x 2 x 3 repeated measures analysis of variance. As predicted, there was a main effect of hand, $F_{(1, 29)} = 4.882, p = .035$, a main effect across electrode sites, $F_{(2, 58)} = 11.758, p < .001$, and a main effect of task, $F_{(1, 29)} = 17.13, p < .001$. No interaction was found between hand and task $F_{(1, 29)} = 0.01, p = .92$, or hand, electrode and task, $F_{(2, 58)} = .916, p = .392$. However, there was an interaction between electrode and hand, $F_{(2, 58)} = 4.045, p = .028$, as well as electrode and task $F_{(2, 58)} = 5.727, p = .011$.

Follow up one sample *t*-tests were next conducted to evaluate alpha-band suppression values in the log transformed scores obtained from each condition for each hand. A Bonferroni correction was applied to the family wise alpha, setting the new rejection *p*-value at $p = .008$. Alpha-band suppression for the right hand condition in electrode C3 was significant during execution $t(29) = -4.148, p < .001$, but not for observation $t(29) = -1.094, p = .283$. Scores for electrode Cz approached significance for suppression during execution $t(29) = -2.446, p = .021$, but not observation $t(29) = -.348, p = .73$, and this pattern repeated in C4 execution $t(29) = -4.646, p < .001$, versus observation $t(29) = -0.45, p = .656$. A graphical display of this information is given in figure 1 of the appendix.

During the left-hand condition, electrode C3 recorded significant values for execution $t(29) = -5.087, p < .001$, and came close to significance for observation $t(29) = -2.708, p = .011$. Suppression scores obtained from Cz were significant for the execution condition $t(29) = -5.18, p < .001$, but not observation $t(29) = -1.277, p = .212$. Finally, *t*-tests for values obtained for recordings taken from electrode C4 were significant for both execution $t(29) = -5.938, p < .001$, as well as observation $t(29) = -4.558, p < .001$. The

only suppression values that failed to reach significance were found in observation conditions for the right hand in C3, Cz and C4, as well as observation of the left hand in Cz, with values for electrodes Cz in the right hand condition and electrode C3 in the left hand condition approaching significance. A graphical display of this information is given in figure 2 of the appendix.

No condition reached significance for any of the occipital electrodes under any of the repeated measures ANOVA. There was no main effect of hand $F_{(1, 29)} = .761, p = .39$, no main effect of electrode $F_{(2, 58)} = 1.102, p = .332$, or main effect of task $F_{(1, 58)} = .449, p = .508$. There was no interaction between hand and electrode $F_{(2, 58)} = 1.964, p = .153$, hand and task $F_{(1, 29)} = 1.49, p = .232$, electrode and task $F_{(2, 58)} = .648, p = .495$, or electrode, hand and task $F_{(2, 58)} = 2.224, p = .126$. Figures 3 and 4 of the appendix provide a graphical display of these results.

All empathy measures were evaluated for correlation with any of the conditions, hands or electrodes. A significant relationship was found between the fantasy subscale and the observation of left-handed tapping in electrode C4, $r(28) = -.425, p = .019$. No other empathy measures reflected a significant relationship with suppression values recorded during the experiment. Additionally, empathy measures were not found to have a significant relationship with any of the suppression values obtained under any condition from electrodes in occipital areas O1, Oz and O2.

Difference scores were then calculated by subtracting scores of alpha-band suppression during observation from execution values in each of the electrodes, and suppression values were assessed for areas being recorded by central motor and occipital electrodes. In regard to difference values obtained from information recorded from

central motor electrodes, there was a main effect of region $F_{(1, 29)} = 24.636, p < .001$ and electrode $F_{(2, 58)} = 4.162, p = .029$. There was no main effect of hand $F_{(1, 29)} = .43, p < .517$. There was an interaction found between region and electrode $F_{(2, 58)} = 5.812, p = .007$, but not between hand and electrode $F_{(2, 58)} = 2.057, p = .141$, region and hand $F_{(1, 29)} = 1.129, p = .297$, or region, hand and electrode $F_{(2, 58)} = .575, p = .562$. Difference scores calculated for occipital data failed to reach significance for any main or interaction effect. These results of difference score *t*-tests for occipital data are displayed in figure 6.

One sample *t*-tests were then performed on each of the difference scores generated from electrodes lying over the sensorimotor cortex. Again, an alpha correction was applied to the family wise error rate, setting the new *p*-value at $p = .008$. In the right hand condition, electrode C3, $t(29) = -3.686, p = .001$, and electrode C4, $t(29) = -4.634, p < .001$ reflected significant suppression values. In the left hand condition, electrode C3, $t(29) = -3.158, p = .004$ and electrode C4 $t(29) = -3.183, p = .003$ also reflected a significant level of alpha-band suppression. Suppression was not significant in electrode Cz for either the right $t(29) = -1.495, p = .146$, or the left $t(29) = -1.74, p = .092$ condition. Difference scores are displayed in figure 5 of the appendix. Correlations were then conducted between empathy values and difference scores for each of the electrodes, again, none of them attaining a significant correlational value with any of the empathy subscales. This was the same for data obtained from the occipital electrodes as well.

