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Motor observation, motor performance, and motor imagery : an ERP study.

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MOTOR OBSERVATION, MOTOR PERFORMANCE, AND MOTOR IMAGERY:
AN ERP STUDY

By

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B.A., University of Kentucky, 2002
M.A., University of Louisville, 2006

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University of Louisville
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A Dissertation Approved on

April 7th, 2011

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John R. Pani

DEDICATION

This dissertation is dedicated to my parents

Mr. Thomas C. Brian

and

Mrs. Barbara V. Brian

for their continued love and support.

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I would like to thank all the other members of my committee, Dr. Dennis Molfese, Dr. Paul DeMarco, Dr. Pavel Zahork, Dr. Joseph Dien, and Dr. John Pani. I am eternally grateful for their time, energy and advice. Special Thanks to Dr. Paul DeMarco and Dr. Joseph Dien for their guidance, advice, and continued support and dedication to my academic success. Without them, I don't know if I ever would have finished. Thank you! I would also like to thank Stephen E. Edgell for opening doors and giving me the freedom to pursue my research interests. I would also like to thank a great many friends and my family for their continued encouragement and support. Lastly, I would like to thank a small but very important group of individuals, namely Erin, Callie, Mary, Katie, Leah, Ashley, Kimmy, Heather, and my good friend Scott Flood for helping find my true path in life.

ABSTRACT

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April 7th, 2011

Two major theoretical models, Direct Mapping and Functional Equivalence, suggest that the observation of action and imagery of action, respectively, involve activation of similar motor related areas. Despite the wealth of evidence that supports these two perspectives, the degree to which these motor-related actions overlap is still only vaguely defined. The present investigation sought to assess both the spatial and temporal characteristics of the brain activity involved in these motor related conditions. Specifically, the present study used ERP technology to assess the neural substrates of Motor Observation, Motor Performance, and Motor Imagery. Participants viewed images depicting two human grasping motions, whole hand grasping or precision finger-to-thumb grasping. Participants were to report, perform, or imagine performing the observed action depicted in the target image. Ongoing EEG was time-locked to the presentation of the target image. The EEG data were filtered, segmented, submitted to a series of artifact correction procedures, then averaged. Subsequently, the averaged data were subject a two-step sequential principal component analysis. These were then subjected to repeated measures

ANOVAs. Additional analyses included amplitude and latency measures, obtained from selected regions across different conditions. These measures were compared and examined for group differences. In addition, Low Resolution Brain Electromagnetic Tomography was used to elucidate the underlying neural activity. Specifically, all three of the motor related experimental conditions were expected to show increased activation of motor related areas on the contralateral hemisphere (left hemisphere) to the instructed action, particularly in the Primary Motor Cortex and Primary Somatosensory Cortex, and increased activation in the Supplementary Motor Area, relative to a nonmotor control condition. However, the statistical analyses failed to support these hypotheses. In the end, a greater understanding of these processes through scientific advances further develops and improves both interventions and treatments aimed at bettering the lives of those suffering from a myriad of psychological, physical and psychophysical disorders resulting from many psychobiological causes including stroke, dismemberment, physical injury, and cognitive dysfunction. While the present study failed to further elucidate these neural mechanisms, this area of study is increasingly important and beneficial to wide ranging areas of medicine, neuroscience, and cognitive and sports psychology.

TABLE OF CONTENTS

	PAGE
ACKNOWLEDGMENTS	iv
ABSTRACT	v
LIST OF TABLES	ix
LIST OF FIGURES	x
CHAPTER	
I. INTRODUCTION.....	1
II. DIRECT MAPPING VIEW OF ACTION UNDERSTANDING.....	3
Mirror Neurons.....	6
Developmental/Behavioral Work.....	13
Electrophysiology and Neuroimaging.....	20
Section Summary.....	24
III. MOTOR IMAGERY.....	26
Behavioral Work.....	28
Motor Potentials and Motor Evoked Potentials.....	30
NeuroImaging Studies.....	33
Section Summary.....	38
IV. CRITICAL ISSUES	40
V. METHODS.....	47
Participants.....	47
Procedures.....	48

VI.	RESULTS	67
VII.	DISCUSSION AND CONCLUSIONS.....	102
	Automatic Motor Recognition	107
	Impact and Relevance to the Field.....	110
	REFERENCES	112
	APPENDIX	135
	CURRICULUM VITAE.....	138

LIST OF TABLES

TABLE	PAGE
1. Observed Actions	8
2. Artifact Removal Summary	65
3. EMG Measures of Maximal Amplitude	68
4. Significant PCA Factors	72
5. Amplitude and Latency Means	79

LIST OF FIGURES

FIGURE	PAGE
1. Broadly Congruent Mirror Neuron	10
2. Neutral Stimulus Image.....	49
3. Target Images.....	50
4. Task Flow	53
5. Visual Imagery Cues.....	55
6. 256-Electrode High Density Array Montage	57
7. Artifact Correction Plots	64
8. EMG Activation	69
9. Average EMG Waveforms	70
10. EEG Grand Averages	76
11. Source Activity at 68 ms	82
12. Source Activity at 112 ms	83
13. Source Activity at 180 ms	84
14. Source Activity in SMA	86
15. Source Activity in M1 at 112 ms	87
16. Source Activity in M1 at 180 ms	88
17. Topographical plot at 68 ms	91
18. Topographical plot at 112 ms	93
19. Topographical plot at 180 ms	94

20. Average EEG During ISI	97
21. Neutral and Target Stimuli	98
22. Response-Locked ERP	100

I. INTRODUCTION

Since the discovery of the mirror neuron system (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Giacomo Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), there has been heightened interest in the neural correlates of human imitation and motor observation. With the advancement in brain imaging technology, there is also a parallel and growing interest in the neural basis of mental imagery and the relative impact of motor imagery on motor performance. Together, these approaches provide an opportunity to examine the roles of observation and imagery on motor control from two different perspectives. Both areas attempt to elucidate the common neural substrates involved in imagining or observing motor actions, and the planning and execution of similar motor movements. Unfortunately, each line of work has progressed largely independent of the other, leaving a gap in the literature. Furthermore, the studies of motor imagery are less conclusive, leaving many remaining questions. However, a close inspection of the literature from these two fields of study reveals a number of commonalities.

These points of convergence, and a common set of questions surrounding motor imagery, provide a unique opportunity for a fresh perspective on this important topic. The overall goals of the present project are to further investigate the neural substrates of motor performance, motor imagery, and motor observation collectively. Specifically, both the spatial and temporal

characteristics of these processes will be examined using Event-Related Potentials. Briefly, a range of behavioral studies investigating short-term visuo-motor interaction, observational learning and stimulus-response compatibility, along with neuroimaging studies and the work on mirror neurons in non-human primates suggest that a matching system such as a Mirror Neuron System may exist in humans. This view proposes that there is a direct relationship between the perception of action and motor performance and that they share common neural substrates. This common neural basis between observation of motor movements and motor action may account for action understanding and human imitation. In addition, comparisons of motor performance and motor imagery suggest that they also share common neural pathways. This Functional Equivalence Model of motor imagery suggests that motor imagery and motor action are functionally and neurologically similar. Investigations of motor imagery involved a range of behavioral, electrophysiological and neuroimaging studies. As will be stated in the following sections, however, there are many remaining questions regarding these neurological similarities. These questions will be brought to the forefront of this discussion.

II. DIRECT MAPPING VIEW OF ACTION UNDERSTANDING

People learn by watching others in a variety of contexts including learning how to behave. This has been referred to as observational learning, modeling, emulating, and imitation (Hodges, Williams, Hayes, & Breslin, 2007). Loosely defined as a process by which we see an action or gesture performed by others and then (attempt to) duplicate that action, imitation is, suggested by some, to be present in humans as early as a few weeks of age (Meltzoff & Moore, 1977, 1983). Meltzoff and Moore (1977) reported that infants as young as 12 to 21 days of age are capable of imitating facial gestures such as tongue protrusion, mouth opening and lip protrusion. Subsequent work replicated and extended these findings to head movements and manual gestures (Meltzoff, 1995; Meltzoff & Moore, 1983, 1989). Others refuted these conclusions raising questions concerning both methodology and analyses (Anisfeld, 1979, 1991, 1996). While much attention was devoted to determining if infants were engaged in imitation or not, Meltzoff and Moore (Meltzoff, 2002; Meltzoff & Moore, 1977) were among the first to posit that a matching process may account for human imitation. They proposed that the infant brain might house a “supramodal” representation system. According to this view, visual information, proprioceptive information and, perhaps, motor information could all be loaded onto a non-modality specific representation through a “matching process.” The notion of a matching process of human imitation has since received much attention. Prinz (1997) proposed a

framework for the relationship between perception and action planning. Similar to a supramodal representation system, Prinz's *Common Coding Approach* contends that planned actions and perceived motor events share a common representational domain. According to this view, incoming sensory patterns and outgoing action programs share some common coding within central processing. In other words, event codes and action codes share a representational domain. This is often closely associated with stimulus-response compatibility, which is a topic we will return to later. Others still proposed that the human neural system matches action observation and execution (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Later, Rizzolatti and colleagues (Giacomo Rizzolatti, Fadiga, Fogassi, & Gallese, 1999) explicitly defined this matching system as it pertained to imitation. The authors suggested a similar explanation of human imitation referring to imitation as "resonance behaviors." According to this view, "in resonance behavior a neural activity that is spontaneously generated during movements, gestures, or actions is also elicited when the individual observes another individual making similar movements, gestures and actions (Giacomo Rizzolatti, et al., 1999, p. 91)."

While a direct matching view gained popularity and fueled a range of investigative studies, an alternative, goal-oriented view garnered support as well (Bekkering, Wohlschläger, & Gattis, 2000; Erlhagen, Mukovskiy, & Bicho, 2006; Heyes, 2001; Hodges, et al., 2007). Some argued that human imitation in children is specific to goal-directed action, that the imitative behaviors of the participants were intended to achieve the same goals rather than simply mirror

motor movements. Although a proponent of a direct matching perspective, Meltzoff (2002) suggested that as children grow older, this mapping process is less direct and instead is based on understanding of the model's intentions. This was followed by others suggesting that infant imitation is not without some *a priori* rationalization as the reasons for the action (Chaminade, Meltzoff, & Decety, 2002; Gergely, Bekkering, & Kiraly, 2002).

The evidence supporting a Goal-Oriented approach defended by Hodges and colleagues (2007) is not necessarily in conflict with direct matching when direct matching is relaxed (i.e. less direct and less well-matched). Indeed, Vogt and Thomaschke (2007) stated that direct matching is "neither as direct nor as well-matched as the name might suggest (pg. 498)." As we will see, mirror neurons show a large degree of generalization (Giacomo Rizzolatti & Craighero, 2004). Further, previous accounts of direct matching were applied only to imitation, often specifically to human imitation, whereas the contemporary view of direct matching may apply to both imitation and action understanding. The direct matching view of action understanding, a.k.a. Direct Mapping, suggests that we understand the actions of others, and subsequently reproduce them, by mapping the visual representation of an observed action onto an existing, internal motor representation of our own for a similar action (Giacomo Rizzolatti, Fogassi, & Gallese, 2001). This perspective relates to action understanding, rather than mere imitation, and that action understanding involves recognizing the purpose of the action. The Direct Mapping view predicts that action observation and action

execution activate a common set of neurons. Such a system is evidenced by the existence of Mirror Neurons in non-human primates.

In support of this Direct Mapping perspective, the characteristics and properties of mirror neurons will be discussed next. The following sections review 3 areas of research that support a Direct Mapping view of action understanding: Studies of Mirror Neurons; Behavioral work; and Neuro-Imaging Studies. The converging evidence from these areas strongly supports Direct Mapping and the existence of a Mirror Neuron System in humans.

a. Mirror Neurons

Although several researchers proposed matching systems to account for human imitation (Meltzoff & Moore, 1977; Prinz, 1997; Giacomo Rizzolatti, et al., 1999), some of these theories were largely based on behavioral data. The location where such a system may reside in the human brain remained elusive. However, in the late 1980s, the functional properties of the frontal agranular cortex of the Macaque monkey were intensely investigated (Gentilucci, et al., 1988; Okano & Tanji, 1987; Giacomo Rizzolatti, et al., 1988; Giacomo Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981a, 1981b). This rostral part of the inferior area 6 is known as area F5 (Matelli, Luppino, & Rizzolatti, 1985). As a result of these investigations, it was reported that area F5 housed motor representations for hand and mouth actions. Specifically, the dorsal portion of F5 is associated with hand movements while the ventral portion is associated with mouth actions. More specifically, the motor representation of these neurons is quite specific, almost exclusively involved in object-oriented actions using fine motor

movements of the fingers and hand such as grasping, manipulating, and tearing (Giacomo Rizzolatti, et al., 1988; Giacomo Rizzolatti, et al., 1981a, 1981b). It was later reported that a small percentage of F5 neurons were also responsive to visual stimuli (di Pellegrino, et al., 1992; Murata, et al., 1997). While investigating the motor properties of the neurons located in the dorsal area of F5, di Pellegrino and colleagues (1992) unexpectedly discovered that some of these neurons also responded to the observation of specific hand actions performed by the experimenters. Put simply, di Pellegrino and associates (1992) discovered a subset of F5 neurons that are responsive to both executed movements and the observation of the same or similar movements performed by the experimenters. This demonstrates that “gesture perception” and motor execution for grasping movements may share common neural circuits that many motor theories of perception, such as Direct Mapping predict. The discovery that F5 neurons are responsive to both executed movements and the observation of similar motor movements fueled extensive investigations of the visual and motor properties of these Mirror Neurons (Gallese, et al., 1996; Giacomo Rizzolatti, Fadiga, Gallese, et al., 1996). Activity from single neurons was recorded while monkeys observed objects, while manipulating objects and while observing either an experimenter or conspecific perform a range of motor actions. Objects alone, faces, emotional gestures, non-object related movements and actions using tools were not effective in activating these mirror neurons. See Table 1.

Table 1. List of observed actions investigated by de Pellegrino, et al., 1992; Gallese, et al., 1996; and Rizzolatti, et al., 1996

<u>Action Types Observed</u>	<u>Examples</u>
Food Grasping	Presenting food to the monkey Placing food or item on a surface Grasping Food Giving food to another experimenter Taking it away from another experimenter
Manipulating	Breaking, Tearing, Folding, Holding items
Intransitive Gestures (non-object related)	Threatening gestures Lifting arms Waving Hands
Hand – Object movements w/o interaction	Grasping Motion in absence of object Grasping objects with tool (e.g. forceps) Simultaneous movement of hand and food, but spatially separated from one another
Conspecific Actions	Food grasping action performed by another monkey

The actions that most frequently visually activated the mirror neurons were grasping, placing and manipulating. Further, Mirror Neurons are better defined by the relationship between the effective observed action and the motor response they code. This relationship is referred to as visuo-motor congruence (Gallese, et al., 1996; Giacomo Rizzolatti, Fadiga, Gallese, et al., 1996). F5 neurons selectively respond during goal-directed motor movements involving hand and mouth action. Similarly, F5 mirror neurons respond to the observation of the same or similar motor actions.

The degree to which the executed and observed actions are related varies. Thus, Mirror Neurons are classified based on this variation into three

categories: *Strictly Congruent*; *Broadly Congruent*; and *Non-Congruent* (Gallese, et al., 1996). *Strictly Congruent* mirror neurons are those “in which the effective observed [actions] and the [effective] executed actions correspond’ in both the “general action (e.g. grasping) and in terms of the way in which the action was executed (e.g. precision grip; Gallese, et al., 1996, p. 601).” Less than one-third of Mirror Neurons are classified as *Strictly Congruent*.

Nearly two-thirds of Mirror Neurons are *Broadly Congruent* Mirror Neurons. *Broadly Congruent* Mirror Neurons allow for some variability in the effective observed action compared to the effective executed action. Take another grasping neuron for example for which the effective executed action is precision grip. For this neuron to discharge during executed actions, the monkey must perform a precision grip, whereas a whole-hand grip will not activate this neuron. On the other hand, the effective observed actions include either precision grip or whole-hand prehension. Here, the grasping neuron discharges during precision grip and also responds to observed actions that are functionally similar. The flexible nature of the *broadly congruent* neurons allows for some variability in the effective observed action. This variability provides the possibility that a range of observed actions can elicit a neural response for a motor representation corresponding to the observed action. See Figure 1.

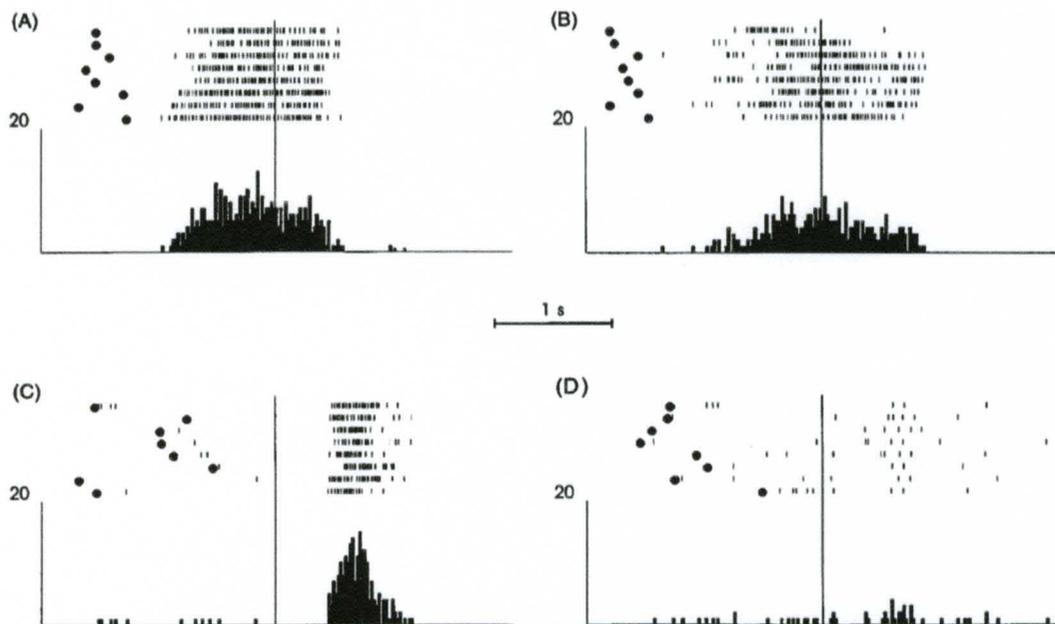


Figure 1. An example of a Broadly Congruent Mirror Neuron – taken from Gallese, Fadiga, Fogassi, & Rizzolatti (1996). Neural discharges (A) while an experimenter uses a precision grip to take hold of a piece of food; (B) while the experimenter uses whole-hand prehension; (C) the monkey grasps the food with precision grip; and (D) the monkey using whole-hand prehension. While the effective executed movement is specific to precision grip, the effective observed actions include both precision grip and whole hand precision.

Lastly, *Non-Congruent* mirror neurons are those that show no clear relationship between the executed and observed action that elicit a response. Visuo-motor congruence has also been reported in neurons located in the Inferior Parietal Lobule shown to exhibit mirror properties (Fogassi, et al., 2005). The

visuo-motor congruence for neurons in this area is consistent with previous findings in that the neurons showed the same specificity for the effective observed action as for the executed actions. Thus, the majority of neurons tested within the inferior parietal lobule were differentially activated depending on the nature of the observed action. This difference in activation was consistent with differences in activation for executed actions.

Additional observations of mirror neuron activity by others have led to some interesting conclusions. Mirror Neurons will respond even when hand-object interactions are inferred rather than seen directly (Kohler, et al., 2002; Umiltà, et al., 2001). F5 Mirror Neurons were examined while observing partially occluded actions and mimed actions (Umiltà, et al., 2001). Specifically, actions were performed in either full view or in partial occlusion and with or without an object present. Nearly half of the mirror neurons showed active neural responses during both the grasping conditions (hidden and full view). This activity was nearly absent in both miming conditions. The authors note that two conditions must be met in order to elicit activity during hidden grasping. The monkey must (1) know the object exists behind the occlusion and (2) must see the hand of the experimenter moving behind the occlusion. This demonstrated that mirror neurons respond to action observation even when the action must be inferred because the hand-object interaction cannot be seen. Kohler's group (Kohler, et al., 2002) examined a small percentage (~13%) of neurons identified with mirror properties. These particular mirror neurons discharged in response to an action related sound as well as the visually observed action. While a variety

of action related and non-action related sounds were used, only those associated with a specific object related action (e.g. tearing paper) were effective in eliciting a neural response. Of the 33 neurons examined, 29 showed auditory selectivity for specific sounds. Of those 29, 22 required a congruency between the visual and auditory stimuli (i.e. visual selectivity for the same auditory action). These lines of work further supported that Direct Mapping involves action understanding rather than mere action observation and imitation.

In short, Mirror Neurons have been identified in two areas of the brain including the rostral area of the ventral premotor cortex, known as F5, and the rostral portion of the inferior parietal lobule, or PF. These neurons discharge during the execution of object-related hand and mouth actions as well as the observation (visual and auditory) of similar motor actions performed by an experimenter or another monkey. Non-object related actions, with and without emotional significance, are ineffective in activating the neurons. The types of objects also do not seem to greatly affect the neural response – actions involving food items or small geometric solids do not produce obviously different neural responses. However, the relationship between observed and executed actions has been associated with different neural activity. Mirror neurons have been classified as highly congruent, broadly congruent or non-congruent. The relationship between the effective executed actions and effective observed actions is much less strict for broadly congruent neurons. This differential activation is present for actions that are seen directly, inferred from partially occluded actions, or heard. The existence of the Mirror Neuron System (MNS) in

non-human primates provides much support for theories proposing that such a matching system exists in humans. In fact, many researchers believe that a MNS may exist in humans (di Pellegrino, et al., 1992; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995), perhaps present in early childhood and infancy (Lepage & Theoret, 2006, 2007).

b. Developmental/Behavioral Work

The existence of the MNS in monkeys provides clear evidence that a similar matching system may exist in humans. The MNS system has been extensively researched using single cell recording techniques. However, such techniques cannot be used on human participants. As a result, unfortunately, proof that a MNS exists in humans is still lacking. Nevertheless, researchers have relied on a wealth of behavioral and neurophysiological evidence to support such a claim. The premise is that if there are in fact common neural correlates for action and perception, then action should directly influence perception and, conversely, perception should directly influence action and that this bi-directional relationship is instantaneous and automatic. A range of behavioral data on stimulus-response compatibility, observational learning, and short-term visuo-motor interaction exists that supports this hypothesis. These methods have been used to obtain observable information that indicates an automatic and bi-directional relationship between visual and motor interaction.

i. Automaticity

A range of behavioral studies has demonstrated that action and perception may be intimately tied to one another. A commonly used paradigm

involves a Serial Reaction Time (SRT) task originally used to examine implicit sequence learning (Nissen & Bullemer, 1987). Briefly, the task required participants to observe a series of asterisks presented in rapid succession on a computer screen and respond to the location of the asterisk with corresponding buttons. Embedded within the apparent random presentations were repeating sequences to which the participants would implicitly develop faster reaction times. Howard, Mutter, and Howard (1992) extended this work to observational learning and addressed an increasingly difficult question of whether performance on SRT tasks was perceptually-based or response-based learning. The response learning view holds that responses are necessary for learning, whereas the perceptually based view does not. Howard and colleagues assigned participants to two groups: a control group and a limited response group. The control group experienced a normal SRT task condition while the limited response group viewed the SRT task, but limited their responding. While the authors note that the observation group made significantly fewer errors, the reaction times for both groups increased significantly during the random block compared to the patterned blocks and were not significantly different from each other. Heyes and Foster (2002) found similar results when they asked participants to observe the key presses of another individual during an acquisition phase of a similar SRT task. In both cases, observation alone during an acquisition or practice phase can dramatically change response characteristics. In other words, pure observation can facilitate motor performance. Flanagan and Johnson (2003) extended these findings to visually

guided actions. They hypothesized that the characteristics of hand-eye coordination would be similar for both observation of and performance on a block-stacking task. Participants were asked to perform and observe a simple block-stacking task. The spatiotemporal relationships between eye gaze and hand movements were analyzed. The results showed that subject gaze was directed at contact points rather than on either the moving blocks or the hands. For both observation and execution, the fixations were directed towards the grasping site when picked up and landing site when placed. Specifically, participants fixated on each grasping and landing site shortly before the fingers grasped the block and before the block was placed, respectively. This pattern held for both the performance and observation conditions. This pattern of fixations illustrated predictive rather than reactive behavior. Given the same pattern occurs for both performance and observation, these results support a direct relationship for visuo-motor interaction predicted by Direct Mapping. Further, additional work on effector-dependent learning provided supplementary evidence in favor of Direct Mapping (Bird & Heyes, 2005; Bird, Osman, Saggerson, & Heyes, 2005; Osman, Bird, & Heyes, 2005). Effector-dependant learning is a form of motor learning in which the training of one set of muscles does not transfer or generalize to another set of muscles. This line of work stemmed from Heyes and Ray's associative learning theory (Heyes, 2001; Heyes & Ray, 2000). This model, consistent with Direct Mapping, suggests that visual information from a model can directly activate motor representations of the observer. Others have demonstrated that observational learning of motor

behavior is effector-dependent (Osman, et al., 2005). This line of work provides a strong indication that observational learning of motor movements is effector-dependent and that the action observation, rather than the sequence observation, is necessary for this type of learning. Taken together, these studies demonstrating an immediate and automatic relationship of visuo-motor interaction consistent with Direct Mapping.

ii. Bi-Directionality

Short-term interactions between perception and action have also received a fair amount of attention as a result of Prinz's Common Coding Approach (Prinz, 1997; Vogt & Thomaschke, 2007). The premise is that visuo-motor interaction should occur in both intentional and unintentional actions. This is often illustrated via Stimulus-Response Compatibility (Hommel & Prinz, 1997). Generally, specific characteristics of a visual display or model interrupt or interfere with motor characteristics of response execution. A common example of this kind of interference is seen in the classic Stroop Effect (Stroop, 1935). Here, participants respond to the color of ink in which color words are printed (e.g. the word "blue" printed in red ink). The semantic information of the word interferes with the participants' ability to respond leading to increased reaction times and more mistakes.

