Summer 8-15-2017

Intrinsic and Extrinsic Biomechanical Factors in a Co-adaptive ECoG-based Brain Computer Interface

Jonathan Carl Landes
Washington University in St. Louis

Follow this and additional works at: https://openscholarship.wustl.edu/eng_etds

Part of the Biomedical Engineering and Bioengineering Commons

Recommended Citation
https://openscholarship.wustl.edu/eng_etds/309

This Dissertation is brought to you for free and open access by the Engineering and Applied Science at Washington University Open Scholarship. It has been accepted for inclusion in Engineering and Applied Science Theses & Dissertations by an authorized administrator of Washington University Open Scholarship. For more information, please contact digital@wumail.wustl.edu.
WASHINGTON UNIVERSITY IN ST. LOUIS

School of Engineering & Applied Science
Department of Biomedical Engineering

Dissertation Examination Committee:
Daniel W. Moran, Chair
Dennis L. Barbour
Eric C. Leuthardt
Baranidharan Raman
Lawrence H. Snyder

Intrinsic and Extrinsic Biomechanical Factors in a Co-adaptive ECoG-based Brain Computer Interface

by

Jonathan Carl Landes

A dissertation presented to
The Graduate School
of Washington University in
partial fulfillment of the
requirements for the degree
of Doctor of Philosophy

August 2017
St. Louis, Missouri
# Table of Contents

List of Figures .................................................................................................................................. v

List of Tables .................................................................................................................................... viii

Acknowledgments .............................................................................................................................. ix

Abstract ............................................................................................................................................. xi

1 Introduction ................................................................................................................................... 1
  1.1 Motivation .................................................................................................................................... 3
  1.2 Specific Aims .............................................................................................................................. 6
  1.3 Organization of the Dissertation ............................................................................................... 8

2 Background ..................................................................................................................................... 9
  2.1 The Cerebral Cortex .................................................................................................................. 10
  2.2 Cortical Representations of Movement ....................................................................................... 13
  2.3 BCI Implementation .................................................................................................................. 17
    2.3.1 Recording Methods ........................................................................................................... 17
    2.3.2 Control Signals for Movement ......................................................................................... 26
    2.3.3 Biofeedback and Cortical Plasticity .................................................................................. 27
  2.4 Significance of Anthropomorphic Schemes .............................................................................. 30
  2.5 Summary .................................................................................................................................... 32

3 General Experimental Methods ................................................................................................... 33
  3.1 Subjects ...................................................................................................................................... 33
  3.2 Behavioral Setup ....................................................................................................................... 34
  3.3 ECoG Arrays ............................................................................................................................. 34
    3.3.1 Silastic Arrays ................................................................................................................... 35
    3.3.2 Polyimide Arrays .............................................................................................................. 37
    3.3.3 Surgical Implantation ....................................................................................................... 39
    3.3.4 Recording and Signal Processing ....................................................................................... 40
  3.4 BCI Tasks .................................................................................................................................... 45
    3.4.1 Classic Center-out Task .................................................................................................... 45
6 Cortical Control of Simulated Muscles for an Intrinsic, Dynamics-based BCI............ 141
  6.1 Introduction........................................................................................................ 141
  6.2 Methods............................................................................................................ 142
    6.2.1 Applied Models for Arm Dynamics and Muscle Forces ......................... 142
    6.2.2 Dynamic BCI Task Implementation.......................................................... 145
    6.2.3 Subjects and Experimental Protocol....................................................... 148
  6.3 Results............................................................................................................... 150
    6.3.1 General Task Performance....................................................................... 150
    6.3.2 Movement Trajectories .......................................................................... 153
    6.3.3 Control Signal Profiles and Properties................................................... 161
  6.4 Discussion.......................................................................................................... 174
References.............................................................................................................. 179
Appendix................................................................................................................ 189
# List of Figures

Figure 1.1: Sensorimotor Transformations During Reaching .................................................. 4

Figure 2.1: Motor and Sensory Homunculi .............................................................................. 12

Figure 2.2: Cosine Tuning in Primary Motor Cortex ............................................................... 16

Figure 2.3: Electrophysiological Recording Modalities ............................................................. 18

Figure 2.4: Cosine Tuning to Movement Direction in Single-unit and LFP .............................. 21

Figure 2.5: Cortical Plasticity in ECoG Control Band .............................................................. 30

Figure 3.1: Design of Silastic Arrays ....................................................................................... 36

Figure 3.2: Design of Polyimide Arrays .................................................................................. 38

Figure 3.3: Signal Processing Chain Occurring in DSP Hardware ......................................... 42

