

ELECTROENCEPHALOGRAPHY (EEG) AND ITS USE IN MOTOR LEARNING AND
CONTROL

by

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Electroencephalography (EEG) is a non-invasive technique of measuring electric currents generated from active brain regions and is a useful tool for researchers interested in motor control. The study of motor learning and control seeks to understand the way the brain understands, plans and executes movement both physical and imagined. Thus, the purpose of this study was to better understand the ways in which electroencephalography can be used to measure regions of the brain involved with motor control and learning. For this purpose, two independent studies were completed using EEG to monitor brain activity during both executed and imagined actions. The first study sought to understand the cognitive demand of altering a running gait and provides EEG evidence of motor learning. 13 young healthy runners participated in a 6-week in-field gait-retraining program that altered running gait by increasing step rate (steps per minute) by 5-10%. EEG was collected while participants ran on a treadmill

with their original gait as a baseline measurement. After the baseline collection, participants ran for one minute at the same speed with a 5-10% step rate increase while EEG was collected. Participants then participated in a 6-week in-field gait-retraining program in which they received bandwidth feedback while running in order to learn the new gait. After completing the 6-week training protocol, participants returned to the lab for post training EEG collection while running with the new step rate. Power spectral density plots were generated to measure frequency band power in all gait-retraining phases. Results in the right prefrontal cortex showed a significant increase in beta (13-30 Hz) while initially running with the new gait compared to the baseline step rate. Previous work suggests the right prefrontal cortex is involved with the inhibition of a previously learned behavior and thus, our results suggest an increase in cognitive load to inhibit the previous full stride motion. After training, this increase in beta over the right prefrontal cortex decreased, suggesting motor adaptations had occurred as a result of motor learning. These results give promising evidence for a new method of ensuring permanent changes in performance that will benefit rehabilitation and athletic performance training programs. The second study in this project sought to understand differences in right and left-handers as they mentally simulate movement. 24 right and left-handed individuals (12 right-handers, 12 left-handers) were shown pictures of individual hands on a screen while EEG was collected. Previous research has shown that while solving this task, participants mentally rotate a mental

representation of their own hand to determine the handedness of the image. Event-related potential results showed that right-handers had an earlier and greater activation in the parietal regions than left-handers, whereas left-handers had a later and greater activation in the motor related brain regions compared to right-handers. These results suggest differing strategies while mentally solving motor related tasks between right and left-handers. We speculate this is a result of left-handers' need to adapt to a majorly right-hand dominant environment. Both these studies show the benefits of using EEG to understand the motor system in physically executed and imagined actions.

ELECTROENCEPHALOGRAPHY (EEG) AND ITS USE IN MOTOR
LEARNING AND CONTROL

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TABLE OF CONTENTS

TITLE PAGE	i
COPYRIGHT PAGE	ii
SIGNATURE PAGE	iii
LIST OF TABLES	vi
LIST OF FIGURES	vii
CHAPTER 1: INTRODUCTION	1
CHAPTER 2: REVIEW OF THE LITERATURE	7
Part I: History of Electricity and the Brain	9
Part II: Methods of Measuring Motor Learning and Control	14
Part III: Electroencephalography	21
Part IV: Benefits of Studying Motor Pathways with EEG	37
CHAPTER 3: METHODS	49
Part I: The Cognitive Demands of Gait Retraining: Psychophysiological Evidence For Learned Motor Skills	49
Introduction	49
Methods	56

Part II: Differing Neural Strategies in Left and Right-Handed Individuals during Motor	
Imagery.....	62
Introduction.....	62
Methods.....	68
CHAPTER 4: RESULTS AND DISCUSSION.....	75
Part I: The Cognitive Demands of Gait Retraining: Psychophysiological Evidence For	
Learned Motor Skills	75
Results.....	75
Discussion.....	81
Part II: Differing Neural Strategies in Left and Right-Handed Individuals during Motor	
Imagery.....	86
Results.....	86
Discussion.....	93
CHAPTER 5: CONCLUSION	98
REFERENCES	101
APPENDIX A: Institutional Review Board Approval-Study 1.....	133
APPENDIX B: Institutional Review Board Approval-Study 2.....	134

LIST OF TABLES

Table 1: Beta and gamma spectral power in the prefrontal cortex for all gait-retraining stages

Table 2: Mu and beta spectral power in the primary motor cortex for all gait-retraining stages

Table 3: Gamma spectral power in the primary motor cortex for all gait-retraining stages

Table 4: Accuracy scores for both groups as they responded to the Hand Laterality Task

Table 5: Reaction times for both groups as they responded to the Hand Laterality Task (HLT)

Table 6: Significant findings for the amplitude of the P1 event related potential (ERP)

component between both groups

Table 7: Significant findings for the amplitude of the N2 ERP component between both groups

Table 8: Significant findings for the amplitude of the P3 ERP component between both groups

LIST OF FIGURES

Figure 1: Experimental set-up for all data collections of the gait-retraining study

Figure 2: Data processing flow-chart for all gait-retraining EEG data

Figure 3: Angles of hand orientation included in stimulus images, diagram of the response pad used by participants to indicate response, and diagram explaining stimulus presentation protocol

Figure 4: Example of ERP components of interest

Figure 5: Power spectral density of all gait-retraining stages in the right prefrontal cortex

Figure 6: Group averages for beta and gamma frequency bands in the prefrontal cortex across all gait-retraining phases

Figure 7: Group averages for mu and beta frequency bands in the primary motor cortex across all gait-retraining phases

Figure 8: Group averages for the gamma frequency band in the primary motor cortex across all gait-retraining phases

Figure 9: Lateralization head plots for the P1, N2, and P3 ERP components for both left and right-handed individuals

Figure 10: ERP plots for both groups in the parietal, premotor cortex (PMC), and supplemental motor area (SMA)

Chapter 1: Introduction

The human brain is made up of roughly 86 billion independent nerve cells (Azevedo et al., 2009). Branch-like dendrites emerge from these nerve cells to receive electrical messages from neighboring neurons. This allows these cells to communicate with other areas of the nervous system. It is this communication between neurons that makes the majority of human function possible. An essential function of the brain is the planning and execution of bodily movement. The following pages discuss the neural brain regions involved with movement and how they can be monitored with the use of electroencephalography (EEG).

Movement is a vital feature of human life. The 1932 Nobel Prize winner, Sir Charles Sherrington, emphasized the importance of movement by saying, "to move things is all that mankind can do, for such the sole executant is muscle, whether in whispering a syllable or in felling a forest." (Sherrington, 1924). Without movement, the life sustaining abilities to eat, walk, reproduce and communicate are lost. Surely, with such a critical aspect of life comes an importance to understand the neural processes involved. The area of study dealing with the understanding of the neural, physical and behavioral aspects of executing movement is known as motor control (Schmidt, 1988). The study of motor control has

provided pivotal information towards understanding human movement since its foundation in the late 1800s (Bowditch and Southard, 1882) and has been accelerated in recent years with the development of technology and brain mapping methods.

Advances in recent technology have allowed for the monitoring and imaging of brain activity. This progress has benefited many disciplines of study across multiple fields such as medical diagnostics, prosthesis research and clinical practice (e.g. Castellano and Falini, 2016; Thut and Pascual-Leone, 2010; Muller-Putz, 2005). In years prior to these developments, the neural networks of the brain were difficult to localize, due to the fast rate at which they operate. However, it is now possible to observe regions of the brain with high temporal precision as they interact with one another. This ability to monitor changes in brain activation at a millisecond level is particularly important in the study of motor control where it seems that the decision to move and movement initiation are instantaneous (i.e. motor commands travel with a velocity of up to 59 m/s and can fire every 0.4 milliseconds; Harayama et al., 1991). An effective tool commonly used to measure these motor pathways is EEG.

Since its first recording by Hans Berger in 1929 (Brazier, 1971), EEG has developed into a standard method of measuring brain activity (Schomer & da Silva, 2011). EEG is collected through electrodes on the scalp that record electrical currents generated below

the skull surface. These currents can be used to identify a general location and magnitude of brain activity. The combination of moderate spatial and high temporal accuracy makes EEG an excellent option for mapping the brain function of sensory, motor and cognitive pathways (Toga & Mazziota, 2002; Shibasaki, 2012).

EEG has been used to benefit the study of motor control in many ways (Babiloni et al., 2009; Stasi et al., 2015; Caviness et al., 2006; Busse & Silverman, 1951; Chuang et al., 2013; Williams et al., 2016). An important area of EEG studies focus on measuring the neural networks of healthy humans involved in task performance. Increasing the knowledge of successful performance can assist in the development of training protocols and performance evaluation. Babiloni and colleagues (2009) compared the EEG of elite gymnasts to non-elite gymnasts. Their results showed a smaller cortical activation in elite athletes compared to non-elite athletes when making sport-related judgments. This gives evidence of an increase in neural efficiency as expertise is developed. Human performance and expertise is of great importance in military populations and thus EEG is commonly used for these purposes. In 2015 a study observed the brain activity of military pilots as they flew helicopters. An increase of EEG activity was shown during highly demanding procedures (i.e., flight take-off and landing). These results suggest that EEG recordings may be used to evaluate a pilot's cognitive performance and thus help to avoid catastrophic

events (Stasi et al., 2015). With the increasing pressure on athletes and soldiers to perform successfully, EEG studies involving human performance continue to increase in popularity.

Another branch of motor control commonly employing EEG is the study of motor dysfunctions. In a system as complex as the nervous system there are bound to be malfunctions and EEG has helped to describe and help improve some of these malfunctions (Duff, 2004; Cao et al., 2008; Cusack et al., 2012; England et al., 1958; Sburlea et al., 2015). Cao and colleagues used a computer algorithm to analyze the EEG data and isolate specific traits of the EEG profile that could be used to classify the severity of mild traumatic brain injury (mTBI)(Cao et al., 2008). This research will benefit many populations including athletes and soldiers due to the increasing knowledge of the long-term effects of mTBI (Almeida-Suhett et al., 2014; McInnes et al., 2017). In a separate study involving upper-limb amputees, differences in brain areas of amputees were seen as they observed and imitated arm actions done by intact demonstrators (with no prosthesis) and amputee demonstrators (with a prosthesis; Cusack et al., 2012). These findings indicate a correction mechanism used to account for the incongruence of a limb that does not match their own. This information is vital for the design of effective rehabilitation techniques. There are several examples of how EEG has been used to help the study of motor dysfunctions and

this number will continue to grow as additional methods of analysis and research techniques are developed.

Progress of recent analysis techniques and EEG collection strategies have paved the way for a large range of possible EEG studies to be done in the future (Gwin et al., 2010; Sburlea et al., 2015; Wagner et al., 2016; Bradford, Lukos & Ferris, 2016; Kelly, Mizelle & Wheaton, 2015). Previously, it has been difficult to collect EEG while participants performed gross motor skills due to the EEG signal being susceptible to noise. Recent studies have developed methods to remove this noise from the EEG signal, making it possible to observe the brain as it coordinates more complex movements (Gwin et al., 2010; Kline et al., 2015). This capability will benefit motor control immensely in both human performance and motor dysfunction. Additional techniques are using EEG coherence to better understand brain connectivity and cortical structure (Kelly et al., 2015; Wheaton et al., 2008). This information can help to understand different types of strokes and rehabilitative practices designed for therapeutic intervention. There are also many new techniques being used in order to develop EEG-based brain computer interfaces (BCI) that, among other purposes, can be used by disabled individuals suffering from movement disorders to interact with the environment (Kaufmann et al., 2014; Bell et al., 2008;

Rajangam et al., 2016; Alison et al., 2008). Clearly, the advent of new, more advanced EEG technologies shows great promise for further development in the future.

The purpose of this work was to better understand the ways in which electroencephalography can be used to measure regions of the brain involved with motor control and learning. In order to achieve this purpose, two experiments were conducted that apply specific methods of EEG collection and analysis to measure the motor systems of interest. One of these studies involved collecting EEG while participants ran with the purpose of determining the cognitive demand of running gait alteration. The second study involved the use of EEG to identify further differences in brain connectivity between right and left-handed individuals during motor simulation. Both of these studies were designed to further develop the use of EEG in motor control and contribute to the study of human movement.

Chapter 2: Review of Literature

Introduction

200 years of research has provided an impressive foundation for the understanding of the brain (Chvatal, 2015; Gross, 2007; Shibasaki, 2008). However, most of the brain's ability to control movement remains a mystery and continues to be at the forefront of scientific research (Amunts et al., 2014; Insel et al., 2013; Shibasaki, 2012). For this cause, EEG has been used to address many of these unknown areas. EEG is an amazing technology used to investigate brain regions in real-time. This technology is beneficial to the study of human movements both simple (e.g. finger movement [Pfurtscheller et al., 2003]) and complex (e.g. running on an inclined surface [Bradford, Lukos & Ferris, 2016]). While using EEG to address movement related questions, it is important to have a knowledge of the physiological sources of the EEG data, the ways in which it is recorded and for what purpose the EEG data is collected. The following sections will thoroughly explain EEG and how it can be used to benefit the understanding of motor learning and control.

This description will start by explaining the discovery of electricity in the brain and the processes through which these electrical impulses reach the scalp surface. Scientists have studied human movement for many hundreds of years and thus, after developing a

clear view of the neural processes used to initiate movement, the history and methods of measuring motor learning and control will be discussed. This description will include psychomotor measures, such as monitoring reaction time and performance errors, as well as neurological measures involving a brief description of fMRI and PET. A more thorough description of EEG will be provided in the following section describing the history and methods of EEG as well as ways in which those methods have been used to measure motor activity.

The final topic discussed in this review will help the reader to understand the great need for the use of EEG in the study of motor processes. Current studies attempting to increase the understanding of brain injuries, neurodegenerative diseases and other motor dysfunctions will be discussed as well as methods to assist those affected by these dysfunctions. This area is currently seeing great improvement, however, the need for further knowledge remains.

At the conclusion of this chapter the reader should have an in depth understanding of early research helping to understand the central nervous system, a surface comprehension of previous research measuring motor learning and performance, and the neural implications of EEG data for motor control in both healthy and impaired individuals.

PART I: The History of Electricity and the Brain

Development of the neuron theory

The body is filled with millions of neuron-driven motor units that excite our muscles to make human movement possible. Even a movement as simple as an eye blink is only possible due to a complex series of neural connections controlling every aspect of the movement. In the current day this is common knowledge, but this has not been the case for long. Luigi Galvani (1737-1798) was among the first to conceptualize the idea that electricity was the cause of human movement in a discovery Galvani called “animal electricity” (Brazier, 1961; Mauro, 1969; O’Leary & Goldring, 1976). Galvani’s experiment involved an electrically powered wire he used to excite dead frog’s legs. This sparked the idea of electricity generated in the body. In the following years, Galvani was forced to ceaselessly defend his hypothesis against many of the days’ top scientists. As a result of Galvani’s persistence, two important ideas came forth that impacted the world’s understanding of the human body: first, animal tissue is a conductor of electricity and second, electricity may be generated from inside the body (Mauro, 1969).

The discovery of “animal electricity” sparked a myriad of research done in efforts to understand the electrophysiological properties of human tissue. In 1836, a German scientist named Christian Gottfried Ehrenberg (1795–1876) proposed the first description

of nerve cells, an idea that he learned from studying the nervous system of leeches (Ehrenberg, 1836). This nerve cell hypothesis was further supported by work being done in Jan Evangelista Purkinje's (1787-1869) lab. Purkinje and his students were able to provide the first microscopic images of these cells, which they labeled "large cells in the cerebellum of mammals" (Purkinje, 1837; Valentin, 1836; Lopez-Munoz, Boya, Alamo, 2006). By the mid-19th century the notion of a human nervous system that controlled movement by means of electrical impulses was beginning to gain credit in the accepted scientific knowledge.

Electricity in the brain continued to be studied for the next 40 years without any real progress. It wasn't until the contention between Camillo Golgi (1843-1926) and Santiago Ramon y Cajal (1852-1934) that progress was made (Lopez-Munoz & Alamo, 2006). In 1873 Golgi introduced the new method of silver chromate staining that made it possible to see cells (Golgi, 1873). Golgi's work with silver staining caused him to support the "reticulum theory" put forward by Josef von Gerlach two years prior (Gerlach, 1871). The "reticulum theory" declared that the entire nervous system, including the brain was one continuous network made up of a dense mesh of thin filament. This was the accepted belief of the time and thus when Ramon y Cajal first contradicted this with the "neuron theory" it was not accepted openly (Lopez-Munoz & Alamo, 2006). Neuron theory stated that rather

than a large continuous system, each nerve cell is a totally autonomous physiological unit (Ramon y Cajal, 1888). Ramon y Cajal used Golgi's method to find images of single nerves with dendritic spines that worked to receive electrical impulses from other nerves. It was Ramon y Cajal that discovered the groundwork for the neuron theory that fuels the way scientists study nerves today. Years later, the discovery of the synapse by Sir Charles Sherrington was inspired by Ramon y Cajal's pivotal research and further developed the knowledge of how the CNS functions. Nerves do not communicate one with another by way of contact but rather, there exists a small space between the terminal branches of the axon and the receiving dendrite (Sherrington, 1906). These findings have fueled hundreds of discoveries of how messages are relayed from cell to cell.

Discovering the motor cortex

In the same period that the neuron theory was gaining its foundation, important research was being done on the brain to localize areas that manage specific functions. In 1870, while doing research on epileptic patients, the English neurologist John Hughling Jackson observed resemblances of common voluntary movements in the seizures his patients were experiencing (Jackson, 1870). This led Jackson to the hypothesis that there exists an area of the brain, just anterior to the central sulcus that plays a meaningful role in controlling movement. It was commonly believed at the time that the cortical brain played

no role in motor function and was nothing but an insignificant “rind” (Gross, 2007). Jackson, however, believed otherwise and his hypothesis fueled the studies of Gustav Fritsch and Eduard Hitzig in Berlin as well as David Ferrier in England (Fritsch & Hitzig, 1870; Ferrier, 1873). These experiments confirmed Jackson’s proposal and provided an important discovery: movements seemed to be localized to specific spots in the brain. The area anterior to the central sulcus was in essence a motor map for the body and particular body parts all had a specific region. When lesions were made in the brains of the dogs used in these studies, motor control of that body part was hindered or lost after healing from the surgery. Schaltenbrand and Woolsley (1964) and Penfield and Jasper (1954) showed that this motor map applied also to humans and other species. The same general topographic map was found across many species although the relative proportions of areas representing body parts were not the same. This fact generated the discovery that the motor map is not a point-to-point representation of the body. Instead, more finely controlled areas, such as fingers and mouth, are represented with larger areas suggesting a greater number of neurons activated for fine control (Kalaska & Rizzolatti, 2013).