A more relevant example comes from Eidelberg (See Vogt & Thomaschke, 2007). Participants performed an action specified by a verbal command. Participants were given this verbal command while simultaneously shown a manual gesture by a model. The gesture performed by the model was

either consistent or inconsistent with the verbal command. When the observed gesture was not the same as the verbal command, participants could not avoid making mistakes even when specifically instructed to perform the verbal command. Subsequent studies investigated the motor aspect of stimulus-response compatibility. For example, Kornblum and Lee (1995) presented participants with an outline drawing of the left and right hands with the middle and index fingers extended. On each trial, a letter was presented on the tip of a finger on the image. The participants were responsible for responding to the letter by pressing a key that corresponded to each letter, regardless of the finger on which the letter appeared. When the cue and response dimensions were congruent, reaction times were faster than when they were incongruent. This form of visuo-motor priming was subsequently extended by Brass and colleagues (2000). The paradigm was tailored to use a video display depicting finger movements of the right and left index and middle fingers. Thus, the finger movements were the same as those used previously by Kornblum and Lee, but used a video model of the finger movements rather than an outline drawing. Again, average reaction times were faster when the observed movements were congruent with the corresponding subject response, replicating and extending the findings of Kornblum and Lee. Subsequent work extended stimulus-response compatibility to action imitation (2000). Participants were shown a video of a model's right hand either spreading or grasping. Simultaneous with the action of the model, the color scheme of the video was altered, modifying the hand color from the normal skin tone to either red or blue. Participants were instructed to

respond to the color change by either spreading or grasping their own right hand, ignoring the action of the model. EMG recordings were used to collect subject responses and to determine response onset. The relevant stimulus (color) was paired with an irrelevant stimulus (grasping or spreading). Note that the subject responses are functionally equivalent to the irrelevant dimension. Thus, on half the trials the displayed gesture was the same as, or congruent with the required subject response. The displayed gestures and required response were incongruent on the other 50% of trials. When the gesture corresponded with the response, reaction times were significantly shorter than when they did not correspond. This indicates that the type of hand gesture modeled on the video influenced the speed of the subject's response. To explore whether movement was necessary for this effect, the authors also explored end-state posture. Instead of the movement of grasping or spreading, participants were shown still images of the end-state of each action (a hand grasped, or spread). Again, only color was the relevant dimension. Similar modulation of reaction times resulted. Participants responded faster when the postured gesture was congruent with the appropriate response than when it was incongruent despite it not being the relevant dimension. This demonstrates that both movement and postures of motor execution can impact a viewer's subsequent motor action. While scant evidence exists that visuo-motor priming does not occur in visually guided actions (Cant, Westwood, Valyear, & Goodale, 2005), others have shown that these visuo-motor priming effects extend to object-oriented prehension actions

and may be restricted to biological motion (e.g. moving hand) as opposed to robotic maneuvers (Castiello, Lusher, Mari, Edwards, & Humphreys, 2002).

Others have also reported reliable results demonstrating motor-visual priming (Craighero, Bello, Fadiga, & Rizzolatti, 2002; Craighero, Fadiga, Rizzolatti, & Umiltà, 1998, 1999). Craighero and associates (1998) presented participants with a white fixation followed by a 'go' signal (red fixation). The go signal prompted the subject to reach for a small bar that was directly in front of them. Simply, the subject would be made aware of the orientation of a rectangular bar before the trial began. Accordingly, the participants were instructed to prepare the related motor movement necessary to grasp the object. A subsequent visual prime (an image of a rectangle) would either be congruent or incongruent with the orientation of the prepared motor act. This design was intended to determine if the visual prime would impact the prepared motor movement. Reaction times were faster on congruent than incongruent trials when the prime was presented 100 ms prior to the "go" signal. The only explanation for this difference in reaction time is that the congruent prime is reinforcing the motor response whereas the incongruent prime is interfering with the motor response. Similar results were reported when extending this design using additional degrees of rotation and mirror images of a hand grasping the bar rather than rectangles for the prime (Craighero, et al., 2002; Vogt, Taylor, & Hopkins, 2003).

Several studies using SRT tasks and effector-dependent learning demonstrated that visuo-motor interaction is immediate and automatic. In

addition Stimulus-Response Compatibility paradigms investigating short-term visuo-motor interaction provided strong evidence that visual perception can both interfere and facilitate motor performance. Similar results have provided a strong indication that motor preparation interferes with the subsequent reaction to a visual signal. Collectively, this automatic and bi-directional relationship for visuo-motor interaction is a strong indication that common neural substrates may exist between action and observation. Recently, neuroimaging and neurophysiological studies, complimentary to the work on Mirror Neurons, have sought to understand the neural basis of these mechanisms.

c. Electrophysiology and Neuroimaging

Mirror neurons were first discovered by happenstance in the early 1990s (di Pellegrino, et al., 1992). Prior to the subsequent reporting of these mirror properties (Gallese, et al., 1996; Giacomo Rizzolatti, Fadiga, Gallese, et al., 1996), those same researchers made an attempt to identify a similar matching system in humans (Fadiga, et al., 1995). Since that time, much attention has been devoted to discovering a MNS in the human brain (Buccino, et al., 2001; Buccino, Binkofski, & Riggio, 2004; Buccino, Lui, et al., 2004; Buccino & Riggio, 2006; Buccino, Solodkin, & Small, 2006; Buccino, Vogt, et al., 2004; Kilner, Neal, Weiskopf, Friston, & Frith, 2009; Giacomo Rizzolatti & Craighero, 2004; Giacomo Rizzolatti, Craighero, & Fadiga, 2002; Giacomo Rizzolatti, et al., 2001; Giacomo Rizzolatti, Fogassi, & Gallese, 2008; Vogt & Thomaschke, 2007; Wilson & Knoblich, 2005). A number of researchers have used a range of electrophysiological and neuroimaging techniques including EEG, PET, fMRI,

Magneto encephalography (MEG), and Transcranial Magnetic Stimulation (TMS). Fadiga, et al. (1995) used TMS and measured motor potentials at the wrist and fingers. The experiment was based on the idea that if observation of motor activity activates similar premotor areas in the human brain, then this should augment the motor evoked potentials elicited by the TMS. Specifically, the activity of the targeted motor areas was enhanced by the observation of motor movements. More specifically, the pattern of activation during observation was remarkably similar to the pattern of muscle activity during the execution of those same actions. This line of work was replicated by Strafella and Paus (2000) and extended by Gangitano, Mottaghy, and Pascual-Leon (2001). Strafella and Paus (2000) used a double-pulse technique to stimulate the left motor cortex. They reported that the activation of the motor areas is significantly modified by the observation of action performed by others. Gangitano, Mottaghy, and Pascual-Leone (2001), using a model performing a finger-to-thumb grasping motion as stimuli, reported that the amplitude of the motor potentials elicited by TMS were modulated by the gap between the finger and thumb across time.

Another early indication that motor observation may share common neural networks with motor execution comes from a few studies that investigated mu suppression (Cochin, Barthelemy, Roux, & Martineau, 1999; Gastaut & Bert, 1954). The mu rhythm is an EEG rhythm encompassed in the alpha range (8-12 Hz). It is recorded from the scalp over the primary motor cortex with maximal amplitude during rest. It is strongly suppressed during the execution of motor actions and is thought to reflect the synchronized discharge of cortical neurons of

the motor cortex and may reflect processes involved in visuomotor integration (Pineda, 2005). Gastaut and Bert (1954) reported a suppression of the mu rhythm in participants when they watched a video depicting human motor actions (e.g. cycling, boxing). They reported that this rhythm was blocked when a subject would change his or her posture and, more interestingly, “it also disappeared when the subject identifies himself with an active person represented on the screen” even when there is no observable change in posture (pg. 439). This work was supported by more recent work using modern technology (Cochin, et al., 1999).

More recent investigations have used MEG (Hari, et al., 1998; Nishitani & Hari, 2000), PET (Decety, Chaminade, Grezes, & Meltzoff, 2002; Decety, et al., 1997; Giacomo Rizzolatti, Fadiga, Matelli, et al., 1996), and fMRI (Buccino, et al., 2001; Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008; Iacoboni, et al., 1999; Kilner, et al., 2009). These methods were used to localize the areas involved in motor observation and execution. Specifically, brain regions were mapped using PET during different grasping, observation, and control conditions (Giacomo Rizzolatti, Fadiga, Matelli, et al., 1996). Analyses revealed significant differences between these conditions. Specifically, there was an increased level of activation for the grasping observation group compared to the group observing the objects alone. The regions showing this increased activation included the left inferotemporal cortex, and the caudal portion of the left inferior frontal gyrus. These results demonstrate that the left inferotemporal cortex and the left inferior

frontal gyrus might be the functional homologues of the monkey superior temporal sulcus and F5, respectively.

In another PET study, participants watched different action related videos depicting either pantomime actions (e.g. opening a bottle, hammering a nail) or physically related, but meaningless actions (Decety, et al., 1997). They instructed participants to either observe the video with the intent to imitate the action or to observe only with the intent to recognize the action later. The authors reported that the pattern of activation was dependent on both the nature of processing and the characteristics of the actions. Observing actions with the intent to recognize led to increased activation in memory related structures (i.e. right parahippocampal gyrus) while observing meaningful action with the intent to imitate activated structures involved in motor planning (i.e. supplementary motor area), voluntary action, and word generation (i.e. dorsolateral prefrontal cortex).

Others, using fMRI, examined strict observation versus imitation of a motor act (Iacoboni, et al., 1999). Half the participants were instructed to observe only, while the other half were instructed to imitate the observed action. The imitation trials showed significantly higher signal intensity. The authors reported this effect in the frontal operculum, parietal operculum and anterior parietal region. It should be noted that the left frontal operculum corresponds to Broca's area (BA 44), a homologous area to F5. Nishanti and Hari (2000) replicated these findings using MEG, and also reported similar activation in Brodman area 44. This provides a strong indication that homologous areas of the human brain to that of the primate MNS may be active during action observation.

Taken together, the presented evidence suggests the observation of action is directly related to the execution of action. A number of researchers employing a wide range of electrophysiological methods have demonstrated a strong connection between action observation and motor execution. These actions have ranged from object and non-object related actions using hands, arms, feet, and mouth. While many of these researchers endeavored to prove the existence of a human MNS, most simply confirmed the possibility that it exists in humans. These studies provide a strong indication that there may in fact be a human homolog of the MNS described in non-human primates. Unfortunately, definitive proof is still lacking. While several electrophysiological and brain imaging studies clearly indicate that common areas of the brain are involved in both action and observation of action, there is no definitive evidence that individual neurons located in these areas are endowed with mirror properties.

d. Section Summary

Prior to the identification of the MNS in non-human primates, a number of researchers proposed matching systems to account for human imitation and action understanding. A preeminent theory of action understanding, Direct Mapping, suggests that we understand the actions of others by mapping the visual representation of an observed action onto an existing motor representation of our own. In other words, action observation and motor execution share common neural substrates and that these commonalities are directly related to the degree to which these observed and executed action are similar. The

discovery of a subset of motor neurons in non-human primates that respond to the observation of similar hand and mouth motor action provided the earliest physiological evidence that such a system exists. While the existence of mirror neurons in non-human primates has been proven via single-cell recordings, their existence in humans is not yet definitive. A wealth of behavioral data demonstrated the visuomotor interactions were automatic and bi-directional. This gave additional support that common neural pathways exist between action observation and motor execution. With the advent of neuroimaging techniques, researchers explored new ways to investigate this issue. Using a range of methods, several researchers showed that observation of hand actions activate areas of the human brain corresponding to, or directly related to BA 44, the human homolog of area F5, and the supplementary motor area. These findings strongly suggest that in the absence of movement or motor preparation, the mere observation of motor action elicits neural responses in areas of the human brain that are homologous to the MNS described in primates. Researchers have directly assessed the merits of a Direct Mapping view of action understanding and the possible existence of a MNS in humans. While the evidence is compelling, it is not conclusive. As yet, there is no definitive proof that these areas contain legitimate mirror neurons.

III. MOTOR IMAGERY

Over the last 60 years, athletes, coaches and sport psychologists have used mental imagery to improve performance in hopes of attaining an advantage over competitors (Moran, 2002). Although the underlying mechanisms remained unclear, researchers using behavioral and physiological measures reported that task performance can be improved via mental imagery (Feltz & Landers, 1983). Until recently, the impact of mental imagery on task performance was a psychological phenomenon. One of the earliest empirical tests of mental imagery was an investigation of the connection between mental activities and the nervous and muscular systems (Jacobson, 1932). Since that time, more specific examinations of mental imagery have been carried out.

Specifically, researchers have been increasingly interested in determining if cognitive experiences and mental activities share properties of perceptual experiences and, more specifically, if these processes potentially share common neural correlates. More specifically, recent work in mental imagery demonstrates distinct dissociations between visual imagery, motor imagery, auditory imagery and olfactory imagery (Jeannerod, 1994, 1995; Jeannerod, et al., 1995; Kosslyn, Ganis, & Thompson, 2001; Kosslyn, et al., 1999; Kosslyn, Thompson, & Alpert, 1997; O'Craven & Kanwisher, 2000). Indeed, neuropsychological studies have demonstrated that visual imagery shares common neural correlates with visual perception

(Farah, 1988; Farah, Hammond, Levine, & Calvanio, 1988; Kosslyn, et al., 1999; Kosslyn, et al., 1997; O'Craven & Kanwisher, 2000). Others have demonstrated that auditory perception shares the same neural substrates as musical imagery (Kraemer, Macrae, Green, & Kelley, 2005; Tinti, Cornoldi, & Marschark, 1997; Zatorre, Halpern, Perry, Meyer, & Evans, 1996). Similar results have been reported for Olfactory Imagery (Bensafi, et al., 2003; Bensafi, Sobel, & Khan, 2007; Kosslyn, 2003; Stevenson & Case, 2005), and Tactile Imagery (Yoo, Freeman, McCarthy, & Jolesz, 2003). Reports on gustatory imagery are similar but inconclusive due to the extensive and interconnected nature of gustatory processing (Jones, Fontanini, & Katz, 2006; Kobayashi, et al., 2004).

Similarly, Johnson (1982) outlined a Functional Equivalence view that such a mechanism exists between motor imagery and movement. This view asserts that imagery and motor movement are functionally equivalent. This also predicts that, aside from muscle contraction, they are neurologically equivalent. While Johnson does not make a strict distinction between visual imagery and motor imagery, a Functional Equivalence view of motor imagery and movement still has merit and the model has received support elsewhere (Jeannerod, et al., 1995; Jeannerod & Frak, 1999; Kosslyn, et al., 2001). The following sections will introduce and discuss different lines of research that support the view that motor imagery and movement are functionally, and, with the exception of muscular activation, neurologically equivalent. These areas include behavioral measures, electrophysiological studies, and neuroimaging studies.

a. Behavioral Work

Sport Psychology abounds with anecdotal and empirical evidence of the facilitative effect of mental practice on task performance. As early as the 1980s, hundreds of studies investigated the impact of mental practice on athletic performance (Feltz & Landers, 1983). Although they do not propose that mental practice directly involves motor elements, the use of imagery to enhance athletic performance was still intensively investigated (Callow & Hardy, 2004; Cooper, Tindall-Ford, Chandler, & Sweller, 2001; Cumming & Hall, 2002; Cumming, Hall, Harwood, & Gammage, 2002; Driskell, Copper, & Moran, 1994; Moran, 2002; Ram, Riggs, Skaling, Landers, & McCullagh, 2007; Short, Tenute, & Feltz, 2005; Taylor & Shaw, 2002). The vast majority of evidence demonstrated that mental practice and imagery facilitate task performance. The earliest indication that imagery and motor execution may share common neural mechanism came from evidence that EMG activity during imagery was similar to the actual muscle activity during certain actions (Jacobson, 1932; Wehner, Vogt, & Stadler, 1984) & Berger and Hadley (1975). Despite these indications, sport psychologists often ignored the neural mechanisms underlying the effects of mental practice and mental imagery.

Others related the similarities of the timing of real and mentally represented actions (Decety, Jeannerod, & Prablanc, 1989; Kosslyn, Ball, & Reiser, 1978; Shepard & Metzler, 1971). Such investigations have included mental scanning (Kosslyn, et al., 1978) and mental rotation of 3-D objects (Shepard & Metzler, 1971). In these cases, the time it takes to mentally scan a

scene, or mentally rotate an object is remarkably similar to the time it takes to actually perform those actions. However, these researchers were not drawing a distinction between visual imagery and motor imagery. Mentally scanning a scene and mentally rotating an object do not necessarily involve imagined motor action. It has been proposed that visual imagery and motor imagery are neurally dissociable processes (Jeannerod, 1994; Jeannerod & Frak, 1999; Sirigu & Duhamel, 2001).

Some have explicitly defined a distinction between traditional visual imagery and motor imagery as well as a distinction between first-person motor imagery and third-person mental imagery (Sirigu & Duhamel, 2001). Mentally represented walking is an example of first-person motor imagery (Decety, et al., 1989). Here, participants walked or imagined walking from a starting point to a target at various distances (5, 10, and 15 m). Time taken to imagine walking was nearly identical to actual walking time. Contemporary views of motor imagery are also referred to as motor ideation, motor simulation, or kinesthetic imagery.

Akin to the work in sport psychology, Mulder and colleagues (Theo Mulder, Zijlstra, Zijlstra, & Hochstenbach, 2004) examined the impact of motor imagery on improving task performance on a simple toe abduction movement. Participants were tested on their ability to abduct their big toe on their dominant foot. Participants were then characterized as those with 'zero' ability to perform the target action or those who could already perform the movement. Half of each group practiced the skill physically while the other half of each group practiced only mentally. Those who began the study with the ability to abduct their big toe

showed significant improvement from either physical or mental practice. The participants with no ability at the beginning only showed improvement from physical practice. This indicated that mental practice may be activating a motor representation for the target action, leading to better performance. The participants without an existing motor repertoire for the given action could not learn one via mental activation. Therefore, there could be no direct connection between motor imagery and a motor program. Thus, the behavioral work on motor imagery has led to a gradual redefinition of motor imagery, ultimately facilitating better research ultimately giving better credence to the possibility that motor imagery involves the same neural mechanisms as motor execution.

b. Motor Potentials and Motor Evoked Potentials

The term Motor Evoked Potential refers to two different electrophysiological components. The first involves recording electromyographic activity coupled with Transcranial Magnetic Stimulation. A number of studies using this technology have been discussed previously. The evoked muscular responses are referred to as "motor potentials" or "motor evoked potentials" because the muscle activity is elicited (or at least augmented) by the TMS. These motor evoked potentials are not to be confused with evoked potentials recorded from the scalp during motor movements. The latter are EEG components time-locked to repeated muscular contractions. Henceforth, the term Motor Evoked Potential will refer to the electromyographic activity elicited by TMS and Motor Potential will refer to the event-related potential recorded from the scalp.

Motor Potentials have been used since the 1960s to investigate motor activity and a contingent negative variation (Walter, Cooper, Aldridge, McCallum, & Winter, 1964) associated with motor planning and motor preparation (Deecke, Scheid, & Kornhuber, 1969; Gilden, Vaughan, & Costa, 1966; Kornhuber & Deecke, 1965; Vaughan, Costa, & Ritter, 1968). Recent work investigated the similarity of the Motor Potentials and motor evoked potentials elicited by motor execution, motor imagery, and motor suppression.

The speculation that common neural pathways may mediate both motor imagery and motor execution raised intriguing questions. Does the pattern of activity differ between execution and imagery, with particular interest in hemispheric differences due to the laterality of motor control? Does this laterality exist in imagery as well? Are the somatosensory and/or premotor cortices involved in motor imagery, in addition to the primary motor areas, as it is in motor execution? A number of researchers employing electrophysiological measures endeavored to answer these questions. Beisteiner and associates (Beisteiner, Hollinger, Lindinger, Lang, & Berthoz, 1995) required participants to either imagine or execute sequenced hand movements in response to different visual cues. The pattern of activity was remarkably similar between imagined and executed trials. Specifically, the authors reported that the unilateral trials led to similar contralateral changes in activation for both imagined and executed movements. To address the previous questions, it appears that neural activation during imagery is very similar to motor activation and as such is also largely lateralized. Subsequent studies would be necessary to determine if

somatosensory areas are involved during motor imagery.

While this line of work demonstrated that motor imagery may be neurologically similar to motor execution, this does not explain why the motor activity is not being initiated. Motor planning and motor inhibition also activate motor representations of movements but, like imagery, are not executed movements. It could be argued that motor imagery may be more similar to motor preparation or motor suppression than motor execution. The use of 'Go-NoGo' paradigms employed by a number of researchers demonstrated that execution and inhibition of motor responses to visual stimuli involve different components, therefore indicating that response inhibition differs neuronally from motor execution (Gemba & Sasaki, 1989, 1990; Jackson, Jackson, & Roberts, 1999; Nativ, Lazarus, Nativ, & Joseph, 1992). Further, Naito and Matsumura (1994) also used a Go-NoGo paradigm to compare motor execution to both motor imagery and motor suppression. The peak latency of a negative deflection observed on imagery trials was similar to movement trials (~ 260 ms) and distinctly different than NoGo trials (-215 ms). In addition, the peak amplitude was smaller for imagery trials (4.7 +/- 1.8 μ V) than NoGo trials (5.5 +/- 1.5 μ V) and corresponded with the amplitude of movement trials (4.4 +/- 1.7 μ V). Thus, the Motor Potentials of imagery trials are more characteristic of movement trials than NoGo trials. This indicates that motor imagery is neurologically similar to motor execution and distinctly different than motor suppression.

Kasai and colleagues (Kasai, Kawai, Kawanishi, & Yahagi, 1997) used motor evoked potentials to further investigate the differences between motor

imagery and motor suppression. In addition to the TMS, Kasai and colleagues also recorded the H-reflex. The H-reflex is an electrically induced muscle reflex similar to the mechanical stretch reflex (e.g. knee-jerk reflex). Together, these methods were used to investigate the role of the primary motor cortex and the spinal chord in motor imagery. While minor EMG activity was recorded during imagery trials, no difference in the H-reflex was found between rest and imagery conditions. This suggests that that absence of overt motor movements during imagery is likely mediated by the primary motor cortex rather than inhibitory signals mediated by the spinal chord.

c. Neuroimaging Studies

As seen with the work on Mirror Neurons, modern neuroimaging technology, predominantly fMRI, has provided considerable contribution to the understanding of the neural basis of motor imagery. While the previous two sections provided some evidence that motor execution and motor imagery may be functionally and neurologically similar, there is little hard evidence. It should be noted that modern views of motor imagery hold that overt motor movements, often measured by EMG activity, are absent during motor imagery trials. This is thought to control for any neural activation responsible for inadvertent muscle activation. Regrettably, completely eliminating EMG during imagery is quite difficult and nearly impossible for some participants. To circumvent this obstacle, many studies provide short training trials to ensure participants understand and are able to execute imagery trials with very little EMG activity and without motor movements. In some, but not all of these cases, trial-by-trial feedback is often

provided to the subject.