Lastly, the repeated measures analysis of variance was conducted on the data, averaging across task (execution and observation suppression scores). This revealed a main effect of hand $F_{(1, 29)} = 4.882, p = .035$, a main effect of electrode $F_{(2, 58)} = 11.758, p < .001$, and an interaction of hand and electrode $F_{(2, 58)} = 4.045, p = .028$. Paired

samples t-tests were then conducted to determine where these differences existed. This revealed that the interaction of hand and electrode is explained by greater mu suppression in electrode C4 in the left hand condition than seen in the right-hand condition, $t(29) = -3.516, p = .001$. Similar effects were not seen for electrode C3, $t(29) = -.761, p = .453$, or for electrode Cz, $t(29) = -1.882, p = .07$. This represents at least half of a laterality effect over area C4, averaged across conditions. These results are shown in figure 7 of the appendix.

CHAPTER 4: Discussion

The purpose of this study was to examine differences in mu suppression based on action-observation versus execution and to evaluate how mu suppression would differ based on the hand of interest in each condition. Specifically, it was hypothesized that mu suppression would be greater during execution than during observation. Secondly, it was hypothesized that laterality effect would occur, based on the hand either being used or being observed. The third hypothesis was that difference scores would reveal significant results based on the hand of interest, and lastly that there would be a correlation found between mu suppression and the IRI. To that extent a laterality effect was found averaging across task, in which the ANOVA revealed a main effect of hand and an interaction between hand and electrode, which is in line with laterality seen in other EEG studies (Nam et al., 2011). Additional paired samples t-tests reflected though that this effect only existed for the left hand values averaging across task. Right-handed conditions did not reflect this same laterality. This seems strange, given that previous experiments using only right-handed conditions have demonstrated a laterality effect with this hand.

Is it possible that right-handedness had a role in this laterality effect? It may be that right-handed participants reflected lateralization only in the left hand because it required the execution combined with the observation of the hand not considered to be dominant. Obviously, participants are familiar with using and observing both hands, but within an experimental condition asking them to use or observe only one at a time, the left hand condition was a more novel stimulus, and it may be for this reason that the same laterality effect did not appear for right hand conditions. Indeed, data reflect that in the alpha-corrected initial one-sample t-tests, observation of right hand conditions did not always reflect significant mu suppression, while left hand observation did.

Since the laterality effect was found by averaging across tasks, it would make sense that the left hand conditions achieved a laterality effect from averaging significant levels of mu suppression in both observation as well as execution. Conversely, this did not occur for the right hand, where mu suppression was frequently only significant during the execution condition. It would be interesting for future research to examine this issue using a sample of participants that are left-handed as a comparison. It may be that the dominant hand was related to the fact that only half of a laterality effect was seen, and a replication using only left handed participants is a future direction for research. Nevertheless, this finding is all the more puzzling, due to the fact that three other experiments in this lab have found a significant correlation between the right-handed condition and electrode C3. At this time though, the reason for this discrepancy is unclear, but may be related to issues with the design of this experiment, described later in the limitations.

Central electrode suppression value difference scores (observation subtracted from execution) reflected no main effect for the hand used, however there were main effects of the electrode and region. Additional one sample *t*-tests verified that suppression difference scores were indeed significant for electrodes C3 and C4 for each hand. The reason that both hands reflected significance in both electrodes is likely because of the nature of subtracting execution, the condition with higher mu suppression, from the observation condition. Mu suppression values for recordings taken from electrode Cz rarely reached significance in one or both conditions for each hand. This seems to suggest that within the context of this study, activity recorded from electrodes C3 and C4 expresses a significant difference between execution and observation suppression levels, regardless of the hand being used.

This experiment may not have found significance in all hypotheses, however it should be noted that activity recorded from electrodes over central motor areas reflected a significant relationship with the task being performed, and that the occipital electrodes consistently did not. It has been suggested that occipital alpha-band activity can contribute to EEG signals recorded in the scalp of central regions of the brain. Pineda (2005) reported previous studies that ruled out volume-conducted effects, and the findings of this study suggest that alpha-band suppression between these two areas is unrelated as well. It appears that any significant values found for measures calculated from alpha-band suppression in the occipital area were likely due to chance probability.

The conditions under which alpha-band suppression achieved significance in the occipital electrodes support this idea. For example, the fact that execution, but not observation conditions reflected a significant level of suppression based on one sample *t*-

tests suggests that the occipital alpha band suppression values observed were not simply a result of visual stimuli. If this were the case, one would expect to see similar values in the observation conditions of this experiment, as both observation and execution should be observing essentially the same thing. This does beg the question though of what might have been viewed differently between these two conditions such that the observation condition did not achieve alpha-band suppression, yet the execution condition did. It may be that participants were not fully attending visually during each condition. However this does not seem likely because suppression was seen in the observation condition from activity recorded from central electrodes. Because attentional allocation was not assessed during the experiment, it is not possible to evaluate the degree to which each participant had attended to the stimuli. Regardless, the suppression values seen in the central as compared to the occipital area suggest that mu suppression is not merely a reflection of activity recorded from occipital electrodes.