What is now known as the motor cortex is made up of three principal regions. It was Campbell (1905) and Brodmann (1908) that first discovered functional divisions when they observed differences in functionality for this new motor area. While dividing the

human cerebral cortex into many different sections they separated the motor map into two functionally distinct areas. The region directly rostral to the central sulcus is now known as the primary motor cortex (M1). This brain region is essential in motor control and plays a role in the generation of movement as well as its kinetics and kinematics (Shibasaki & Hallett, 2006; Georgopoulos et al., 1982; Kalaska et al., 1989). The area of the motor cortex that lies anterior to M1 is called the premotor cortex. The premotor cortex participates in many motor functions, which include: the representations of peripersonal space, the coordination with sensory inputs to direct motor reactions, the formulation of specific plans for reaching movements and the learning of motor skills (Avenanti et al., 2012; Cisek & Kalaska, 2005; Fogassi et al., 2005; Mitz et al., 1991). Years after these two motor areas had been discovered, Woolsey (1951) would identify a third area involved with voluntary movement that, unlike the previous two regions, evoked movements on both sides of the body when stimulated. This area, located on the medial surface of the cerebral hemisphere, is now known as the supplementary motor area (SMA) and is known to play a role in movement planning, the sequential organization of multiple movements and the monitoring and evaluation of movement outcomes (Hoshi & Tanji, 2004; Scangos et al., 2013; Tanji, 2001). It is these three units of the brain, the primary motor cortex, the premotor cortex, and the supplementary motor area that make up the motor cortex that is

known today. The ability to monitor these three constituent regions as they process and perform motor actions has only been possible in recent years and has played a pivotal role in the measurement of motor learning and control.

PART II: Methods of Measuring Motor Learning and Control

In 1997 Robert Christina wrote a review article explaining and assessing the most popular methods of measuring motor learning and control at that time. In this paper, Christina states that the biggest challenge in studying motor learning is the inability to measure motor learning as it happens in the brain and that it must be inferred from motor performance (Christina, 1997). It has only been twenty years since Christina's remarks and already the barriers he mentioned have been overcome. With the use of electroencephalography, fMRI and other methods of brain imaging it is now possible to monitor changes in the brain that suggest learning has taken place. Using information from studies involving both observed motor performance and brain imaging, a more complete understanding of what is happening in the brain during movement can be formed. In the following section, methods used to track motor learning and control will be discussed. These include measurements of behavior and performance, as well as the neurological measures, which were alluded to previously.

Performance measures

Although early studies in motor learning were limited to performance measures, major contributions were made in the discipline nonetheless. Since the late 1800s, multiple methods have been developed to investigate the way in which the brain coordinates and learns motor skills (Bowditch & Southard, 1882; Fullerton & Cattell, 1892). Three methods that have proven to be effective are monitoring reaction time (Henry & Rogers 1960; Klapp, 1975), measuring performance errors (Henry, 1974; Hancock et al., 1995), and kinematic measures (Hall, 2003).

A common approach to studying the mechanisms that control movement is the process of monitoring reaction time. Reaction time is the interval between the presentation of a signal and the initiation of movement (Rose & Christina, 2006). Researchers have used reaction time repeatedly to better understand the decision-making process (Henry & Rogers 1960; Christina et. al 1982). These studies have provided important insight into the way the brain processes, decides and plans motor tasks. Reaction time has been further broken into multiple types that depend on multiple variables such as the number of stimuli to choose from and the number of movement options. As early as 1885, scientists understood that the number of possible responses/stimuli caused an increase in reaction time (Woodworth, 1938). A widely

known explanation of this effect was provided by Hick (1952) and Hyman (1953) which states that choice reaction time is linearly related to the log of the number of stimulus alternatives. This finding gives powerful insight into the way the brain interprets signals from the environment and uses them to decide on the appropriate response. Henry and Rogers (1960) discovered a similar relationship with task complexity instead of stimulus alternatives. They saw an increase in RT with respect to task complexity. These findings suggest the increase in reaction time is due to an increase in time needed to plan and program the movement. Both Hick and Hyman and Henry and Rogers used reaction time to provide significant information into the neural pathways of the brain without the ability to measure them directly.

An additional method commonly used to assess a participant's ability to perform or learn a skill is by measuring performance errors (Henry, 1974; Patrick, 1971). Successful performance of a motor task may require the correct application of speed, timing, force, accuracy, or any combination of them all. There are multiple techniques of measuring error such as absolute error, constant error, and variable error, which can be used to detect the participant's bias or inconsistency with respect to certain performance outcomes. These approaches can help the researcher to understand any connections that may exist between specific types of error/outcome and physical performance aspects (such as too

high or too low) as well as possible causes of the error. With this knowledge, researchers can better understand the processes of motor execution that are most difficult and why.

A third method commonly used to measure movement and motor control is to measure the characteristics of movements with the use of kinematics. Kinematics is the study of the geometry, pattern, or form of movement with respect to time (Hall, 2003). This type of performance measure often uses tools such as cameras and motion analysis technology to provide information on the characteristics of movement. Commonly measured aspects are joint or limb velocity, displacement and acceleration (Kennedy et al., 2015; Enoka, 2002). This can be very beneficial when attempting to understand specific movement characteristics and how they may change with training.

Neurological Measures

Despite the fact that scientists have been studying motor control since the late 1800s, measuring motor learning and control on a neurological level has mainly been developed in the last century. These developments have greatly impacted our realization of the events occurring in the brain that result in physical movement. The most familiar means by which we can study the neurological patterns of the brain are divided into two categories: invasive and non-invasive techniques. Two examples of invasive techniques that have been

employed to study motor control will be discussed in this section as well as three commonly used non-invasive measures.

Although generally limited to animal studies, intracellular recordings are an example of an invasive method that has been used to understand the brain and movement. With this technique, a sharp micropipette is inserted into the brain and used to measure intracellular electric potentials during the planning and execution of movement. Intracellular recording measures were among the first to clarify the roles of the basal ganglia and cerebellum in the planning, control and learning of movements (Connor & Abbs, 1991; DeLong, 1972; Gilbert & Thach, 1977). Another invasive technique restricted to animals is the study of lesions and ablations. These two methods involve either cutting out or damaging certain structures in the brain, respectively. Fritsch & Hitzig (1870) used this method in their pivotal discovery of the topographical motor map and development of the motor cortex mentioned previously. These findings were quite significant and contributed greatly to the area of study. However, due to their highly invasive nature, the techniques of using lesions and ablations to study the motor cortex are not commonly practiced by many motor control scientists.

Non-invasive methods are more commonly practiced in today's study of motor learning and control. They provide clear data of brain functions, yet are not harmful to the

participants. Three examples of these techniques that have made large impacts on the study of motor control are positron emission tomography (PET), functional magnetic resonance imaging (fMRI), and electroencephalography (EEG).

Started by a group of scientists in the 1970's, PET has proven to be an effective method to view the neurological elements involved with motor processes (Oldendorf, 1980; Grafton et al., 2002; Ghatan et al., 1995). PET is obtained by injecting radioactive positron-emitting isotopes into the blood stream, which then can be tracked by a computerized reconstruction procedure to create a tomographic image. Different radioisotopes are used to identify specific areas of the body and, when used in motor control studies, can demonstrate specific areas associated with certain functions. Among the first to use this method in motor control were Ghatan and colleagues, who used PET to see motor cortex activity during perceptual motor tasks and navigation plans (Ghatan et al., 1995). PET has been used in years since to study many other areas of motor control including neurodegenerative diseases and sequence learning (Grafton & Ivry, 2002; Grafton, Hazeltine and Ivry, 1995; Bohnen et al., 2014; Loane & Politis, 2011).

An additional non-invasive method of measuring the brain is with the use of functional magnetic resonance imaging (fMRI). This technique measures changes associated with blood flow in the brain to understand the neural activation of a task. fMRI does this by

generating a series of images of the brain taken in sequence and statistically identifying differences that may exist between each image. The spatial precision of fMRI is superior to many other brain imaging techniques and thus has been a benefit in the study of motor learning and control (Rose & Christina, 2006). This ability has been useful in many areas including the identification of neural structures involved in the acquisition and retention of motor skills (Coynel et al., 2010; Karni, 1996). While in the MRI machine, the participant must stay relatively still, and thus the motor skills performed while collecting fMRI data must be rather simple in nature. This drawback of fMRI has limited its ability to study more complex movements. However, fMRI has been greatly helpful to the study of motor imagery. Gerardin et al. (2000) used fMRI to show similar neuronal activity in the motor cortex, basal ganglia and cerebellum during both real and imagined movements. This finding has sparked many other studies using fMRI to understand the neural activity of motor imagery (Guillot et al., 2008; Chen et al., 2016; Wang et al., 2014). Aside from motor learning and imagery, fMRI is beneficial to many other areas of study with its superior spatial precision. However, it is not as temporally precise as other methods such as electroencephalography.

PART III: Electroencephalography

Electroencephalography (EEG) is a neurological technique commonly used to measure motor learning and control. With the use of electrically conductive electrodes placed on the scalp, EEG measures electrical currents generated by the brain that reach the scalp surface. Although EEG lacks the spatial resolution of fMRI, EEG is superior in temporal resolution taking up to 20,000 samples per second from each electrode. This ability has made EEG a dominant tool used to identify the neural networks activated during the execution and planning of motor skills. The following section will be dedicated to the explanation of EEG and how it can be used to measure the planning and execution of motor tasks.

History of EEG

In the mid 19th century there was a great amount of excitement surrounding the electrical activity of the body. The study of electricity as a whole was a very young science and, as described earlier, man's understanding of the nervous system was still developing. The contention between Luigi Galvani and Alessandro Volta had fueled the discovery of electrophysiology but the concept of independent nerve cells would not be understood for a few more years (Brazier, 1961; Mauro, 1969; O'Leary & Goldring, 1976). In 1848, Dr. Emil du Bois-Reymond published a study that laid the foreground of our understanding of

the action potential (Du-Bois-Reymond, 1848). Du Bois Reymond was able to record a negative variation from excited peripheral nervous tissue that he defined as, “muscular current.” This current is an essential concept that makes electroencephalography possible.

It was Du Bois Reymond’s success in measuring current from a peripheral nerve that sparked an idea for Richard Caton in 1875 (Caton, 1875). Caton concluded that if currents could be measured in the periphery, it must be possible to measure currents directly from the brain. Caton put this idea to work with an oxyhydrogen lamp shown on the mirror of a galvanometer and two electrodes placed at different points on the surface of an animal brain. This process made it possible to see small currents passing through the multiplier. From this experiment and following experiments done by Caton, it was discovered that electric current can be measured at the brain level, and may have a relation with specific movements.

The study of EEG continued to be developed by many researchers across the globe but it was not for another 40 years that developments towards a successful EEG would be made. In 1913, a Russian scientist named Vladimir Vladimirovich Pravdich-Neminsky published the first images of electroencephalograms measured from the unopened skull of a dog (Pravdich-Neminsky, 1913). In this early EEG recording, Pravdich-Neminsky recognized electrical oscillations that varied in frequency from 12-20 per second, all the

way up to 35 per second. These frequency bands were very similar to the alpha and beta bands that would be described by Hans Berger in later years.

In 1929, a young German psychiatrist named Hans Berger was the first to record electroencephalogram in human subjects (Berger, 1929). Using platinum wires as electrodes, Berger identified and named the frequency bands of alpha and beta and witnessed changes in their activity caused by eye opening, painful stimuli, loud noises, and mental effort. Since Berger's discovery, scientists have combined EEG results with a firm knowledge of the nervous system to further understand the many underlying functions of the brain.

The Neurophysiology of EEG

The collected EEG data appears in waveforms. These waveforms represent electric currents measured by the electrodes at the scalp surface. The majority of these currents are generated from the extracellular field potentials of millions of nerve cells as they communicate through specific neural processes of the brain. This section will provide a brief background into the neurophysiological processes involved in these currents in order to best understand and interpret the collected EEG data.

Generation of an action potential

The simplest unit of the central nervous system is the nerve cell. It is the communication between these cells that allows all human function. This communication is made possible through a small electrical signal called an action potential. The currents that make up an EEG signal result from a chain of events that begins with the action potentials of many nerve cells. The generation of an action potential begins with many protruding branches called dendrites reaching out from the cell body of a neuron in search of the axon terminal branches of surrounding neurons. The space between the terminal branch of the relaying neuron (known as the pre-synaptic neuron) and the dendrite of the receiving neuron (known as the post-synaptic neuron) is known as the synapse or synaptic gap. The pre-synaptic neuron releases neurotransmitter into the synapse, which then binds to a ligand-gated ion channel specific for that neurotransmitter. Once the neurotransmitter is bound, the channel opens and, due to a concentration gradient of sodium ions, these positively charged ions rush into the intercellular space of the neuron and by result, slightly raise the membrane potential of the nerve from its resting point of -70 mV. If this channel is acting in solitude, nothing will happen and the cell will return to resting potential. However, if many ion channels open simultaneously, the depolarization will summate to the threshold point of -55 mV. Once the membrane potential hits the threshold of -55 mV

this triggers the opening of the voltage-gated ion channels of the axon at the neuron hillock to open and sodium enters at a very fast rate. This generates an action potential that then travels the length of the axon to the axon terminal and prompts the exit of neurotransmitter filled vesicles into the synaptic gap to be received by other post-synaptic neurons. When sodium enters the axon it causes the membrane potential of the cell to rise to roughly +30 mV. Upon reaching this potential, potassium channels then open and allow potassium to leave the cell, repolarizing the cell in effort to restore resting membrane potential.

The action potential traveling down the axon of the neuron creates an electric current. However, it is not this current that the EEG signal represents. The currents generated by action potentials inside the axon are impossible to track, due to the insulating myelin sheath and the simultaneous firing of surrounding neurons that cause the currents to cancel out. The EEG signal comes from the electric dipoles that result from the action potentials of many neurons in synchrony.

Electric Dipoles and EEG measurement

At the beginning of the action potential generation process, ligand-gated ion channels are opened. When these channels open, the extracellular space that is populated by positively charged sodium ions, due to the concentration gradient, becomes much more

negatively charged because of the sudden vacancy of these positive sodium ions. This extracellular negativity is known as the sink. Later in the process, the action potential is created. As a result, the membrane potential reaches +30 mV and the voltage gated potassium channels open. This causes a rapid outflow of positively charged potassium into the extracellular space and results in a much more positively charged extracellular space in the area of the axon terminal. This extracellular positivity is known as the source. The combination of the sink near the cell body and the source near the axon terminal creates a very small magnetic dipole. When this process involves many millions of neurons, it generates a magnetic dipole large enough to trigger an electric current that can be measured at the scalp level. It is these currents that create the different waveforms of the EEG signal.

EEG and Waveforms

Neurons are not able to continuously produce action potentials the way that a fire hose delivers water. After an action potential has traveled down an axon and caused the release of neurotransmitter, neurotransmitter will not again be released until the firing neuron has had an opportunity to repolarize, hyperpolarize and depolarize once again. The speed of this process and the firing rate of a neuron depends on its location and what networks it is involved in (Adrian & Mathews, 1934; Van Wijk et al., 2012). These diverse

firing patterns cause distinctive wave oscillations observed in the EEG signal and can be divided into six groups: delta, theta, alpha, mu, beta and gamma. The following paragraphs will briefly discuss each of these wavelengths.

Delta waves are the slowest waves and have a duration of .25 seconds or longer. This implies a frequency band of 0-4 Hz. Delta waves are mostly generated in both the thalamus and cortex and are commonly found during sleep and anesthesia (Walter, 1936). Theta waves oscillate at a frequency of 4-7 Hz and are commonly found in the hippocampus and cortex. Theta waves have generally been associated with learning and recognition tasks as well as in spatial navigation (Cornwell et al., 2008; Raghavachari et al., 2001). However, In a more recent study, theta oscillations were used to locate activity in the anterior cingulate cortex during error processing of motor behaviors (Arrighi et al., 2016).

The frequency band above theta is known as alpha and is best seen in a relaxed, awake state with eyes closed. It was the alpha band that Hans Berger first saw in his early EEG studies (Berger, 1929). Alpha frequency covers the span of 8-13 Hz. Classic alpha activity is said to originate in the visual cortex but there are also rhythmic activities within the alpha band found elsewhere in the cortex. The mu rhythm (10-12 Hz) is a sub-frequency band within alpha that is commonly associated with motor learning and control (Pfurtscheller et al., 2006; Tangwiriyasakul et al., 2013; Yi et al., 2016). It is found at its

highest power over the sensorimotor cortex while the subject is in a state of muscular relaxation (Schomer & Lopes de Silva, 2011). Pfurtscheller and colleagues confirmed this observation in 2006 (Pfurtscheller et al., 2006). During hand motor imagery tasks, the mu amplitude above the hand area of the motor cortex decreased. However, the same area showed an increase in mu amplitude during foot or tongue motor imagery and hand imagery was absent providing further evidence that the mu rhythm plays a role in the control of movement. Houdayer (2016) was able to show neurophysiologic evidence of motor learning in the mu rhythm by tracking a change in this frequency band following two weeks of piano training. Due to a proven role in movement, the mu frequency band within alpha is often analyzed in studies involving motor learning and control.

Following alpha and mu, is the beta frequency band (14-30 Hz). Beta is generally associated with motor planning and control and is often weakened during motor activities. Such was the case with Jurkiewicz et al., (2006) as they observed a peak in beta amplitude immediately following a finger movement. It is also common for changes in beta amplitude to be seen in greater movements involving many joints and muscle groups. This denotes a role in movement coordination and control. Wagner and colleagues (2012) confirmed this role as they attempted to determine the cortical activity in subjects with robotic assisted walking. Their results showed a depression of both mu and beta activity while participants

actively tried to move their legs with the robot. Participants doing the same task, but instead passively allowing the robot to move their legs showed the opposite in mu and beta amplitude. The next frequency band, gamma, also followed the same pattern in Wagner's robotic walking study.

Gamma waves are classified as anything above 30 Hz, with the assumption that all frequencies behave the same after 30 Hz. However, this concept was recently contradicted by Seeber and colleagues (2015). They observed a difference in amplitude direction in high and low gamma frequencies. This has sparked ongoing studies into possible functional differences in these higher frequencies. Gamma waves are currently believed to be involved with movement coordination, increased focus or attentional demand and the binding together of populations of neurons for the purpose of performing a certain cognitive or motor task (Schomer & Lopes da Silva, 2011; Murthy & Fetz, 1992). The effect of attentional demand on gamma power was shown by Wagner (2014) who had participants walk with robot assistance on a treadmill while being shown a virtual environment in which they were walking without assistance. Participants in the virtual environment condition had a decrease in beta and gamma power compared to two control groups not involved with the virtual environment. These findings confirm the concept of the gamma bandwidth participating in the cognitive demands of motor tasks.

The difference in functionalities in these waveforms can provide important insight into what is happening inside the brain as it performs different actions. With this knowledge, motor control researchers have developed many techniques to learn more from the EEG waveforms resulting from motor activities (Wagner et al., 2012; Castermans et al., 2014; Babiloni et al., 1999; Pfurtscheller et al., 2003).