The earliest investigation using neuroimaging technology took measures of regional cerebral blood flow using PET (Ingvar & Philipson, 1977). Measures were taken during rest, motor imagery, and motor movements. Real and imagined movements involved the rhythmic opening and clinching of the right hand. While the present investigators did not control for overt movements during imagery, the results nevertheless suggested that different areas of the brain, rather than common areas, are involved in motor imagery and actual execution. This indicated that two separable mechanisms for motor execution and motor ideation. They reported that increases in blood flow during action were seen in the Rolandic areas, whereas increases during ideation were seen in frontal and temporal areas. This would seem to indicate that the mechanisms involved in motor ideation differ from those involved in motor movement.

However, a subsequent follow-up of this work suggested otherwise (Roland, Larsen, Lassen, & Skinhoj, 1980). Here, regional cerebral blood flow was measured during the same types of conditions: rest; motor planning; and motor execution. There were increases in blood flow in the contralateral primary motor area only during execution. In contrast, bilateral activation of the supplementary motor area was found for both motor planning and motor execution. Contrary to Ingvar and Philipson (1977), the supplementary motor area was shown to be involved in both motor execution and motor planning.

In more recent investigations, brain imaging has employed the use of event-related and time-resolved fMRI (Cunnington, Windischberger, & Moser,

2005; Leonardo, et al., 1995; Lotze, et al., 1999; Porro, Cettolo, Francescato, & Baraldi, 2000; Porro, et al., 1996; Rao, et al., 1993; Roth, et al., 1996; Sabbah, et al., 1995). Leonardo and colleagues (Leonardo, et al., 1995) tested participants with alternating periods of rest and rehearsal of a finger-to-thumb sequence. Rehearsal of this sequence was either real or imagined movement. This was one of the first studies that made an attempt to control EMG activity during imagery trials. The authors identified several regions of interest. These regions were defined as primary sensorimotor cortex ('sensorimotor' is an ambiguous descriptor for both the precentral and postcentral gyri), posterior parietal cortex, inferior parietal lobe, primary motor cortex, and premotor cortex. These areas were directly compared across the different conditions. Areas showing significant signal intensities from motor movements included the sensory/motor areas, posterior parietal areas and premotor cortex. Similar regions were activated by motor ideation including sensorimotor cortex and premotor cortex. These results replicated findings from previous work (Rao, et al., 1993).

While this is a strong indication that both motor movement and motor imagery are activating common motor areas, it leaves the question why the primary motor area was not showing increased activity, particularly during motor movements. Subsequent work, on the other hand, did find activation in the contralateral primary motor cortex (Roth, et al., 1996). Motor execution led to significant activation of the contralateral primary motor cortex, primary sensorimotor cortex and premotor cortex. Mental simulation of this movement also led to a significant activation of the contralateral primary motor cortex and

premotor cortex, but to a lesser extent than during movement trials. Activation of the sensorimotor cortex during the movement condition was not shown in imagery. This was also the first indication that the primary motor cortex, often associated with movement conditions, was also activated by imagery conditions.

Subsequent work has replicated these findings (Lotze, et al., 1999; Porro, et al., 2000; Porro, et al., 1996), namely, the activation of the contralateral primary motor cortex during imagery. A critical difference between this and prior work was the direct comparison to visual imagery. Visual imagery was considered a control condition to tease apart any activation during motor imagery that is characteristic of the imagery component rather than the motor component of the mental activity. The visual imagery condition required participants to mentally represent a familiar landscape. The experimenters gave specific instructions not to imagine themselves moving any part of the body, but to scan the scene and focus on particular objects within it. Similar movement and motor imagery conditions were used, each of which included real or imagined sequential finger-to-thumb opposition movements. Different regions of interest were compared across conditions. The regions of interest included anterior and posterior portions of the precentral gyrus, and the postcentral gyrus (Porro, et al., 1996). Movement trials showed significant increases in activation in all areas compared to both motor imagery and visual imagery. Similarly, motor imagery, compared to visual imagery, also showed significant increases in mean activation levels in the anterior and posterior precentral gyrus, and postcentral gyrus. Follow up work also identified increased activity in the contralateral

premotor cortex and supplementary motor area, but to a lesser extent during the imagery trials (Porro, et al., 2000).

Lotze, and associates (1999) using a full brain scan rather than specific regions found comparable results. The contralateral primary motor and somatosensory cortices were found to be significantly activated along with weaker bilateral activation of the supplementary motor area during movement conditions. In addition, ipsilateral activation of the cerebellum was also significant. Imagery trials showed a stronger bilateral activation of the supplementary motor area, but weaker activation of the primary motor and somatosensory cortices.

While even the most recent work admits that the degree to which the neural substrates of motor imagery and motor performance overlap remains unclear (Hanakawa, Dimyan, & Hallett, 2008), there still exists strong evidence to suggest that imagined and executed movement activate similar motor areas, particularly the contralateral primary motor cortex (Lotze, et al., 1999; Porro, et al., 2000; Porro, et al., 1996; Roth, et al., 1996; Sabbah, et al., 1995) and premotor areas (Leonardo, et al., 1995; Rao, et al., 1993; Roth, et al., 1996). While these areas were commonly activated by motor imagery and motor execution, it is also quite clear the signal intensities were weaker for motor imagery than motor execution. This provides good groundwork for future research. Specifically, the evidence suggesting that the supplementary motor area, or the somatosensory cortex is involved in motor imagery is mixed.

d. Section Summary

The impact of mental imagery is well established and has been intensively investigated since the 1960s (Feltz & Landers, 1983; Richardson, 1967). Sport psychologists, coaches and athletes regularly used mental activities to improve performance. These activities included but are not limited to psychological preparation (i.e. getting psyched up), visual imagery and motor imagery. These activities were thought to physically and mentally prepare someone for athletic competition. However, the mechanisms by which these effects worked remained unknown.

After a number of behavioral studies examined mental imagery and motor execution, subsequent investigations of motor imagery were specific to imagined motor movements from a first-person perspective. Such investigations evidenced a possible neural connection between motor imagery and motor execution. Specifically, it was hypothesized that motor imagery and motor movements are functionally equivalent (Jeannerod, 1994; Jeannerod & Frak, 1999; Johnson, 1982; Kosslyn, et al., 2001).

As a result of this speculation, electrophysiological and neuroimaging techniques were employed to test this hypothesis. What can be gleaned from that work is that motor imagery is remarkably similar to motor performance. While it is not proven to be functionally and neurologically identical, the two activities do in fact share common neural pathways. It is clear that executed and imagined movements activate similar motor areas including the contralateral primary motor cortex and, likely, the premotor cortex. However, results indicating

bilateral activation of the supplementary motor area and a number of parietal areas including the somatosensory cortex are a bit more idiosyncratic. The roles of these areas in motor imagery and motor execution need to be further investigated. In addition, it should be noted that while common areas of activation are reported between motor imagery and execution, the mean activation levels are consistently weaker during imagined movements compared to those that are executed. This suggests that while common areas are stimulated, the degree to which they are activated is modulated by the task.

IV. CRITICAL ISSUES

Two bodies of literature were reviewed, each lending support to major, distinct theoretical models involving human motor control. Direct Mapping offers a neurological explanation to account for observational learning, action understanding, and human imitation. The Functional Equivalence model of motor imagery proposes that motor execution and motor imagery are functionally equivalent, thus offering a neurological explanation for the relative impact of motor imagery on motor performance. In each case, the models suggest clear predictions that common neural pathways exist for multiple motor-related functions. Direct Mapping suggests that we understand the actions of others by mapping the visual representation of an observed action onto an existing motor representation of our own. Thus, neural mechanisms responsible for motor execution are also involved in action observation. Similarly, the Functional Equivalence model of motor imagery suggests that motor imagery and motor execution are functionally the same. Underlying this assumption is the implication that the neural mechanisms responsible for motor execution are also activated during motor imagery. Despite the apparent similarities and the relationship with motor execution, these two perspectives are investigated largely independent of each other. Each line of work serves to elucidate a number of questions and predictions concerning these models. Despite the apparent differences in these fields of work, the content is not all that dissimilar, each

drawing connections to the neural substrates of motor execution. While the two fields progressed largely independent of each other, the majority of the methods are common between them, often reporting comparable results. A comparison of these two bodies of literature reveals a number of interesting commonalities; most notably are the motor related areas of the brain reported to be involved in these activities. These areas include the frontal operculum (BA 44), dorsolateral prefrontal cortex (BA 45), primary motor cortex (M1) including Rolandic areas, the premotor cortex (BA 6) including the supplementary motor area (SMA), the somatosensory cortex (S1) and other inferior portions of the parietal lobe.

While some areas have been strictly associated with action observation, and others with motor imagery, many are directly related to motor execution. Specifically, the SMA, often associated with motor planning and execution has been implicated to some degree in both motor observation and motor imagery. Unfortunately, few researchers have addressed both motor imagery and motor observation in concert. It is reasonable to hypothesize that even if similar activation occurs, the sequence in which these areas are activated may differ between these motor related processes. In short, despite the wealth of evidence supporting both Direct Mapping and Functional Equivalence, the degree to which the processes outlined by these models and the related brain areas overlap remains unsettled. Even if these activities lead to activation of similar motor areas of the brain, it is unclear if these areas are activated in the same sequence and order. In other words, the manner and extent to which motor observation and motor imagery compare is still largely overlooked. Such a comparison would

benefit both fields tremendously. The major goal of the present project is to further investigate both the spatial and temporal characteristics of motor observation and motor imagery in concert.

The first major aim of this project examines the spatial characteristics of the neurological differences and similarities between motor observation, motor performance and motor imagery. A number of neuroimaging studies have established that several brain areas are involved in both motor observation and motor execution. These areas include portions of the inferior frontal gyrus and the inferior parietal lobule (Buccino, et al., 2001; Buccino, Binkofski, et al., 2004; Iacoboni, et al., 1999; Nishitani & Hari, 2000; Giacomo Rizzolatti, Fadiga, Matelli, et al., 1996). These areas correspond nicely with F5 and PF of the MNS identified in non-human primates. However, only mixed results exist suggesting that other motor-related areas, such as premotor areas, M1, or S1 are involved in motor observation (Buccino, et al., 2001; Cochin, Barthelemy, Lejeune, Roux, & Martineau, 1998; Cochin, et al., 1999; Decety, et al., 1997). Still, both PET (Decety, et al., 1997; Decety, et al., 1994) and fMRI studies (Buccino, et al., 2001) indicated that the SMA might also be involved in motor observation. With these considerations in mind, it can be hypothesized that the SMA, along with the inferior frontal and angular gyri are responsive to motor observation, while M1 and S1 are not.

Furthermore, several neuroimaging studies also assessed the role of motor-related brain areas involved in motor imagery. The earliest work using Single Photon Emission Computed Tomography provided only conflicting reports

(Ingvar & Philipson, 1977; Roland, et al., 1980). Since that time, more recent investigations, primarily using fMRI, have reported more consistent conclusions. Strong evidence demonstrates that motor imagery involves contralateral activation of M1 and S1 as well as activation of the SMA (Leonardo, et al., 1995; Lotze, et al., 1999; Naito, Roland, & Ehrsson, 2002; Porro, et al., 2000; Porro, et al., 1996; Roth, et al., 1996; Sabbah, et al., 1995). However, the signal intensity of the activation of the SMA is characteristically weaker than the activation of M1 and S1. Based on the available evidence, the following hypotheses are advanced:

Hypothesis 1: All three motor-related experimental conditions (Motor Observation, Motor Performance, and Motor Imagery) will involve activation of the SMA compared to a non-motor related control (Visual Imagery). In addition, the activation of the SMA will be weaker in both Motor Observation and Motor Imagery compared to Motor Performance

Hypothesis 2: Motor Performance and Motor Imagery will lead to activation of the contralateral primary motor and somatosensory cortices compared to both Motor Observation and Control.

Hypothesis 3: Motor Performance and Motor Observation will show activation in the posterior portion of the inferior frontal gyrus (BA 44) and the angular gyrus (BA 39), predominantly in the left hemisphere.

The second major aim of the present project is to explore the temporal characteristics of these processes. The coordination among these areas across these different motor functions has been almost entirely ignored. Currently,

Movement-Related Potentials are characterized by both pre- and post-movement components (Brunia & van den Bosch, 1984; Kornhuber & Deecke, 1965; Vaughan, et al., 1968). The earliest pre-movement component is the *Bereitschaftspotential* (Kornhuber & Deecke, 1965). This preparatory potential is a slow negative shift that begins as early as 2 seconds prior to movement. It is also referred to as the *readiness potential*, or the N1. In some cases, it is separated into two separate components: an early bilateral negativity and a later lateralized negativity. A lateralized positive wave (P1) known as the Pre-Movement Positivity follows the readiness potential. Lastly, the Motor Potential, or N2, is a negativity recorded over the contralateral primary motor cortex that occurs about 60 ms prior to movement.

Post-movement potentials occur simultaneously with movement execution and the characteristics of these components tend to be task specific (e.g. goal-directed, movement monitoring, directed attention, relaxation potentials). It should be noted that the N1, P1, and N2 components just described should not be confused with the N1, P1, and N2 components recorded from visual and auditory event-related potentials. The eliciting events, latencies, amplitudes and topographical distributions of visually and auditorally evoked potentials are distinctly different than the motor-related components just described. To be clear, all references to N1, P1, and N2 will, henceforth, refer only to the motor related components.

Few studies exploring the human motor potential have compared motor movement to motor inhibition. These studies use Go-NoGo paradigms (Gemba

& Sasaki, 1989, 1990; Jackson, et al., 1999; Naito & Matsumura, 1994; Nativ, et al., 1992). In addition, few directly compared motor execution to motor imagery (Beisteiner, et al., 1995; Caldara, et al., 2004; Naito & Matsumura, 1994; Pfurtscheller & Neuper, 1997; Romero, Lacourse, Lawrence, Schandler, & Cohen, 2000). Taken together, much of the evidence suggests that motor imagery is distinctly different than motor inhibition and more similar to motor execution. Specifically, these investigations reported that motor imagery and motor execution share similar ERP components, reflecting comparable neural activity in S1 (Pfurtscheller & Neuper, 1997), Premotor areas (Romero, et al., 2000), and M1 (Caldara, et al., 2004). However, most agree that the component amplitudes are smaller for motor imagery than motor execution (Beisteiner, et al., 1995; Naito & Matsumura, 1994).

Others employing EEG have also compared motor execution to motor observation (Babiloni, et al., 2002; Babiloni, Carducci, et al., 2003; Babiloni, Del Percio, et al., 2003; Calmels, Holmes, Jarry, Hars, et al., 2006; Holz, Doppelmayr, Klimesch, & Sauseng, 2008). While the series of studies by Babiloni and colleagues (Babiloni, et al., 2002; Babiloni, Carducci, et al., 2003; Babiloni, Del Percio, et al., 2003) report conflicting accounts, others have provided good evidence indicating that motor observation and motor performance share similar ERP components (Calmels, Holmes, Jarry, Leveque, et al., 2006; Holz, et al., 2008).

Further, Holz and associates (2008), in contrast to the majority of neuroimaging work, reported activation of M1 and premotor areas including the

SMA during motor observation. This unique difference raises the question of whether the primary motor cortex is involved in motor observation. With this in mind, the following three additional hypotheses are also presented.

Hypothesis 4: Because the SMA may be activated in all three experimental conditions (Hypothesis 1), there should be a comparable N1 component in all three experimental conditions compared to the control. In addition, the amplitude of the N1 is also likely to be larger for Motor Performance compared to both Motor Imagery and Motor Observation. Further, all three experimental conditions will also share similar latencies of the N1 component.

Hypothesis 5: Similarly, contralateral sensorimotor areas, thought to be responsible for the Premovement Positivity should result in a comparable P1 during Motor Performance and Motor Imagery, and be distinctly different than both Motor Observation and the control. While Holz and colleagues (2008) reported activation of M1 during Motor Observation, this is in stark contrast to the majority of electrophysiological and neuroimaging work investigating the neural substrates of motor observation.

Hypothesis 6: Lastly, the N2 is associated with the initiation and accompaniment of movement, respectively. As such, the presence of these components will be restricted to Motor Performance and will be absent in both the Motor Imagery and Motor Observation conditions.

V. METHODS

a. Participants

Twenty-Seven adult volunteers between 18 and 25 years of age participated. Participants were recruited from the undergraduate student population at the University of Louisville. They were recruited through online advertisements and bulletin boards. Each participant was paid \$10.00 for participation. All Participants provided written informed consent prior to participation. An estimated effect size of 0.35 and a power estimate of 0.8 were used to calculate an expected sample size of 8. Similar estimates are cited within the literature (Romero, et al., 2000). This standard was met for both male and female participants. The study was approved by the University of Louisville's Institutional Review Board. Participant confidentiality was also maintained according to the standards set forth by that Board.

Screening Procedures:

All Participants had normal or corrected to normal vision and were screened for history of neurological disorders, head injury, and medications that affect the EEG response. The Neuropsychological Screening Questionnaire involved 8 self-reported yes-or-no questions concerning Neuropsychological History. In addition, all participants completed the Edinberg Handedness Inventory (Oldfield, 1971) to assess hand preferences. This scale ranges from +1.0 (strongly right-handed) to -1.0 (strongly left-handed). Further, a generic 4-

point, Likert Type rating scale was used to assess the participants' ability to perform mental and motor imagery required by the task (1 = always performed imagery, 2 = often performed, 3 = rarely performed, 4 = never performed). One participant was omitted due to a history of head injury. Five (5) were omitted due to various prescription medications shown to disrupt recordings of ongoing EEG. Three (3) participants were omitted due to low Imagery Ratings exceeding a value of 2.0 that indicated a persistent inability to perform either the mental imagery or motor imagery required during the task.

Participant Characteristics:

Eighteen adult participants (10 Female, Mean Age = 22.8 years) were included in the analyses. All participants were strongly right-handed (LQ = 74.43, St. Dev = 20.7). Mean imagery ratings for Motor Imagery and Visual Imagery were 1.40 (.339) and 1.29 (.3), respectively.

b. Procedure

Stimuli:

The stimuli consisted of a fixation point (a small plus sign in the center of a computer monitor), a neutral image and two target images. All images were gray-scale images of a human right hand situated above two small objects. The hand was presented from a third-person perspective. The two objects were a baseball-sized sphere and a small marble. The *Neutral Image* depicted the hand in a neutral and relaxed posture, ambiguously located above and in between the two objects. See Figure 2.

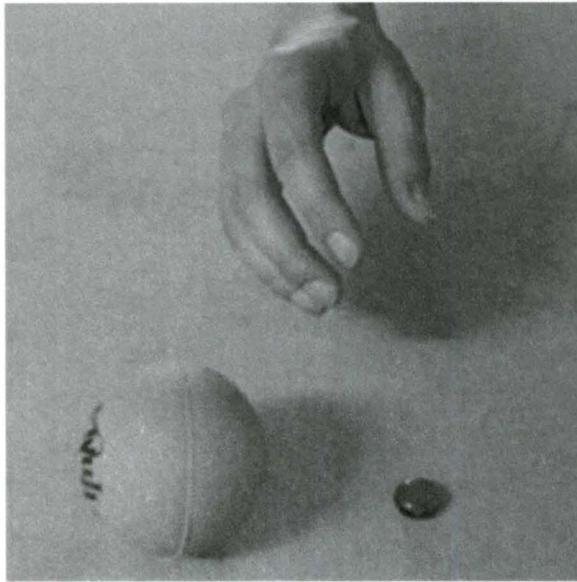


Figure 2. The Neutral Image depicting a hand in a neutral position presented from a third-person perspective.

The *Target Image* depicted the hand grasping one of the two objects. The perspective of the image is important, as it represents an action performed by another person. Therefore it is presented from a third-person perspective. Further, the difference in target images (which object is grasped) requires two different types of goal directed, object-related actions. One requires whole hand prehension, while the other requires more precise finger-to-thumb opposition. See Figure 3.

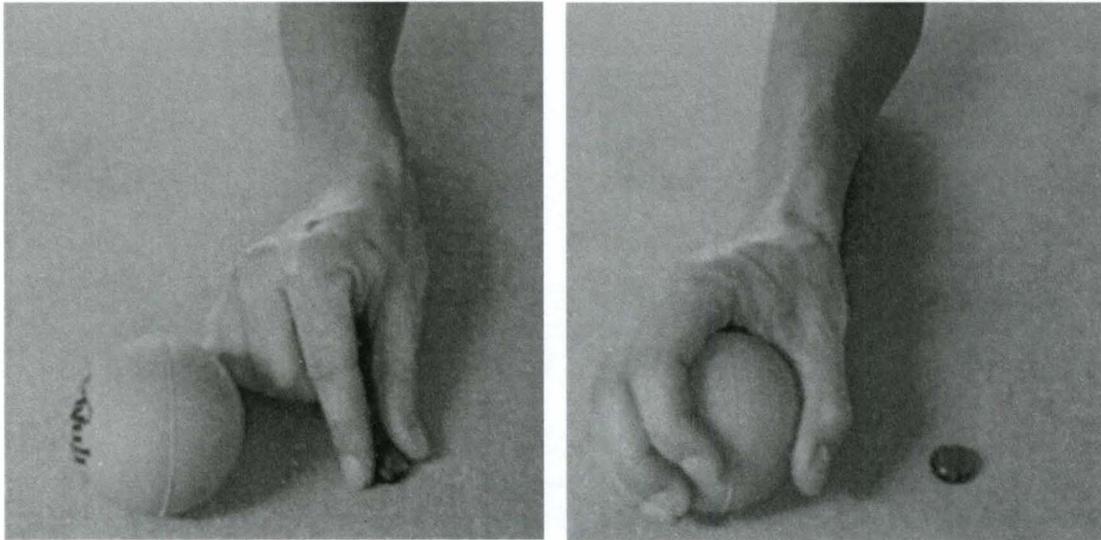


Figure 3. The Target Images; The left image depicts a hand using a finger-to-thumb motion to grasp the marble while the right image depicts a hand using a whole-hand prehension to grasp the ball.

This is consistent with the tasks involved in the majority of the existing literature supporting both Direct Mapping and Functional Equivalence. In addition, having two separate and distinct images prevented the participant from anticipating the motor act and activating a motor program prior to the onset of the target stimulus. In addition, still images were chosen rather than a video presentation to ensure an abrupt onset of the stimulus needed to elicit the ERP. The need for a punctual stimulus is imperative.

Using a still image is a common and well-accepted alternative to movement-based stimuli. A number of studies have illustrated that still images depicting hand-actions are effective in motor-visual and visuo-motor priming effects (Castiello, et al., 2002; Craighero, et al., 2002; Vogt, et al., 2003).

Further, Sturmer, Aschersleben, and Prinz (2000) illustrated that images depicting end-state postures of hand related actions such as grasping were effective in producing visual and motor priming effects. The authors concluded that movement-based and state-based mechanisms correspond to process-oriented and result-oriented forms of imitation, respectively. Thus, state-based, result-oriented forms of imitation involve attempts to attain the same goal. This relates nicely to the distinction made between strictly and broadly congruent Mirror Neurons. The majority (~60%) of Mirror Neurons are classified as broadly congruent Mirror Neurons where the effective observed and effective executed actions correspond in terms of the type and the goal of the action. The authors ultimately concluded that goal-correspondence may be stronger than process-correspondence.

A few fMRI studies report that Mirror Neurons are also responsive to inferred action when the action itself cannot be seen directly. This effect occurred using partially occluded actions (Umiltà, et al., 2001) and action-related sounds (Kohler, et al., 2002). For the present project, an image depicting a hand in a neutral state precedes the target image that illustrates the grasping action. Taken together, the two images give the impression or illusion of motion allowing the observers to infer the action taken by the model. While the imperative stimuli are identical, the intention of the observer is the key manipulation. Decety (1997) demonstrated that the intention of the observer leads to differential activation. Participants instructed to observe actions with the intention of recalling them later showed activation of memory related structures, where as participants instructed

to observe with the intent to imitate showed activation of areas related to motor planning. In the present study, participants observed the stimuli with different intentions: Motor Observation, Motor Performance, Motor Imagery, and Visual Imagery. These different conditions are described in the next section.