Figure 3.4: Pre-processing of Neural Features in Software ...................................................... 44

Figure 3.5: Novel 2-D Joint Angle Task ................................................................................... 47

Figure 3.6: BCI Control Schematic ....................................................................................... 49

Figure 3.7: Daily Training Protocol ....................................................................................... 54

Figure 4.1: Overview of Implanted ECoG Arrays .................................................................. 59

Figure 4.2: Cosine Tuning Example ....................................................................................... 65

Figure 4.3: Mean Vector Length Example ............................................................................... 67

Figure 4.4: Average Movement Trajectories .......................................................................... 70

Figure 4.5: Daily Task Psychophysics .................................................................................... 72

Figure 4.6: Feature Tuning Relationships .............................................................................. 75

Figure 4.7: R² and Weight Magnitudes by Frequency Band ...................................................... 79

Figure 4.8: Mean vs. Depth of Modulation in Monkey P ........................................................ 81

Figure 4.9: Overview of Encoding and Decoding Directions ................................................... 83

Figure 4.10: Regression R² differences between motor (Red) and sensory (Blue) electrodes .... 85
Figure 4.11: Decoding weight differences between motor (Red) and sensory (Blue) electrodes 87
Figure 4.12: Motor vs. Sensory Preferred Directions.......................................................... 88
Figure 4.13: Left vs. Right Hemisphere Preferred Directions.............................................. 89
Figure 4.14: Three Control Columns....................................................................................... 92
Figure 4.15: K-means clustering with $K = 2$ ....................................................................... 94
Figure 4.16: Push and relax strategy, monkey G.................................................................. 97
Figure 4.17: Push, push, and push strategy, monkey I............................................................ 98
Figure 5.1: Joint Angle Task Overview.................................................................................. 104
Figure 5.2: Joint Space Error Direction Represented in Cartesian Space......................... 106
Figure 5.3: Experimental Protocol......................................................................................... 110
Figure 5.4: Cursor Path Trajectories in Cartesian Space..................................................... 116
Figure 5.5: Cursor Path Trajectories in Joint Space.............................................................. 117
Figure 5.6: Cursor Velocity Profiles...................................................................................... 121
Figure 5.7: Control Signals Projected onto the Center-Target Line..................................... 124
Figure 5.8: Dot Product Temporal Profiles for Cartesian and Joint Angle Control........... 125
Figure 5.9: Percentage Weight Contributed by each Frequency Band................................. 128
Figure 5.10: Daily Decoding Weights over Time................................................................. 130
Figure 5.11: Correlation of Decoding Weights...................................................................... 132
Figure 5.12: Cosine Tuning $R^2$ by Frequency Band........................................................... 134
Figure 5.13: Exemplar Feature from Monkey G................................................................. 136
Figure 6.1: Musculoskeletal Model ....................................................................................... 142
Figure 6.2: Cursor Path Trajectories in Cartesian Space..................................................... 155
Figure 6.3: Cursor Path Trajectories in Joint Angle Space.................................................. 156
Figure 6.4: Temporal Profiles of the Dot Product for Each Control Scheme....................... 159
Figure 6.5: Cursor Velocity Profiles from Monkey G............................................................ 160
Figure 6.6: Magnitudes of the Control Signals for Monkey G ........................................... 162
Figure 6.7: Dynamic Range of Control Signals .................................................................. 164
Figure 6.8: Muscle Activation Profiles for Monkey G ........................................................ 166
Figure 6.9: Muscle Activation Profiles and Correlations for all Subjects ............................. 167
Figure 6.10: Co-activation of Antagonistic Muscle Pairs .................................................. 169
Figure 6.11: Proportional Torque Contributions for Simulated Reaches ............................ 171
Figure 6.12: Proportional Torque Contributions: Simulation vs. Data ............................... 173
Figure 6.13: Co-activation of opposed control signals during extrinsic kinematic control ....... 175

Figure A.1: Percentage of Features Recruited as a function of mean $R^2$ ............................... 189
Figure A.2: Individual Monkey Range of Modulation .......................................................... 190
Figure A.3: Individual Monkey Mean vs. Depth of Modulation Relationships ...................... 191
Figure A.4: Regression $R^2$ distributions for motor and sensory electrodes ......................... 192
Figure A.5: Decoding weight distributions for motor and sensory electrodes ....................... 193
Figure A.6: K-means clustering with $K = 3$ ....................................................................... 194
Figure A.7: Jacobian Determinant from Joint Angle Space to Cartesian Space ....................... 196
Figure A.8: Mean Decoding Weight Vectors, from Chapter 5 .............................................. 197
Figure A.9: Cosine Tuning Preferred Directions, from Chapter 5 ......................................... 198
Figure A.10: Magnitudes of the Control Signals for Monkey O, from Chapter 6 ................... 200
Figure A.11: Magnitudes of the Control Signals for Monkey I, from Chapter 6 ..................... 201
Figure A.12: Dot products between the applied torque and velocity vectors .......................... 202
Figure A.13: Torque-velocity dot products in the absence of joint friction ............................ 203
List of Tables