Methods of Collecting EEG Data with an emphasis on motor learning and control

EEG is a tool that can be used in many ways. As explained above, there are many techniques of using EEG that can be employed to analyze the EEG signal. Certain of these techniques have proven to be particularly beneficial in the realm of motor learning and control. The following sections will give a brief insight into the differences of these methods and give examples of how they have been employed by researchers in the field.

1. Event Related Synchronizations/De-Synchronizations

The networks of the brain involved in sensorimotor processing and control involve many millions of nerve cells that oscillate together primarily within the frequencies of the theta, alpha, beta and gamma bands (>4 hz). The power of these frequencies is dependent on the synchronization of the neural networks involved and the many millions of nerve cells that comprise them. When a demand is placed upon the brain, such as a necessity for greater attention or a physical movement executed by the motor pathway, these neural

networks decrease in synchrony as they begin to fire in many different directions and rhythms to respond to the new demand. This suppression of nerve synchrony in response to an outside event is known as an event-related desynchronization (ERD). The opposite effect, an increase in frequency amplitude, is known as an event-related synchronization (ERS) (Pfurtscheller and Lopes de Silva, 1999). The observance of ERDs/ERSs has shown that voluntary movement results in a desynchronization in the upper alpha and lower beta bands, localized close to sensorimotor areas (Babiloni et al., 1999). Research using unilateral upper limb movements with right-handed individuals has shown that this desynchronization begins in the mu wave band about 2 s prior to movement onset on the contralateral side. As the movement initiation draws closer, the desynchronization becomes bilaterally symmetrical immediately before movement execution (Pfurtscheller and Aranibar, 1979; Pfurtscheller and Berghold, 1989; Derambure et al., 1993; Toro et al., 1994; Stancak and Pfurtscheller, 1996b; Leocani et al., 1997). ERDs/ERSs have been observed to find many significant findings in motor control and are thus regularly monitored in EEG studies.

2. Event Related Potentials

Another event-related method in EEG studies is the measuring of the event-related potential (ERP). ERP is defined as the electrical activity that is triggered by the occurrence

of particular events or stimuli (Schomer & Lopes Da Silva, 2011). Commonly used forms of stimuli involve sensory events such as visual cues, auditory signals or somatosensory stimuli. These electrical changes are ever so slight and too small to observe in a single trial. In order to visualize and observe the ERPs, all trials must be layered on top of each other and averaged together. This allows for the removal of signal that is not involved with the stimulus response, as well as the negation of unwanted artifact due to muscle activity or eye movement. The result of this process is a single waveform from each channel that is time locked to the stimulus event. When used as a research tool, ERPs have been very helpful in understanding the timing of neural activity generated during cognitive processes, as well as gain a better knowledge of the cortical distribution of specific neural functions (Toga & Mazziota, 2002). General characteristics of the ERP show positive and negative variations at specific periods after or before the movement. These variations have been used in many studies to understand mental workload, information processing, and motor planning (Falgatter et al., 2000; Reitschel, 2014). Rossini and colleagues (1989) used ERPs to identify a specific difference between patients with Parkinson's disease and a control group of healthy individuals. The difference was seen in a component of the ERP, 30 ms after the stimulus was given. Names of these ERP components are given due to their direction, positive or negative, and either their latency from the stimulus or their order

from the stimulus. Thus, the component seen by Rossini was named the N30 wave (i.e. N30 is in the negative direction and 30 ms following the stimulus). In the parkinsonian patients, the wave component was absent in the frontal electrode sights specifically over the supplementary motor area (SMA). This information was used to better understand the network connecting the basal ganglia and the SMA. This early work with Parkinson's disease using ERPs has sparked many similar studies including the work of Solís-Vivanco et al. (2015) who identified an ERP component with amplitude that correlates with Parkinson's disease severity. Due in part to its timely precision, the mentioned studies have shown the ERP to be effective in better understanding the processes involved with stimulus response and motor planning.

3. Event Related Spectral Perturbations

Although the ERP is effective in tracking specific reactions to an event by the time-locked EEG data, it is ineffective in reporting changes in wave band power. Event related spectral perturbations (ERSPs) are a way in which this is done. By averaging the amplitude of all trials time locked to the stimulus event, it makes it possible to see the changes in frequency power as the brain reacts to the event. The 2-dimensional image that is produced allows researchers to localize a specific area involved in the processes being studied and compare the image across study conditions (Makeig, et al., 2004). ERSPs have

been utilized in many ways to identify synchronizations and de-synchronizations in different wave frequencies in response to certain stimuli (Brooks & Kerick, 2015; Rossi, 2014; Li et al., 2011; Chen et al., 2013). ERSPs are particularly beneficial in studies involving mental workload (Brooks & Kerick, 2015) and motor imagery (Chen et al., 2013).

4. Movement related cortical potentials

The movement related cortical potential (MRCP) is a slow negative shift in the EEG recording that is observed around 2 seconds prior to the initiation of movement and has been measured to develop the understanding of the nerve pathways that govern movement initiation (Wright et al., 2011). It was Bates in 1951 (Bates, 1951) that first attempted to identify this potential change in the cortex over the precentral gyrus prior to the onset of movement. Bates was unsuccessful in this attempt but he was successful in demonstrating the use of EEG simultaneously with EMG. Kornhuber and Deecke (1965) were inspired by the methods of Bates and essentially replicated his study with a simple finger movement task instead of a grip task. A negative potential in the lower frequency was shown roughly a second prior to movement initiation. Kornhuber and Deecke named this potential the Bereitschaftspotential (BP), which has often been called the readiness potential. Further studies of the Bereitschaftspotential potential helped to gain a greater understanding of this wave and it was discovered that the readiness potential was a component of the greater

MRCP. Recent studies have shown that MRCP initially starts in the supplementary motor area and makes its way into the premotor cortex and shortly thereafter into the primary motor cortex (Shibasaki, 2012). This discovery has helped to form our understanding of the planning role of the supplementary motor area in voluntary movement and the usefulness of MRCPs in measuring motor control.

5. EEG Coherence Analysis

EEG coherence is a method of gathering EEG that reflects functional connectivity between brain regions. Previously discussed methods have measured differences with respect to time or waveband, EEG coherence analysis measures the phase consistency between pairs of signals in each frequency band (Nunez et al., 1997; Shaw, 1983). Two examples of how this method has been used are to determine differences in the activity in the brain with respect to separate cerebral hemispheres (Wheaton et al., 2008; Kelly et al., 2015) and regional connectivity involved in learning (Wu et al., 2014).

6. Principal and independent component analysis

Amid the collected EEG data are many different components that may not all stem from a source inside the head or may be from brain regions unrelated to the task. These unwanted components, known as artifacts, can come from movement of the electrodes, muscle or eye movement, line noise and many others. The raw EEG data is put through a

detailed protocol to filter these unwanted aspects of the signal from the brain waves to be measured. This review will not cover this process in depth, however with respect to EEG studies of motor control, PCA and ICA are of prime importance due to their dynamic nature and will be briefly described.

The measurement of brain activity with only one electrode would serve no purpose due to many events happening in the brain at one time. The collected brain signal can be related to the ripples that result from dropping a rock in an otherwise calm pond, greater activity is seen closest to the signal and as the signal travels outward it becomes less extreme. With the use of many electrodes and computer algorithms designed to compute activity across all the electrodes it is possible to locate specific regions as the source of the observed activity. This is made possible by methods of analysis known as principal component analysis (PCA) and independent component analysis (ICA). As a general statement, fMRI is a more accurate technique for locating specific sources of brain activity. However, with recent developments in PCA and ICA, EEG is gaining ground in the conversation of source location. PCA is a method used to remove variance in the signal that is unwanted and irrelevant to the study (Skrandies, 1989; Kayser & Tenke, 2005). PCA first determines the maximum amount of data variance and then works backwards towards the maximum amount of residual variance determined by the user. This is particularly useful

in extracting components of an ERP that are due to a difference in condition (Schomer & Lopes Da Silva, 2011). The main purpose of ICA is to decompose the signal as a whole into individual components (Makeig et al., 1997; Delorme et al., 2007). In the example with the rock thrown into a pond, imagine many rocks are being thrown into the pond simultaneously. ICA would work to take the measurements from all the ripples and locate every rock's location in time and space that it first splashed into the pond and to remove any ripples not due to the rocks. This tool is particularly helpful in studies collecting EEG simultaneous with physical movement. The movement causes artifact in the signal that can overshadow the underlying brain waves. ICA is an effective tool that has been used to remove this noise without affecting the brain activity underneath and has allowed for the gathering of EEG during complex body movements (Wagner et al., 2016; Gwin et al., 2011; Bulea et al., 2015; Castermans et al., 2014; Bradford, Lukos & Ferris, 2016).

Part IV: Benefits of Studying Motor Systems with EEG

Introduction

As described previously, EEG can be a very helpful tool to better understand the inner working of the brain. It can help to identify and observe specific regions of the sensorimotor cortex and measure the oscillations and electric potentials that are involved with the planning, control and execution of motor tasks. EEG by itself, however, is no more

than a tool and is useless without the correct application. This section will focus on ways researchers have utilized the EEG techniques discussed in this review to provide useful knowledge benefiting the study of sports and human performance as well as the study of sickness, disease and injury.

EEG in Sport and Athletic Performance

In an age where improving sport performance is of great interest, studying the brain's involvement in athletic performance has received much attention in recent years (Ofori, Coombs & Vaillancourt, 2015; Chuang et al., 2013; Zhu et al., 2015). However, a regular limitation to this area of study has been the inability to monitor the brain while sport related skills are performed. Notwithstanding, many techniques with EEG have been developed to compensate for this limitation and continue to determine the neurophysiology of successful athletic performance (Thompson et al., 2008). The following section will discuss common methods to overcome this limitation as well as frequent study design techniques used to understand the brain activity involved with sport and performance.

An important technique used by electroencephalographers to study the neural pathways involved in sport performance is motor imagery. This approach avoids the dilemma of movement affecting the EEG signal yet still allows for the monitoring of neural

processes involved with movement. A study done in 1990 set the stage for motor imagery by showing changes in mean alpha band frequency as participants imagined themselves swimming a distance of 100 M (Beyer et al., 1990). Since then, multitudes of EEG studies have contributed to the understanding of motor imagery and its role in physical performance (Cebolla et al., 2015; Wilson et al., 2015). Cebolla et al., (2015) used ERPs, and ERD/ERS to show the effects of an imagined ball throw on brain activity. These findings provide important insight for the use of motor imagery with athletes and its ability to be used as a practice method to benefit athletic performance.

An additional method of using EEG to monitor motor pathways involved with sport performance is to identify characteristics of a sport movement and gather EEG while only portions of the movement are being executed (Ofori et al., 2015; Pastotter et al., 2012). Ofori and colleagues exemplified this practice in 2015 while studying tennis serves and other overhead ballistic movements. Ofori et al. used event related spectral perturbations (ERSPs) and a ballistic arm rotation task to discover a correlation between the theta band power of the left motor area and contralateral arm acceleration (Ofori et al., 2015). These findings provide significant insight into the underlying neural framework that characterizes a successful tennis serve as well as give implications to be able to do the same in many other sport related tasks.

The final method of researching EEG during sport and athletic performance has only been possible in recent years. Although the practice of gathering EEG during gross body movements does produce movement artifact, recent studies have been successful in removing these artifacts and observing the neural activity underneath. This has been made possible with the use of a specific data analysis process that involves recently developed algorithms. Gwin et al. (2010) recorded EEG while participants ran and then clearly explained a method to remove the movement artifacts from the EEG data. These methods have since been repeated to measure the neural pathways involved with running at different speeds (Bulea et al., 2015; Lisi, Morimoto, 2015), avoiding obstacles while walking (Wagner et al., 2016), walking at different levels of incline (Bradford, Lukos and Ferris, 2016), and the maintenance/loss of balance during walking (Sipp, Gwin, Maekig & Ferris, 2013) among many more (Bertrand et al., 2013; Castermans et al., 2014; Kline et al., 2015; Wagner et al., 2012; Urigüen and Garcia-Zapirain, 2015; Wagner et al., 2014; Lisi and Morimoto, 2015; Sipp et al., 2013). This new ability to measure the brain as complex actions are being performed may allow us to see how the brain coordinates the kinematic and kinetic skills across multiple joints and limbs simultaneously. This ability sparks multiple directions for possible science implications but could indeed help to create different training protocols towards specific athletic performance goals.

The above paragraphs provide exciting information as to how these brain regions can be measured and monitored. However, with these methods, how does one apply them to develop effective study designs that help to understand the brain activity in sport and athletic performance? A common method of addressing this question is to make comparisons of EEG profiles. A common comparison made by researchers is to compare the EEG data from novices to that from experts. Doppelmayr et al. (2008) compared novice rifle shooters to experts. In rifle shooting, a calm composure and steady hand is key. This was shown using spectral analysis to show an increase in frontal midline theta 3 seconds prior to shooting for experts that was absent in novices. These findings denote a greater ability to focus attention in experts vs. novices.

Another common comparison made in EEG data is to compare successful trials to unsuccessful trials. Chuang, Huang, and Hung (2013) used this technique effectively to show that a higher frontal midline theta power was common in the preparatory stage of successful free-throw basketball shots than in unsuccessful free-throw shots. This study gives neurophysiological evidence for the need to control arousal and attention.

In summary, electroencephalography is an incredible tool for the research of sport and athletic performance. It gives researchers the ability to monitor similarities between imagined and executed motions. It also allows for the measuring of neural activity during

the execution of both simple and complex motions. These new methods, and the research that applies them will benefit athletes and coaches as they strive to improve sport performance as well as researchers as they strive to understand motor dysfunctions of the CNS.

EEG in Motor System Dysfunctions

Many people are affected by dysfunctions of the central nervous system or injuries that have impacted its function. EEG has been a helpful tool for researchers striving to better understand a number of these dysfunctions and develop effective methods of assisting the populations that they affect. The following section will briefly explain a few of these cases in which EEG has proven to be helpful and give specific examples of each. The cases discussed will be: mild traumatic brain injury, Parkinson's disease, strokes, and the development of brain computer interfaces designed to benefit these populations.

Brain Injury

It is reported by the Center for Disease Control and Prevention that 1.7 million people every year suffer from traumatic brain injury (TBI) (CDC, 2010). These injuries come from a number of areas including car crashes and work accidents; however, a type of head injury that has received a large amount of attention in recent years is injuries experienced during sport participation known as mild traumatic brain injuries (mTBI) or

concussions. Recent studies have begun to discover the long-term affects that result from these head injuries (Guskiewicz et al., 2005; Lehman et al., 2012; Randolph et al., 2013). This has fueled current research on the neurophysiological symptoms of head injuries, and training programs to help improve them. One of these symptoms, oculo-motor based problems, was addressed by Yadev and colleagues in 2014. Yadev used visual evoked potentials (VEP), a type of ERP, and alpha frequency to investigate the efficacy of an oculomotor vision rehabilitation (OVR) program. It was shown that six weeks of OVR was effective in increasing both the VEP amplitude and alpha band power, thus showing that OVR can help to treat mTBI symptoms (Yadev et a., 2014).

Another branch of traumatic brain injury research uses EEG to assist in the assessment and classification of mTBI. Cao, Tutwiler, and Slobounov recognized that many athletes were returning to play before neurophysiological symptoms had ceased and designed an algorithm to be applied to EEG data isolating band frequencies that may still show signs of mTBI effects (Cao, Tutwiler & Slobounov, 2008). Slobounov et al. (2011) provided a technique for a similar purpose that uses virtual reality while collecting EEG. This technique uses ERSPs in the theta frequency band to assess mTBI (Slobounov et al., 2011). Methods and research such as these will continue to use EEG to benefit the understanding of mTBI and its long-term effects.

Parkinson's disease

Parkinson's disease is a chronic and progressive movement disorder that is associated with malfunction and death of nerve cells found in the basal ganglia of the brain. EEG has long been a fundamental tool for scientists as they have striven to understand the causes and underlying factors of Parkinson's disease (England, Schwab, Peterson, 1958; Laidlaw & Catling, 1964). In recent years EEG continues to benefit the study of Parkinsonism as researchers study the different symptoms and neural activity associated with this disease. Malgari et al., used EEG frequency analysis to identify specific wave bands that are effected by dopamine replacement therapy (DRT) with hopes to understand the impacted brain oscillations regularly seen in patients with PD (Melgari et al., 2014). Caviness et al. (2006) researched postural tremor, and with coherence analysis, observed a correlation in small amplitude postural tremor and corticomuscular coherence. This finding suggests that the sensorimotor cortex has a direct role in the small amplitude postural tremor observed in PD. Although there is much that we do not know about this disease and many others like it, EEG has proven to be a valuable tool as researchers address the remaining questions of these diseases.

Stroke

A stroke is the result of a blocking of blood flow to certain areas of the brain, which

results in neural cell death. This neural cell death can happen in many different parts of the brain and affect many of the brain's functions. Although there are multiple kinds of strokes, it is common for many to impact different brain systems that play a role in sensorimotor control resulting in apraxia, or impaired motor activity. This can affect the individual's ability to execute voluntary actions and interact with their environment such as waving goodbye or using a toothbrush. EEG has helped practitioners to isolate nerve systems involved with these types of strokes and construct useful rehabilitation programs. Part of this task involves further research into the way the brain coordinates praxis, or performed action, in healthy adults which can then help to create more accurate hypotheses related to those who have brain damage from stroke. Research using EEG has shown that planning self-paced praxis movements begins up to 3 seconds prior to movement initiation in the left parietal region and then enlists premotor and motor areas bilaterally before initiation (Wheaton, Shibasaki, Hallett, 2005; Wheaton & Hallett, 2007; Shibasaki & Hallett, 2006). This has been used to help understand specific types of stroke and the neural sequences that they affect (Wheaton & Hallett, 2007; Wheaton et al., 2008). Another common use of EEG in stroke research is in the development of rehabilitation programs (Ang et al., 2015; Kober et al., 2015; Sburlea et al., 2015; Sharma et al., 2006). EEG's ability to localize brain activity is beneficial and allows the identification of changes

made in response to specific training regimes. This has been used in programs involving mental imagery with stroke victims mentally executing movements in efforts to repair the damaged areas (Sharma et al., 2006). Ang et al. used EEG combined with a brain computer interface (BCI) in a 4-week study that improved motor recovery after stroke for participants with upper-limb hemiparesis. In Ang's study, participants' effected arm was attached to a robot exoskeleton that was controlled by the alpha and beta frequency power collected from 27 electrodes positioned over their frontal and parietal cortex.

These studies show many promising findings including: motor imagery can be effective in promoting neuroplasticity following a stroke, and also, a brain computer interface can be an effective tool for the rehabilitation and assistance of those with motor dysfunctions.