In addition to calculating suppression values for each condition, calculating difference scores, and averaging execution and observation values together across electrode site, empathy measures were also taken using the IRI. The IRI was used with the expectation of finding a correlation between the empathy subscales and alpha-band suppression values. Specifically, it was hypothesized that there would be a correlation between the perspective taking subscale and difference scores obtained by subtracting observation from execution conditions, based on previous research from this lab (Woodruff, Martin & Bilyk, 2011; Woodruff & Klein, in preparation). While a correlation between perspective taking and difference scores was not evident, the fantasy subscale did reflect a significant correlation with the left-hand observation condition. The

fact though that only the fantasy subscale revealed a significant correlation and only under the left-hand observation condition is curious, because fantasy has not previously reflected a significant correlation in other studies. Additionally, it is important to note that while the correlation found with the fantasy subscale was mathematically negative, it represents a positive relationship with mu suppression and the fantasy measure. The reason for this is that greater mu suppression values are represented by values that are more negative.

One could postulate that it makes sense that a scale involving imaginative creativity would reflect a correlation with the observation condition, as observation to some extent would involve invoking some level of fantasy. The fantasy subscale is defined as “the tendency to imaginatively transpose oneself into fictional situations (Davis, 1994).” It could be the case then, that fantasy to some extent is involved in observing and understanding another’s actions, especially when these actions are observed in an artificial video and applied to a physical circumstance. In regard to the current experiment, it was observing a hand movement in the video, and then preparing for this future movement that elicited a correlation with the fantasy scale. Having a significant correlation would suggest that greater expressed levels of fantasy might be related to greater mu suppression during observation, especially of the non-dominant hand. If this were true, it would put this finding in line then with the laterality effect observed for the left hand as well. However, it should be noted that the fantasy subscale has not been found to have any significant relationship with suppression in another study conducted by this lab (Woodruff, Martin & Bilyk, 2011).

Because of this fact, making a statement of some kind of relationship between these measures may be premature. Since the fantasy sub scale was the only measure to reflect a significant correlation, it may be that the task simply was not socially relevant enough to functionally evoke a greater correlation in other empathy measures. Why exactly this is though remains unclear, as perspective taking correlations have been found in two other studies from this lab (Woodruff, Bilyk, & Martin, 2011; Woodruff and Klein, in preparation). Other studies have demonstrated correlations between putative mirror neuron activity and empathic abilities other than perspective taking (Perry et al., 2010; Schulte-Ruther et al., 2007; Yang et al., 2009), and it may be that this empathic relationship has something to do with levels of fantasy that previously has not been as robust in other research.

Limitations

Limitations of this study did occur. Of secondary interest in this experiment was the recording of sub-threshold motor activity using EMG. This involved adhering electrodes to record motor activity from participants' arms prior to beginning the experiment. While such a process seemed rather innocuous as an additional measure initially, in practice it presented problems. Because it was necessary that the participant move his or her arms when executing the hand tapping action, occasionally electrodes would come loose from where they had been attached. EMG electrodes would then require adjustment and reapplication, sometimes in the middle or following the completion of one of the trial blocks. The fact that this meant the participant's attention was directed elsewhere and that full attention may not have been paid to the task at hand could have been what affected this study's ability to reveal more robust results in regard

to some hypotheses. Specifically, issues with these electrodes may have affected the ability to find a laterality effect with the right hand, because this was the hand that EMG electrode cords had to travel the longest distance to reach, involving going behind the computer screen in order to reach the subject. If EMG cords came loose during the experiment, it was more likely to happen to the right hand. The other issue related to the use of EMG, was that both EEG and EMG recording were feeding into the same computer. The fact that both of these systems were recording at the same time may have been related to the glitch or freezing that occurred during the experiment for a few of the participants.

Another issue that presented itself for some of the final participants used in this experiment was in regard to the EEG cap used. Prior to analyzing EEG data as with any other type of data, it is important to remove any artifacts before analysis. This is an essential step because of the obvious effect that artifacts can have in proper data interpretation. In this case, before analyzing EEG data, it is necessary to remove eye blinks. It would not be desirable to request participants to not blink their eyes for eighty seconds at a time, however because these muscles are interconnected with other muscles of the scalp, these artifacts must be removed from the data before beginning analysis. The issue for some of the final participants was that the electrodes meant to record eye blink behavior (electrode Fp1, Fpz and Fp2), had difficulty reaching the desired level of impedance. While it does not appear that the data obtained from these participants were significantly different, it is possible that it may have been related to some issues with being unable to remove complete eye blink artifacts as effectively. However, it is not desirable to change equipment in the middle of an experiment because of concerns with

discrepancy in measurement between old and new tools, and for this reason it was deemed appropriate to finish the experiment with these same tools and procedures with which it began.

Finally, there may have been an issue with presenting the empathy questionnaire at the end of the study. The reason for doing this was the concern that taking an empathy questionnaire at the beginning of the study might bias EEG data related to aspects of empathy. By presenting the questionnaire to participants at the end of the study it may have prevented the survey from biasing EEG data, but it did not prevent the EEG experiment from biasing how the participant chose to fill out the IRI. The fact that this experiment lasted for an average of an hour may have left some participants feeling rushed when completing this questionnaire.