Task:

Participants sat in a dimly lit room. Stimuli were presented on a Dell 17" LCD computer monitor positioned 1 meter directly in front of and with the center of the screen at eye-level to the participant. Participants were instructed to sit as still as possible and to position the head and body comfortably. The use of a chin rest ensured limited movement of the head and shoulders by the participant. Any such movement could cause a physical distortion of the electrical signal. Each trial began with the fixation point (a plus [+] sign presented in the center of the screen), followed by the presentation of the *neutral image*. This image was presented for 1.0 second and was followed by a blank screen lasting for a variable interval (750 ms – 1250 ms). The variability in the interstimulus-interval reduced the likelihood of any preparatory responses, such as contingent negative variation or hesitation effects (Walter, et al., 1964). Following this interval, the target image was presented for 1.0 second. A blank screen replaced the *Target Image* and lasted long enough for the participant to complete the condition-specific behavior (approximately 500ms). The task flow is illustrated in Figure 4.

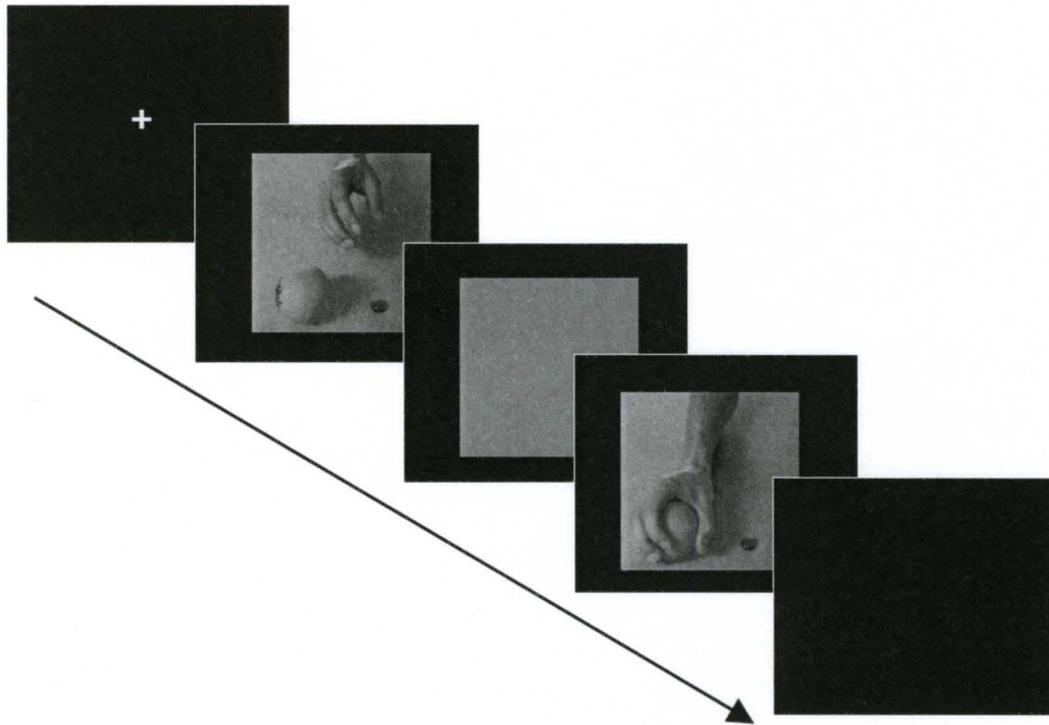


Figure 4. Representation of the presentation of the task images. Each trial began with the fixation point [+], followed by the Neutral Image, each presented for 1.0 second. The Neutral Image was followed by a blank gray square with similar dimensions and luminance as the neutral and target images. This blank image was presented with a variable inter-stimulus interval of 750 – 1250 ms. Subsequently, the Target Image presented for 1.0 second. The final blank screen was presented for an additional 500 ms allowing the participant to complete the condition specific task demands.

MOTOR OBSERVATION (MO): During Motor Observation trials, the participants were responsible for reporting which of the two actions (whole-hand grasping of the larger of the two objects, or precision grasping of the smaller object) the image depicted. Responses were made with right hand, using a 4-button response pad. Buttons 1 and 4 were used to collect responses and were counterbalanced across participants.

MOTOR PERFORMANCE (MP): During Motor Performance trials the participants were instructed to perform or imitate the action depicted in the image. This included reaching and grasping one of the two same objects. The objects were present and placed on the table 3 inches in front of the participant's right hand. A wrist pad served as a starting/resting position, allowing the participant to reach and grasp the objects without eye movements; otherwise, eye saccades would severely disrupt the EEG.

MOTOR IMAGERY (MI): During Motor Imagery trials the participants imagined performing the action depicted in the image. The imperative objects were presented as described in the MP condition.

VISUAL IMAGERY (VI): Imagining one of two landscape scenes based on the state of the target image served as the control condition. This was chosen as a control for both the motor-related and imagery-related aspects of the experimental conditions (Porro, et al., 1996). Example images, depicting either a desert or lake scene, were provided as examples at the beginning of the study and at the beginning of each block of control trials. See Figure 5.

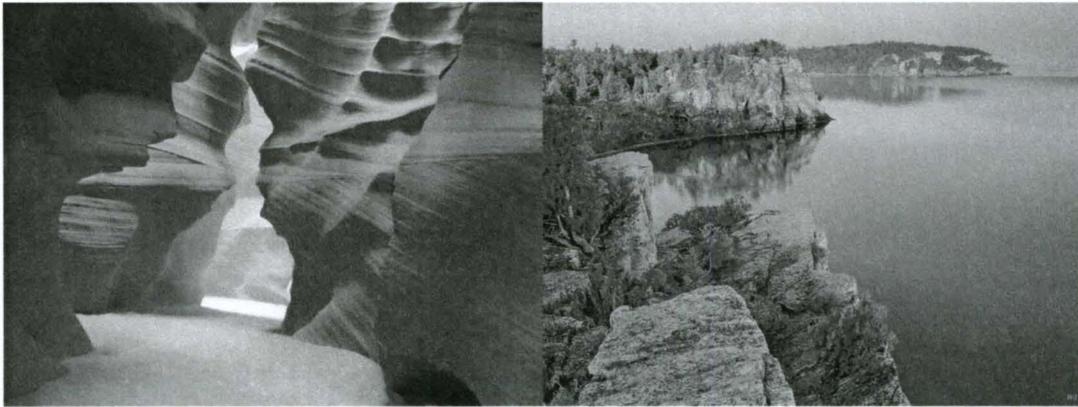


Figure 5. Visual Imagery Cues: Left image depicts a dry desert scene, intended to be in stark contrast in both content and color to the lake scene in the right image. The stark contrast between the images is intended to help facilitate visual imagery during the task.

The participants successfully completed 16 practice trials (4 trials of each condition) to familiarize themselves with the task. The participants then completed 200 experimental trials (50 of each condition). Trials were organized in 20 blocks of 10 trials of the same condition. Each block was comprised of five trials depicting whole-hand grasping and five depicting finger-to-thumb precision grip. The block order was organized in a Latin Square so that no condition would be repeated in succession. This also controlled for the order of presentation across participants. Stimulus presentation was controlled by E-Prime (Psychology Software Tools Inc, Pittsburg PA). E-Prime was also used to send a digital signal to two separate computers, each responsible for recording the ongoing EEG and EMG signals. This digital signal was used to time-lock the stimulus presentation to the ongoing recordings for later analysis.

Hardware and Software Setup:

Participants were fitted with two surface electrodes on the right forearm. Surface EMG was recorded from the Extensor Digitorum Communis and Flexor Digitorum Profundus of the forearm. The Extensor Digitorum Communis connects to tendons that extend into the second and third phalanges (forefinger and middle finger respectively). The Flexor Digitorum profundus also has tendons that run through the carpal tunnel and attach to the phalanges. The recordings from these two muscles provide a clear indication of any movement of the fingers for either flexion (i.e. grasping) or extension (i.e. spreading) of the hand. The electrodes were referenced to the upper forearm using two additional surface electrodes.

In addition to the surface electrodes on the arm, participants were fitted with a 256-electrode high-density hydrocel net (EGI, Eugene OR). Following standard procedures, the electrode net was soaked in a warm saline solution for approximately 10 minutes prior to application to ensure proper hydration of all electrodes. The saline solution is composed of 1.5 tablespoons of potassium chloride dissolved in one liter of deionized water with a drop of baby shampoo to help break up oils on the scalp. This solution was warmed for the participants' comfort. The net was then placed on the participant's scalp. The layout for these electrodes can be seen in Figure 6.

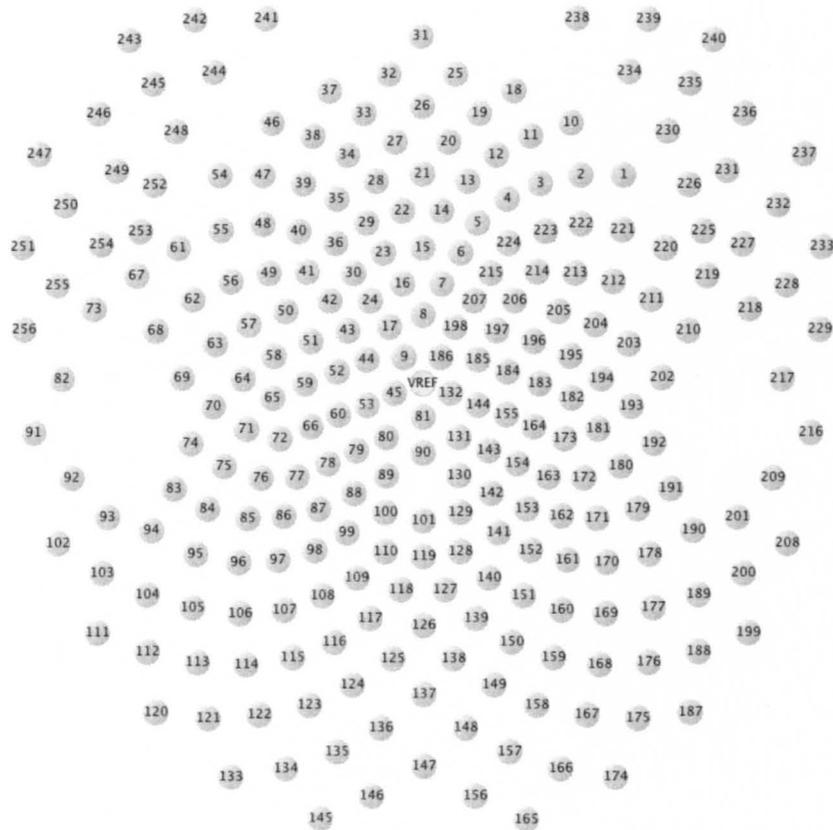


Figure 6. The 256-Electrode High Density Array Montage. Electrode E31 rests on the Nasion, just superior to the bridge of the nose. Sites E1, E10, E18, E25, E32, E37, E46 and E54 rest on the forehead. Sites E238 and E241 rest below the eyes and are used along with electrode sites E18 and E37, respectively, to detect eye blinks. Similarly, sites E230 and E248 are used to detect eye saccades. The VREF at the center is located at the vertex of the scalp and used as the reference during data acquisition. Later, the data are re-referenced to an average reference off-line. The empty spaces located laterally from the VREF are ear holes in the net structure. The most posterior (bottom of the image) electrode sites, E102, E111, E120, E133, E145, E165, E174, E187, E199, E208 and E216, are located along the base of the skull, just above the neckline.

Impedances were measured and reduced to 40 K Ω or less prior to the start of the task. The electrodes were initially referenced to Cz (vertex of scalp) during data acquisition and later re-referenced to an average reference off-line prior to analysis. Both the EEG and the EMG were each collected and recorded using separate Macintosh laptops running OSX 10.4. Specifically, the ongoing EEG was collected and recorded using a Macintosh Laptop running NetStation 4.3 (EGI, Eugene OR). The ongoing EEG was collected at a sampling rate of 250 Hz (one sample/4 milliseconds) using a digital high pass filter of 0.1 Hz and a low pas filter set to 100 Hz. The EMG data were also measured at a sampling rate of 250 HZ using a BIOPAC MP-150 system (BIOPAC Systems, Goleta, CA). The EMG data were then recorded on separate Macintosh laptop running *AcqKnowledge*, version 3.9.2.

Traditionally, ERP components elicited by visual and auditory stimuli are characterized by latencies and positive and negative deflections (peaks and valleys) that occur in response to the triggering stimulus. Thus, the latencies of these components refer to time intervals that occur immediately following stimulus onset. In contrast, early ERP studies investigating motor potentials often attempted to time-lock the ERP waveforms to the EMG onset, rather than the triggering stimulus (Mushiake, Inase, & Tanji, 1991; Nativ, et al., 1992; Okano & Tanji, 1987; Thickbroom & Mastaglia, 1985; Thickbroom, Mastaglia, Carroll, & Davies, 1985). This method allowed researchers to reference the pre- and post-movement potentials to the movement rather than the triggering stimulus. This was often necessitated by the fact that the movements were either self-paced or

set to a metronome-paced tone. Thus, a discrete triggering stimulus did not elicit an ERP in the traditional sense. The only event to which the evoked potentials could be tied was EMG onset. However, more recent investigations of visually triggered motor-related potentials examine the ERP waveforms that are time-locked to the triggering stimulus (Romero, et al., 2000; Senkfor, Van Petten, & Kutas, 2002; Thayer & Johnson, 2006). Because the motor movements of the present study were visually triggered, the ongoing signals were each time-locked to the onset of the Target stimuli described above using a digital signal originating from the E-Prime software responsible for stimulus presentation. This was achieved by placing an electronic marker at the time point within the ongoing EEG when the target image was presented. This digital flag was used to identify the time of stimulus onset. Therefore, the waveforms remained time-locked to onset of the Target Image.

Pre-Analysis Processing: EEG

In order to identify the discrete waveforms within the EEG, the data were subjected to a series of artifact correction procedures. These included applying filters, epoch segmentation, artifact correction, bad channel replacement, averaging, re-referencing, and baseline correction. The first of these is the application of a 30 Hz low-pass filter. The electroencephalogram is the collection of recorded voltage changes measured from various locations across the human scalp over a given time period. Fluctuations in these recordings are described or classified by their relative frequencies: Delta waves (~0.5 – 4 Hz), Theta waves

(~5-7 Hz), Alpha waves (8-12 Hz), Beta waves (13-30 Hz), and Gamma waves (~31-50 Hz). Thus, a 30 Hz low-pass filter is applied which allows all frequencies below 30 Hz to pass through the filter unaffected. Frequencies above 30 Hz are attenuated. This essentially filters out high frequency artifacts such as high frequency EMG and electrical interference.

Further, recorded voltage changes result from either endogenous or exogenous neural activity. The present investigation is particularly interested in the exogenous activity, that is, those fluctuations directly related to an eliciting event, a.k.a. evoked potentials. These ERP components are hidden within all the endogenous activity. However, these exogenous components of interest have a temporal relationship to the eliciting event, where as the endogenous, background activity does not. Therefore, averaging discrete EEG epochs together will cause the endogenous background activity to average out to near zero while the evoked responses that are temporally related will remain present, appearing as positive and negative deflections (Van Boxtel, 1998). Before averaging, these discrete segments in time need to be defined.

The continuous EEG, then, is segmented using an electronic marker into discrete segments ranging from 100 ms before the onset of the imperative stimulus to 1500 ms after the onset of the stimulus. Specifically, the filtered data was segmented into 1600 ms segments, ranging from 100 ms prior to the onset of the *Target Image* to 1500 ms after the onset of the *Target Image*. All continuous EEG outside of those 1600 ms segments is essentially cut out. These filtering and segmentation procedures were carried out using NetStation

version 4.3 (EGI, Eugene OR). The filtered and segmented data were exported, and all subsequent processing steps were carried out using the ERP PCA Toolkit (Dien, 2010).

Once the data were reduced to the specific epochs, those epochs were examined for various artifacts; extraneous variations in the waveforms. Such artifacts are caused by eye blinks, eye movements, and physical movements or simply by electrode sites with high impedance. Epochs or even individual channels with these various artifacts were identified and then were either corrected or removed from the average all together. Before checking individual epochs for movement artifacts, the data were examined for globally bad channels. Channels are checked statistically using correlations with each channel's direct neighbors and the reference channel. Simply, each channel is checked for very low correlations or perfect correlations amongst its direct neighbors, and for having a perfect correlation with the reference channel. Given the close proximity of the electrodes, those sites that are closer together theoretically should measure similar, but not identical, voltage changes. Channels further apart are theoretically measuring voltages generated by very different areas of the brain and therefore may not share similarities in electrical activity. As such, low correlation between two adjacent channels indicates that one or both channels may include extraneous noise or may have a poor signal. Thus, channels whose highest absolute correlation with its directly adjacent neighbors falls below 0.4 are considered globally bad and are excluded from further processing and analysis. Similarly, having a perfect correlation with either

the reference channel or a direct neighbor (indicating arching between channels) also generates a warning. These channels may also be removed from subsequent stages of processing and analysis.

Once these bad channels were identified, individual epochs were examined for eye blinks. The 100 ms pre-stimulus baseline is individually corrected to ensure the quality of the eye blink corrections. The technique in the present study for correcting eye blinks used an individually defined eye blink for each subject. Given the idiosyncratic nature of eye blinks, it was best to define each participant's eye blink, rather than comparing a generic blink template to all participants. This was achieved by running an Independent Component Analysis routine to identify trials where the upper eye channel pairs (specifically, sites E18 [Right Eye] and E37 [Left Eye]) covary with each other and negatively vary with the lower eye channels (sites E238 [Right Eye] and E241 [Left Eye] respectively). These are used to generate a blink template that will then be compared to the data set. The artifact detection routine runs an independent component analysis and compares these components to the blink template. Components that correlated highly with the blink template were subtracted trial-by-trial on an individual basis. Similarly, Horizontal Eye Movements are identified by a difference of greater than 55 μ V between horizontal eye channels, specifically channels E230 and E248.

In addition to blink correction, additional movement artifacts must also be corrected. A temporal principle component analysis was used to identify

components with highly variable minimum and maximum values with a difference greater than 200 μV . Any such activity identified by the PCA was removed.

Once these artifacts were removed from the data set individual trials were examined. This process is similar to marking channels globally bad, but was performed on individual trials rather than individual channels. Simply, segments defined with more than 30 μV difference at some point in the segment from the six directly adjacent channels, or having more than 100 μV difference between the minimum and maximum values are marked as bad segments. Trials with greater than 10% bad segments are marked bad and are removed from further analysis. Once all the movement artifacts were corrected and removed, the bad channels and bad trials were marked, and either corrected or removed. Individual trials marked bad are zeroed out, while bad channels are replaced using interpolating data from the good channels. The EPR PCA Toolkit generated a log file detailing each these corrections along with an Artifact Correction Plot representing the data segments during the course of these procedures. The plots from one participant are found in Figure 7 and the quality control measures behind these corrections are summarized in Table 2.

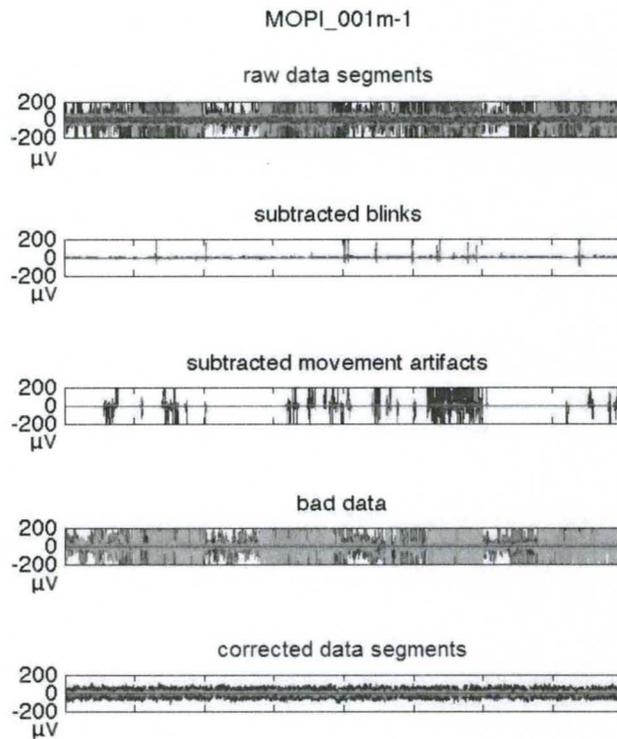


Figure 7. Artifact Correction Plots illustrating sequential artifact correction procedures for an individual participant. The scale on the vertical axis is in microvolts and only pictures data within +/- 200 microvolts. The first plot at the top shows the raw data segments, laid end to end, prior to any corrections. The second shows the eye blinks to be removed from the data. The next graph pictures the subtracted movement artifacts. The next graph shows data identified in bad channels and bad trials. The final graph is the resulting data set with all bad data removed from the segments.

Table 2. Artifact Removal Summary. *Trials* – number of trials per condition; *Blinks* – proportion of trials containing eye-blinks to be corrected; *Movement* – proportion of trials containing movement artifacts; *Bad Trials* – proportion of trials marked bad; *Bad Channels* – proportion of channels marked globally bad; *Noise* – Measure of noise obtained by inverting every other trial and then summed together to provide a measure of noise within trials.

	<u>Motor Observation</u>	<u>Motor Performance</u>	<u>Motor Imagery</u>	<u>Visual Imagery</u>
TRIALS	49.4444	48.6111	48.6111	49.8333
BLINKS	0.3575	0.3613	0.3614	0.3590
MOVEMENT	0.2530	0.2733	0.4416	0.2451
BAD TRIALS	0.0111	0.0091	0.0278	0.0033
BAD CHANNELS	0.0228	0.0241	0.0368	0.0237
NOISE	1.4011	1.2925	1.4701	1.3991

Following artifact correction, segments were averaged together, for each channel, participant, and condition. The final two steps before analysis include re-referencing the data to an average reference and baseline correction. During acquisition and the previously described artifact detection routines, the data were referenced to a single electrode located at the vertex of the scalp. All data were re-referenced to an average reference. Similarly, all data were also adjusted to a pre-stimulus onset period, so that all data points within the 100 ms baseline average out to zero.

Pre-Analysis Processing: EMG

Only minor processing steps were needed for the EMG. The raw electromyograms from the Extensor Digitorum Communis and Flexor Digitorum Profundus of the forearm were first filtered using a 15 Hz highpass filter. The filtered data were then converted to an Average Rectified Signal. Simply, this converts the raw electrical signal to the absolute value of the voltage changes being recorded. The reason for this conversion is that the signal activity from muscle contractions is oscillatory in nature, which results in a zero-mean Gaussian distribution. As such, when averaged together, the signals would theoretically average out to zero. Thus, using the absolute value of the voltage changes allows for data averaging. Analysis included measures of Maximum Voltage and Time of Maximum Voltage.

VI. RESULTS

Analysis 1: EMG

Measurements from two muscles were recorded across the four experimental conditions resulting in a 2 Muscle (extension, flexion) x 4 Condition (Observation, Performance, Imagery, Visual) design. These data were subjected to a Repeated Measures ANOVA. Sphericity was not assumed, and significance was tested using the Greenhouse-Geisser correction. Analysis of the maximum amplitude revealed a main effect for muscle, $F(1, 17)=44.725$, $p<0.001$, and for condition, $F(1.301, 22.114)=73.535$, $p<0.001$. The interaction was also significant, $F(1.968, 33.449)=26.585$, $p<0.001$. The analysis of the simple effects revealed significant differences between conditions for both flexion, $F(1.160, 19.723)=44.479$, $p<0.001$, and extension, $F(1.557, 26.461)=91.842$, $p<0.001$. Simple effects between muscles were also significant for Motor Observation, $F(1,17)=8.415$, $p<0.010$ (max Flexion =0.76; max Extension =1.0), and Motor Performance, $F(1,17)=51.51$, $p<0.001$ (max Flexion =2.0; max Extension =2.92). The Simple Effect of muscle for Motor Imagery, $F(1,17)=3.267$, $p=0.088$, was not significant (max Flexion =0.29; max Extension =0.40). Surprisingly, however, the Simple Effect of muscle for the control was also significant, $F(1,17)=9.737$, $p=0.006$ (max Flexion =0.25; max Extension =0.31). Follow-up comparisons indicated that MP was significantly higher than VI, $t=10.308$, $p<0.001$, MO was

significantly higher than VI, $t=8.397$, $p<0.001$, and MP was significantly higher than MO, $t=7.157$, $p<0.001$. Group means are presented in Table 3.