Brain Computer Interface

Recent developments in neurophysiology have developed an approach known as EEG-based brain-computer interface (BCI). An important goal of BCI is to use specific features from the user's EEG profile and translate them into signals that operate a computer-controlled device and assist patients with motor dysfunctions (Allison et al., 2008; Pfurtscheller and da Silva, 1999; Bell et al., 2008). Because this is a developing area

of study, this review will not expound on BCI extensively, but two examples of its use in motor learning and control will be discussed.

A group of individuals that can benefit most from effective BCIs are those who suffer from partial or full paralysis. In a recent study (Muller-Putz et al., 2005), a neuroprosthetic device was applied to recognize the EEG alpha band frequency recorded while the participant imagined himself performing a hand-grasping task with his paralyzed hand. With only three days of training the participant was successful in transporting an object from one location to another on the table in front of him. This research gives evidence that a neuroprosthetic may be effective in regaining at least partial control of a paraletic hand. Another promising study sought to increase the functionality for teraplegic patients. Kaufmann et al., (2014) developed a BCI that allowed for participants to navigate a wheelchair through a virtual course by focusing on specific body parts. As participants focused on body regions representing directions of movement, the resulting ERP could be recognized and applied to control the wheelchair's movement. This will help many of those with severe nervous system dysfunctions to transport themselves in a wheelchair and thus increase independence and quality of life (Rajangam et al., 2016). These two examples of helpful BCIs give promising evidence for their future capabilities. An increasing knowledge

of EEG and its ability to measure motor learning and control will greatly benefit this area of study and improve the quality of life for many with motor system dysfunctions.

Conclusion

87 years have passed since Hans Berger recorded the first EEG of a human. In the time since, our understanding of the brain and the ways in which it plans and executes movement have been defined. The availability of the electroencephalogram has made it possible to monitor and measure specific populations of nerves as they communicate throughout the cerebral cortex. With 86 billion nerve cells inside the human brain, a perfect understanding of this organ's ability to successfully plan, coordinate and execute movements may not be available for years to come. However, the current knowledge has benefited greatly from the abilities of researchers to use EEG and explain the complexities of neurons that control human movement.

Chapter 3: Methods

As discussed in chapter one this project will involve two separate experiments. Both these studies have been designed and carefully planned to utilize the methods and techniques discussed in previous chapters in order to answer specific questions filling a void in the available literature. Chapter three will provide a brief background for each of these studies and clearly explain the proposed methods for how the research question will be addressed.

Part I: The Cognitive Demands of Gait Retraining: Psychophysiological Evidence for Learned Motor Skills

Introduction

One of the most essential characteristics of motor learning is a permanent capability to perform the skilled behavior. Changes in behavior that are easily reversed with time, fatigue or mood are not to be considered learned (Schmidt, 1988). The ability to learn new skills and consistently perform them is essential to all humans. Athletes that can efficiently learn new techniques and reliably produce them are often more successful. Soldiers must permanently learn combat operations in order to ensure the protection of themselves and those they serve. Patients who suffer from harmful injuries rely on their ability to permanently re-learn common movements to gain independence and quality of life. Due to

the importance of permanently learning new skills, much research has been done to recognize when learning has become permanent.

Fitts and Posner (1967) proposed a three-stage learning model for getting motor skills to be permanent and automatic. The first stage is the cognitive, or verbal stage. In this stage learners strive to understand what exactly needs to be done and often have to talk themselves through the execution of the movement. Performance is jerky and inefficient in the cognitive stage. Cognitive demand is high in this stage and often is difficult to perform other tasks. In the second stage, the associative stage, performance becomes more consistent from trial to trial and only slight movement adjustments are made. Co-contractions of competing muscle groups decreases, causing performance to appear smooth and effortless. Certain aspects of the task become automatic and cognitive demand decreases allowing some attention to be given to other tasks. In the final stage, the autonomous stage, performance is automatic, very consistent and requires little to no attentional resources. When attempting to permanently learn a new skill, athletes, soldiers and patients strive to be in the autonomous stage of learning. For this purpose, motor learning research has striven to develop reliable methods to measure learning as it occurs.

Until recent years, research has relied on performance to measure motor learning. When performance is consistent and error free, it is easy to recognize a transition from the cognitive stage to the associative stage. The transition from the associative stage to the autonomous stage is more difficult to recognize. For this purpose, dual-task performance is used to measure cognitive demand of motor skills to recognize an increase in attentional reserve. However, in recent years, electroencephalography (EEG) has been used to recognize an increase in the neural efficiency of motor skill performance. Attempting to perform a new task places a large workload on the brain as additional neural networks are recruited to accommodate the new demand. With EEG, this new workload can be identified and tracked. As learning takes place, neural adaptations occur to create a more efficient network to execute the task. The increase of neural efficiency can be seen in the resulting electrical currents measured by EEG. Houdayer et al. (2016) sought to identify EEG markers as participants learned to play piano. His results showed mu (10-12 Hz) frequency power to decrease while first performing the piano task. With time and training, this decrease in mu power while playing was lessened although performance improved. These results show that EEG can be used to track the neurological changes that occur as a result of learning. However, similar to Houdayer et al. (2016), many EEG studies track learning only for motor skills that require small minor hand movements (Reitschel et

al., 2014; Mathewson et al., 2012). For many patients, amputees and athletes, the motor skill to be learned is more complex and requires more bodily movement.

Gait retraining

Many athletes, soldiers and recreational runners suffer from overuse injuries such as stress fractures. These injuries come from the prolonged use of a biomechanically harmful running gait that results in small bone fractures in the lower extremities. Military recruits with stress fractures miss substantial training time that hinders their physical fitness development and costs the military extra money for medical charges. Crowell and Davis (2011) reported that the annual cost of Army recruits being discharged because of stress fractures is \$6.2 million. This cost, in combination with recovery times up to 8 weeks, creates a significant problem. Stress fractures can remove an athlete from competition for the majority of a competitive season and discourage recreational runners from continuing to run, due to the high recurrence rate. Hauret and colleagues (2001) observed a 36% recurrence rate for military recruits with stress fractures. With the impacts of stress fractures as detrimental as these mentioned, there is a great need to find effective ways to re-train these individuals to permanently alter the way that they run. An example of a successful training protocol is provided by Willy et al. (2015). This study sought to develop an in-field gait-retraining program for participants at risk for tibial stress fractures. They

did this by promoting a 5-10% increase in step rate. A small increase in step rate has shown to decrease ground reaction forces and hip adduction while running at the same speed, and thus reduce risk factors for these types of injuries (Heiderscheit et al., 2011; Hobara et al., 2012). An in-field training computer system was used with an accelerometer attached to the participant's shoe to track step rate per minute. The accelerometer synced with a mobile biofeedback computer worn on the wrist that provided strategic feedback to promote an increased step rate. Ground reaction forces, motion capture data and step rate were measured at baseline, following the retraining period, and one month post retraining. Results showed that the decrease in step rate lowered risk factors for tibial stress fracture and step rate was maintained one month post retraining. These results give optimistic results that the new gait had begun to become a learned motor skill. Similar to the study by Willy et al. (2015), most gait-retraining research has used performance retention as evidence that the new gait has become learned and transitioned into the autonomous stage (Willy et al., 2015; Willy et al., 2014; Crowell & Davis, 2011; Willy, Scholz & Davis, 2012; Fitts and Posner 1967). However, brain adaptations measured by EEG would be a more accurate indicator of permanent behavioral changes.

Until recently, obtaining EEG data while participants ran has not been possible. The constant motion of running causes a large amount of artifact in the EEG data that

overshadows the electrical signal from brain activity. However, Gwin, Gramann, Makeig, and Ferris (2010) developed a strategy of data analysis to mathematically isolate and remove these artifacts from the EEG signal that result from running. With the use of this strategy it is now possible to gather brain activity while participants perform complex movements such as walking and running. The purpose of this study is to employ similar methods of data analysis used by Gwin and others in an attempt to determine the cognitive demand of a gait-retraining program and identify evidence of motor learning throughout the training protocol.

Since Gwin and colleagues' 2010 discovery, there have been many studies done to analyze the cortical activations during gait modification in walking, but, none have been done to address these activations while running (Gwin et al., 2011; Seeber et al., 2014; Seeber et al., 2015; Lisi et al., 2015; Peterson et al., 2012; Kline et al., 2015; Haefeli et al., 2011; Bradford, Lukos & Ferris, 2015; Bulea et al., 2015). Wagner et al. (2016) found, while giving auditory cues to instruct participants to walk with shorter steps, participants showed an increase in beta power over the prefrontal areas and a decrease in beta power over the central midline and parietal regions. Wagner and colleagues' results in the prefrontal areas perhaps suggest a greater engagement of motor resources to inhibit the accustomed full-stride action.

Similar to Wagner et al., many studies have shown a decrease in mu or beta power over the sensorimotor areas in response to lower limb movement, suggesting this region to play a large role in gait planning, initiation and control (Weiser et al., 2010; Presacco et al., 2011; Seeber et al., 2014; Gwin et al., 2011; Wagner et al., 2014). In addition to these findings in the mu and beta bands, Seeber et al. (2015) found an increase in gamma amplitude (>30 Hz) over these regions while walking. These results suggest that this increase may facilitate enhanced motor processing, which would likely result from an altered running gait.

Based on previous studies using EEG to measure learning combined with recent studies using EEG to measure neural activity during gait, it was hypothesized that while initially learning a new gait (increasing step rate 5-10%) an increase in beta and gamma amplitudes over the pre frontal areas would be shown in the EEG data. Such a response would indicate that cognitive load was increased with the new task, a characteristic of Fitts and Posner's cognitive stage. It was further hypothesized that as a result of training, this increase in beta and gamma would decrease, giving evidence that the new skill had become learned and in either the associative or autonomous learning stage. Similarly, it was hypothesized that the mu and beta band frequencies would initially decrease in amplitude over the primary motor cortex as the brain plans, initiates and controls the new gait. In

response to training, it is hypothesized that this initial decrease will subside and that mu and beta power will be higher after training than in the early stages of learning. Due to Seeber and colleagues' findings in the gamma band over the primary motor cortices, we lastly hypothesized that as runners increased their step rate, gamma amplitude would show similar responses and initially increase during early skill acquisition then decrease after training. If shown, these results would give hopeful evidence for the permanent maintenance of an altered running gait and suggest learning to have transitioned towards the autonomous stage proposed by Fitts and Posner (1967).

Methods

Participants

13 undergraduate student volunteers of both sexes that were currently active runners (run at least 8 miles/week) and injury-free were recruited for this study (mean age = 20.1; SD=1.2). All participants provided written informed consent to participate in the study.

Procedure

Using methods similar to Willy et al. (2014), participants first attended a baseline data collection. In order to ensure similar performance parameters for all data collections,

fully instrumented, three-dimensional kinematic and ground reaction forces were collected using motion capture technology (The MotionMonitor, Chicago, Illinois, USA) and an instrumented dual force-plate treadmill (Bertec, Worthington, Ohio, USA) collected at 200 Hz and 1000 Hz, respectively. Upon entering the lab and prior to EEG cap preparation, each participant was issued a pair of shoes for testing and attached with the proper reflective balls for the motion capture. To acquire EEG data, a QuickCap 64-channel EEG cap (modified 10–20 system) from Neuroscan was used with a Neuroscan SynAmps2 64-channel amplifier from Compumedics (El Paso, TX). All data was referenced between electrodes Cz and CPz, and grounded anteriorly to Fz. Saline solution was used to ensure that impedance remained below 5 K Ω on all electrodes prior to data collections. Prior to collecting the baseline EEG data, participants ran at a self-determined pace for a five-minute warm up period. After warming up, one minute of EEG baseline data was collected as the participant ran with their preferred step rate. Using motion data from the baseline period, the increased step rate was calculated by an increase of the preferred rate by 5-10%. Participants were then instructed to increase their step rate 5-10% at the same running speed measured during their baseline run. Once participants successfully maintained a step rate within this 5% window, one minute of EEG was collected and further referred to as the new gait data.

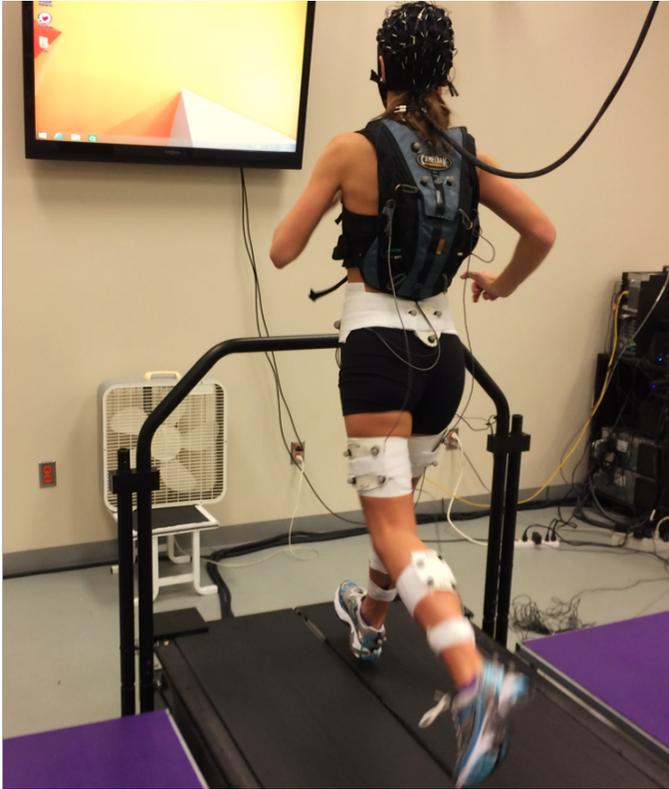


Fig. 1. Participant running on the instrumented treadmill while kinetic, kinematic and EEG data is collected.

At the end of day 1 testing, participants were given a Garmin Forerunner70 (FR70, Garmin Corporation, Olathe, Kansas, USA) wrist computer and a paired Garmin foot pod that was firmly affixed to each participants' right shoe. The foot pod is a triaxial accelerometer that wirelessly transmits a signal (1000 Hz) to the wrist computer allowing for the real-time calculation and recording of step rate and running pace. Participants were shown how to use the wrist computer and instructed to wear it while completing 8 runs of at least 3 miles. During these 8 runs, bandwidth feedback was given by the sound of a beep from the wrist computer. The wrist monitor alerted the participant if they fell below or

above the prescribed 5-10% step rate increase. Participants' running data from the biofeedback computers were downloaded periodically to assess in-field step rate and running volume. After 8 runs were completed successfully with the biofeedback wrist computer, the participants were released for 1 month to run on their normal running routine. Participants were encouraged to run 3 times a week during this period and continued to wear the wrist computer and foot pod while running but received no real-time feedback. During this training period, the wrist computer only allowed participants to know of their results after the run had finished if they chose to look at them.

Following the intervention protocol, participants returned to the laboratory to be tested with exactly the same measures as the day 1 testing (e.g. kinematic, kinetic and EEG data). After set up was completed, equipment was proven functional and a five minute warm up period, participants ran for one minute at their preferred pace while EEG data was collected. No step rate instruction was given. This minute of EEG data is further referred to as the posttest data.

Data Processing

Using methods similar to those used by Gwin et al. (2010), Wagner et al. (2016), Snyder et al. (2015), and Chaumon et al. (2015), all EEG data processing was done with custom scripts written in Matlab 2016b (The MathWorks) using EEGLAB version 13

functions (Delorme & Makeig, 2004). All data were put through a three-stage artifact-reduction process (explained in figure 2) in order to eliminate noise that resulted from running with the EEG cap. The three stages focused on rejecting artifact at the channel, epoch and component levels.

With the purpose of testing the research hypotheses involving frequency activations associated with learning a new gait, a power spectral density plot was calculated for each participant in each condition. Following data processing, a mean spectral power value for each frequency band was calculated for the brain regions of interest and plugged into a one-way ANOVA with repeated measures (baseline data, new gait data, post test data) in order to track changes in EEG spectral power during gait retraining stages. An alpha level of $p < 0.05$ was considered statistically significant for all analyses and effect sizes were calculated using Cohen's d . For these effect sizes, values of 0.1 were considered small, 0.3 were considered medium and anything above .4 was considered large (Cohen, 1988). Tukey's post-hoc test and pairwise comparisons were calculated for all main effects and interactions.

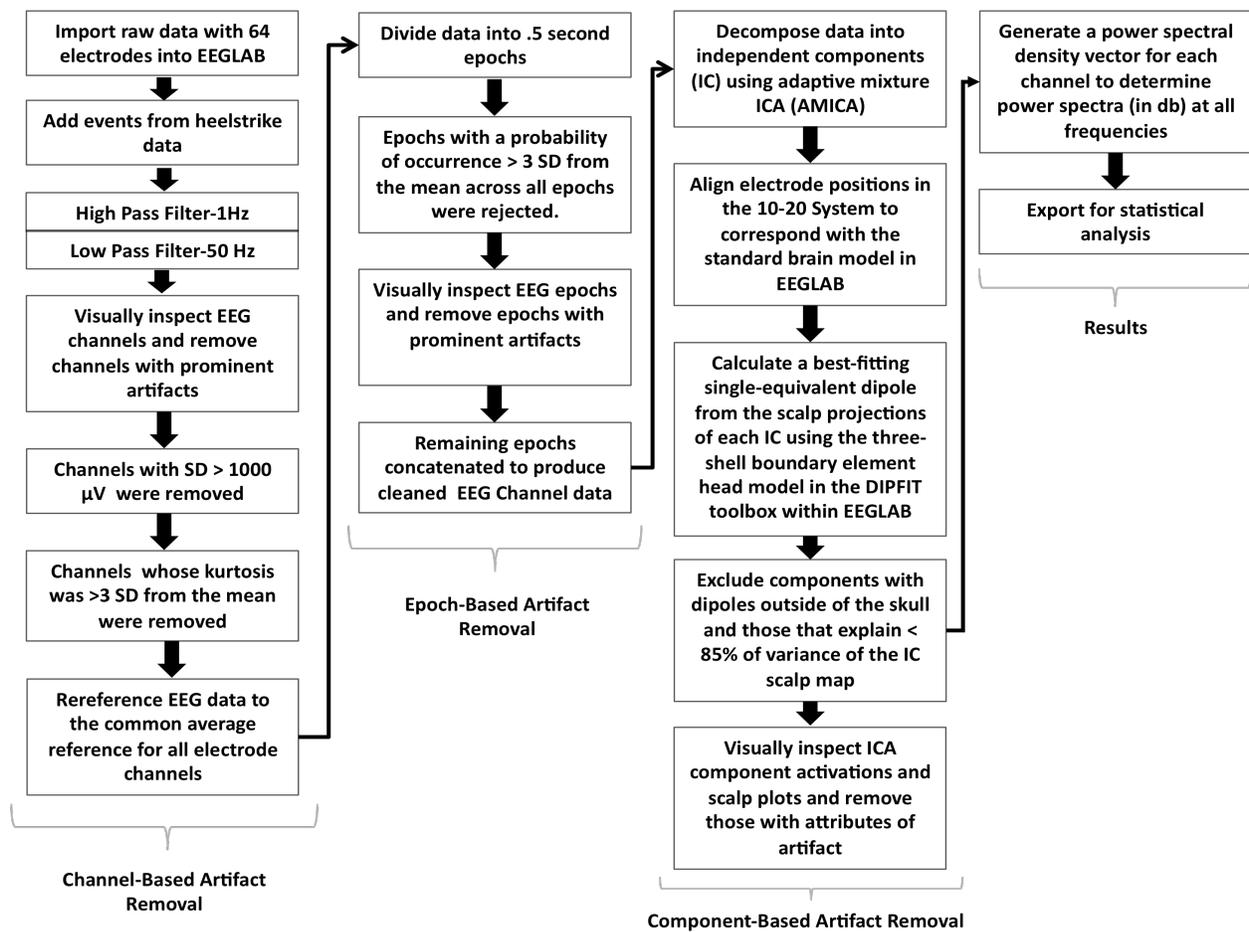


Fig. 2

Part II: Differing neural strategies in left and right-handed individuals during motor imagery

Introduction

Many cognitive tasks that inherently do not require physical movement generate activity in areas of the brain that are also involved in physical movement (Jeannerod, 1994; Decety 1996; Lotze et al., 1999; Parsons, 1995). This shared neural activity occurs as we attempt to understand the actions of others and develop successful motor plans ourselves. Jeannerod's simulation theory (2001) suggests that with every overt action comes a covert mental representation of that action. This mental representation of previously executed movement assists us to successfully complete future motor tasks and understand the actions of others. Frak et al. (2001) showed that while estimating the feasibility of a motor action, participants mentally simulated themselves performing the action in order to provide a response. Although we may not be aware of it, this ability to mentally simulate movement is used daily as we observe, plan and execute actions. Without the capacity to mentally simulate physical movements, we would be incapable of many essential motor tasks such as tool use, reaching out to grasp a pen, or waving goodbye (Clark et al., 1994; Mutha, Sainburg & Haaland, 2010).