Rather than thoughtfully evaluating each statement, it may be that completing a survey represented yet an additional task and could have biased feelings related to empathy, such as perspective taking. It could be possible that one would be less concerned with accurately answering questions after a long experiment involving repetition of very similar activities. Alternatively, perhaps the perspective of others is not at the forefront of one's mind following completion of a tedious activity. Regardless, this experiment did have important findings and future research should look to evaluating the connection between mu suppression and empathy measures within different contexts as well.

One area not evaluated in this study was empathy and mu suppression within the context of gender. No hypothesis was made in relation to the gender of participants involved in this study, however other research suggests that gender may play an

important role in social sensitivity and emotion recognition, such that women tend to be more aware of these issues (Schulte-Ruther et al., 2008). Indeed, female participants in the study conducted by Schulte-Ruther et al. (2008) expressed a higher degree of activation in areas thought to contain mirror neurons, as compared to males. This has led to the hypothesis that perhaps males and females rely on different cues when assessing distinctions between the self and other. Had the current study had a more representative sample of males, it would have been interesting to assess differences in activation and empathy levels between groups. Unfortunately, the subsample of males was too small to allow adequate analysis. Additionally, the videos used in the current study displayed the same, clearly male hand in all conditions. It is not clear how gender of the hand may have affected results, however it would be fascinating to replicate this experiment using a female hand in the videos. It may be that gender differences affected results in this study in unexpected ways, and future research that more adequately addresses this question may serve to elucidate this issue.

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Appendix:

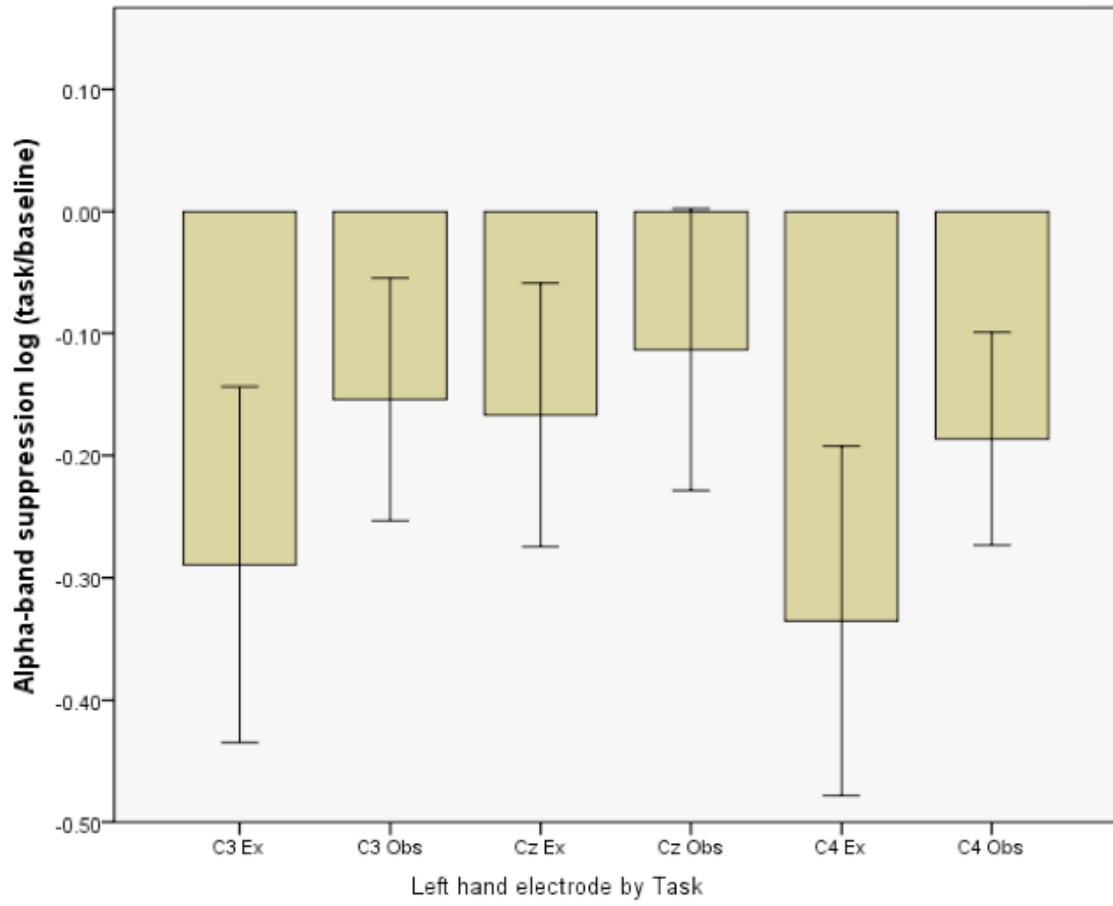


Figure 1. Alpha-band suppression in central electrodes during left handed execution and observation hand tapping tasks.