Table 3. Maximum Amplitude (StdDev), and marginal means for each condition as a function of muscle movement. Units in Microvolts; see text for details.

	Average Maximum Amplitude (StDev), By Condition Units in Microvolts, N=50				
	<u>Motor Observation</u>	<u>Motor Performance</u>	<u>Motor Imagery</u>	<u>Visual Imagery</u>	
Flexion	0.76(0.28)*	2.00 (0.97)*	0.29(.14)	0.25(0.06)	0.82(0.23)
Extension	1.00(0.40)*	2.92(0.87)*	0.40(0.39)	0.31(0.10)	1.16(0.25)
	0.88(0.30)	2.46(0.89)	0.34(0.26)	0.28(0.07)	

* Reached significance

Taken together, one can conclude that motor movements occur in motor performance and motor observation conditions and that there is a much greater activity in the extensor muscle than the flexor. The activity in the motor observation condition is significantly less than that during motor performance. This activity may simply be the result of preventing the wrist and fingers from resting on the buttons of the response pad. Thus, the minimal activity in MO is likely the result of the minor activity required to use the response pad whereas the movement in the motor performance condition is the result of the extension of the hand and forearm and grasping of the object. This becomes evident when graphing the mean activation for each muscle across the different conditions. (Figure 8). Ultimately, these data support the notion that executed movements requiring grasping occurs only during MP and is consistent with the demands of the experiment.

Average Maximum EMG Amplitude by Condition

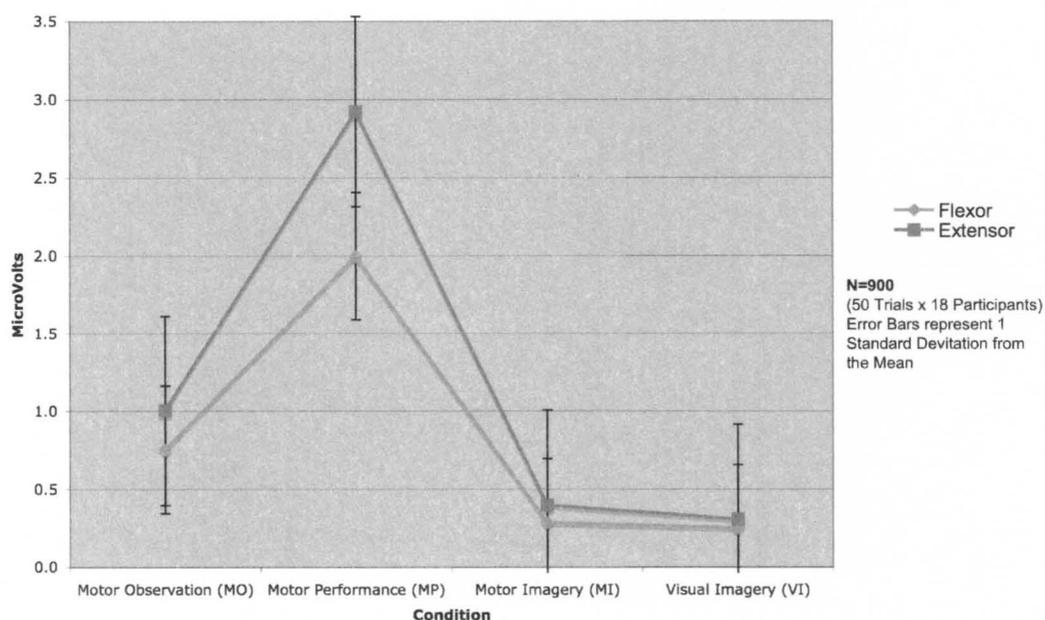


Figure 8. Mean activation of the extensor is significantly higher than mean activation of the flexor. Further, the graphed means illustrate the significantly greater activity in the MP.

In addition, measures of reaction time and maximal flexion were also calculated to determine the point at which the participants initiated and executed these movements. Average reaction time to execute movements, obtained from the reaction time of MO trials, was just over a one half second, $M=526.5(113.1)$ ms. This compares quite well the EMG data. Specifically, the time of the maximum amplitude for the extension occurred at 495.48 ms (134.3ms) after the onset of the target image. Initiation of movement occurs around 200 ms. See Figure 9.

Grand Average EMG

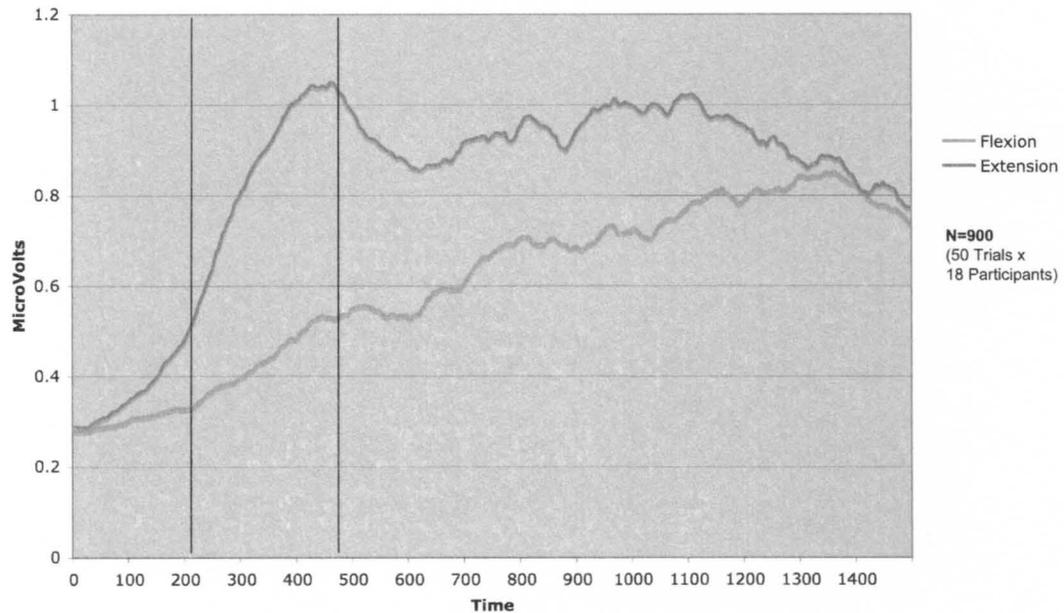


Figure 9. Average EMG during Motor Performance. Initiation of movement (first vertical black line) occurs at approximately 200 ms. The peak amplitude for the extensor muscle (second vertical black line) occurs at approximately 500ms. The initial increase in extension is followed by gradual increase in the flexor muscle before returning to a relaxed state. This is consistent with the task which requires the extending of the arm and opening of the hand followed by a gradual closing of the hand to grasp the object.

Lastly, the argument that similar motor areas of the cerebral cortex are involved in the three experimental conditions simply due to physical movement present in all three experimental conditions cannot be supported because real

muscular contractions necessary to reach and grasp objects were present in only the motor performance condition.

Analysis 2: ERPs-PCA

A Spatiotemporal Principal Components Analysis was used to reduce the data into manageable ERP components (Dien, Beal, & Berg, 2005; Dien & Frishkoff, 2005). These procedures were implemented using the ERP PCA Toolkit (Dien, 2010). Specifically, the first step is a Temporal PCA using Promax rotation (Kayser & Tenke, 2003) and the second is spatial, using an Infomax rotation. In the present analysis, the temporal PCA yielded 20 factors and the spatial PCA yielded an additional 5 factors for each temporal factor, resulting in 100 total components. The numbers of factors retained resulted from the use of a Scree Plot and a parallel test (Horn, 1965). This directly compares the Scree plot of the experimental data set to that from a random data set. The intersection of these two lines was used to determine the recommended number of factors to retain.

It was expected that specific components would correspond with motor related activity. Specifically, it was expected that the sequential PCA would reveal components that would correspond with peaks associated with motor evoked potentials. For example, a component corresponding with the N2 would likely have a negative polarity occurring just prior to 200 ms with maximal amplitude in the left hemisphere around C3 (E59). Theoretically, the motor related activity prior to the initiation of motor movement during Motor

Performance would be the generator for this component. However, none of the components obtained from the PCA correspond in time course or location that might reflect or be related to activation of motor related areas. The full list of factors can be found in Appendix 1.

While several components were identified that occur prior to and up to 200 ms, the spatial location at maximal amplitude is irregular and does not correspond to any motor related areas. Typically, components corresponding to possible motor related activity based on a-priori hypotheses would be subjected to ANOVAs. However, given the erratic nature of these components, any component meeting a minimum criterion 0.5% of the variance was subjected to ANOVAs to examine differences between conditions. Of the 100 PCA components, only 39 met this criterion, and only eight factors reached significance. These results are summarized in Table 4. The results of the analysis are not straightforward, as they are unrelated to any expected motor related activity.

Table 4. The eight significant PCA factors and electrode sites, latencies and the associated amplitudes across the four conditions.

Factor	Latency	Site	Level of Significance	Motor Imagery	Motor Observation	Motor Performance	Visual Imagery
TF01SF1	328	E128	4.97, p=0.048	3.350	4.490	4.270	3.890
TF01SF4	328	E145	6.08, p=.016	0.730	1.700	0.540	0.730
TF01SF5	328	E199	3.83, p=.084	0.200	0.240	-0.860	0.550
TF03SF3	884	E37	5.74, p=.02	0.950	-0.150	-0.250	0.210
TF04SF1	564	E175	4.68, p=.032	-0.330	-0.470	-0.720	0.750
TF04SF3	564	E18	20.13, p=.0015	0.810	-0.800	0.870	0.310
TF06SF2	212	E90	7.43, p=.011	-0.580	-0.830	-2.010	-0.380
TF13SF2	116	E119	4.4, p=.044	-0.140	-0.500	-1.230	-0.580

Robust ANOVA procedures using Welch-James Approximate Degrees of Freedom Solution, Trimmed Means, and Winsorized Variances (TWJt/c) were used to test for differences between conditions for each factor. Only three components occur early enough to be of interest, TF06SF2, TF13SF2, and TF01SF1. Of these three, the earliest occurs at 116 ms and is maximal in the parietal area. While this demonstrates an increased negativity during MP, $TWJt/c(3.0, 14.2)=4.4, p=.044$, this component occurs too early to be related to any sensory feedback. In addition, this demonstrates a negativity that corresponds with the P1, thus making this result difficult to reconcile. The next component occurs at 212 ms and is maximal at E90 – centrally located just posterior to Cz. This could be the result of activity in the somatosensory cortex in response to the initiation of movement. However, one would expect to find this activity in the contralateral hemisphere (left hemisphere) rather than centrally or bilaterally. The most interesting component reaching significance is the first spatial factor for the first temporal factor, $TWJt/c(3.0, 14.2)=4.97, p=0.048$. This component accounts for the most variance (7.5%) and is maximal at E128. While parietal activity would be expected, it would, again, only be expected in the left hemisphere. Further, the difference occurs between MI and MO, $TWJt/c(1.0, 17.0)=8.94, p=0.0085$, as there are no differences between MO, MP and VI, $TWJt/c(2.0, 15.1)=0.43, p=0.69$. In the end, these components do not lend any support to the spatial hypotheses.

The other 6 components reaching significance may share temporal similarities with the imagining or execution of grasping movements, but the

spatial distributions are very diffuse and not likely related to any motor activation. Specifically, areas at which these components are maximal include two different eye channels and electrode sites on the back of the scalp along the neckline. Taken together, it is highly unlikely that many of the components revealed by the sequential PCA share any relationship with any possible motor planning, motor movement, nor any sensory feedback. The majority of components resulting from the sequential PCA are inexplicable and additional analyses were necessary to further elucidate the characteristics of the EEG. Specifically, measures of specific peaks within the waveforms were obtained for each condition and compared. Namely, the N1, P1 and N2 described in previous sections. The peak latencies and peak amplitudes of the raw data were specifically compared for differences between the three experimental conditions and the control condition.

Analysis 3: ERPs-Windowed ANOVA

Windowed measures were examined by obtaining peak amplitude and peak latency measures at specific time points from selected electrode channels of interest. These measures were obtained using the ERP PCA Toolkit. Specifically, the N1, P1, N2, were examined by taking measures of peak latency and the relative peak amplitude within specific time windows from selected channel clusters. For example, measures of N1 were obtained from sites clustered around FCz. This cluster included seven electrode sites including FCz (E15) and the six adjacent channels – E6, E7, E14, E16, E22 and E23. Further,

measures of P1 and N2 were clustered around C3 (E59, and the six surrounding electrode sites - E51, E52, E58, E60, E65, and E66) and C4 (E183, and the six surrounding sites – E155, E164, E182, E184, E195 and E196). FCz is believed to measure activity from SMA and C3 and C4 are believed to record activity from the left and right hand area of M1, respectively (Homan, Herman, & Purdy, 1987; Jasper, 1958; Towle, et al., 1993). The N1 occurred between 40-80 ms. The P1 occurred between 80-150 ms. The N2 occurred between 150-200 ms. This time course corresponds nicely with the initiation of movement observed in the EMG. These peaks can be seen in Figure 10.

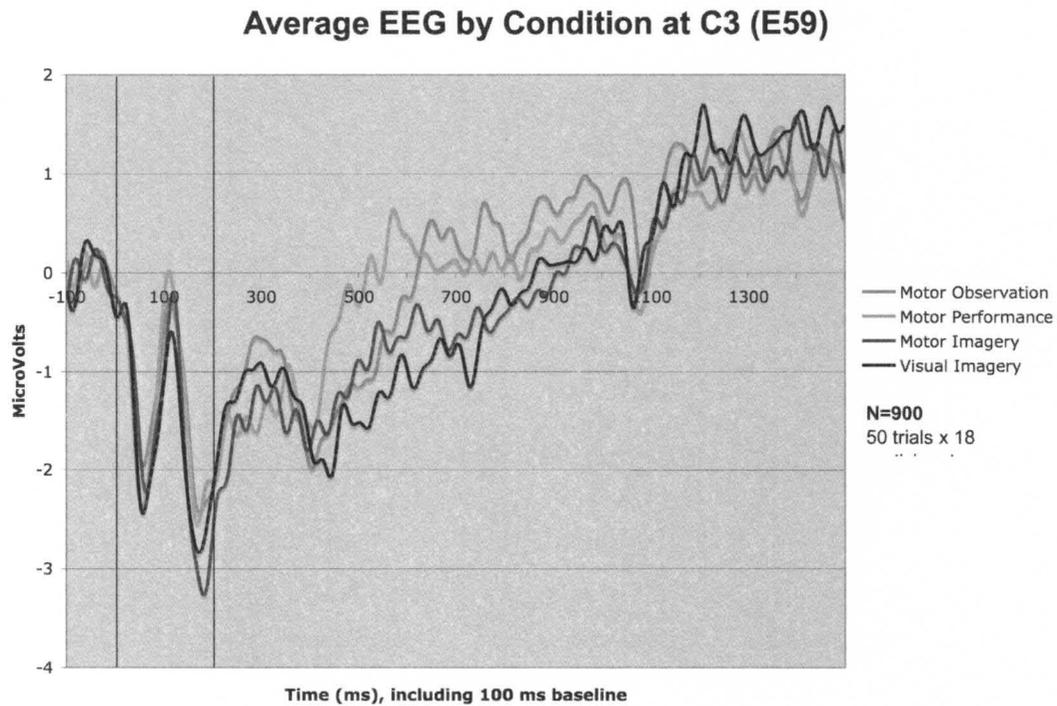


Figure 10. The average EEG waveforms across the four conditions recorded from C3. Vertical black lines indicate, moving chronologically, stimulus onset and EMG onset (~200ms). The N1, P1, and N2 peaks are apparent in all four conditions, and occur around 65ms, 110ms, and 180ms, respectively.

As previously noted, Robust ANOVA procedures using Welch-James Approximate Degrees of Freedom Solution, Trimmed Means, and Winsorized Variances (TWJt/c) were used. Here, measures were investigated for latency and amplitude differences between conditions for each peak at the described channels clusters. For the P1 and N2, an additional factor of hemisphere was also investigated. These specific analyses test temporal hypotheses 4, 5 and 6.

Latency measures were obtained first in order to better identify the window within which peak measures were to be obtained. While the hypotheses suggest differences in amplitude, or in some cases the presence or absence of peaks, there is little to no evidence to suggest that there should be differences in peak latencies. With this in mind, it should be noted that, theoretically, there should be no difference in peak latency where peaks should occur. Indeed, the first temporal hypothesis suggests a comparable N1, and thus, no differences in latency are expected. The first ANOVA indicated that there are no differences in the latencies at N1, TWJt/c (3.0, 14.2)=1.13, $p=0.39$ (MO=63.75, MP=61.78, MI=69.21, VI=66.41). Similar results were found for both the P1 and N2, measured around C3 and C4: P1 condition main effect, TWJt/c(3.0, 14.2)=0.38, $p=0.78$ (MO=110.46, MP=111.6, MI=112.51, VI=108.98); Hemisphere, TWJt/c(1.0, 17.0)=3.89, $p=0.067$ (Left=107.06, Right=114.72); ConditionXHemisphere interaction, TWJt/c(3.0, 14.2)=0.55, $p=0.70$; N2 condition main effect, TWJt/c (3.0, 14.2)=1.31, $p=0.34$ (MO=182.60, MP=179.83, MI=178.41, VI=175.24), Hemisphere, TWJt/c(3.0, 14.2)=0.23, $p=0.63$, and interaction, TWJt/c(3.0, 14.2)=0.17, $p=0.92$. While this is not theoretically interesting, it is of some empirical value as it demonstrates that there is no need to modify the time windows used to obtain the measures of maximum amplitude.

Measures of maximum amplitude were obtained from the same time windows and from the same clustered regions described above. These measures were also subjected to robust ANOVAs. According to the fourth hypothesis, each of the motor related conditions should show a comparable N1

peak, and each should differ from the control condition. The ANOVA revealed no significant differences: TWJt/c (3.0,14.2)=1.04, $p=0.43$ (MO= -2.27, MP= -2.66, MI= -2.51, VI= -2.73). While the motor related conditions ought not to be different, the average peak amplitude for the control condition also does not differ. Based on the available evidence there should be no N1 present in control condition. However, not only is the waveform present, it does not differ significantly from the experimental conditions. The presence of this peak in the control condition is a topic that will be addressed in the discussion.

Next, there should be a lateralized P1, primarily during MP and MI trials. Unfortunately, this assumption is not supported. While the peaks are visually evident in the waveform, the ANOVAs still failed to reach significance for the Condition main effect, TWJt/c(3.0, 14.2)=0.55, $p=0.67$ (MO=0.20, MP=0.38, MI=0.26, VI=0.37), main effect of Hemisphere, TWJt/c(1.0, 17.0)=1.0, $p=0.33$ (left=0.17, right=0.43), or the interaction, TWJt/c(3.0, 14.2)=3.75, $p=0.11$.

Lastly, the N2 peak is likely to show the more robust differences given that this peak should just precede motor movements. Therefore this peak should occur in the MP condition just prior to 200 ms. Further, this peak should also be lateralized in the left hemisphere. The ANOVA did reveal a strong main effect for Hemisphere, TWJt/c(1.0, 17.0)=9.81, $p=0.0058$ (left=-1.75, right=-0.69) indicating and greater negativity in the left hemisphere as expected. While the main effect for condition did not reach significance, TWJt/c(3.0, 14.2)=2.02, $p=0.18$

(MO=-1.12, MP= -1.40, MI= -1.35, VI=-1.01), there was a trend toward significance for the interaction, $TWJt/c(3.0, 14.2)=3.49, p=0.072$. All means are compiled in Table 5.

Table 5. Mean Amplitude (Latency) for the N1, P1, and N2 waveforms for each condition at each electrode region along with marginal means for hemisphere.

	<u>Motor Observation</u>	<u>Motor Performance</u>	<u>Motor Imagery</u>	<u>Visual Imagery</u>	<u>Hemisphere</u>
N1@SMA	-2.27 (63.75)	-2.66 (61.78)	-2.51 (69.21)	-2.73 (66.41)	
P1	0.2 (110.46)	0.38 (111.60)	0.26 (112.51)	0.37 (108.98)	
P1@C3	-0.13 (104.32)	0.68 (108.79)	-0.13 (108.29)	0.27 (106.83)	0.17 (107.06)
P1@C4	0.52 (116.50)	0.08 (114.41)	0.65 (116.73)	0.47 (111.14)	0.43 (114.72)
N2	-1.12 (182.60)	-1.40 (179.83)	-1.35 (178.41)	-1.01 (175.24)	
N2@C3	-1.91 (184.03)	-2.04 (180.44)	-1.76 (181.05)	-1.31 (175.71)	-1.75 (180.31)
N2@C4	-0.33 (181.17)	-0.77 (179.21)	-0.95 (175.78)	-0.71 (174.76)	-0.69 (177.73)

Although these comparisons fell short of statistical significance, the overall picture is still revealing. Specifically, several of these conditions are supposed to share similarities rather than differences. For example, the only group expected to show a difference in the N1 was the control condition. The three experimental conditions were supposed to yield an N1, and the peak characteristics ought to be comparable, with one exception. Namely, motor performance was expected to show increased activation compared to the other motor related conditions. Motor performance was supposed to lead to a maximal N1, compared to both motor imagery and motor observation. Looking that the means presented in Table 6, it is clear that in all cases except the P1 in the right hemisphere, the

peak amplitude for motor performance in numerically higher. While this is not statistically significant, it does persist across all amplitude measures. So, this finding suggests that the SMA may be involved in all three motor-related experimental conditions. In another case, both motor performance and motor imagery were expected to contain a pre-movement positivity, the P1. Again, these peaks are evident when they are supposed to occur, leaving only the question of why the peak is present and comparable when it is not supposed to occur, especially during Visual Imagery. Thus, the greatest cause for questioning these results is not the failure to find statistical differences among the experimental conditions. Rather, the most curious result is the mere presence of these peaks where they are not expected at all, especially in the control condition. Further investigations of the data may elucidate this matter and it will also be addressed in more detail in the discussion.

Analysis 5: Source Localization

Low Resolution Brain Electromagnetic Tomography (LORETA) was used to estimate the 3D distribution of the generating neural activity based on the topographical distribution of the EEG. LORETA is a Laplacian weighted minimum norm method used to solve the *inverse EEG problem*. Given known dipole locations, known head volume, geometry and conductivity, the EEG voltage of the scalp can be predicted at known sensory locations. This is known as the *forward EEG problem*. Working in reverse, knowing the sensor locations, scalp voltages and head model to estimate the underlying brain activation is the

inverse EEG problem. The estimated 3-dimensional activation can be viewed at various coordinates layered over three MRI slices at designated time points: Horizontal, Sagittal, and Coronal slices. Images depicting neural activity at time points corresponding to the peak latencies were reviewed. Images of activity at 68ms where the MRI slices intersect at the point of maximal activation can be seen in Figure 11. Source activity at 112 ms and 180ms can be seen in Figures 12 and 13, respectively. Voltage ranges from low to high using a white (zero) to red (relative maximal voltage of approximately 0.8-1.2 μV) gradient. Small black triangles along the top and left edge of each slice indicate the axial location of the other two slices. X, Y, Z values are provided, indicating the coordinates corresponding to the point of maximal activation at which the three slices intersect.