Mental simulation of movement without physical execution is known as motor imagery (MI) and would not be possible without a mental representation developed through previous experiences of performing similar actions (Schwartz & Black, 1999). Thus, motor tasks that have been completed more regularly generate a mental representation that can better aid in motor imagery compared to a less familiar task (Gentilucci et al., 1998a; Takahashi et al., 2005). Given that hand-dominance can greatly affect the magnitude of familiarity a motor task has for each hand, the purpose of this study is to better understand the neural differences in right and left-handers as they mentally simulate physical movements to assist in cognitive tasks.

Hand dominance has been shown to affect motor imagery ability (Takeda et al., 2009; Ni Choisdealbha et al., 2011; Gentilucci et al., 1998b). Based on behavioral data, many studies have shown that while mentally simulating action, participants are more proficient while imagining action with their dominant hand (Takeda et al., 2009; Ni Choisdealbha et al., 2011; Gentilucci et al., 1998b, Parsons 1987, 1994; Parsons et al., 1995). The dominant hand is used habitually and more often for a wide range of tasks and thus, a lateral preference is possible while mentally simulating action.

This preference for the dominant hand is also reflected in neuroimaging studies (Parsons et al., 1995; Vingerhoets et al., 2002; Osuagwu & Vuckovic, 2014). Parsons et al.

(1995) were among the first to show dominant laterality in the supplemental motor area (SMA), premotor cortex (PMC) and anterior cingulate during motor imagery of an upper extremity movement. Parsons and colleagues also reported a greater bilateral activation of the inferior parietal lobe during MI with the dominant hand compared to its non-dominant counterpart. In recent years, many studies have found similar results to prove an effect of hand dominance on both the behavior of motor imagery and its neural components (Hanakawa, 2016; Iacoboni et al., 1999; Vingerhoets et al., 2002; Osuagwu & Vuckovic, 2014; Jeannerod & Frak, 1999; Jongsma et al., 2013).

The majority of action simulation research, as well as motor function research as a whole, have primarily focused on right-handed individuals. Because left-handed individuals make up 4-16% of the population, (varies by culture (Perelle and Ehrman, 1994)) most studies focus on right-handers only. It has been assumed that the left-dominant contralateral cortical activity, which is seen in right-handers, would be identical in the opposite right-hemisphere for left-handed individuals (Goldenberg, 2013; Vingerhoets et al., 2012; Goble et al., 2009). However, this has not been proven and recent research would suggest otherwise. Kelly, Mizelle and Wheaton (2015) showed that left-handed individuals, while mentally simulating the use of a tool, did not show contralateral activation in the premotor and parietal regions relative to the imagined hand, but rather

showed a bilateral activation of both regions regardless of hand imagined. Martin, Jacobs and Frey (2011) also reported a bilateral activity of both the parietal and premotor areas in left-handers in a similar task. While planning a grasping motion with either hand, left-handed participants showed bilateral activation in the ventral premotor cortex (vPMC) and anterior intraparietal sulcus (aIPS) while the right-handed group was left-hemisphere lateralized, failing to exceed baseline activity in the right ventral premotor cortex in all conditions. These results challenge previous assumptions and suggest fundamental differences in the way left-handers mentally process motor-related tasks. A better understanding of these differences will advance the current knowledge of hand dominance and the role it plays in information processing. In addition, this work will assist in the development of proper rehabilitation practices for individuals with disease and injury to the brain regions involved with this essential task. Thus, more research is needed to understand MI in both right and left-handers.

The hand laterality task (HLT) is a standard test used in research to understand the neural and cognitive mechanisms involved with motor imagery and mental simulation (Cooper & Shepard, 1975; Parsons, 1987; Parsons, 1994; Osuagwu & Vuckovic, 2014; Lyu et al., 2017). In the HLT, participants are shown an image of a hand and asked to identify it as a left or right hand. It has been shown repeatedly that while solving this task,

participants mentally rotate a mental representation of their own hand to match the observed hand in order to identify it as right or left (Parsons, 1987, 1994, 2001; Parsons et al., 1995; Gentilucci et al., 1998a, 1998b; Takeda et al., 2010; Ni Choisdealbha et al., 2011). Parsons (2003) suggests that this cognitive task is solved in five phases, i.e., a) visual encoding, b) analysis of the orientation difference between the target and mental template, c) mental rotation of the appropriate body part from the current to the target position d) comparing the images to determine laterality and e) response execution. Many previous studies have used spatially precise neuroimaging techniques, such as fMRI and PET, to locate the brain regions involved in this mental task at the expense of temporal exactness (Parsons et al., 1995; Perruchoud et al., 2016, Iacoboni et al., 1999). However, many participants complete all five phases of the HLT in less than one second, making temporal accuracy imperative in understanding the neural components involved.

Due to its fine temporal precision, EEG has frequently been used to understand the temporal patterns of motor-related cognitive tasks, but has only recently been used to evaluate the neural activity during the HLT (Osuagwu & Vuckovic, 2014; Lyu et al., 2017; Jongsma et al., 2013). When presented with a visual stimulus, an electrophysiological response known as an event-related potential (ERP) can be seen in the EEG data and used to understand the way the brain processes information (Herrmann & Knight, 2001).

Certain components of the ERP could be helpful to understand the temporal patterns of the phases involved in solving the HLT. The N2 (a large negative shift generated around 200 ms after stimulus onset) has been characterized with recognizing the similarities or deviations of a stimulus from a previously developed mental template in order to give meaning to visual stimuli (Folstein & Van Petten, 2008). Lyu and colleagues (2017) observed a decrease in magnitude of the N2 for amputees imagining movement of their amputated hand compared to their intact limb while completing the HLT. Interestingly, it was also shown by Lyu and colleagues that the magnitude of decrease in the N2 was correlated with the amount of time since losing their limb. This finding implicates that the degree of familiarity of an action should be shown in the amplitude of N2. Thus, it is possible that N2 amplitude may be reduced for mentally simulated actions with the non-dominant hand. As follows, it was hypothesized that N2 would be greater over the intraparietal sulcus area in the contralateral hemisphere for right-handed individuals as they view right hands compared to left hands. It was further hypothesized, that the magnitude of N2 in the same region would not differ across hemispheres for left-handed individuals regardless of the stimulus hand laterality.

The P3 component of the ERP (a large positive shift occurring roughly 300 ms after stimulus onset) is believed to be the most prominent ERP component sensitive to cognitive

processing (Herrman & Knight, 2001). Considering the greater latency of the P3, it can be expected to provide insight on the later stages of the HLT task. Based on the findings from Martin et al. (2011), it was hypothesized that right-handers would show greater amplitude of P3 in the contralateral premotor cortex relative to stimulus hand and that P3 would not differ across hemispheres of left-handers regardless of hand presented. Due to its short temporal latency, no differences were expected in the P1 (a positive shift occurring within 80-130 ms after stimulus presentation) component of the ERP.

Methods

Participants

Twelve right-handed individuals and twelve left-handed individuals aged 18 to 35 years from both sexes participated in the study. All participants were generally healthy and had no history of neurological illness or injury. The Edinburgh handedness inventory (EHI) was used (Oldfield, 1971) to evaluate the degree of hand dominance. The median laterality quotients (LQ) for the right and left-handed group were 80.5 and -70, respectively. All participants gave written informed consent before participating in this study.

EEG

Participants were seated in a chair and fitted with a standard 64-channel EEG electrode cap (Neuroscan, Charlotte, NC) in the standardized 10-20 electrode configuration to record neural activity (1000 Hz) using SynAmpsRT (Neuroscan, Charlotte, NC). The cap was referenced between Cz and CPz, and grounded anteriorly to Fz. Electrode impedance was brought below 5 k Ω s for all data collections. Eye movements were recorded with electrodes placed above and below the left eye to capture electrooculographic (EOG) activity. Using StimTracker (Cedrus Corporation, San Pedro, CA), stimulus onset and participant responses were synchronized to the EEG continuous data, which allowed the data to be epoched and analyzed.

Hand Images

In order to control for a learning effect and to promote consistent motor imagery, pictures included hands in multiple positions, angular orientations, and visual angles. Gentilucci et al. (1998a) suggested that unique hand postures promoted a greater amount of mental simulation than commonly seen hand images. Thus, three levels of image complexity were included in this study: simple images (either an open palm or closed fist), familiar hand posture images (pointing finger, thumb up, handshake, etc.), and unique hand images (non-recognizable, novel postures). All hand images were drawn randomly from a

bank of 672 images (336 right-hands, 336 left-hands), consisting of a front and back image of each hand posture in each complexity level rotated at 45° angles (fig.7a).

Procedure

Participants were seated in a chair with fingers placed on a response pad (RB-840, Cedrus Corporation, San Pedro, CA) in order to provide behavioral responses (fig. 7b). EEG was recorded while participants were shown randomized images of individual hands on a 47 in. (119.38 cm) visual monitor. To promote mental simulation of movement, participants' hands were occluded with a towel draped over their hands. Upon stimulus presentation, participants were instructed to determine the laterality of each hand and respond by pressing the corresponding button on the response pad as fast and accurately as possible. To monitor behavioral data, response times and response accuracy were recorded. The inter-stimulus period contained a black fixation cross, located in the middle of the screen that lasted 3 seconds (fig. 7c). All images were preceded by a visual warning cue varying between 1.5-3 seconds prior to picture presentation. Once the image was presented, if participants did not respond in 3 seconds, the inter-stimulus fixation cross would appear and continue into the next trial. Data collections consisted of four blocks of 60 images each (240 trials total).

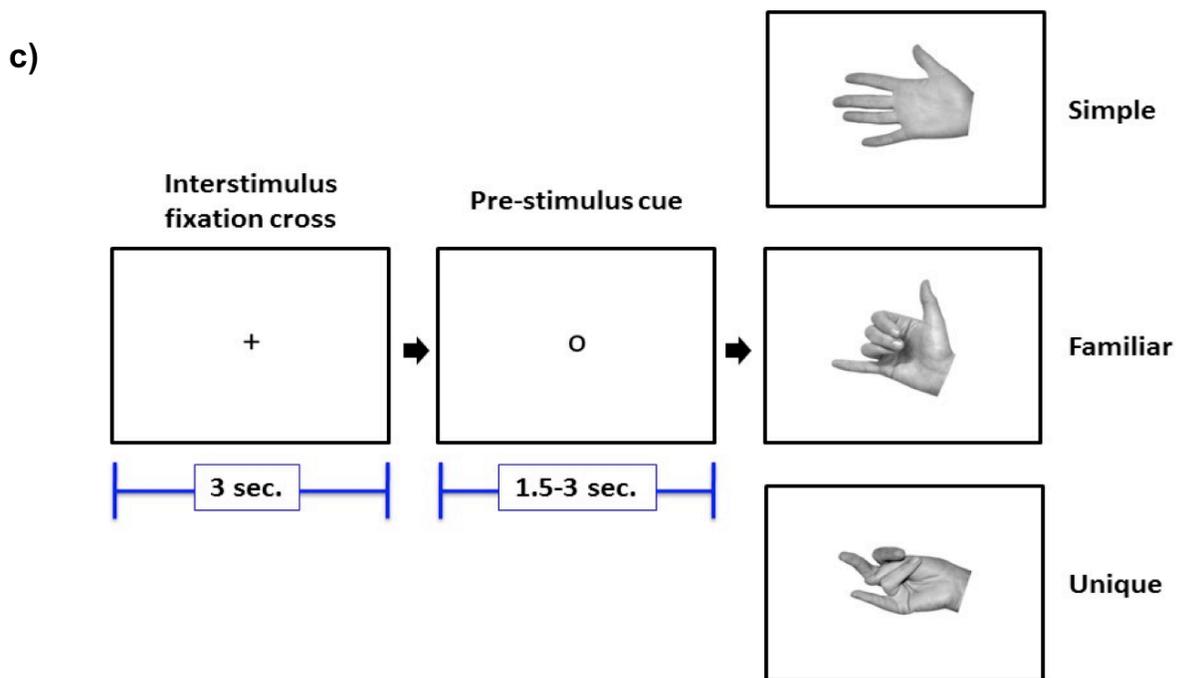
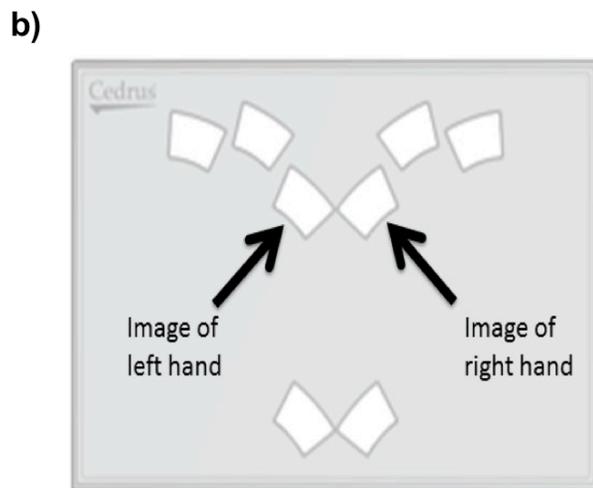
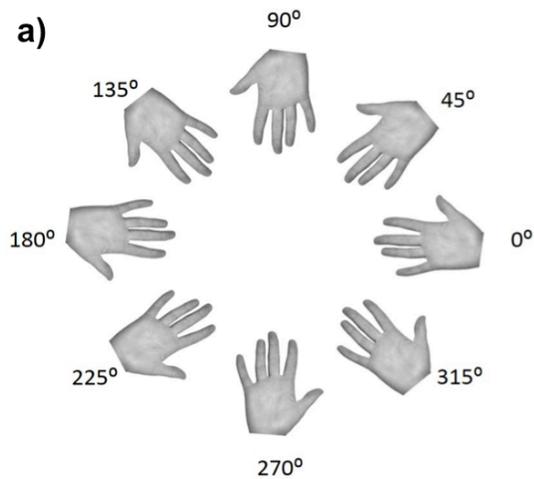


Figure 3. a) All images presented in a randomized 45° increment. b) Diagram of respond pad on which participants indicated if the presented hand was a left or right hand. c) Each hand image was preceded by an interstimulus fixation cross and pre-stimulus warning cue.

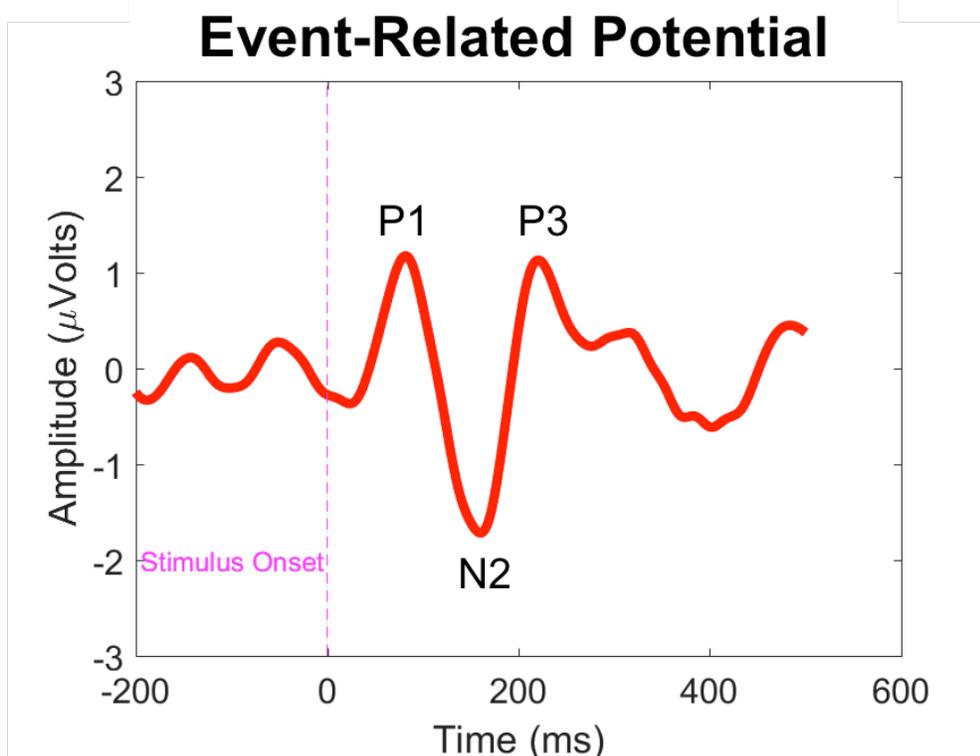


Figure 4. Components of interest in the visual event-related potential

Analyses

Behavioral data

In order to monitor response time and accuracy differences between left and right-handers, a one-way multivariate analysis of variance (MANOVA) was calculated in IBM SPSS Statistics 22. Alpha was set at $p = .05$ as the critical level of significance.