Table 3.1: Summary of Experimental Subjects ................................................................. 35
Table 4.1: Subjects Background .......................................................................................... 58
Table 4.2: Task Related Parameters for 2-D Center-out BCI ............................................. 61
Table 4.3: General Task Performance .................................................................................. 68
Table 4.4: Single Trial Performance Metrics ...................................................................... 69
Table 4.5: BCI Pentathlon Scoring Chart ............................................................................ 71
Table 4.6: Feature Tuning Relationship Regression Statistics ............................................. 76
Table 4.7: Percent Significant Tuning by Band ................................................................... 78
Table 4.8: Significant Relationships between Mean and Depth of Modulation .................. 82
Table 4.9: Significant differences between motor and sensory ........................................... 85
Table 5.1: Joint Angle Task Parameters .............................................................................. 103
Table 5.2: General Task Performance / Data Collection Summary ..................................... 114
Table 5.3: General Task Performance / Daily Averages ± Standard Deviation .................... 114
Table 5.4: General Task Performance / Block Averages ± Standard Deviation .................... 114
Table 5.5: BCI Trajectory Metrics in each Reference Frame ............................................... 119
Table 6.1: Dynamic Model Parameters ............................................................................... 143
Table 6.2: BCI Gain Parameters .......................................................................................... 150
Table 6.3: General Task Performance / Data Collection Summary ..................................... 152
Table 6.4: General Task Performance / Daily Averages ± Standard Deviation .................... 152
Table 6.5: General Task Performance / Block Averages ± Standard Deviation .................... 152
Table 6.6: BCI Trajectory Metrics in each Reference Frame ............................................... 157

Table A.1: Cosine Tuning of Kinematics vs. Frequency Bands ........................................... 195
Table A.2: Percent correct with single worst block removed from each day, from Chapter 6... 199
Acknowledgments

As the completion of this dissertation brings my graduate school career to a close, I would like to take this opportunity to acknowledge those who have supported me throughout this amazing journey. First, I would like to thank the National Science Foundation, who funded my research through the Mind, Machines, and Motor Control (M3C) program (NSF EFRI 1137211). Without this financial support the ideas, strategies, and findings resulting from this work would not be possible. I would like to thank the BME department at WashU for providing a welcoming atmosphere and the opportunity to pursue my education and research goals.

I would like to thank each of the members of my thesis committee for broadening my horizons by providing valuable advice, insights, and critiques from a fresh perspective. I must thank my advisor, Dan Moran, for all of his guidance, encouragement, and enthusiasm. I would also like to thank the past and present members of the Moran lab, who helped form a solid foundation for engineering and neuroscience research. It truly was a pleasure to work with each of my ECoG BCI comrades in the lab: Jesse Wheeler, Piyush Karande, and Keith Dyson. Additionally, I owe a very special thanks to Donna Reedy, for her help in training and caring for the monkeys.

Last but not least, I would like to thank my friends and family. I am forever grateful for their continuous love and support.

Jonathan C. Landes

Washington University in St. Louis

August 2017
Dedicated to mom and dad.
Paralysis, due to spinal cord injury, amyotrophic lateral sclerosis (ALS), or stroke, is the result of severed communication between the brain and the motor periphery. Brain computer interfaces (BCIs) are neuroprosthetic devices that create novel communication pathways by measuring and transforming neural activity into operational commands. State of the art BCI systems measure brain activity using penetrating electrode arrays able to record from hundreds of individual cortical neurons simultaneously. Unfortunately, these systems are highly susceptible to signal degradation which limits their efficacy to 1-2 years. However, electrocorticography (ECoG) signals recorded from the surface of the brain deliver a more competitive balance between surgical risk, long-term stability, signal bandwidth, and signal-to-noise ratio when compared to both the aforementioned intracortical systems and the more common non-invasive electroencephalography (EEG) technologies.