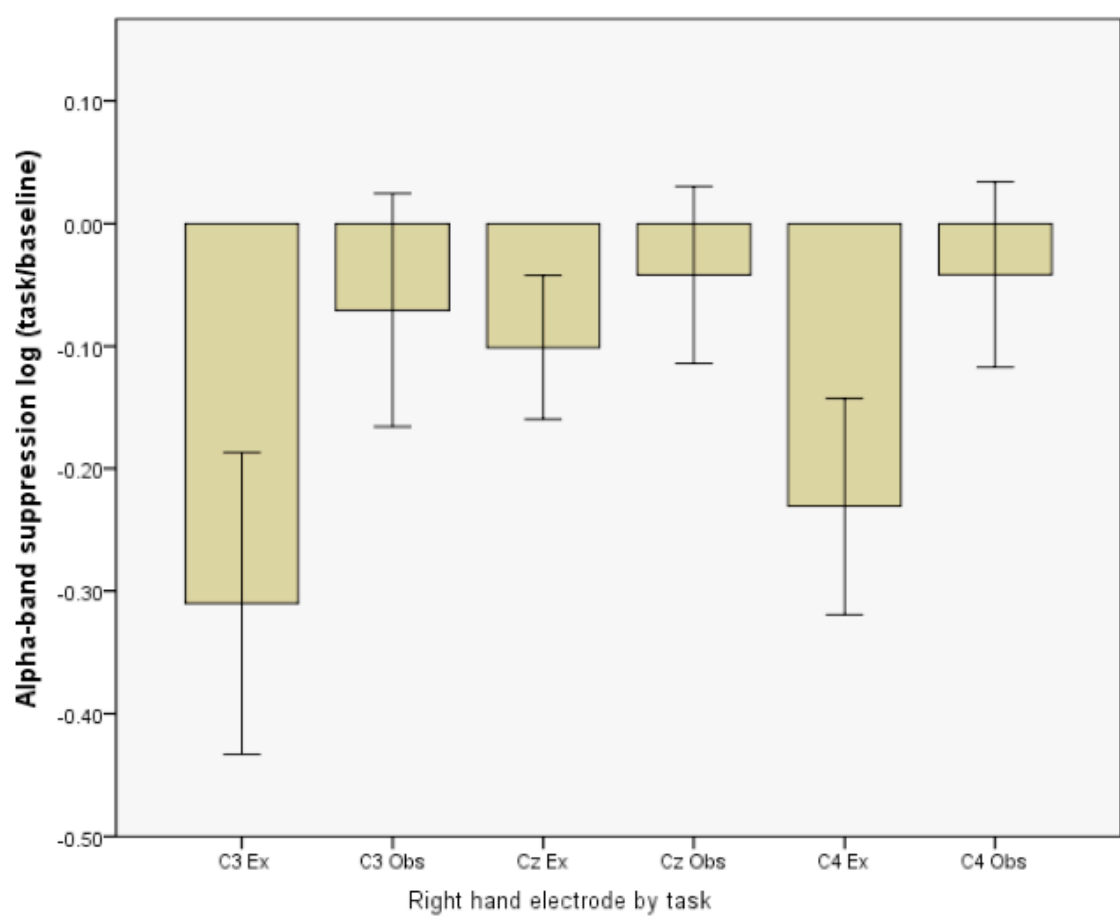


Figure 2. Alpha-band suppression in central electrodes during right handed execution and observation hand tapping tasks.