EEG Data:

Data from each participant were visually analyzed to locate and remove any prominent artifact resulting from eye and muscle activity. Afterwards, using custom scripts written in

Matlab 2016b (The MathWorks) and employing EEGLAB functions (Delorme & Makeig, 2004), all data were filtered using a 4-35 Hz band-pass filter, re-referenced to the average of M1 and M2 (left and right earlobes), and epoched to include 1 second before and after picture presentation for each stimulus condition. Based on the unique EEG marker generated by StimTracker for each picture presentation, epochs were sorted into each trial condition (simple image-right hand, unique image-left hand, etc.) for each participant. To reduce the effect of inter-subject variability in the amplitude of the evoked responses, the data for the 12 subjects in both groups were resampled to the average number of trials that all participants saw each stimulus condition (Mizelle & Wheaton, 2010, 2011). After resampling, trials in each condition were averaged, individually, for all participants of each group to result in a 64 (channels) x 2000 (time points) data matrix for each participant in each condition. Based on the prominence of the negative shift of the N2, peak values for the three ERP components were identified in the data and used for the remainder of data processing.

In order to test the hypotheses of laterality differences in left and right-handers, a custom Matlab script was created that compared the peak values of an ERP component in each of the 62 electrodes from all participants of a group to its contralateral counterpart (t-test) (Mizelle et al., 2011). In this script, if a lateral preference exists across hemispheres

that is statistically different ($p < .05$), the corresponding brain region is colored over in a lateralization head plot. Different preferences of hemisphere between right and left-handers become evident in the side-by-side comparison of each group's head plot.

To further understand differences in the brain activity involved with motor imagery in right and left-handed individuals, a one-way multivariate analysis of variance (MANOVA) was conducted for the brain regions of interest to determine the effect of stimulus type on the ERP wavelet magnitudes in these regions. An alpha level of $p < 0.05$ was considered statistically significant for all analyses and effect sizes were calculated using Cohen's d and partial eta squared. For Cohen's d , values of 0.1 were considered small, 0.3 were considered medium and anything above 0.5 was considered large (Cohen, 1988). For partial eta squared, values of .0099, .0588, and .1379 were considered small, medium, and large effect sizes, respectively (Richardson, 2011).

Chapter 4: Results and Discussion

Part I: The Cognitive Demands of Gait Retraining: Psychophysiological Evidence for Learned Motor Skills

Results

Due to excessive artifact, the data from two subjects were excluded from the study. In addition, two participants failed to report back for post testing and thus, the results include data from 11 subjects for the baseline and new-gait stages and 9 subjects for the posttest stage. To test the three research hypotheses, a one-way repeated-measures ANOVA was conducted. In the ANOVA, the factor was gait-retraining stage (baseline, new gait, post-test) and the dependent variable was mean spectral power (dB) across all epochs. The means, p values, and effect sizes for spectral power are presented in tables 1-3. First, it was hypothesized that there would be an increase in both beta and gamma power over the prefrontal brain regions following an increase in step rate and that these measures would reduce as a result of training. The repeated-measures ANOVA showed a main effect of gait-retraining stage in the right prefrontal cortex within the beta frequency band ($F(2, 7) = 4.939, p < .05, d = .861$) as well as the gamma frequency band ($F(2, 7) = 4.246, p < .05, d = .844$). Post-hoc tests indicated a significant spectral increase from baseline to new gait in the beta and gamma frequencies. Post-hoc tests did not show the decreases in beta and gamma power over the right prefrontal area from new gait to post training to be significant.

However, as shown by the Cohen's *d* scores (figure 3), the effect sizes were large for both the increase from baseline to new gait as well for the decrease in these measures as a result of training. The increase in power in the left prefrontal cortex was not significant in the beta or gamma frequency bands and showed only moderate effect sizes ($F(2, 7) = 2.432, p > .05, d = .399$; $F(2, 7) = 2.222, p > .05, d = .337$, respectively). The findings in the right prefrontal cortex support our first research hypothesis and suggest that there is a greater engagement of cognitive resources in this region to inhibit the previously accustomed full stride motion.

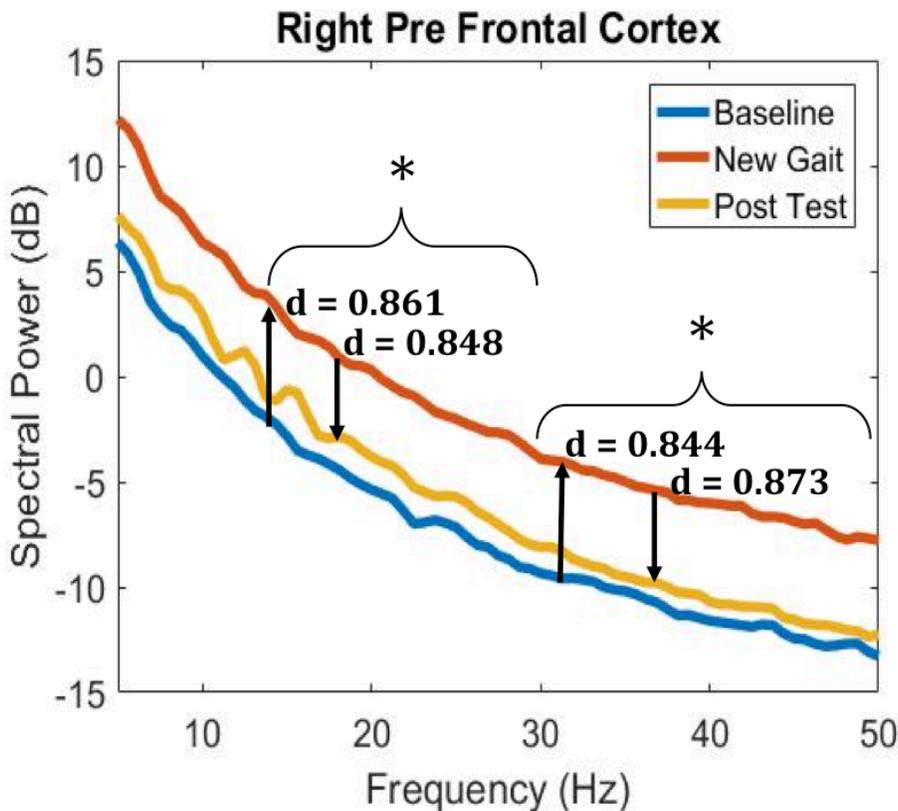


Fig. 5. Mean power spectral density for all participants in the right prefrontal region.
 * = $p < .05$

It was further hypothesized that both mu and beta frequency bands would initially decrease in power over the primary motor cortices as participants increased their step rate and then rise in response to training. This hypothesis was not supported by the repeated measures ANOVA in either the left primary motor cortex (mu $F(2, 7) = 3.213$, $p = .067$, $d = .750$; beta $F(2, 7) = 3.226$, $p = .066$, $d = .747$) or the right primary motor cortex (mu $F(2, 7) = 3.511$, $p = .054$, $d = .780$; beta $F(2, 7) = 2.982$, $p = .079$, $d = .562$). It should be noted that the mean spectral power in both the beta and mu frequency bands in the primary motor cortex increased in both hemispheres with participants increasing their step rate and then decreased after training. This was opposite to the expected direction and contrary to many studies' findings in similar conditions (Weiser et al., 2010; Presacco et al., 2011; Seeber et al., 2014; Gwin et al., 2011; Wagner et al., 2014). Although these findings were not significant, their large effect sizes merit the attention of future research (table 2).

Finally, it was hypothesized that gamma spectral power would first increase over the primary motor cortices as participants increased step rate and decrease as the new gait was learned. Although there were large increases in these measures, the repeated measures ANOVA was not significant for both hemispheres (left $F(2, 7) = 2.993$, $p = .079$, $d = .716$; right $F(2, 7) = 2.758$, $p = .094$, $d = .557$). However, all the effect sizes were large for the changes in gamma power over the primary motor cortices.

Hypothesis 1 Results

		Mean Spectral Power over all epochs (db)				Cohen's d			
		Baseline	New Gait	Post-Training	F	Sig.	BL-NG	NG-PT	NG-PT sig.
Beta	Left Pre Frontal Cortex	-4.999	-2.560	-2.952	2.432	.120	0.399	0.064	.332
	Right Pre Frontal Cortex	-4.723	0.990	-4.180	4.939	.021	0.861	0.848	.266
Gamma	Left Pre Frontal Cortex	-10.438	-8.454	-8.981	2.222	.141	0.337	0.090	.298
	Right Pre Frontal Cortex	-10.361	-4.967	-10.298	4.246	.033	0.844	0.873	.196

BL = Baseline data, NG = New gait data, PT = Post test data

Table 1

Hypothesis 2 Results

		Mean Spectral Power over all epochs (db)				Cohen's d			
		Baseline	New Gait	Post-Training	F	Sig.	BL-NG	NG-PT	NG-PT sig.
Mu	Left Primary Motor Cortex	-6.530	-3.578	-5.614	3.213	0.067	0.750	0.510	.125
	Right Primary Motor Cortex	-5.591	-0.052	-4.021	3.511	0.054	0.780	0.560	.361
Beta	Left Primary Motor Cortex	-8.153	-3.173	-6.279	3.226	0.066	0.747	0.515	.134
	Right Primary Motor Cortex	-7.291	-2.519	-4.565	2.982	0.079	0.562	0.293	.374

BL = Baseline data, NG = New gait data, PT = Post test data

Table 2

Hypothesis 3 Results

		Mean Spectral Power over all epochs (db)				Cohen's d			
		Baseline	New Gait	Post-Training	F	Sig.	BL-NG	NG-PT	NG-PT sig.
Gamma	Left Primary Motor Cortex	-13.681	-8.983	-12.517	2.993	0.079	0.716	0.620	.113
	Right Primary Motor Cortex	-13.297	-8.843	-10.922	2.758	0.094	0.557	0.309	.377

BL = Baseline data, NG = New gait data, PT = Post test data

Table 3

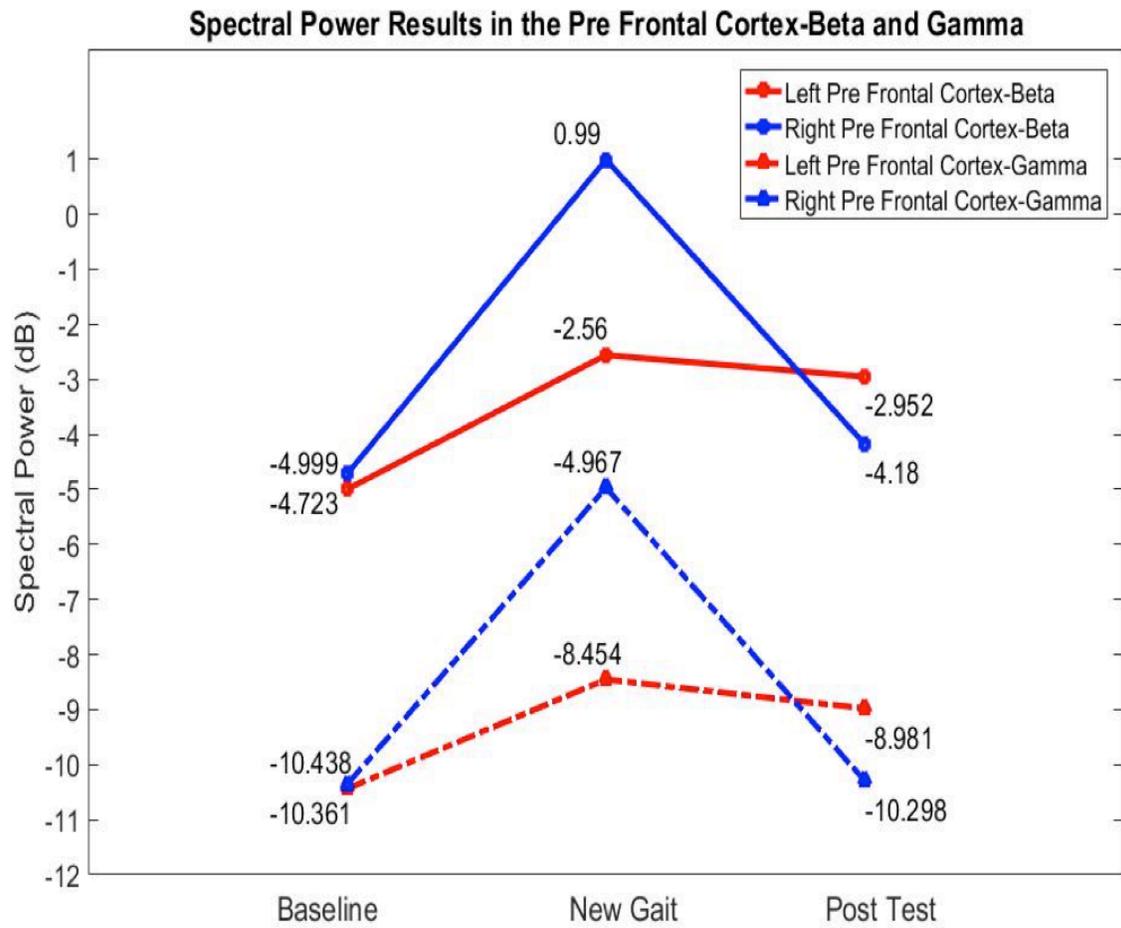


Fig. 6. Mean spectral power in the beta and gamma frequency bands across all gait retraining phases in the prefrontal cortices.

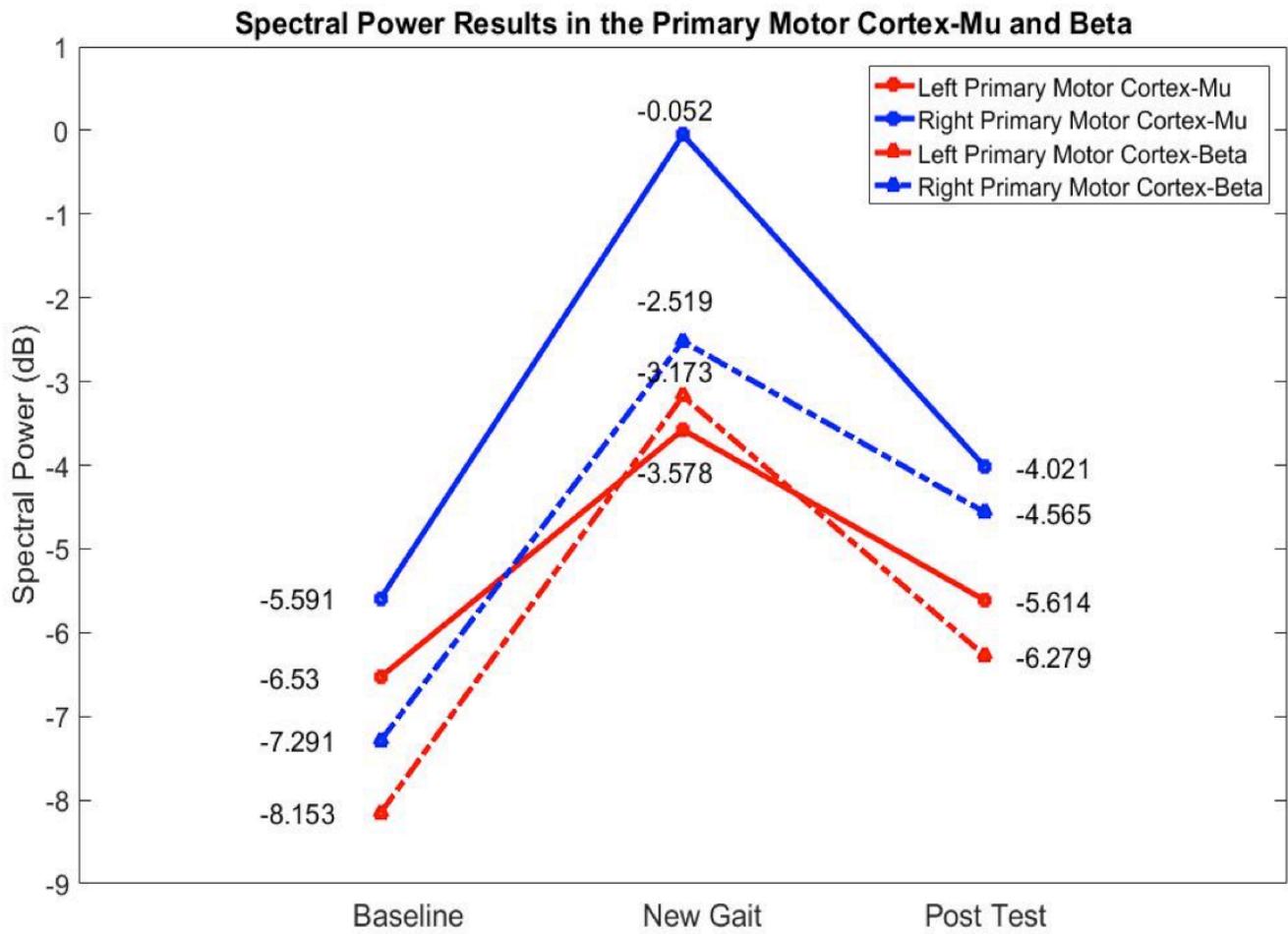


Fig. 7. Mean spectral power in the beta and mu frequency bands across all gait retraining phases in the primary motor cortices.