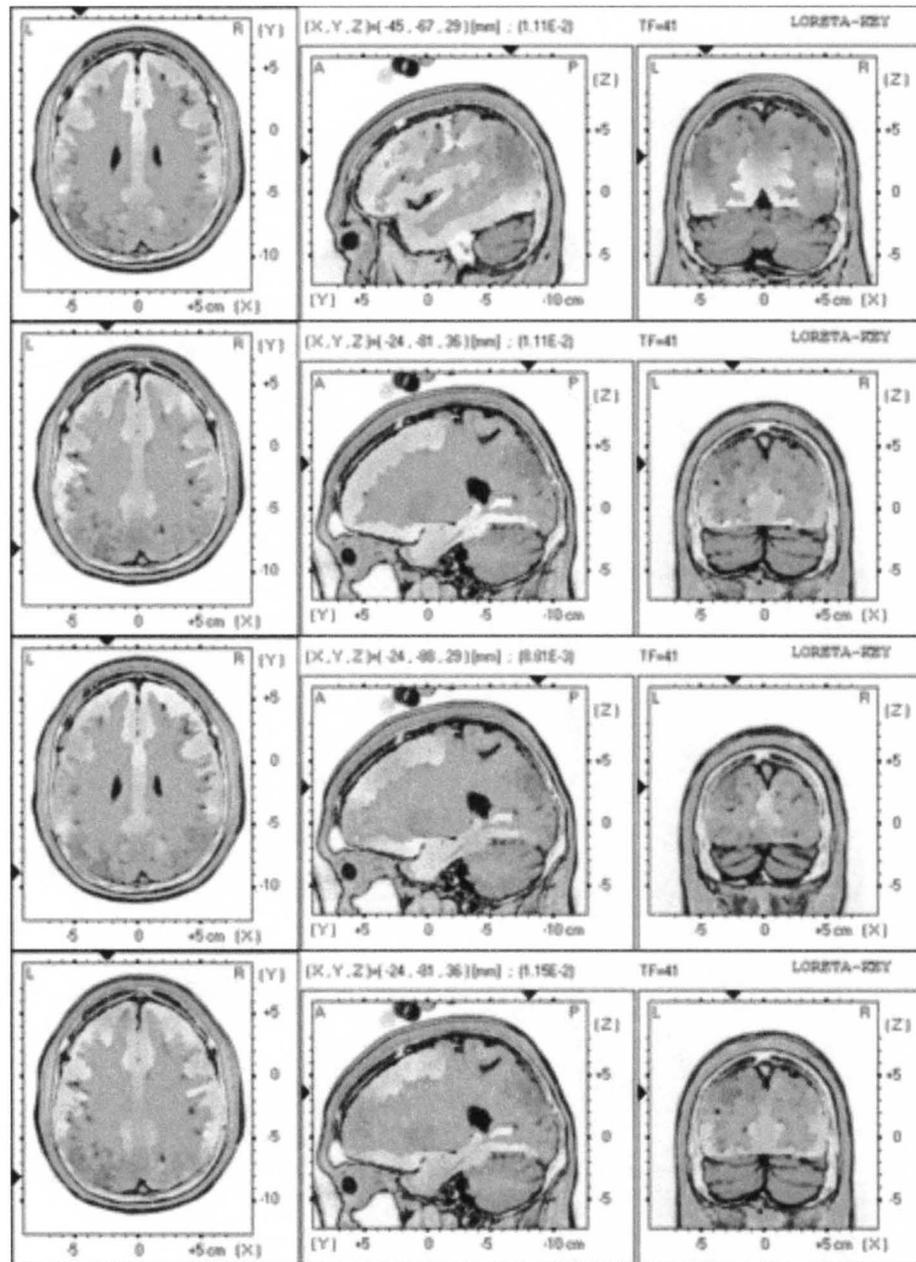


Figure 11. Source Activity at 68ms as shown by the LORETA Values. Slices intersect at the point of maximal voltage. Moving from top row to bottom, conditions are as follows: images during Motor Observation, Motor Performance, Motor Imagery, and Visual Imagery. Activation ranges from zero (white) to relative maximal voltage (red).

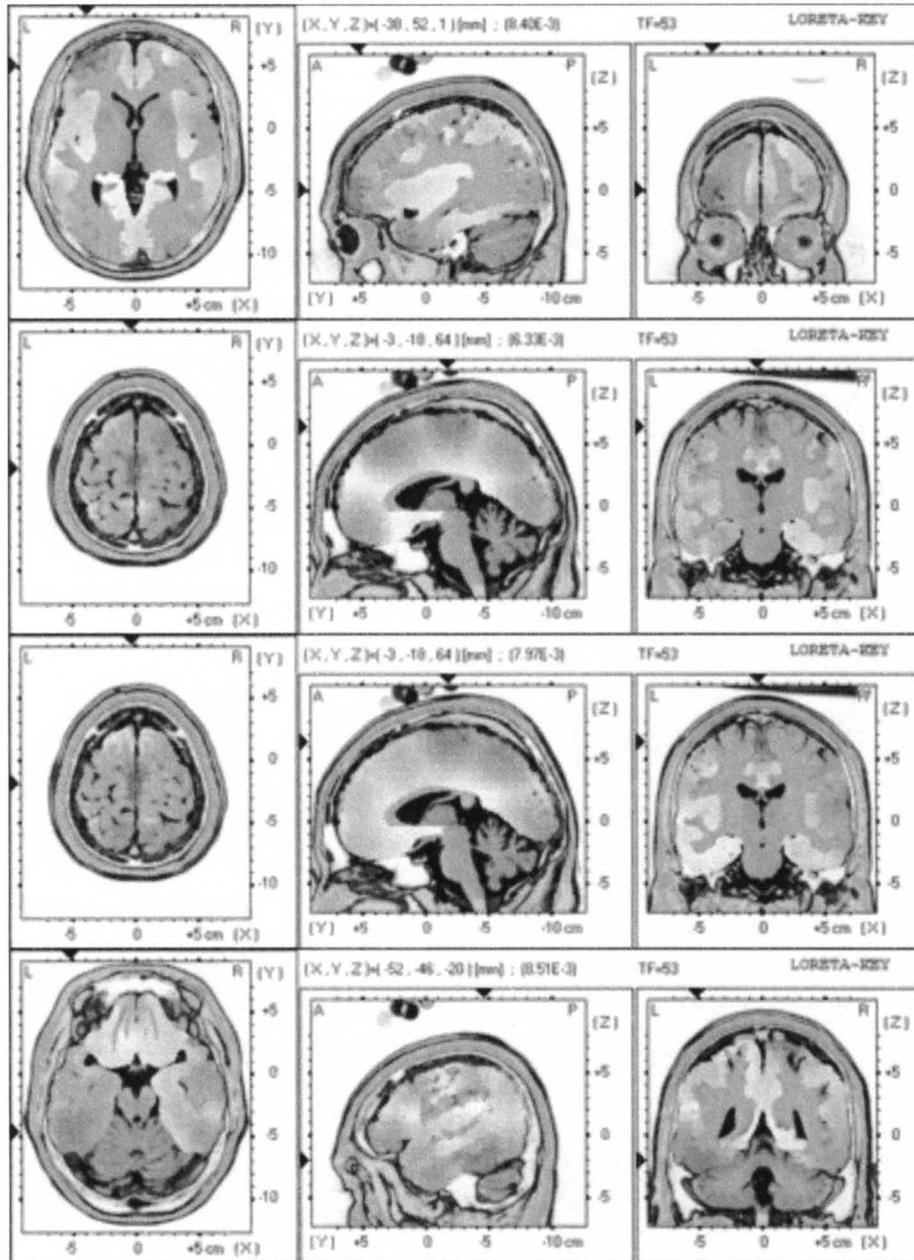


Figure 12. Source Activity at 112ms as shown by the LORETA Values. Slices intersect at the point of maximal voltage. Moving from top row to bottom, conditions are as follows: images during Motor Observation, Motor Performance, Motor Imagery, and Visual Imagery. Activation ranges from zero (white) to relative maximal voltage (red).

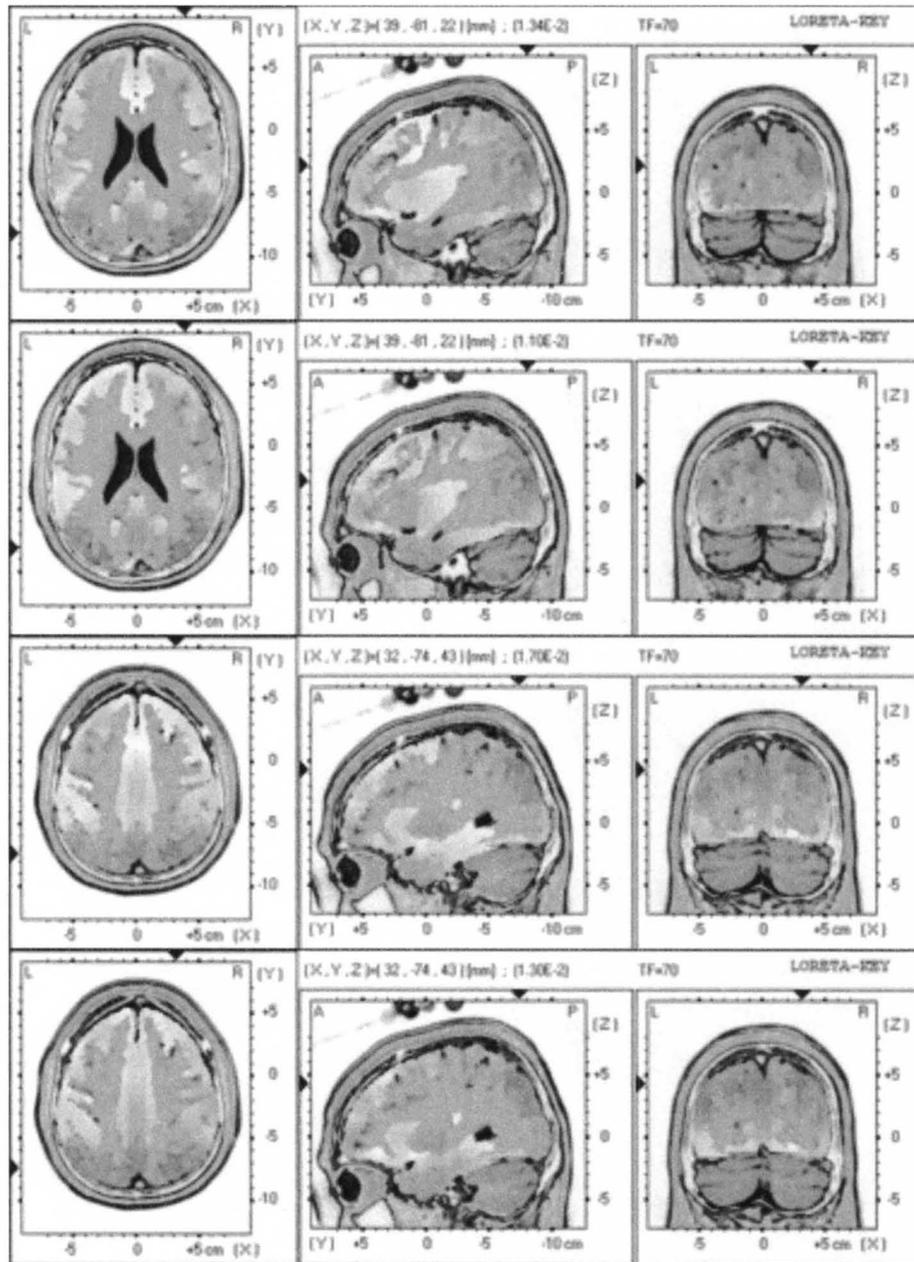


Figure 13. Source Activity at 180ms as shown by the LORETA Values. Slices intersect at the point of maximal voltage. Moving from top row to bottom, conditions are as follows: images during Motor Observation, Motor Performance, Motor Imagery, and Visual Imagery. Activation ranges from zero (white) to relative maximal voltage (red).

Activity at 68ms was maximal in the left parietal cortex in all four conditions. While the activity appeared to be consistent between conditions, it did not reflect activation that would be expected to be related to motor activity. Activation at 112s was more diffuse, ranging from inferior left frontal activation during motor observation, to posterior portions of the temporal lobe during visual imagery. During motor performance, on the other hand, the point of maximal activation occurred in the precentral gyrus. However, this activity occurred medially, rather than laterally and therefore does not reflect activation in the hand area of M1. Activity occurring at 180ms, contrary to expectation, was maximal in the right hemisphere in all conditions. These data show the location of maximal activation, but do not indicate other areas that may also be activated. In other words, several areas of the brain may be activated, but the slices shown in Figures 11, 12 and 13 only show areas of maximal activation. As a comparison, slices of activity were also viewed at locations that intersect the SMA and M1. Rather than using locations of maximal activation, these latter slices were used to investigate activity in two specified, motor related areas. These slices were taken at the same three time points of 68ms, 112ms and 180ms, respectively. The images are shown in Figures 14, 15, and 16.

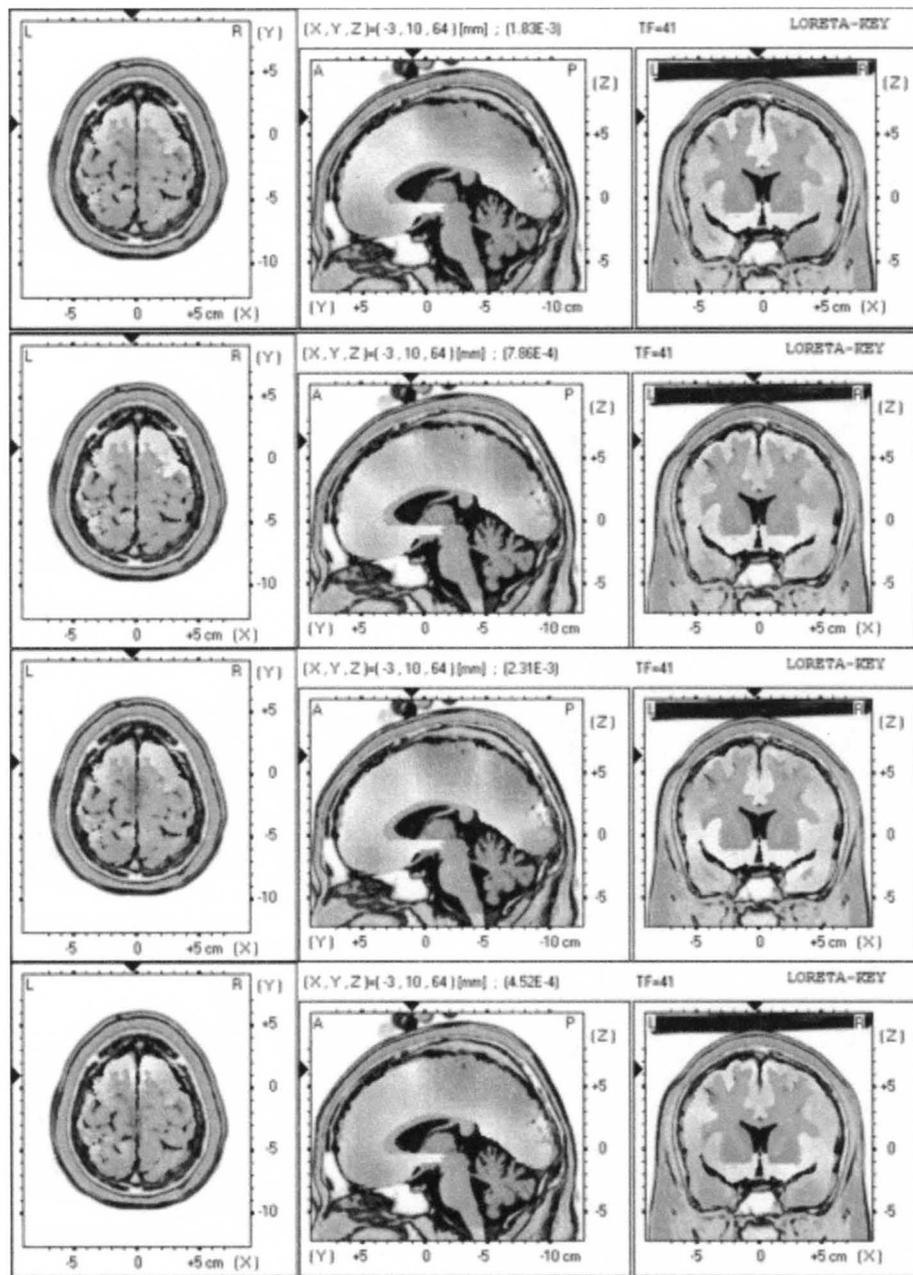


Figure 14. Source Activity in the SMA at 68ms as shown by the LORETA Values. Slices intersect at the SMA. Moving from top row to bottom, conditions are as follows: images during Motor Observation, Motor Performance, Motor Imagery, and Visual Imagery. Activation ranges from zero (white) to relative maximal voltage (red).

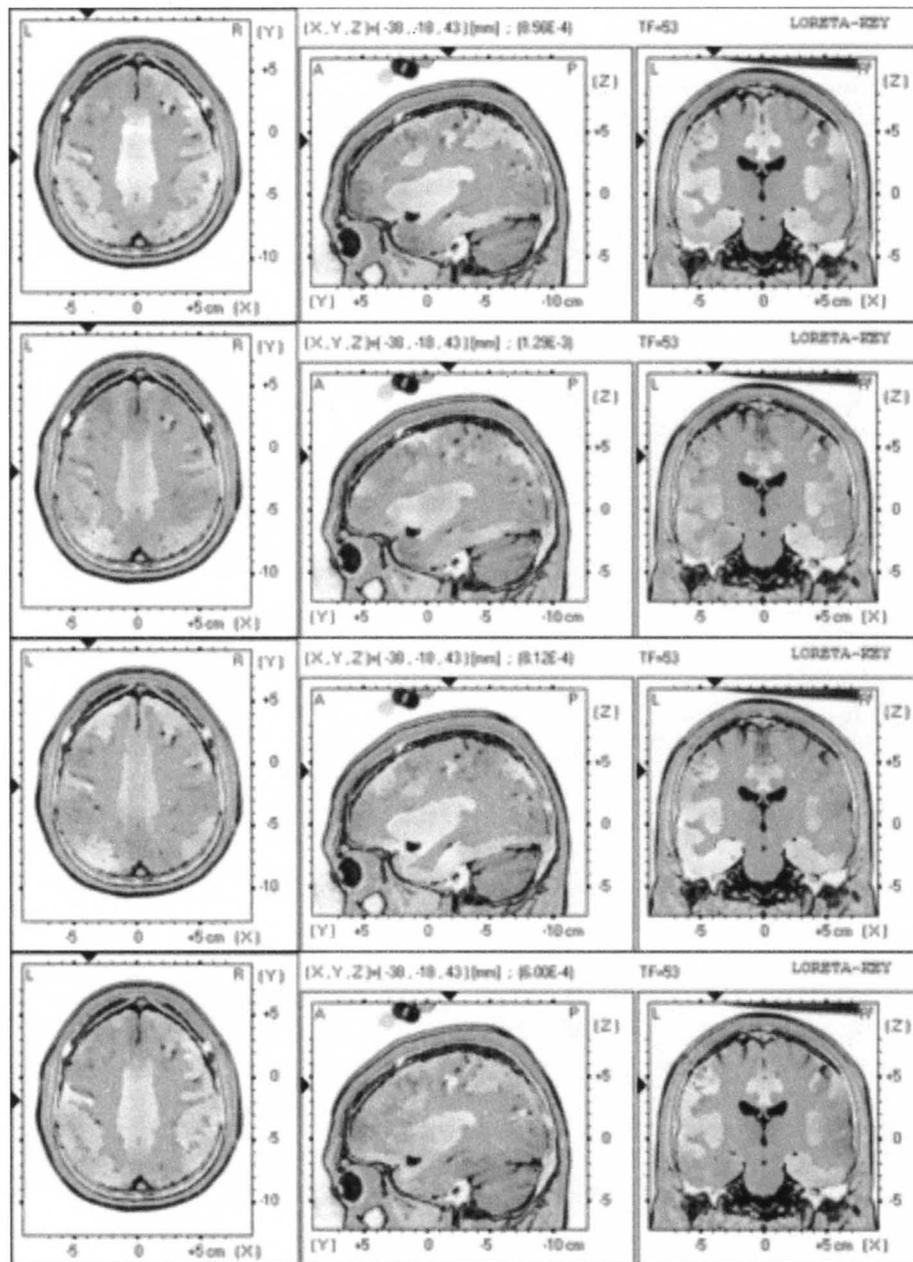


Figure 15. Source Activity in area M1 at 112ms as shown by the LORETA Values. Slices intersect at area M1. Moving from top row to bottom, conditions are as follows: images during Motor Observation, Motor Performance, Motor Imagery, and Visual Imagery. Activation ranges from zero (white) to relative maximal voltage (red).

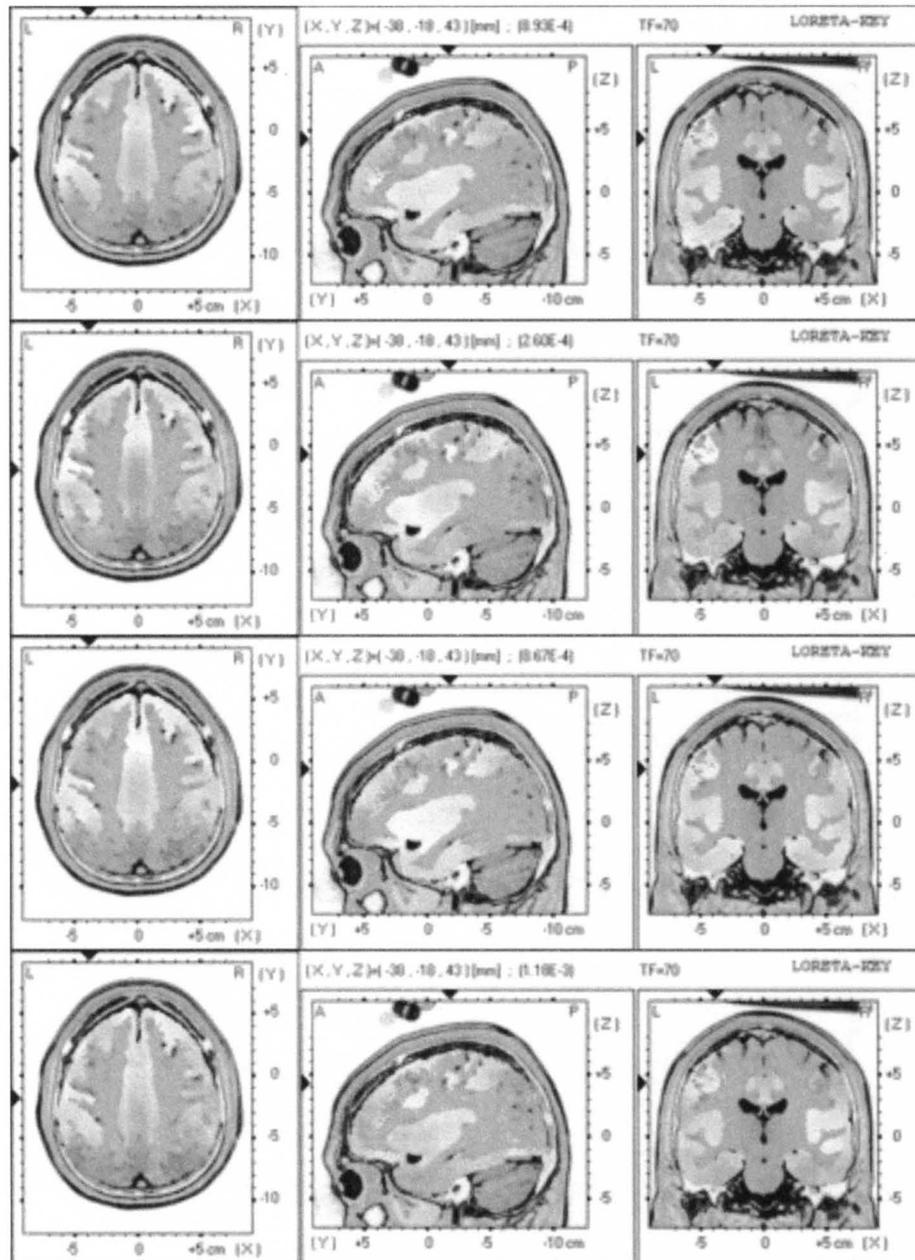


Figure 16. Source Activity in M1 at 180ms as shown by the LORETA Values. Slices intersect at area M1. Moving from top row to bottom, conditions are as follows: images during Motor Observation, Motor Performance, Motor Imagery, and Visual Imagery. Activation ranges from zero (white) to relative maximal voltage (red).

Slices intersecting at SMA at 68 ms revealed medial activity across all conditions, but occurred at more central and parietal areas than near the SMA. The activity at 112 ms is rather diffuse and leads to activity predominantly in the parietal and occipital areas at 180 ms. Further, the specific sites of interest, namely SMA and M1, do not show much activation. While the source activity was expected to occur in motor related areas, it mirrored more the ambiguity resulting from the sequential PCA. The estimated source activity was intended to elucidate the neural activity responsible for generating the peaks in the waveforms.