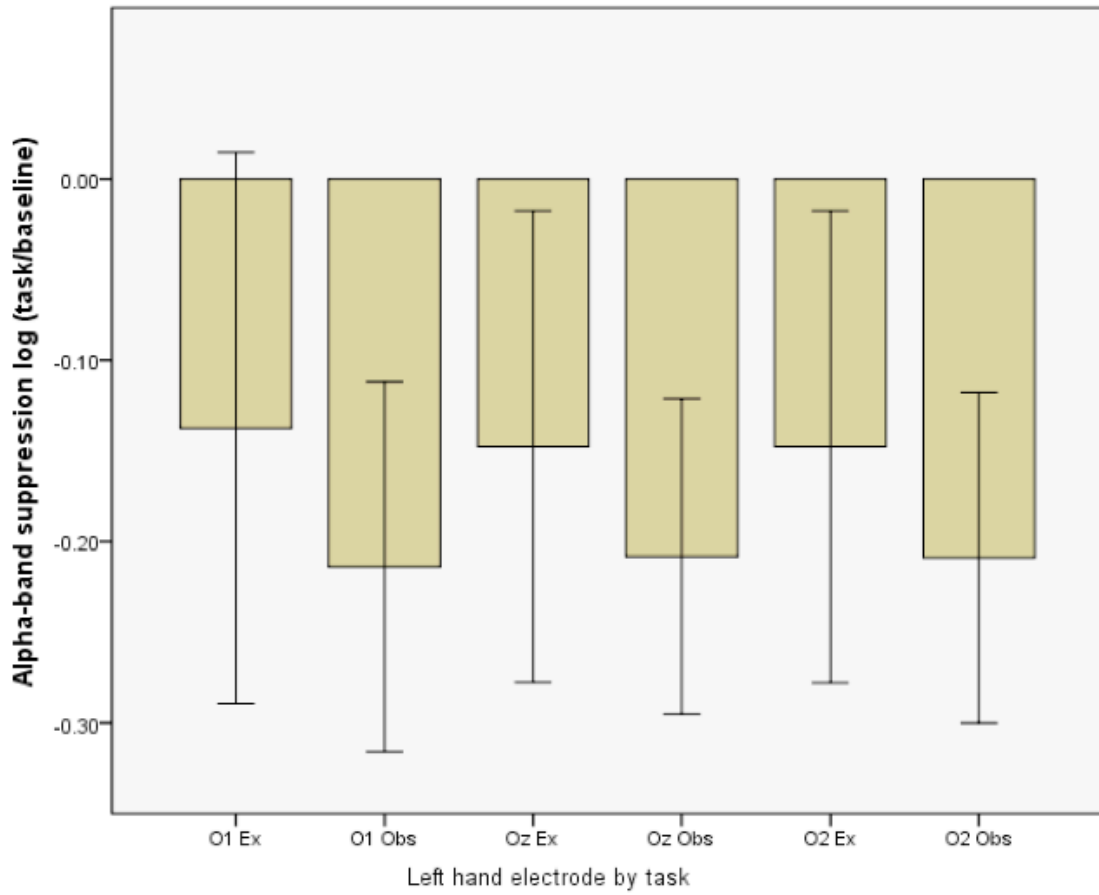


Figure 3. Alpha-band suppression in occipital electrodes during left handed execution and observation hand tapping tasks.

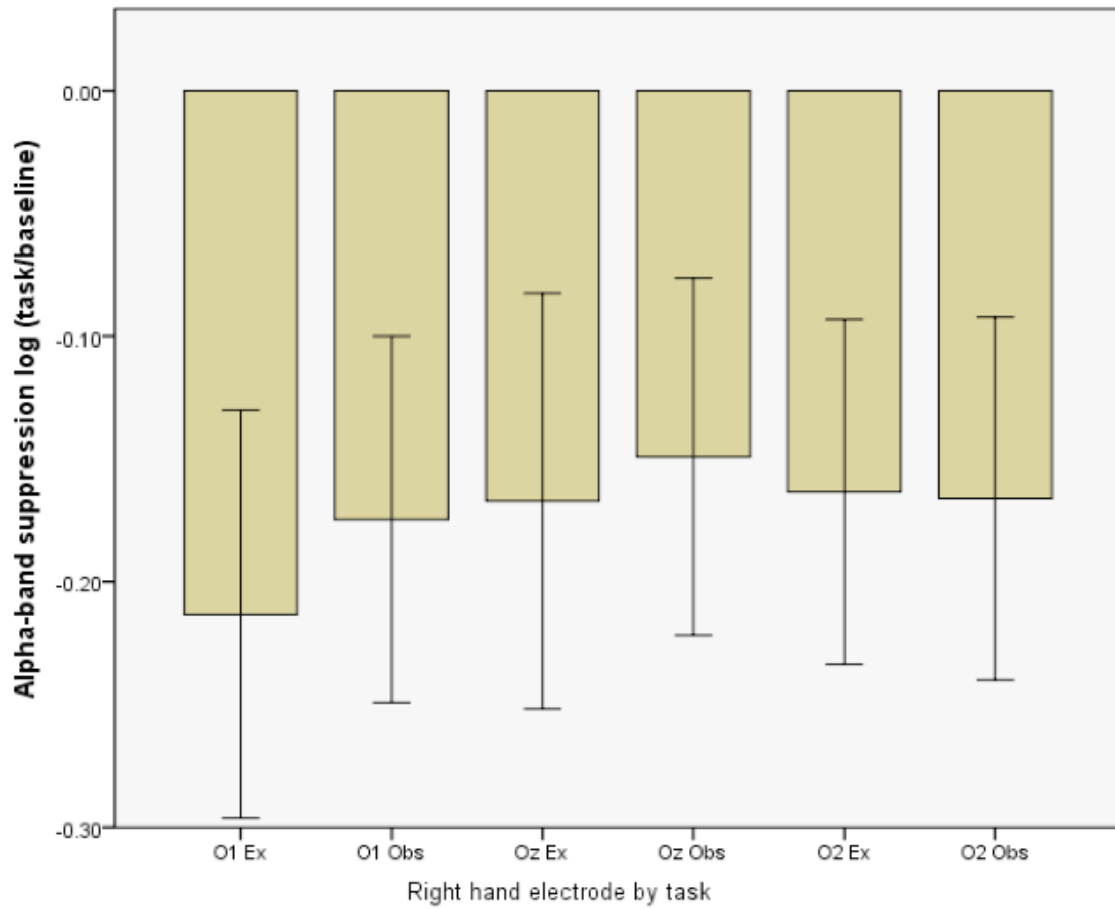


Figure 4. Alpha-band suppression in occipital electrodes during right handed execution and observation hand tapping tasks.