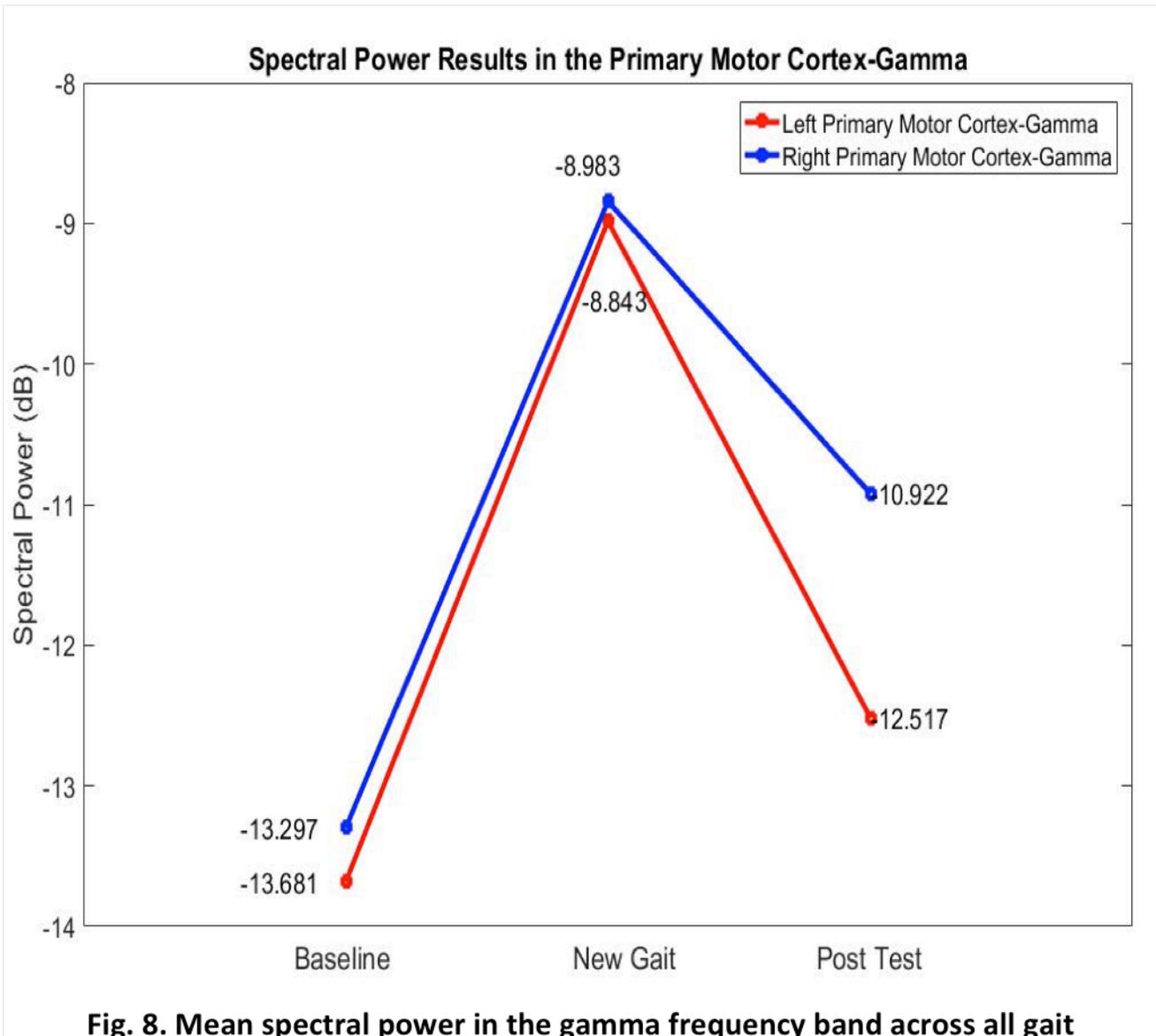


Fig. 8. Mean spectral power in the gamma frequency band across all gait retraining phases in the primary motor cortices.

Discussion

To our knowledge, this is the first study to use EEG to track learning during walking or running. The purpose of this study was to determine the cognitive load of running with an altered gait and identify EEG biomarkers that provide evidence of motor skill learning. Our findings showed that as runners increase their step rate, the greatest changes in brain activity are seen in

the prefrontal and motor regions and suggest a greater cognitive demand compared to the baseline step rate. We also give EEG evidence that cognitive load decreases in response to training, a characteristic of later learning stages. Our findings in the prefrontal and primary motor regions, along with suggestions for future research will be discussed below.

As participants ran with the new step rate for the first time, they showed a significant increase in beta power over the right prefrontal cortex. These findings are consistent with previous EEG studies and give evidence for an increase in cognitive load typical for the early cognitive stage in Fitts and Posner's learning model (1967) (Wagner et al., 2016; Swann et al., 2009; Aron et al., 2014). Based on results from a finger-tapping task, Swann et al. (2009) suggest that the right prefrontal region is part of a larger inhibitory network with the basal ganglia and primary motor cortex that serves to stop previously learned responses. Wagner et al. (2016) showed similar results during gait. They reported large increases in beta power in the right prefrontal hemisphere while participants reacted to walking with shorter steps compared to reacting to longer steps. Our findings provide further evidence for this function of the right prefrontal region and show that it is consistent in more complex movements, such as running.

The results of the current study also show that as the novelty of a new task wears off with practice, this increase of activation in the right prefrontal cortex begins to attenuate towards baseline levels. Whether this increase of beta power in the right prefrontal cortex would be observed in other methods of running gait alteration could be the focus of future research. This

finding gives promising evidence for the permanent maintenance of the new gait pattern and offers a unique method of monitoring the motor learning process. Future work could apply these methods to identify learning in athletes as they perform sport related movements, amputees as they adapt to prostheses, and soldiers as they perform novel combat operations.

In addition to activity in the right prefrontal region, interesting results were seen in the primary motor cortex. Although these differences lacked significance at $p = .05$, their large effect sizes suggest it to merely be a sample size issue. As participants initially increased their step rate, there was a power increase in the mu, beta and gamma bands of both hemispheres. In addition, all of these frequency bands reported spectral power in the direction of their baseline values after training. This pattern suggests that mu, beta and gamma may also be indicators of motor learning and may be used in future studies to track motor skill acquisition. Interestingly, many studies have seen a decrease in the mu and beta bands over the primary motor cortex during lower limb movement and thus, this finding was not expected (e.g., Presacco et al., 2011, Severens et al., 2012; Wagner et al., 2012; Weiser et al., 2010). Freeman et al. (2016) suggested that increasing cognitive workload may set the motor system into a suppressed state that results in an increase in mu frequency power over the motor areas compared to a low cognitive workload. It is possible that a similar phenomenon occurred in result of increasing cognitive workload by altering runners' step rate. With respect to the increase of beta power, Gwin et al. (2011) used similar methods of mobile EEG to suggest differences in brain activation across the gait cycle. They found

there to be an increase in beta power over the sensorimotor region contralateral to the pushing off foot during the end of stance phase. It is possible that this burst of beta power is amplified as participants attempt to push off with less force as they seek to take more steps. This research falls in line with previous research that shown an increase in gamma power over the primary motor cortex during gait. These findings further this research by showing the increase in spectral power to subside in response to training.

Limitations

Although these findings are promising, there are a few limitations to the current study. The selected sample size hinders the ability to infer these results onto the population. Two of the three hypotheses were not statistically significant at the $p < .05$ level. However, based on the large effect sizes, this lack of significance is likely due to a small sample size. A large amount of movement artifact is inherent to mobile EEG research and, in combination with the variability that already exists in EEG data, merits a need for proper planning of sample size to ensure significant findings. In addition, it is possible that the amount of electrodes used may be seen as a limitation. Many of the mobile EEG studies recently published used an EEG cap with more than 100 electrodes, whereas the cap used for this study had only 64. As a result of our rigorous data processing methods, multiple electrodes were removed from analysis because of artifact contamination. This generally resulted in around 50 electrodes used for data processing. When using independent component analysis algorithms, more electrodes allow for better spatial

accuracy of the EEG components. However, recent research has shown that as little as 35 electrodes are necessary for sufficient spatial and temporal precision of the resulting ICA components (Lau, Gwin & Ferris, 2012). These results suggest the findings of Lau et al. (2012) to also be applicable to mobile EEG research.

Conclusion

An essential characteristic of motor skills is a permanent capability to perform the behavior that is not quickly diminished with time, fatigue or mood. Previous research has used performance indicators as a sign for permanent behavioral change. This research provides psychophysiological evidence that neural changes are being made to result in the permanent execution of the new gait pattern. The current study showed an increase in beta power over the right prefrontal cortex as runners increase their step rate. This increase in right prefrontal beta power is indicative of an increase in cognitive workload as the individual strives to inhibit the previously learned running pattern. It was also shown that with time and proper training, these changes in brain frequency power can be diminished towards baseline levels, a hopeful biological marker for permanently learned motor skills.

Part II: Differing neural strategies in left and right-handed individuals during motor imagery

Results

Behavioral results

Behavioral results from the one-way multivariate ANOVA are shown in table 4 and 5. The ANOVA revealed no significant differences in either accuracy scores or reaction time between right-and left-handers in any condition. There was effectively no difference in behavioral performance across these two groups.

Stimulus Response Accuracy Score

	Mean		F	sig.	Partial η^2	Cohen's d
	Righties	Lefties				
Simple right-handed images	0.87	0.82	0.45	0.51	0.02	0.29
Simple left-handed images	0.87	0.88	0.06	0.81	0.00	0.10
Familiar right-handed images	0.83	0.82	0.03	0.86	0.00	0.08
Familiar left-handed images	0.83	0.84	0.01	0.92	0.00	0.04
Unique right-handed images	0.85	0.83	0.35	0.56	0.02	0.26
Unique left-handed images	0.83	0.81	0.05	0.83	0.00	0.10

Table 4. One-way multivariate ANOVA results for response accuracy scores for both left and right-handers.

Stimulus Response Reaction Time (ms)

	Mean		F	sig.	Partial η^2	Cohen's d
	Righties	Lefties				
Simple right-handed images	1414.89	1492.23	0.53	0.48	0.03	0.31
Simple left-handed images	1436.83	1577.72	2.71	0.12	0.12	0.70
Familiar right-handed images	1501.33	1573.78	0.55	0.47	0.03	0.32
Familiar left-handed images	1519.18	1540.85	0.05	0.82	0.00	0.10
Unique right-handed images	1547.49	1615.90	0.58	0.45	0.03	0.33
Unique left-handed images	1588.31	1601.56	0.03	0.88	0.00	0.07

Table 5. One-way multivariate ANOVA results for reaction time for both left and right-handers.

Laterality Head Plots

The resulting lateralization head plots can be seen in figure 9. It was first hypothesized that when shown images of right hands, the right-handed group would show greater contralateral amplitude of the N2 component in the parietal lobe than was seen in the right-hemisphere when shown images of left hands. As can be seen in figure 9b, little contralateral preference was observed in the parietal cortex regardless of image complexity or hand seen. Interestingly, a significant contralateral activation was seen in the premotor cortex when shown right hands in a unique position.

Next, it was hypothesized that amplitude of the N2 would not differ across hemispheres in the parietal lobe for all image types in the left-handed group. Thus, it was expected that no color would be seen in the lateralization head plots of the left-handed group in this region. Based on the lateralization head plots of the N2 component, left-handers' N2 component was equal across hemispheres only when shown images of hands in simple hand postures. Right-handers also showed this bilateral activation for simple hand postures. The activation of the N2 component for the other two image complexity levels was inconsistent with a slight preference for the right parietal region regardless of hand shown.

Further, it was hypothesized that for right-handers, greater amplitude of P3 would be seen in the premotor cortex of the hemisphere contralateral to the stimulus hand. This contralateral

preference was not observed in the resulting lateralization head plots. Activation of the P3 in the premotor cortex was generally bilateral in activation regardless of hand shown and brain area. In line with our fourth hypothesis, this trend was also shown for left-handers with the exception of an ipsilateral activation in P3 when shown images of right hands in a familiar posture.

ANOVA Results

In addition to the laterality head plots, a one-way multivariate ANOVA was calculated in order to identify any further differences in ERP components between these two populations (tables 6-8). Interestingly, all significant findings in the parietal lobe indicated a greater activation for the right-handed group. However, all significant findings in the PMC and primary motor cortex showed a greater activation for the left-handed group.

P1

Due its short latency, no differences were expected in the P1 component between right and left-handers. However, the right-handed group showed a significantly greater P1 activation in the parietal lobe for unique left-handed images in the left hemisphere ($F(22,1) = 13.183, p < .01; d = 1.482, \eta_p^2 = .375$) and the right hemisphere ($F(22,1) = 4.806, p < .05; d = 1.482, \eta_p^2 = .179$) (fig. 10a-b and table 6) . For right-handed images in simple positions, the right-handed group showed a significantly greater P1 activation in the supplementary motor area in the left hemisphere ($F(22,1) = 6.361, p < .02; d = 1.030, \eta_p^2 = .224$) and the right hemisphere ($F(22,1) = 12.936, p < .01;$

$d = 1.468, \eta_p^2 = .370$) (fig. 10e-f and table 6). Left-handers did not show significantly greater activation of the P1 in any condition.

N2

Right-handers showed larger activation of the N2 in the parietal region as well, but only in the left hemisphere. The N2 for right-handers was significantly larger than left-handers in this area when shown unique left hands ($F(22,1) = 4.942, p < .05; d = .908, \eta_p^2 = .183$) and simple right hands ($F(22,1) = 4.667, p < .05; d = .882, \eta_p^2 = .175$) (table 7). Generally, the left-handed group showed greater activation in the SMA, PMC and primary motor cortex of both hemispheres when shown left hands.

P3

All significant findings in the P3 favored the left-handed group, included all stimulus conditions and were located in the motor related brain regions. The greatest of these significant findings were in both hemispheres of the SMA and PMC while looking at left hands (SMA-left $F(22,1) = 21.852, p < .001; d = 1.908, \eta_p^2 = .498$) (SMA-right $F(22,1) = 20.541, p < .001; d = 1.850, \eta_p^2 = .483$) (PMC-left $F(22,1) = 15.012, p < .002; d = 1.582, \eta_p^2 = .406$) (PMC-right $F(22,1) = 18.832, p < .001; d = 1.772, \eta_p^2 = .461$).

Left Hemisphere

Right Hemisphere

P1

Left Handed Images										Right Handed Images									
Brain Region	Image Complexity	Mean Righties	Mean Lefties	F	Sig.	Partial η^2	Cohen's d		G.A.	Brain Region	Image Complexity	Mean Righties	Mean Lefties	F	Sig.	Partial η^2	Cohen's d		G.A.
SMA	Simple	3.494	1.574	5.675	0.026	0.205	0.973	Righties		Parietal	Familiar	2.191	1.585	6.009	0.023	0.215	1.001	Righties	
Parietal	Unique	1.903	1.045	13.183	0.001	0.375	1.482	Righties		Parietal	Unique	2.154	1.440	4.806	0.039	0.179	0.895	Righties	
Right Handed Images										Left Handed Images									
SMA	Simple	4.080	2.688	6.361	0.019	0.224	1.030	Righties		SMA	Simple	3.476	1.851	12.936	0.002	0.370	1.468	Righties	

G.A. = Greater activation

Table 6

N2

Left Handed Images										Right Handed Images									
Brain Region	Image Complexity	Mean Righties	Mean Lefties	F	Sig.	Partial η^2	Cohen's d		G.A.	Brain Region	Image Complexity	Mean Righties	Mean Lefties	F	Sig.	Partial η^2	Cohen's d		G.A.
SMA	Simple	-3.941	-5.279	10.830	0.003	0.330	1.344	Lefties		SMA	Familiar	-3.072	-3.991	6.078	0.022	0.216	1.006	Lefties	
PMC	Simple	-3.223	-4.251	10.655	0.004	0.326	1.333	Lefties		M1	Familiar	-2.450	-3.106	6.151	0.021	0.219	1.013	Lefties	
M1	Familiar	-2.329	-3.229	5.500	0.028	0.200	0.957	Lefties		PMC	Familiar	-2.252	-2.968	5.853	0.024	0.210	0.988	Lefties	
PMC	Familiar	-2.557	-3.396	5.635	0.027	0.204	0.969	Lefties		SMA	Simple	-3.938	-5.118	6.270	0.020	0.222	1.022	Lefties	
SMA	Familiar	-3.137	-4.209	9.508	0.005	0.302	1.259	Lefties											
Parietal	Unique	-2.614	-1.976	4.942	0.037	0.183	0.908	Righties											
Right Handed Images										Left Handed Images									
Parietal	Simple	-4.775	-3.666	4.667	0.042	0.175	0.882	Righties		M1	Unique	-2.200	-3.165	4.382	0.048	0.166	0.855	Lefties	

G.A. = Greater activation

Table 7

P3

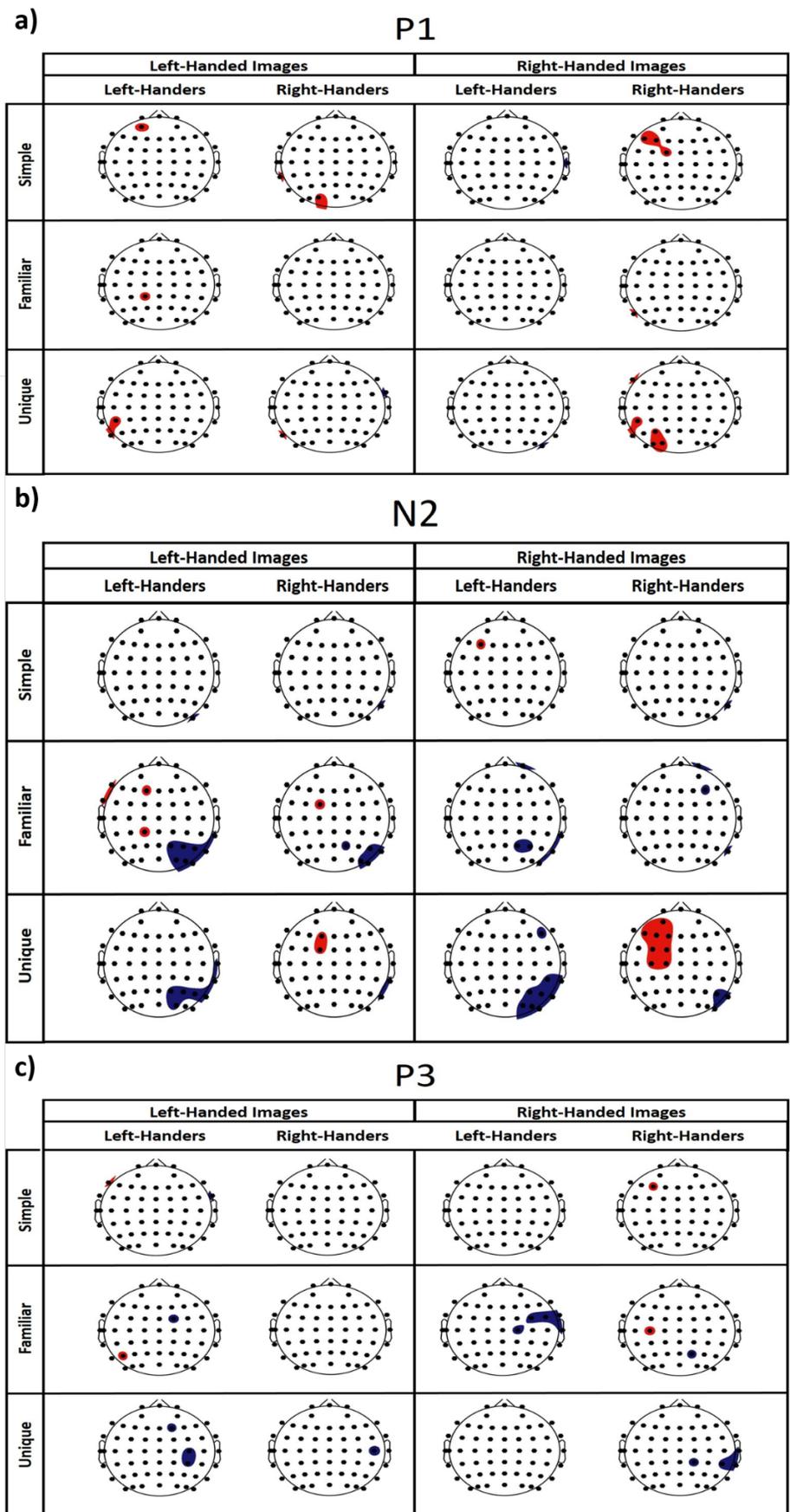
Left Handed Images										Right Handed Images									
Brain Region	Image Complexity	Mean Righties	Mean Lefties	F	Sig.	Partial η^2	Cohen's d		G.A.	Brain Region	Image Complexity	Mean Righties	Mean Lefties	F	Sig.	Partial η^2	Cohen's d		G.A.
SMA	Simple	3.633	6.062	9.272	0.006	0.296	1.243	Lefties		SMA	Simple	4.088	5.641	4.763	0.040	0.178	0.891	Lefties	
SMA	Familiar	2.154	3.645	21.852	0.000	0.498	1.908	Lefties		PMC	Familiar	1.612	2.918	18.832	0.000	0.461	1.772	Lefties	
PMC	Familiar	1.801	2.917	15.012	0.001	0.406	1.582	Lefties		SMA	Familiar	2.063	3.505	20.541	0.000	0.483	1.850	Lefties	
PMC	Unique	1.845	2.650	7.918	0.010	0.265	1.149	Lefties		SMA	Unique	2.451	3.077	4.741	0.040	0.177	0.889	Lefties	
										M1	Unique	1.507	2.401	12.317	0.002	0.359	1.433	Lefties	
										PMC	Unique	1.728	2.407	7.182	0.014	0.246	1.094	Lefties	
Right Handed Images										Left Handed Images									
PMC	Familiar	1.913	2.843	13.261	0.001	0.376	1.487	Lefties		SMA	Familiar	2.565	3.548	5.803	0.025	0.209	0.983	Lefties	
SMA	Familiar	2.550	3.652	13.409	0.001	0.379	1.495	Lefties		PMC	Unique	1.385	3.036	19.324	0.000	0.468	1.795	Lefties	
SMA	Unique	2.206	3.643	12.314	0.002	0.359	1.433	Lefties		M1	Unique	1.401	2.735	13.452	0.001	0.379	1.497	Lefties	
PMC	Unique	1.702	2.979	12.625	0.002	0.365	1.451	Lefties		SMA	Unique	1.953	3.733	19.696	0.000	0.472	1.812	Lefties	
M1	Unique	1.847	2.724	4.360	0.049	0.165	0.852	Lefties											

G.A. = Greater activation

Table 8

	Right-handed group
	Left-handed group

Figure 9. Lateralization head plots for statistical comparison of left-right hemisphere preferences for the ERP components of interest. Significant differences ($p < .05$) are colored over the electrode that showed greater activation. For visualization purposes, combinations where left electrode was greater than right electrode are colored red. Combinations where right electrode was greater than left electrode are colored blue.