To be clear, the purpose behind reviewing the source activity was to lend support to the notion that motor related areas were involved in both motor observation and motor imagery in addition to motor performance. The areas most likely to show activation are the SMA, M1 and S1. Additional areas expected to show activation included Broca's Area (BA 44) and the Angular Gyrus (BA 39), as these are both areas that have been implicated in Mirror Neuron System. While these areas may show some activation, the pattern of activation over time does not reflect that of motor activity. For example, both figures depicting activity at 68 ms show activation of the left parietal cortex. However, this pattern of activity would not be expected so early as it could not reflect any sensory (real or imagined) processing. While these data do not support the hypotheses, additional visual inspections of the data are reviewed next to help make sense of these idiosyncrasies.

Comparative Waveforms and Topo Plots:

Additional examinations of the data were carried out to better make sense of the results. The windowed measures were only snapshots of the data recorded from selected regions and LORETA provided an estimation of the source activity. Further, the sequential PCA did not identify any temporal or spatial components that could be tied to or related to motor related activity. However, given the unusual nature of those results, further investigations were necessary to make sense of the disconnect between the apparent waveforms demonstrating the expected motor evoked potentials and the ambiguous outcome of the PCA and source localization.

First, the raw voltage changes were viewed using topographical plots, 2-dimensional representations of the scalp voltages. The topographical plot at 68 ms reveals a clear negativity centrally located at the frontal electrode sites. See Figure 17. This explains the strong N1 at that time point measured from SMA and its presence in all four conditions. This frontal negativity coincides with a strong positivity along the back of the scalp, which could simply be a result of visual processing.

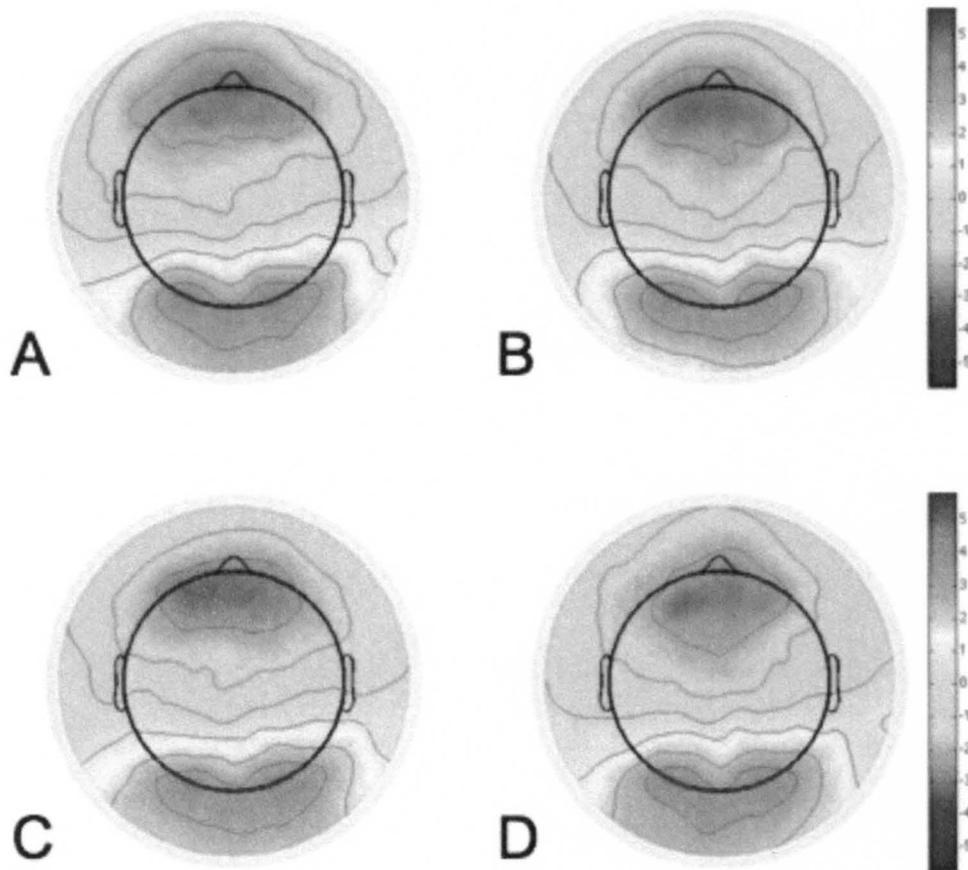


Figure 17. Topographical plot at 68 ms. Voltages range from -5 microvolts (blue) to +5 microvolts (Red). Plots depict scalp voltages during (A) Motor Observation, (B) Motor Performance, (C) Motor Imagery, and (D) Visual Imagery. The negativity explains the presence of the N1 measured at the SMA across the four conditions. A coinciding positivity is present in posterior electrodes sites. This negativity is apparent across all four conditions. Indeed, statistical analysis of amplitude measures obtained from a cluster of electrodes sites above the SMA revealed no differences between conditions.

More diffuse activation is present at 112 ms. See Figure 18. While the peak itself is quite apparent in the waveform measured at C3, the voltage amplitude is very close to zero. This positivity seems quite diffuse across the scalp. However, in the motor performance conditions, there appears to be a greater positivity in the left frontal area. With this in mind, a windowed measure of amplitude was obtained from F7 (E47), which measures activity of the inferior frontal gyrus – the home of Broca’s area that is implicated in the Mirror Neuron System. The ANOVA performed on these measures revealed a significant effect of condition, $TWJt/c(3.0, 14.2)=4.04, p=0.049$ illustrating a significantly higher activation during motor performance (MO=1.00, MP=1.71, MI=0.82, VI=0.81). This area is believed to be involved with the mirror neuron system. Therefore this result is not surprising and, in part, lends support to hypothesis 3 that posits the involvement of Broca’s area in motor performance and motor observation. The caveat is that there is no support for the involvement of this area during Motor Observation, nor the involvement of the Angular Gyrus.

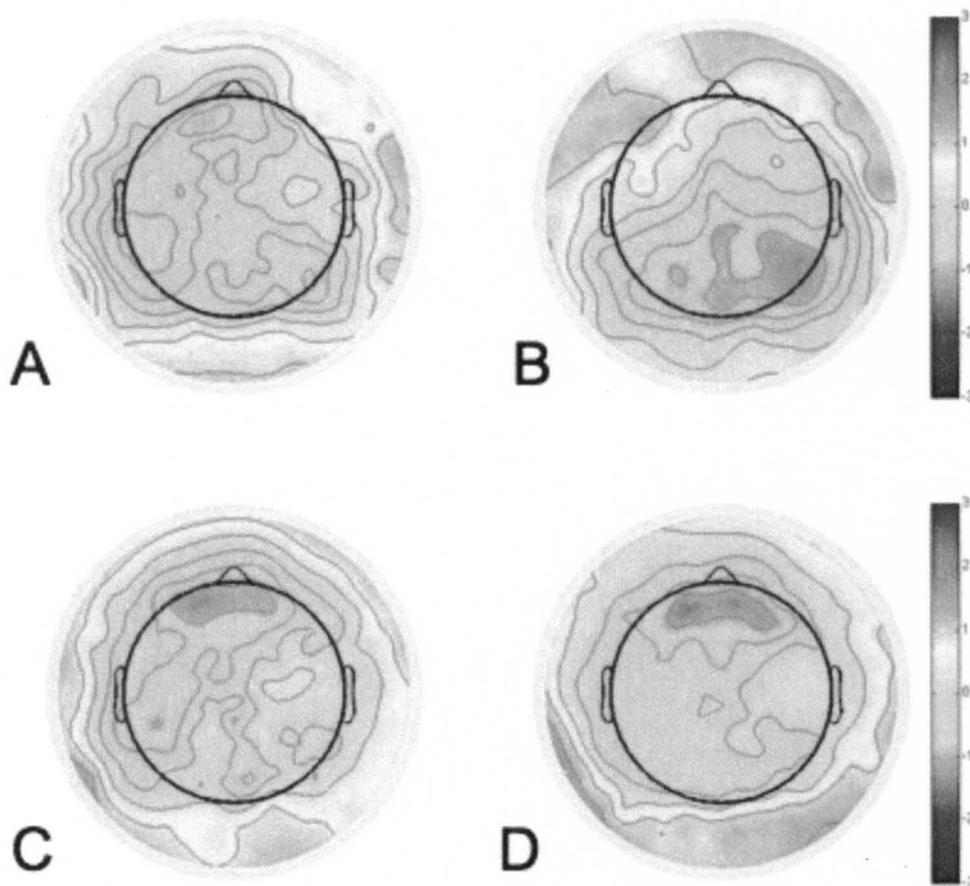


Figure 18. Topographical plot at 112 ms. Voltages range from -5 microvolts (blue) to +5 microvolts (Red). Plots depict scalp voltages during (A) Motor Observation, (B) Motor Performance, (C) Motor Imagery, and (D) Visual Imagery. A lateralized positivity appears in the frontal areas during motor performance. Statistical analysis of amplitude measured at F7 revealed a significantly higher activation in Motor Performance. This activity could be related to activation of Broca's area, part of the Mirror Neuron System.

The third topographical plot illustrates the voltage changes at 180 ms. See Figure 19. This pattern of activity is similar to the pattern of activity observed during the first negative peak, showing a strong negativity, centrally located in frontal electrode sites with a coinciding positivity along parietal and occipital areas.

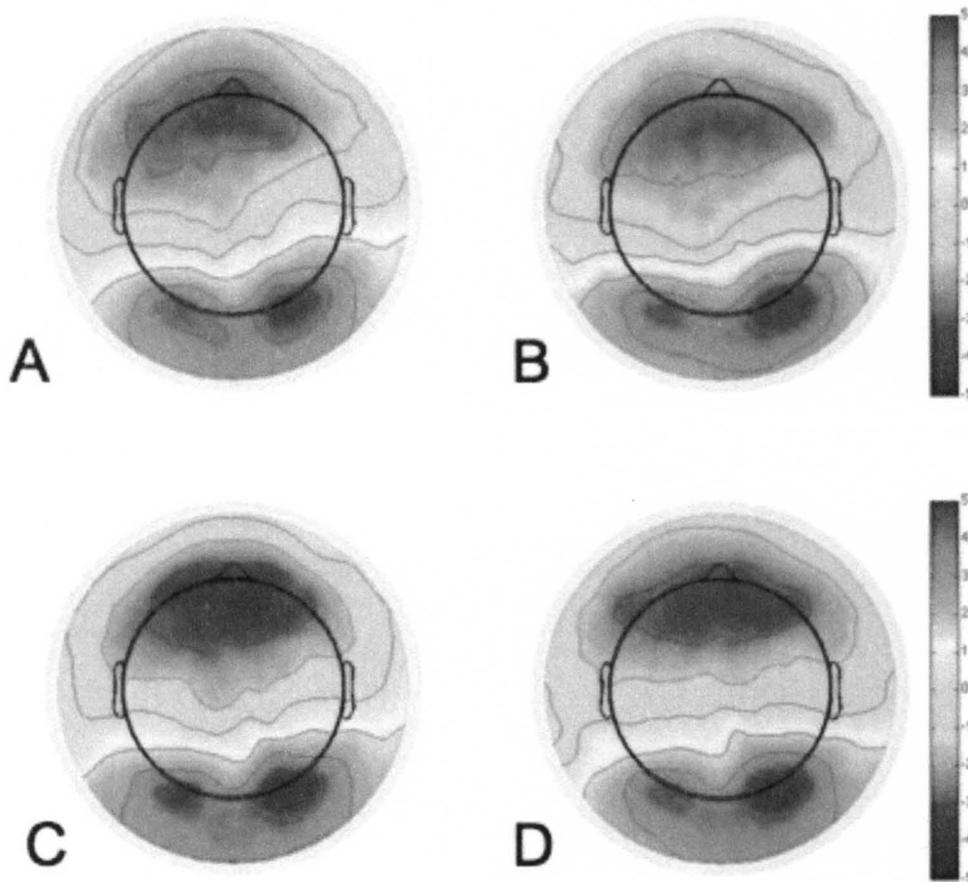


Figure 19. Topographical plot at 180 ms. Voltages range from -5 microvolts (blue) to +5 microvolts (Red). Plots depict scalp voltages during (A) Motor Observation, (B) Motor Performance, (C) Motor Imagery, and (D) Visual Imagery.

In contrast to the PCA and the LORETA results, the topographical voltage changes provide a level of consistency to the results. There is a strong polarity coinciding with the N1 followed by a more diffuse pattern of activity that returns to another strong polarity. To be fair, the observed motor evoked potentials measured at specific locations are simply a subset of the full montage presented in these 2D topographical plots. Still, the data depicted in these images are in stark contrast to the rather erratic results from the PCA and LORETA that seemed to have no relationship with the observed motor evoked potentials.

To further investigate the nature of the waveforms, three additional comparisons were made. The first was a comparison to the pattern of activity in response to the visual information available during the inter-stimulus interval. The second comparison evaluated the morphology of the waveform elicited by the Neutral Image. These comparisons were chosen to investigate the possibility that some of the activity being observed in response to the target image was simply due to visual processing. The third comparison was made to the response-locked ERP during the motor observation condition. This comparison was chosen to determine if any of the putative motor evoked peaks would be revealed by locking the EEG to the motor response, rather than the triggering stimulus. For each of these comparison waveforms, ongoing EEG was subjected to the same preprocessing steps described previously. However, the critical difference was the time point to which the segments would be locked. The EEG during the ISI was time locked to the onset of the gray inter-stimulus interval. The second comparison required the EEG to be time-locked to the onset of the

Neutral Image. The response-locked average was obtained by averaging segments based on the button response recorded during motor observation. Button responses were collected by which the participants reported which of the two actions were depicted in the target image. Therefore, a response-locked average was obtained for MO only, as it was the only condition that required and recorded participant responses.

The ongoing EEG during the ISI was chosen as a comparison to the originally segment ERPs to investigate the nature of the EEG during visually similar information but which contained no visually meaningful information, namely any visual or motor information. The grey square presented during the ISI contained the same luminance to prevent a strong visual evoked potential in order to provide a better controlled evoked potential in response to the target image. Amplitude means were obtained from the same C3 cluster and graphed in the same manner as those data presented in Figure 10. The graph of the ISI averages for each condition can be seen in Figure 20. The only difference in how these data were processed was the visual stimulus to which they are time-locked. The graphs are presented on the same scale to provide the best possible comparison.

Grand Average EEG by Condition during ISI at C3

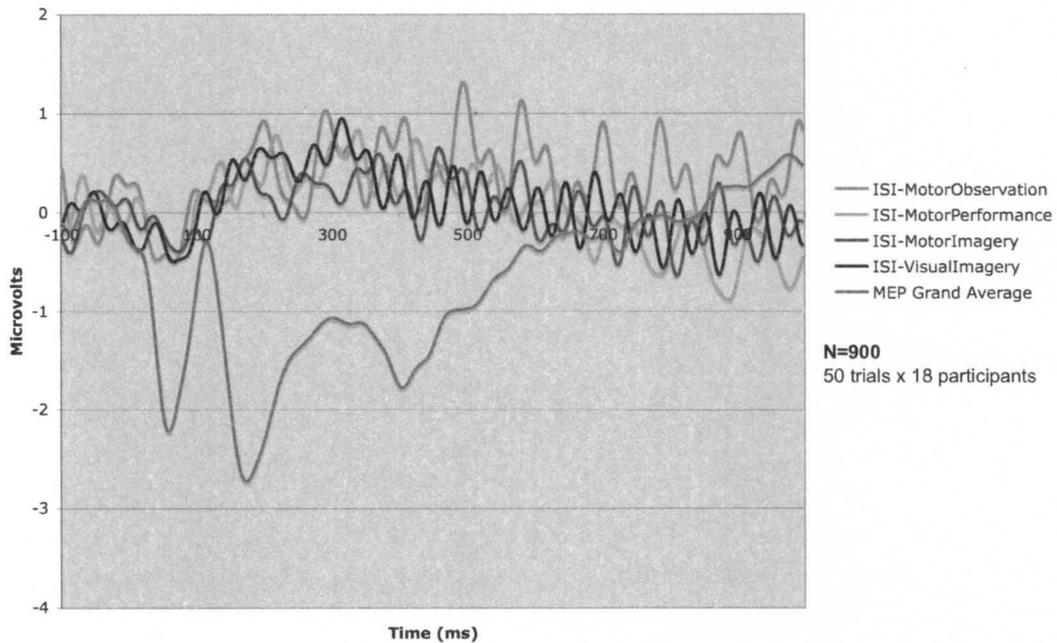


Figure 20. Average EEG waveforms for the four different conditions recorded around C3 (E59, E51, E52, E58, E60, E65, and E66) during the Inter-stimulus interval. The Grand Average for the EEG following the Target Image is provided for comparison.

There is no apparent evoked potential during the ISI. There also does not appear to be much of a relationship in the EEG between conditions. Further, and most important, there is also no apparent comparison to the EEG time locked to the target image. What can be gleaned from this comparison is that the evoked potential time locked to the target imaged is not likely visually evoked response. This not only provides credence to the experimental design, but it provides a

better indication that the evoked potential observed in response to the target image is not simply a result of visual processing.

To further validate this point, a comparison was also drawn between the Neutral and Target Images. The Neutral Image should elicit quite a large visually evoked potential due to the absence of any images or brightness leading up to the presentation of the Neutral Image. Secondly, the Neutral image still contains the presence of the objects and the human hand. However, the grasping motion is not presented until the target image. These waveforms are presented in Figure 21.

Grand Average ERPs, Neutral and Target Stimuli

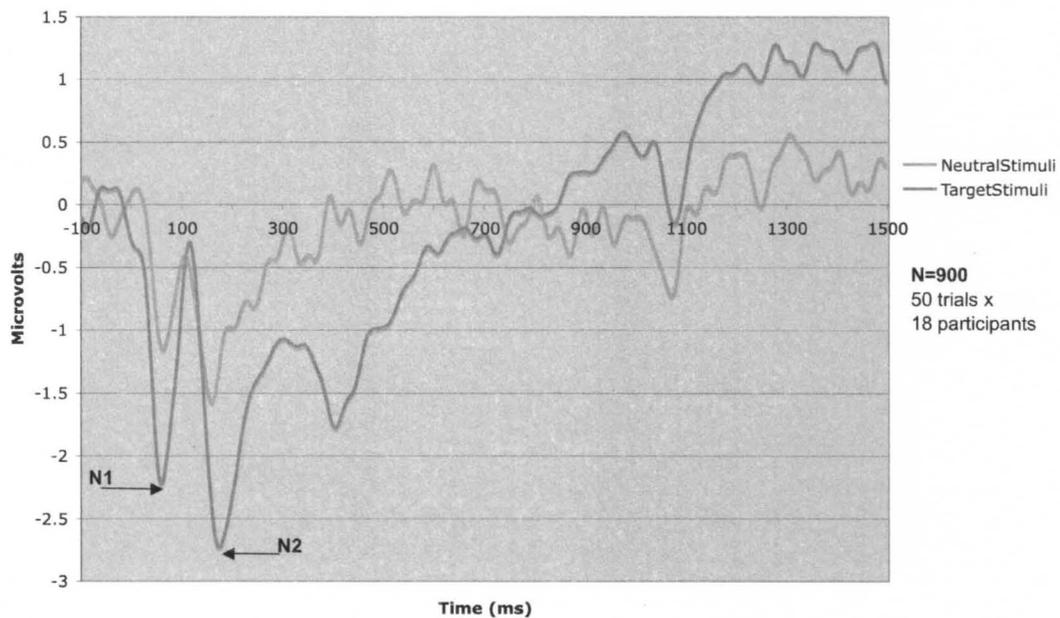


Figure 21. ERPs during the presentation of both the Neutral and Target Stimuli. The amplitude of the peaks believed to be related to motor observation are significantly greater for the N1 and N2.

The peaks identified in the waveforms as an N1, P1 and N2 are present in both waveforms. However, the amplitudes for the N1 and N2 are significantly greater in response to the Target Image: N1, $t(1, 54)=11.075$, $p<0.001$; N2, $t(1, 54)= 9.909$, $p<0.001$. If these peaks were visually related rather than motor related, it would be expected that the peaks would have a larger amplitude in response to the Neutral Image than to the Target Image. This is not the case. As such, it is not likely that these peaks are only visually related. While there is a clear visual component to the observed peaks, they not expected to be observed at C3. Further, given the increased amplitude to the Target Image, there is an additional component augmenting the amplitude of these peaks. This augmentation is believed to be the motor related activation.

On the other hand, each stimulus appears to be eliciting these peaks to some degree. With this in mind, it is important to note that both stimuli contain similar object characteristics. Therefore, it could be argued that the evoked potentials may be due in part to object recognition rather than a traditional visually evoked potential or the possibility of a motor related response. While the visual characteristics of luminance remained constant from the neutral image to the target image, there is a presence of the objects in the target image that is absent during the ISI. To better investigate this possibility, another comparison to a response-locked ERP was also investigated. Early investigations of motor evoked potentials were typically time-locked to EMG onset during repeated motor movements that were paced to a metronome or self paced (Mushiake, et al., 1991; Nativ, et al., 1992; Okano & Tanji, 1987; Thickbroom & Mastaglia, 1985;

Thickbroom, et al., 1985). This strategy was used to obtain a response-locked average. During motor observation, participants were required to report which of the two actions they observed in the target image. These button responses were used to generate a response-locked average as opposed to the stimulus-locked averages previously examined. The response-locked waveform contains some of the same features as the stimulus-locked waveforms. See Figure 22.

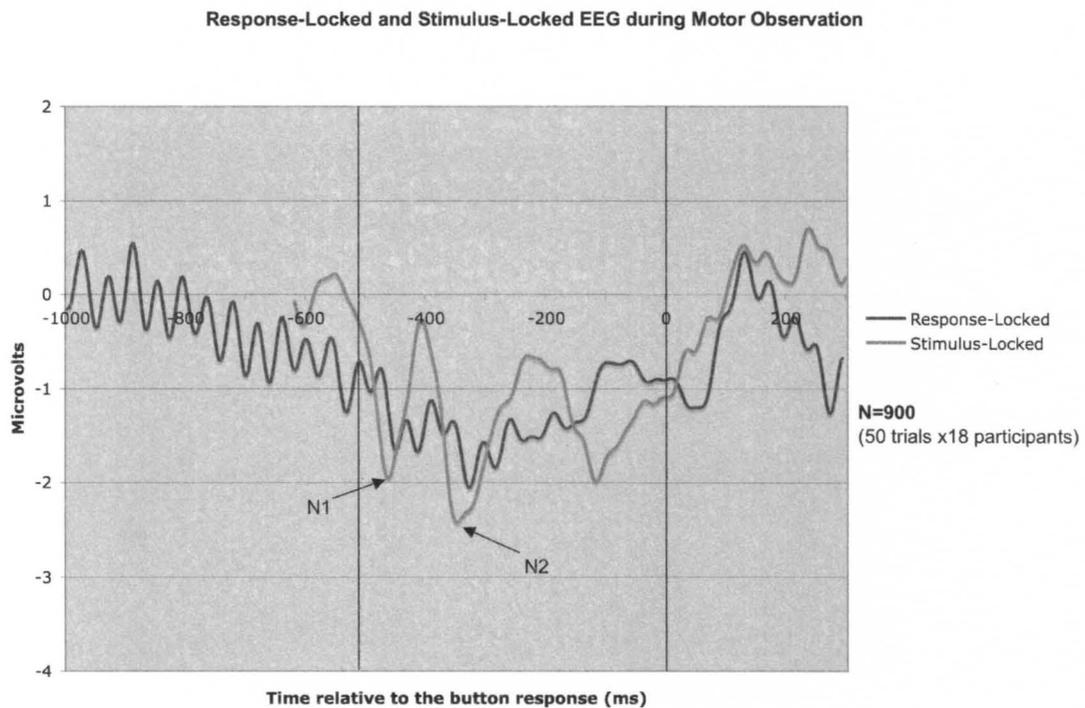


Figure 22. Response-Locked ERP during Motor Observation. The vertical black line on the right side of the graph is at zero and represents the time at which the button response was made. The average response time during motor observation was approximately 526 ms. Moving backward from there, the vertical black line on the left represents the approximate onset of the target image. The

average stimulus-locked ERP (including baseline) is added for comparison beginning at -626 ms.