Historically, neural signals for controlling a computer cursor or robotic arm have been mapped to extrinsic, kinematic (i.e. position or velocity) variables. Although this strategy is adequate for use in simple environments, it may not be ideal for control of real-world prosthetic devices that are subject to external and unexpected forces. When reaching for an object, the trajectory of the hand through space can be defined in either extrinsic (e.g. Cartesian) or intrinsic (e.g. joint
angles, muscle forces) frames of reference. During this movement, the brain has to perform a series of sensorimotor transformations that involve solving a complex, 2nd order differential equation (i.e. musculoskeletal biomechanics) in order to determine the appropriate muscle activations. Functional neuromuscular stimulation (FNS) is a desirable BCI application because it attempts to restore motor function to paralyzed limbs through electrical excitation of muscles. Rather than applying the conventional extrinsic kinematic control signals to such a system, it may be more appropriate to map neural activity to muscle activation directly and allow the brain to develop its own transfer function.

This dissertation examines the application of intrinsic decoding schemes to control an upper limb using ECoG in non-human primates. ECoG electrode arrays were chronically implanted in rhesus monkeys over sensorimotor cortex. A novel multi-joint reaching task was developed to train the subjects to control a virtual arm simulating muscle and inertial forces. Utilizing a co-adaptive algorithm (where both the brain adapts via biofeedback and the decoding algorithm adapts to improve performance), new decoding models were initially built over the course of the first 3-5 minutes of each daily experimental session and then continually adapted throughout the day. Three subjects performed the task using neural control signals mapped to 1) joint angular velocity, 2) joint torque, and 3) muscle forces of the virtual arm. Performance exceeded 97%, 93%, and 89% accuracy for the three control paradigms respectively. Neural control features in the upper gamma frequency bands (70-115 and 130-175 Hz) were found to be directionally tuned in an ordered fashion, with preferred directions varying topographically in the mediolateral direction without distinction between motor and sensory areas. Long-term stability was demonstrated by all three monkeys, which maintained performance at 42, 55, and 57 months post-implantation. These results provide insights into the capabilities of sensorimotor cortex for control of non-linear multi-joint reaching dynamics and present a first step toward design of intrinsic, force-based BCI systems suitable for long-term FNS applications.
1 Introduction

In humans, the nervous system consists of two main parts, the Central Nervous System (CNS) and Peripheral Nervous System (PNS), that work together to transform intentions into actions. The CNS is comprised of the brain and spinal cord and is responsible for generating and processing signals, while the PNS consists mainly of nerves that transmit these signals to every other part of the body. Nerves that transmit motor commands from the brain are called motor or efferent nerves and mediate voluntary movement. Movement related malfunction of the nervous system can occur as a result of degenerative motor neuron diseases like Amyotrophic Lateral Sclerosis (ALS) or trauma to the spinal cord. In either case, the body’s motor output commands are disrupted before movement can be produced. Although patients with conditions ranging from spinal cord injury to late-stage ALS and locked-in syndrome may have fully intact cognitive function, their ability to interact with the world around them is severely compromised.

By merging the fields of neurophysiology and engineering, movement can be restored in motor impaired individuals by interpreting their intentions, which can then be used to control machines. This field of study is widely known as neuroprosthetics and is used to build the class of devices called Brain Computer Interfaces (BCIs, also referred to as BMIs or brain machine interfaces). BCI implementation can facilitate actions as simple as moving a cursor on a screen or as complex as controlling a prosthetic limb. Over the past 20 years, researchers have made great strides improving the application of brain signals for the control of external devices. The development of clinical BCI systems has largely focused on improving functional independence for patients with severe motor impairments, including providing tools for communication and mobility.
To bypass the damaged peripheral nervous system, BCI devices must record and decipher the motor intentions represented in the brain. Electroencephalography (EEG), Intracortical Single-Unit and Multi-Units, and Electrocorticography (ECoG) are three primary recording modalities used in the research and development of BCI systems. Depending on which is used, there is a trade-off between surgical invasiveness and robustness of signal. At the one extreme, EEG relies on signals from noninvasive electrodes placed directly on the scalp. While multi-dimensional movement control has been demonstrated with EEG systems [1], [2], poor accuracy and learning rates have limited their efficacy compared to other methods of BCI. In stark contrast, intracortical single- and multi-unit electrode systems have proven to be effective and accurate sources for BCI applications in both monkeys and humans. However, these types of recordings require complicated, highly invasive surgeries resulting in elevated risk of CNS infection. Additionally, the quality of these recordings tends to decay over time as electrodes become physically encapsulated and electrically insulated by the immunologically reactive tissue.