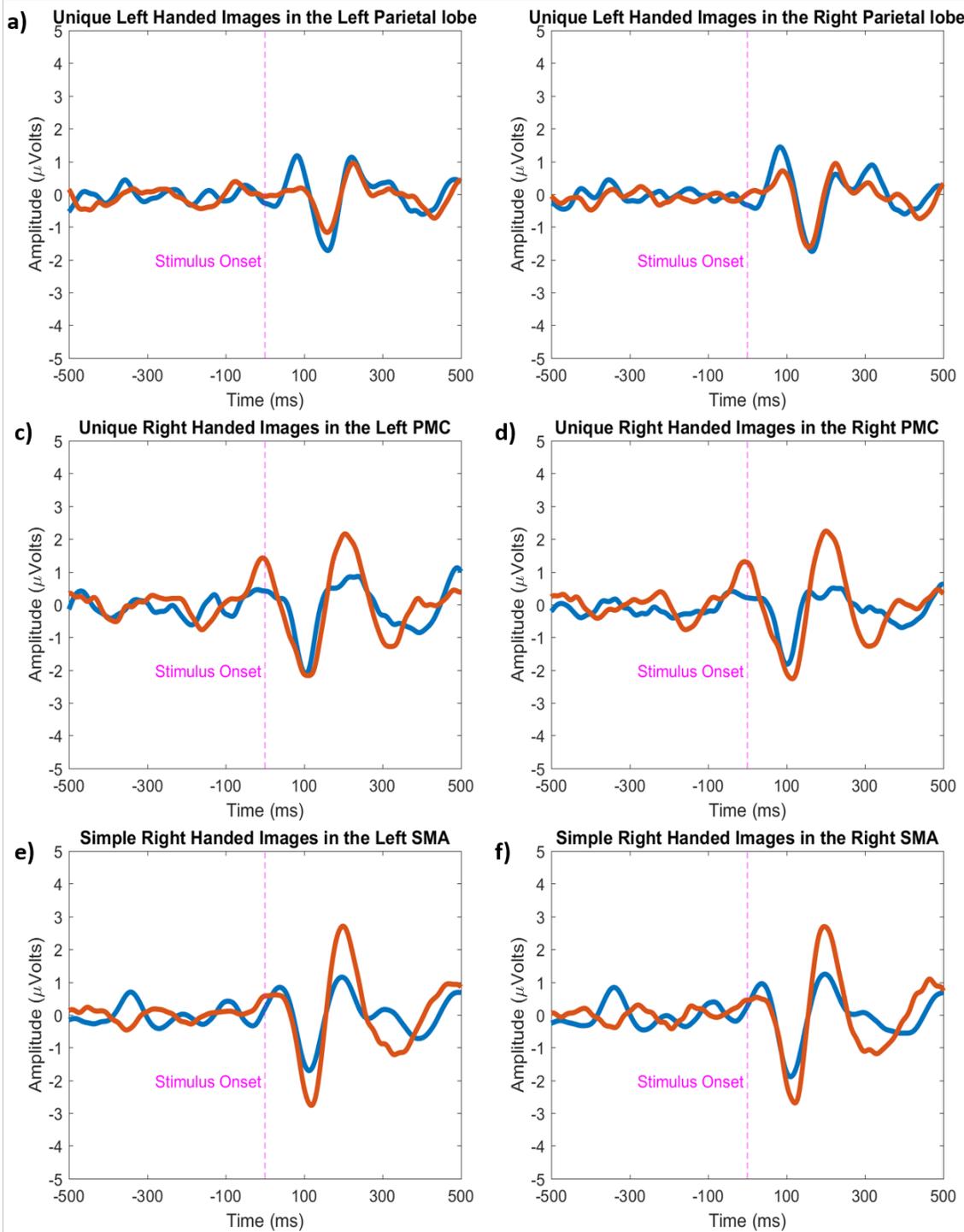


Figure 10. Event related potentials for both hemispheres in the parietal lobe, premotor cortex, and supplementary motor area.



Discussion

In this study, we hypothesized there to be a difference in laterality of premotor and parietal brain regions between right and left-handers as they mentally simulate movements. Previous research with fMRI and EEG coherence has shown left-handers to have more bilateral activation than right-handers and thus, we expected to find similar results with EEG. In our results, differences in lateral activation between these groups were not as prevalent as the differences in anterior-posterior activity. While solving the HLT, the left-handed group showed greater activation in the motor-related areas of the brain and right-handers showed more activation in the parietal brain regions. The following section will discuss these deviations from the expected findings and provide explanations and implications for the observed results.

Due to the findings from Kelly et al. (2015) and Martin et al. (2011), it was hypothesized that the laterality of N2 and P3 would differ between left-and right-handers. Our results showed little differences in laterality and generally showed both hemispheres to be equally involved for both populations. In the research by Kelly and colleagues (2015), participants were introduced to hand tools used for drilling and removing screws. After a period of physically using the tools, participants were shown pictures of these tools being used and asked to indicate if the screw was being inserted or removed from a board in the picture. Their results showed imaginary coherence between the parietal and premotor areas to be greatest in the hemisphere contralateral to the stimulus hand for the right-handed group. For the left-handed group, this coherence was

generally equal for both hemispheres regardless of the stimulus hand used. Martin et al. (2011) had a similar study design and allowed participants to physically execute an upper extremity reaching task before mentally simulating the same task. Although both of these studies share similarities with our current study, they both employ inherently different tasks and methods of measurement. Both of these tasks involve a mental simulation of a physical action that had recently been executed by the participant. In contrast, our study involved the understanding of an image that possibly had never been seen prior to data collections. These variations in task parameters may be the reason for discrepancies in the results found. It may be that when mentally simulating a familiar action (physically executed in recent past) these lateral differences become evident, but during initial object understanding, hemispheric preferences are not shown for either group. Another possible cause for the variance in these findings may be due to the method of measurement. Kelly et al. (2015) showed lateral preferences to be highest from 280-526 ms after stimulus onset. Martin and colleagues' (2011) results were taken from a three second window following stimulus presentation. As can be seen in figure 10, all of the ERP components of interest to this study occurred within 300 ms of stimulus onset. Results from this study suggest that laterality differences do not emerge during the initial phases of the HLT. Further work is needed to better understand the temporal development of laterality differences in these populations. It is possible that a study examining frequency-based measures of EEG during the HLT may provide more understanding in this area.

Instead of a hemispheric preference between right and left-handers, our results showed anterior-posterior differences in brain activity to solve the HLT. The P1 component reflects early visual processing and is affected by the spatial characteristics of an object. No differences in visual processing were expected between these groups and thus, the P1 component was not expected to differ across these groups. However, right-handers showed greater activation of the P1 in the SMA and parietal regions than left-handers. Recent research has shown the amplitude of P1 in the parietal lobe to reflect top-down modulation (Zanto & Gazzaley, 2009; Zanto et al., 2011). Thus, a difference in P1 may suggest a greater ability to use multi-sensory input to focus on task-relevant stimuli. According to Parsons (2003), the first three steps of solving the HLT are first, visual encoding, second, analysis of orientation differences between the target and mental template and third, mental rotation of the appropriate body part from the current to the target position, respectively. These results indicate that right-handers may be more efficient during visual encoding than left-handers. The ability to recognize task-relevant cues in the stimulus picture would assist them to form a mental template from previous motor experiences and rely less on the mental simulation of actually reproducing the hand posture. This suggestion is consistent with the findings over the SMA, PMC and primary motor cortices which all revealed a greater amplitude in N2 and P3 for left-handers. It is possible that left-handers rely on the motor system to more effectively mentally simulate movement of the appropriate limb to determine image laterality. This may be due to the fact that left-handers live in an environment that favors right-handers and

thus, are faced with the task of using common objects with their non-dominant hand (scissors, school desks, computer mouse, etc.) that right-handers do not face. This forced use of the non-dominant hand, may cause left-handers to rely on motor imagery to solve tasks that right-handers can solve by using visual and context clues. Interestingly, even though activation of brain regions differed between these two groups, behavioral results denote no difference in physical performance. This variation of active brain regions suggests that left and right-handers differ in neural strategies during motor imagery. Future research should attempt to clarify these differences by isolating the different stages involved in the HLT task.

Limitations

A limitation of this study is that electromyography (EMG) was not recorded from the arm muscles in order to quantitatively dismiss the possibility that participants attempted to imitate the image seen. Vision of hands was occluded and the experimenter monitored all participants, but EMG would confirm that EEG activity was reflective of action simulation and not execution. An additional limitation was that the picture bank of hand images contained more images classified as 'unique' than the other two complexity levels ('familiar' and 'simple'). This resulted in all participants seeing more unique images than familiar and simple images. In order to understand the involvement of image complexity on these neural markers, equal amounts of all levels should be included in the study procedure.

Conclusion

This work sought to better explain the differences in neural activity between right and left-handers during motor imagery. Our results suggest that in addition to a difference in hemispheric laterality between right and left-handers, there exists a difference in neural strategies that rely on different areas of the brain during motor imagery. This work can help clinical researchers to better understand the behavioral consequences of individuals with damage to these brain regions. Development of valid and efficient rehabilitation practices is centered on a sound understanding of the neural activates involved in the motor and cognitive tasks affected. Future work will focus on how these differences in the neural strategies of motor imagery affect behavior and physical actions.

Chapter 5: Conclusion

Since 1929 electroencephalography has been used to further the current knowledge of the human brain. It has been applied in many different ways to shine light on brain function during multiple different tasks. The purpose of this study was to better understand the ways in which electroencephalography can be used to measure regions of the brain involved with motor control and learning. For this purpose, a background of EEG was provided, followed by the description of two separate research studies that used EEG in different modalities to understand aspects of motor learning and control. These closing paragraphs will layout the main takeaways from this research and elaborate on their significance to this area of study.

In concluding this work, many key points were evident from this research. The first main takeaway from this study is that EEG can effectively be used to track neural changes in the brain throughout the learning process of complex movements, such as gait. Along with other uses, this new ability will benefit populations who suffer from gait disturbances (e.g., stroke, amputees, multiple sclerosis, Parkinson's disease, etc.) throughout their rehabilitation and assist them to gain independence. The second highlight gathered from this work is that left and right-handers differ in the way they use motor imagery to understand and plan movements. Based on our results, left-handers apply a greater degree of motor simulation while preparing for movement and understanding the movement of others. The underlying cause of this difference, as well as the

role of hand-dominance in motor function as a whole will be the focus of future research. A third key point gathered from this research is the need for proper experimental design and data collection preparation. Due to the variable and noise-prone nature of EEG, the collected signal, in its raw form, is habitually laden with unwanted noise. Thus, it is imperative to design research studies that collect enough EEG signal to successfully filter out the unwanted noise and measure the underlying neural activity of interest. Moreover, the careful preparation of the EEG cap to the head of the participant is essential, especially in studies involving physical movement, such as our gait-retraining project. A final pivotal takeaway from this work was the need for further research in motor learning and control. Since Ramon y Cajal first discovered the neuron (Ramon y Cajal, 1888), our understanding of how the brain understands, plans and executes movement has grown immensely. However, there is still so much that is unknown about this complex system. The intricacies of how sensory information is coordinated to result in successful motor execution are still largely a mystery. In this search for a greater understanding of the human motor system, the use of EEG will be valuable due to its temporal precision and ability to monitor brain processes during movement.

The two research projects included in this study were chosen because of their relevance to the current directions of motor control research with EEG. One of these projects involved collecting EEG during a complex movement involving multiple joints and planes of motion. This research is essential as these types of movements are executed daily and imperative to

independent living. Previously all motor control research using brain imaging has been done on stationary patients executing very simple movements. However, it is now possible to monitor brain activity as individuals execute movements common to daily life. Our work adds to this field by showing that EEG can be collected during running and can be used to monitor motor learning. The second study included in this research used EEG to monitor active brain regions during motor imagery. It is only recently that we know of the similarities in brain activity during imagined and physically executed actions. Thus, much research has been dedicated to understanding the underlying neural correlates involved in this shared activity. Our second study on motor imagery and hand-dominance highlights that this shared activity between imagined and executed movements is not uniform across the whole population. We showed that although physical behavior did not differ, the mental strategies used and mental representations recruited are affected by the dominant use of a hand. This discovery will assist in future research seeking to clarify the complexity that surrounds motor cognition research.

In summary, EEG has, and will continue to be, a vital tool in the area of motor learning and control research. The two studies included in this work exemplify how EEG can be used to monitor these brain processes during simple, complex and imagined movements of all sorts. This work emphasizes a need for further research into the motor systems of the brain and declares that EEG will be an essential tool in doing so for many years to come.

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APPENDIX A

Institutional Review Board Approval-Study 1



EAST CAROLINA UNIVERSITY
University & Medical Center Institutional Review Board Office
4N-70 Brody Medical Sciences Building Mail Stop 682
600 Moye Boulevard · Greenville, NC 27834
Office 252-744-2914 · Fax 252-744-2284 · www.ecu.edu/irb

Notification of Initial Approval: Expedited

From: Biomedical IRB
To: [Richard Willy](#)
CC:
Date: 2/28/2014
Re: [UMCIRB 13-002858](#)
The effect of increasing step rate on lower extremity loading

I am pleased to inform you that your Expedited Application was approved. Approval of the study and any consent form(s) is for the period of 2/27/2014 to 2/26/2015. The research study is eligible for review under expedited category #4,6. The Chairperson (or designee) deemed this study no more than minimal risk.

Changes to this approved research may not be initiated without UMCIRB review except when necessary to eliminate an apparent immediate hazard to the participant. All unanticipated problems involving risks to participants and others must be promptly reported to the UMCIRB. The investigator must submit a continuing review/closure application to the UMCIRB prior to the date of study expiration. The Investigator must adhere to all reporting requirements for this study.

Approved consent documents with the IRB approval date stamped on the document should be used to consent participants (consent documents with the IRB approval date stamp are found under the Documents tab in the study workspace).

The approval includes the following items:

Name	Description
Debriefing statement_steprate.docx	Debriefing Statement
Informed_Consent_steprate_2014_Submitted_ECU.docx	Consent Forms
NASA scale	Surveys and Questionnaires
Steprate_Recruitmen_Flyer-1.docx	Recruitment Documents/Scripts
Study_protocol_to_be_uploaded_steprate.docx	Study Protocol or Grant Application
Tegner Activity Scale	Surveys and Questionnaires
Treadmill Running Comfort Questionnaire	Surveys and Questionnaires

The Chairperson (or designee) does not have a potential for conflict of interest on this study.

IRB00000705 East Carolina U IRB #1 (Biomedical) IORG0000418
IRB00003781 East Carolina U IRB #2 (Behavioral/55) IORG0000418

APPENDIX B

Institutional Review Board Approval-Study 2



EAST CAROLINA UNIVERSITY
University & Medical Center Institutional Review Board Office
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600 Moye Boulevard · Greenville, NC 27834
Office 252-744-2914 · Fax 252-744-2284 · www.ecu.edu/irb

Notification of Initial Approval: Expedited

From: Social/Behavioral IRB
To: [Chris Mizelle](#)
CC: [Chris Mizelle](#)
Date: 10/6/2016
Re: [UMCIRB 16-001491](#)
Motor Imagery and Mental Rotation in Left and Right-Handed Individuals

I am pleased to inform you that your Expedited Application was approved. Approval of the study and any consent form(s) is for the period of 10/6/2016 to 10/5/2017. The research study is eligible for review under expedited category # 4. The Chairperson (or designee) deemed this study no more than minimal risk.

Changes to this approved research may not be initiated without UMCIRB review except when necessary to eliminate an apparent immediate hazard to the participant. All unanticipated problems involving risks to participants and others must be promptly reported to the UMCIRB. The investigator must submit a continuing review/closure application to the UMCIRB prior to the date of study expiration. The Investigator must adhere to all reporting requirements for this study.

Approved consent documents with the IRB approval date stamped on the document should be used to consent participants (consent documents with the IRB approval date stamp are found under the Documents tab in the study workspace).

The approval includes the following items:

Name	Description
Edinburgh Handedness inventory	Data Collection Sheet
Edinburgh.Handedness.Inventory.docx	Additional Items
Email Language	Recruitment Documents/Scripts
Informed consent	Consent Forms
Informed Consent Spanish	Translated Consent Document
Recruitment flier	Recruitment Documents/Scripts
Whittier.Mizelle.Protocol.docx	Study Protocol or Grant Application

The Chairperson (or designee) does not have a potential for conflict of interest on this study.