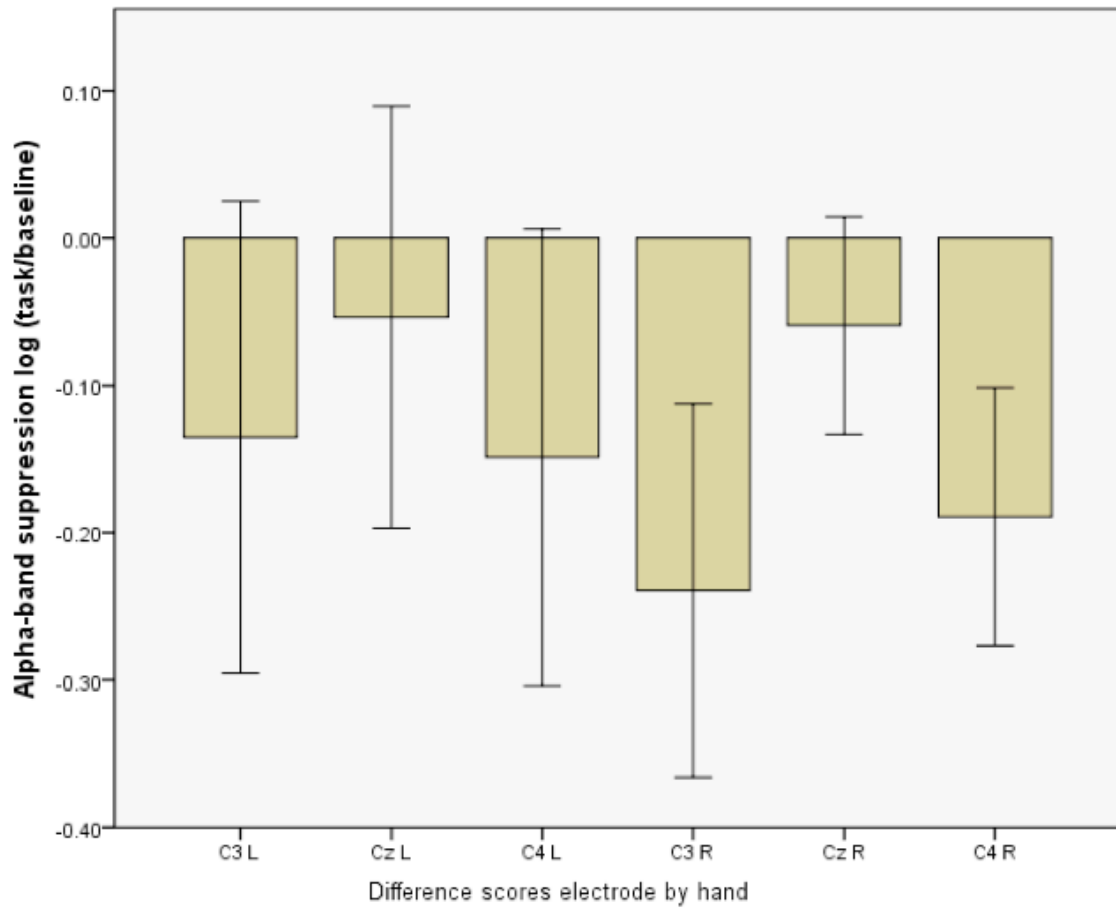


Figure 5. Alpha-band suppression difference scores (execution – observation) in central electrodes during left and right handed tasks.