ERPs time-locked to stimulus presentations are characterized by peak latencies that occur after the onset of the stimulus. Response-locked ERPs are characterized by latencies that occur prior to the onset of EMG or, as in the present case, prior to a punctual participant response. The point at which the participant's respond, and the point at which the waveform is time locked will be referred to as Response Time. Activity prior to this time point shows a gradually increasing negativity, which peaks about 300 ms prior to response time. This peak negativity coincides with the N2 when comparing the relative time course of the stimulus-locked ERP. There also appears a comparable peak coinciding with the N1. It was difficult to determine if there is a similar peak comparable to the P1. Still, the response-locked average yields a fairly similar waveform that was observed in the stimulus-locked EEG. This comparison, yet again, provides an additional level of consistency within the data, lending more support that the observed waveforms are not simply a response to visual information. This further supports the notion that the observed activity is more likely to be related to some kind of motor activity.

VII. DISCUSSION AND CONCLUSIONS

Two major theoretical models, Direct Mapping and Functional Equivalence, suggest that the observation of action and imagery of action, respectively, involve activation of similar motor related areas. Both perspectives attempt to elucidate the common neural substrates involved in imagining or observing motor actions, and the planning and execution of similar motor movements. Despite the wealth of evidence that supports these two perspectives, the degree to which these motor-related actions overlap is still only vaguely defined. The present investigation sought to assess both the spatial and temporal characteristics of the brain activity involved in these motor related conditions. Specifically, the present study used ERP technology to assess the neural substrates of Motor Observation, Motor Performance, and Motor Imagery. All three of these experimental conditions were expected to show increased activation of motor related areas on the contralateral hemisphere (left hemisphere), particularly in the Supplementary Motor Area, Primary Motor Cortex and Primary Somatosensory Cortex.

The data were subjected to a sequential PCA to reduce the data into manageable ERP components. Specifically, the PCA was expected to produce components that would reflect previously identified motor evoked potentials, namely the N1, P1, and N2. The analysis revealed 100 components, only eight of which reached significance. Of these eight, three are maximal in parietal

areas. None are maximal in motor related areas. The three components that are maximal in the parietal areas are two early to be sensory feedback during motor movements. The third is not maximal in the left parietal area where it would be expected with a motor movement of the right hand. Ultimately, the analysis did not reveal any temporal components that corresponded to any of the expected peaks associated with motor evoked potentials, nor any other components that might reflect any expected motor related activity. Thus, the three temporal hypotheses were not supported by the temporal spatial PCA.

The three spatial hypotheses were addressed in part by estimating the source activity using LORETA. LORETA attempts to solve the inverse EEG problem which estimates the source activity within the brain based on the scalp voltages, electrode locations and what is known about the average human brain and the skull that houses it. Initial slices were obtained by locating areas of maximal activation. However, much of the activity revealed by the LORETA values suggest very diffuse sources of brain activity, ranging from frontal areas to occipital areas, all having very little to do with motor control. Secondly, specific motor related areas were targeted to investigate activity possibly occurring in these areas, namely the SMA and M1. Contrary to expectations, LORETA values did not demonstrate that there was activity present in these areas.

Given the paucity of support for the hypotheses, as well as the general lack of consistency among these analyses, additional investigations of the data were warranted. Specifically, identified peaks within the waveforms were subjected to ANOVAs, and 2-dimensional views of the scalp voltages were

examined to better understand the nature of the data. Each was intended to compliment the primary analyses, while providing a better picture of what can be learned from the data. These subsequent examinations of the data were also intended to provide some insight and rationale for the unanticipated results yielded by the PCA and LORETA results.

The greatest source of useful information came from the windowed ANOVAs. Here, windowed measures were obtained for specifically identified peaks within the waveforms. These windowed measures provided minimal support for the temporal hypotheses. These amplitude measures were subjected to robust ANOVAs. MO, MP and MI all share an N1 as expected. However, this peak was also present during the VI. The presence of this peak in the control condition makes this outcome a bit suspect. Similarly, MP and MI also share a P1 as expected. Still, this peak is also present during MO and the control. Lastly, the N2 was only supposed to be present during MP, but was quite apparent in all four conditions. While there was a hemisphere affect for the N2, demonstrating a greater negativity in the left hemisphere, there were no differences between conditions at any of these peaks. One remaining question is why there are not identifiable differences between conditions.

The literature suggests that there are a number of similarities among Motor Observation, Motor Performance, and Motor Imagery. Specifically, these similarities include activation of motor related areas. While subtle differences among these conditions theoretically exist, the similarities eclipse any differences that might be present, thus making it ever more difficult to detect those

differences. In other words, the experimental conditions themselves may have been too similar in nature, making it increasingly difficult to detect subtle differences between the participant tasks. While previous work suggested that the intention of the observer leads to differential activation (Decety, et al., 1997), there is no indication that same manipulation worked here. This could account for the similarities between the experimental conditions. While participants understood the task demands and may have performed honestly, all three motor related experimental conditions required the participants to observe the same motor information. While the intention varied, the imperative stimuli did not. It was believed that despite the similarities in stimuli, the differences in intention would be robust enough to lead to differences in motor processing and therefore result in differences in recorded waveforms. As such, the ERPs would demonstrate the expected differences in motor processing. This was not the case. Had the experimental stimuli differed between the conditions, the outcome would not have weighed so heavily on the intention of naïve participants. While this explanation can account for the similarities between the experimental conditions, it fails to explain the similarities to the control condition.

Ultimately, the last question begging to be answered was why are these peaks present even under conditions where they are not expected to occur? There are two probable explanations, including confusion with visually evoked potentials, or the presence of motor related activity across all the conditions.

To tease these apart, specific comparisons were made between three additional waveforms. Specifically, comparisons were drawn between the EEG

during both the Neutral Image and the inter-stimulus interval. A third comparison was made to a response-locked ERP. Close inspection of the EEG in response to the inter-stimulus interval demonstrated that the ERPs elicited by the presentation of the target images were uniquely different than the waveforms during the ISI. The ISI followed directly the presentation of the neutral images. Essentially, the participants viewed a novel visual stimulus of identical size and luminance as the target images. However, the EEG during this presentation was nearly unaffected and did not contain any elicited response. The additional comparison to the Neutral Stimulus revealed a similar morphology to that elicited by the Target Image. However, significant differences were found between measures of maximum amplitude. These differences demonstrate a significantly greater response to the Target Image than the Neutral Image. Thus the waveforms time-locked to the target images were not simply evoked by the presentation of a novel visual stimulus. Therefore, the peaks under investigation could not be confused for visually evoked potentials.

There were two critical differences between the visual display during the neutral images, the inter-stimulus interval, and the target images. One is the presence of a human hand, and the two objects. The second is the presence of the motor related activity inherent in the image. The latter of these two is the basis for the present investigation. It is the motor related information that is the fundamental issue. Therefore, an additional comparison was made to a response-locked average obtained during the motor observation condition.

During the motor observation trials, participants were instructed to report using a response pad which of the two target images they saw. In addition to the recorded response, the ongoing EEG was also marked when these responses were made. The EEG was segmented using these markers and averaged together. This average was then compared to the time-locked ERP for the same condition. The waveforms shared similar characteristics including the N1 and N2 peaks. It was difficult to determine if a positive deflection the response-locked average was comparable to the P1. Nonetheless, this comparison provides support that the peaks could still be related to motor activity. What is most interesting is the presence of this activity in all four conditions, especially the purported non-motor related control. The following explanation is presented.

a. Automatic Motor Recognition

As previously explained, the theoretical similarities among the three motor related conditions could explain the remarkable commonalities between these conditions. However, this explanation does not explain the similarities to the control condition. Secondly, this explanation relies on the assumption that viewing motor information alone elicited these motor evoked potentials. This assumption would further suggest there is more motor related activity involved in motor observation than previously thought. Essentially what may be happening here is a kind of automatic motor recognition. Much like object recognition, but recognition of motor information. This explanation is plausible given the line of work of visuo-motor priming previously introduced.

Several studies using Serial Reaction Time (SRT) tasks demonstrate that action and perception directly affect one another. Specifically, these tasks illustrate the direct relationship between observed motor information and motor behavior (Heyes & Foster, 2002; Howard, et al., 1992) such as visually guided actions (Flanagan & Johansson, 2003). This idea is further supported by Heyes and Ray's Associative Learning Theory (Heyes, Bird, Johnson, & Haggard, 2005; Heyes & Foster, 2002) that suggests visual information from a model can directly activate motor representations of the observer. These lines of work validate the suggestion that the peaks found in the present data set may be due to this automatic relationship between motor observation and action understanding.

However, there are some additional concerns regarding the present study including both methodology and the number of participants. The present investigation relied on only 18 participants using a within-subjects design. As such, participants experienced all four conditions. While these were presented in blocks of 10, it could be argued that motor related activity present during one motor related condition, could carryover to the next block of trials, including the control condition. This could possibly lead to some kind of priming or carryover effect that could theoretically account for the similarities found between the different conditions. As such, the conclusion that the similarities between the conditions are caused by an automatic motor recognition as part of motor observation is tempered by these methodological issues mentioned above.

In order to evaluate if motor observation is in fact responsible for these similarities and the observed evoked potentials in all four conditions, only a few

simple changes to the present design would be necessary. Essentially, only a few modifications to the methodology would be necessary. Specifically, these modifications would include changes to the imperative stimuli, namely the target images, increasing the number of participants, and using a between subjects design to prevent any kind of carryover or priming effects from one condition to another. Removing the motor related information from all but the motor observation condition could be enough. Simply using an arrow or some other indicator during those conditions would suffice. The task and intention of the observer would not change, nor would the nature of the stimuli aside from the absence of the motor information. The motor information would simply be removed from the image. In the end, only the Motor Observation condition would employ the Target Image in its present form – that is containing the hand performing the grasping motion. Therefore, only the Motor Observation condition would require the subject to actually observe motor related behavior. Similarly, only the Motor Performance condition would require actual motor behavior on the behalf of the participant, and only the Motor Imagery condition would require the expected kinesthetic motor imagery. Therefore, by augmenting the target stimuli, any differences that theoretically exist between the motor processes would be more pronounced and more likely to be observed and identified statistically. Further, any automatic motor recognition would not confound the other experimental conditions or the control condition.

b. Impact and Relevance to the Field

The most recent investigations concerning the MNS in humans suggest that this system plays several vital roles from action understanding, human imitation, response facilitation and observational learning to higher cognitive functions such as language understanding, empathy, and even mind reading (Frith & Frith, 1999; Gallese, 2001; Gallese & Goldman, 1998; Hickok, 2010; Kelley & Bass, 2010).

From a clinical perspective, the dysfunction of the putative MNS has been suggested to be involved with autism (G. Rizzolatti, Fabbri-Destro, & Cattaneo, 2009; Williams, 2008). In addition to the purported impact on motor execution and athletic performance, motor imagery may play a role in stroke rehabilitation (Garrison, Winstein, & Aziz-Zadeh, 2010), relearning locomotor skills (Malouin & Richards, 2010) and prehabilitation. Prehabilitation is the practice of engaging in rehabilitation prior to surgery by incorporating resistance training and flexibility training. This strategy is employed in order to facilitate better post-surgery outcomes (Ditmyer, Topp, & Pifer, 2002). In the event that an injury prevents any kind of physical prehabilitation, it could be argued that motor imagery could be employed as a substitute. In other words, if one can't exercise the muscles before surgery, perhaps exercising the neural pathways for those actions may have a benefit (T. Mulder, 2007).

Taken together, there may be numerous benefits of understanding the common neural substrates of motor imagery and motor observation by taking advantage of those commonalities in a variety of settings involving sensory-motor

dysfunction. Flor, Diers and colleagues are among the first to employ both motor imagery and motor observation in addition to motor execution to facilitate cortical reorganization in an effort to treat a variety of sensory and motor abnormalities such as stroke, dystonia and tinnitus (Diers, Christmann, Koeppel, Ruf, & Flor, 2010; Flor & Diers, 2009).

While the methodology of the present study failed to further elucidate these neural mechanisms, this area of study is increasingly important and beneficial to wide ranging areas of medicine and psychology. Studies that aim to provide better understanding of the neural substrates of motor imagery and motor observation and how they relate to motor execution ultimately benefit a growing and thriving body of literature. In the end, a greater understanding of these processes through scientific advances further develops and improves both interventions and treatments. Each are aimed at bettering the lives of those suffering from a myriad of psychological, physical and psychophysical disorders resulting from many psychobiological causes including stroke, dismemberment, physical injury, and cognitive dysfunction.

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APPENDIX 1

Factors resulting from Sequential PCA. The Temporal PCA yielded 20 factors, followed by a Spatial PCA yielding 5 factors for each temporal component for a total of 100 components. The first temporal factor (TF01-) with the first spatial factor (-SF1) is listed first, followed by the additional spatial factors for the first temporal factor. The latency of the component and the channel where the component is maximal is listed along with the polarity and the amount of variance accounted for by the factor.

Factor	Latency	Channel	Polarity	FacVar	FacVarQ
TF01SF1	328	E128	1	0.0746	0.0442
TF01SF2	328	E134	-1	0.0215	0.0128
TF01SF3	328	E169	-1	0.0163	0.0096
TF01SF4	328	E145	-1	0.0093	0.0055
TF01SF5	328	E199	1	0.0078	0.0047
TF02SF1	1372	E18	-1	0.0455	0.0221
TF02SF2	1372	E234	1	0.0256	0.0124
TF02SF3	1372	E34	-1	0.0138	0.0067
TF02SF4	1372	E18	-1	0.0086	0.0042
TF02SF5	1372	E187	-1	0.0056	0.0027
TF03SF1	884	E133	1	0.0267	0.0104
TF03SF2	884	E208	1	0.0134	0.0052
TF03SF3	884	E37	1	0.0113	0.0044
TF03SF4	884	E18	1	0.0092	0.0036
TF03SF5	884	E188	1	0.0065	0.0025
TF04SF1	564	E175	1	0.0279	0.0117
TF04SF2	564	E199	1	0.0132	0.0055
TF04SF3	564	E18	-1	0.0103	0.0044
TF04SF4	564	E10	-1	0.005	0.0021
TF04SF5	564	E217	1	0.0036	0.0017
TF05SF1	64	E148	-1	0.0202	0.0096
TF05SF2	64	E101	-1	0.008	0.0038
TF05SF3	64	E95	1	0.0033	0.0016
TF05SF4	64	E136	1	0.0025	0.0012
TF05SF5	64	E101	-1	0.0013	5.97E-04
TF06SF1	212	E169	-1	0.0174	0.009
TF06SF2	212	E90	1	0.012	0.0062
TF06SF3	212	E150	-1	0.0023	0.0012
TF06SF4	212	E178	-1	0.0019	9.96E-04
TF06SF5	212	E102	1	0.0013	6.76E-04
TF07SF1	156	E19	1	0.0206	0.0082

TF07SF2	156	E90	-1	0.0083	0.0033
TF07SF3	156	E192	1	0.0027	0.0011
TF07SF4	156	E150	-1	0.0018	7.04E-04
TF07SF5	156	E13	-1	0.001	4.20E-04
TF08SF1	1120	E101	1	0.0196	0.0089
TF08SF2	1120	E213	1	0.0027	0.0012
TF08SF3	1120	E66	1	0.0024	0.0011
TF08SF4	1120	E212	-1	0.0017	7.83E-04
TF08SF5	1120	E18	-1	0.0017	7.77E-04
TF09SF1	436	E127	1	0.0123	0.0059
TF09SF2	436	E216	1	0.007	0.0034
TF09SF3	436	E94	1	0.0029	0.0014
TF09SF4	436	E256	1	0.0025	0.0012
TF09SF5	436	E202	-1	0.0019	9.22E-04
TF10SF1	1484	E101	-1	0.0214	0.0114
TF10SF2	1484	E112	1	0.0025	0.0017
TF10SF3	1484	E213	-1	0.0025	0.0013
TF10SF4	1484	E51	1	0.0013	6.71E-04
TF10SF5	1484	E101	1	6.85E-04	3.57E-04
TF11SF1	1060	E101	-1	0.0179	0.0092
TF11SF2	1060	E149	-1	0.0024	0.0013
TF11SF3	1060	Cz	1	0.0021	0.0011
TF11SF4	1060	E212	1	0.0013	6.54E-04
TF11SF5	1060	E199	1	9.78E-04	5.09E-04
TF12SF1	32	E101	-1	0.0219	0.0105
TF12SF2	32	E84	-1	0.0024	0.0013
TF12SF3	32	E212	1	0.0018	8.56E-04
TF12SF4	32	E90	-1	0.0011	5.54E-04
TF12SF5	32	E139	-1	7.19E-04	4.10E-04
TF13SF1	116	E168	-1	0.0177	0.0144
TF13SF2	116	E119	-1	0.0055	0.0046
TF13SF3	116	E159	-1	0.0014	0.0011
TF13SF4	116	E116	1	7.97E-04	6.72E-04
TF13SF5	116	E28	-1	4.87E-04	4.14E-04
TF14SF1	1184	E18	-1	0.01	0.0054
TF14SF2	1184	E242	-1	0.003	0.0016
TF14SF3	1184	E208	1	0.0017	9.76E-04
TF14SF4	1184	E213	1	0.0011	6.22E-04
TF14SF5	1184	E208	1	7.10E-04	4.01E-04
TF15SF1	716	E101	1	0.008	0.0048
TF15SF2	716	E213	-1	0.0025	0.0015
TF15SF3	716	E208	1	0.0019	0.0011
TF15SF4	716	E90	1	0.0012	6.85E-04
TF15SF5	716	E213	-1	8.08E-04	4.82E-04
TF16SF1	252	E101	-1	0.0095	0.0042
TF16SF2	252	Cz	-1	0.0024	0.0011
TF16SF3	252	E72	-1	0.0013	5.66E-04
TF16SF4	252	E90	-1	7.30E-04	3.53E-04
TF16SF5	252	E151	-1	4.93E-04	2.30E-04

TF17SF1	692	E54	-1	0.0077	0.006
TF17SF2	692	E213	1	0.0016	0.0012
TF17SF3	692	E66	-1	0.0012	9.34E-04
TF17SF4	692	E90	-1	9.83E-04	7.76E-04
TF17SF5	692	E213	-1	8.13E-04	6.34E-04
TF18SF1	132	E101	1	0.0092	0.0063
TF18SF2	132	E213	-1	0.0027	0.0019
TF18SF3	132	E103	-1	8.65E-04	6.11E-04
TF18SF4	132	E213	-1	7.49E-04	5.18E-04
TF18SF5	132	E90	1	4.64E-04	3.27E-04
TF19SF1	16	E101	1	0.0067	0.0047
TF19SF2	16	E213	1	0.0019	0.0013
TF19SF3	16	E213	-1	9.32E-04	6.59E-04
TF19SF4	16	E90	-1	8.45E-04	5.99E-04
TF19SF5	16	E90	-1	4.71E-04	3.35E-04
TF20SF1	1500	E230	-1	0.0039	0.0037
TF20SF2	1500	E185	-1	0.0013	0.0013
TF20SF3	1500	E208	-1	9.38E-04	9.15E-04
TF20SF4	1500	E46	1	5.43E-04	5.32E-04
TF20SF5	1500	E90	-1	4.20E-04	4.21E-04

CURRICULUM VITAE

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EDUCATION:

UNIVERSITY OF LOUISVILLE, Louisville, KY
MA of Psychology: May 2007
PhD of Philosophy: Anticipated May, 2011

UNIVERSITY OF KENTUCKY, Lexington, KY
Bachelor of Arts, Psychology: December 2002

TEACHING EXPERIENCE:

2003-20010

University of Louisville, Graduate Teaching Assistant, 2003-2006

- Assisted Primary Instructors in Introductory Psychology, Cognitive Processes, Statistics, and Tests & Measurements

University of Louisville, Graduate Research Assistant, 2006-2010

Developmental Neuropsychology Lab, Supervisor: Dennis L. Molfese,

Ph.D.

- Responsible for data collection, data processing and data analysis procedures using ERP Technology
- Responsible for writing and programming experimental paradigms to be used with ERPs
- Administered behavioral assessments including Repeatable Battery for the Assessment of Neuropsychological Status (RBANS),

- Conner's Performance Test – II (CPT-II), and Spaceflight Cognitive Assessment Test for Windows (WinSCAT)
- Mentored summer undergraduate students through process of creating, preparing, submitting and presenting poster presentation at national conferences.

Brescia University, Course Instructor, Owensboro KY, 2010

- Primary Instructor for Online Courses in Lifespan Development and Psychological Testing

CONFERENCE PRESENTATIONS:

Dien, J., Brian, E., Molfese, D. L., and Gold, B. T. (October, 2010). Combined ERP/fMRI Evidence For Lexical Effects In The Language Formulation Area. Talk presented at the meeting of the Psychonomics Society, Saint Louis, Missouri.

Dien, J., Brian, E., Molfese, D. L., and Gold, B. T. (October, 2010). Combined ERP/fMRI Evidence For Lexical Effects In The Language Formulation Area. Talk presented at the meeting of the Society for Psychophysiological Research, Portland, Oregon.

O'Brien, K.M., Brian, E., Garrod, K.N., Kheirandish-Gozal, L., Molfese, V., & Molfese, D. (February, 2009) The Effects of Minor Sleep Restriction Elicited by an Oddball Task. International Neuropsychological Society, Atlanta Georgia

Emerson, J., Brian, E., Kheirandish-Gozal, L., Molfese, V., & Molfese, D. (April, 2008) Impact of Simulated Microgravity and Sleep Restriction on Speech Perception in Adults. Conference on Human Development, Indianapolis, IN.

Brian, E., Kheirandish-Gozal, L., Molfese, V., & Molfese, D. (June, 2008). The Effects of Sleep Loss and Simulated Microgravity in Adults using a Rock-Paper-Scissors Paradigm. Associated Professional Sleep Societies, Baltimore MD.

Brian, E., Emerson, J., Kheirandish-Gozal, L., Molfese, V., & Molfese, D. (Oct, 2007). The Effects of Simulated Microgravity on Speech Perception Under Different Sleep Conditions. Research Louisville, Louisville KY.

Molfese, D.L., Waford, R., Warren, C., Pratt, N., Brian, E., Barnes, M., Gozal, D., & Molfese, P. (February, 2007). Brain organization during an attention task changes following minor sleep loss and head-down tilt. NASA Human Research Program Investigators' Workshop, League City, Texas.

Edgell, S.E., Harbison, J.I., & Brian, E. (November, 2005). Saliency effects in learning in a probabilistic Environment. Society for Judgment and Decision Making, Toronto, Canada

EDITORIAL EXPERIENCE:

Science Fair Judge, Kentucky Junior Science & Humanities Symposium, 2007

COMPUTER SKILLS:

Familiar with both PC and Macintosh operating systems

Programming in E-prime/E-Studio

Programming in HTML (Hypertext Markup Language)

Programming in ANSI C

Familiar with standard Microsoft Office programs

PROFESSIONAL EXPERIENCE:

2000-2003

The Southwestern Company, Nashville, TN

Manager/Salesperson, 2000 – 2003

- Personally recruited, trained, managed, and motivated salespersons for direct sales
- Worked 80+ hrs/wk and managed sales efforts
- Attended over 200 hrs of advanced sales, time management, managerial and motivational training
- Established success principles through direct sales (i.e. schedule, positive attitude, goal setting, & self –motivation, managerial and public speaking skills)
- Prospected and approached over 3,000 families of various socio-economic levels
- Relocated to Alabama, Nebraska, Missouri, and Arkansas

PROFESSIONAL ACHIEVEMENTS:

- Top Experienced Salesperson (top 3% nationally)-Southwestern Company: 2002
- Top First-Year Salesperson (top 3% nationally)-Southwestern Company: 2000
- President's Club (over \$2,400 profit in a week)-Southwestern Company: 5 times
- Gold Seal Gold (worked 80+ hours per week)-Southwestern Company: 2000-2003
- Monte Blanc Pen (first to 45 customers in a week)-Southwestern Company: 2000
- Big Check Award (net savings over \$5000) – Southwestern Company: 2000-2003

- Growth Award (increase of \$21,600 in retail sales)-Southwestern Company: 2002
- Dean's List – University of Kentucky
- University of Kentucky Men's Club Volleyball, Club President, 2000-2002

PROFESSIONAL ASSOCIATIONS:

American Volleyball Coaches Association

Psi Chi Honor Society