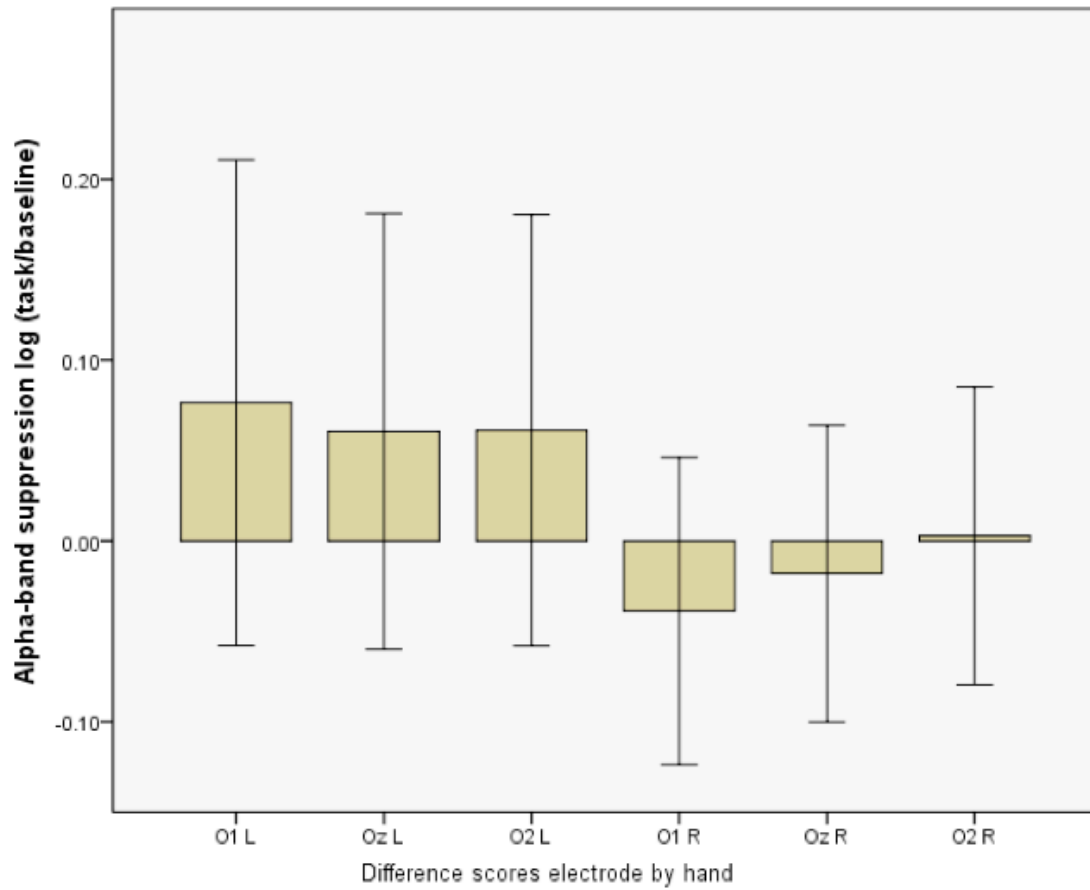


Figure 6. Alpha-band suppression difference scores (execution – observation) in occipital electrodes during left and right handed tasks.

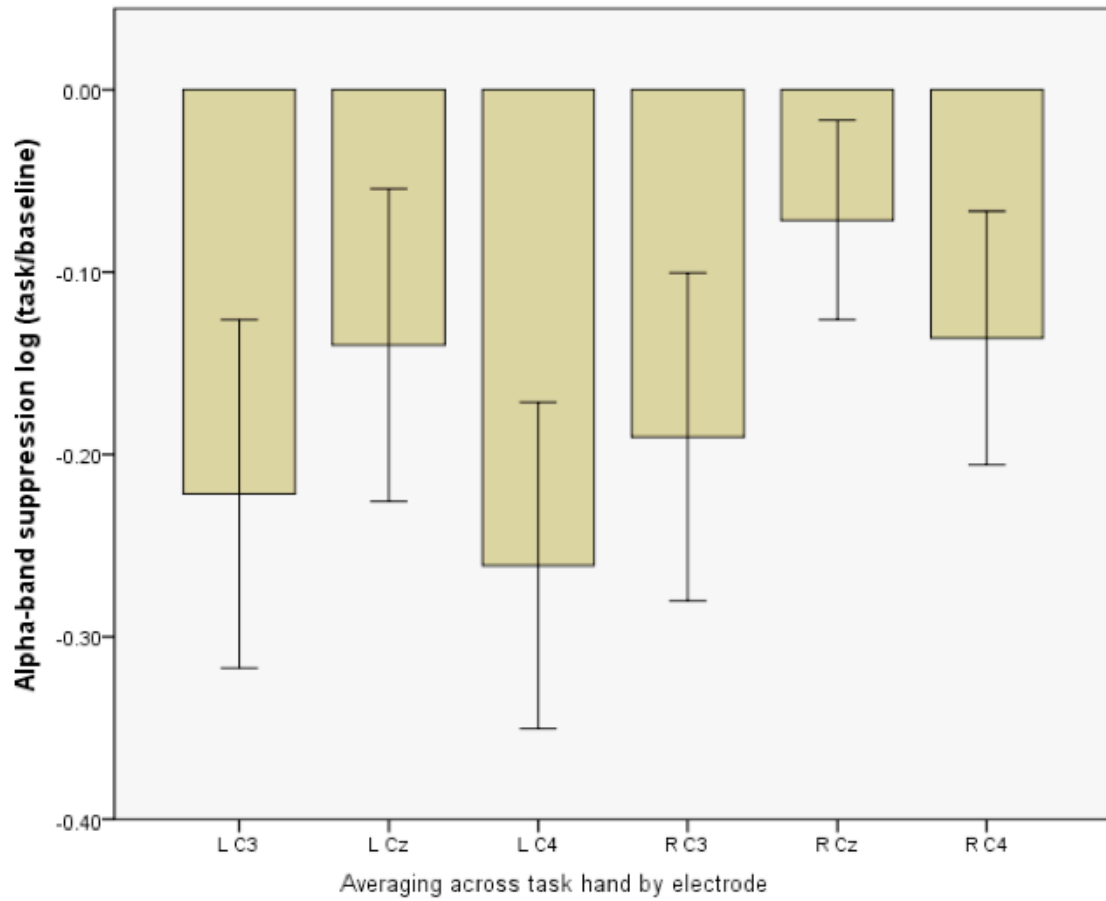


Figure 7. Alpha-band suppression averaging across task (execution and observation) in central electrodes for the left and right hand.