Electrocorticography (ECoG) is a well-balanced technique that records brain signals from the surface of the cortex in either the subdural or epidural space. Both subdural and epidural ECoG configurations are less invasive than intracortical recordings because they are not piercing into the brain parenchyma. Since the first demonstration of ECoG-based BCI in humans by Leuthardt and colleagues [3], its clinical and academic applications have been extensively studied in both humans and non-human primates. Due to recording extracellular field potentials from inside the skull, ECoG exhibits higher spatial (on the order of millimeters) and spectral (up to roughly 200 Hz) resolution than EEG (centimeters and up to 50 Hz). Unsurprisingly, advances in ECoG BCI remain a step ahead of EEG in terms of the complexity and accuracy of
acquired control. However, intracortical systems typically exhibit superior control signal bandwidth and continue to advance the field in terms of outcome expectations in the realm of dexterous limb control [4], [5].

1.1 Motivation

Simple prosthetic arms and legs can help to restore mobility for otherwise healthy individuals suffering from limb loss by redirecting residual motor function to control of the device. However, those with the least ability to move and communicate have arguably the greatest need, and these individuals lack comparable therapies. Possible remedies include the technique of Functional Neuromuscular Stimulation (FNS), which aims to reanimate paralyzed limbs by electrically stimulating the intact muscles. FNS is certainly considered a worthwhile candidate for BCI technologies because many of the control strategies required for meaningful function of paralyzed limbs are analogous to those for directing fully robotic arms.

Consider the act of reaching for a glass of water. In order to be successful, the goal (reach the glass) must be translated to a series of muscle activations (in robotic arms this would be analogous to the torques exerted by joint actuators) as illustrated in Figure 1.1. These sensorimotor transformations are non-unique; for example there are an infinite number of hand paths possible that would result in success. On the flip-side, a defined hand path uniquely describes the end state or goal. These forward and inverse transformations are known as many-to-one and one-to-one mappings respectively. These many-to-one transformations are not performed consciously, but rather several cortical and subcortical brain structures play a large role in estimating the most desirable transformation.
Spatial goals, such as reaching to a location in space, are converted to muscle activity through a sequential series of intermediary representations or coordinate frames. Neural recordings, primarily in motor cortex, have been demonstrated to correlate with each of these reference frames to varying degree under specifically designed behavioral tasks. (Figure adapted from Scott [6])

Parameters measured with respect to the external world, such as the Cartesian coordinates of the hand, are considered parameters of extrinsic space (e.g. A and B). Conversely, quantities like the forces exerted by individual muscles or the angular velocities of the shoulder and elbow joints are considered intrinsic in nature (e.g. C, D, and E) because they are measured relative to the object being controlled (in this case, the arm itself). Both extrinsic and intrinsic factors are essential in the way humans perform daily activities and are just as significant in the design of prosthetic BCIs for restoring meaningful function to people with disabilities.

Extrinsic, kinematic features of upper limb movement are well represented in single-unit activity of motor cortex, while intrinsic properties like joint kinematics and muscle forces appear to be less significant [7], [8]. BCI systems have taken advantage of this knowledge for continuous control of cursors or prosthetic limbs, utilizing extrinsic, kinematics-based user commands such as hand position or velocity. Traditionally, only desired target locations or hand kinematics are decoded for control, resulting in the BCI system being responsible for the remaining sensorimotor transformations. While these signals are satisfactory for control of
simulated objects such as those found in virtual environments, they may not be ideal for control of real-world prosthetic devices that are subject to external and unexpected forces. For cases in which the physical model of the limb is unknown or incomplete, using an inverse model to estimate intrinsic dynamics from the users’ extrinsic-kinematic control signal can result in large errors and unproductive movements. In order to minimize these errors it may be more effective to map brain activity to muscle activation directly and allow the brain to develop its own transfer function between muscle stimulation and limb movement. Some evidence for the long-term decoding of intrinsic features in ECoG has also recently surfaced, lending credibility to the idea that these features can be used for control in a BCI format [9]–[11].

With this in mind, we wish to expand the breadth of utility of current ECoG systems by developing an intrinsic-based BCI that may be more suitable for applications of this nature. This work involves alternative control schemes for ECoG-based brain computer interfaces. As more degrees-of-freedom (DOF) become possible for BCI (i.e. more attainable limb states), the shift to a more anthropomorphic scheme could prove advantageous moving towards dexterous control or prosthetic limbs that can functionally replace their natural counterparts.

In addition, our results may enhance our understanding of the functional organization of motor cortical areas and their encoding strategies. Nearly all BCI systems have utilized activity from primary motor cortex (M1), decoding kinematic variables for control. Assessing M1’s ability to control intrinsic-based BCI applications could directly address several controversial theories of motor control and lead to new models of M1’s capacity to interact directly with machines.
1.2 Specific Aims

Our lab has worked almost exclusively with extrinsic-velocity-based control signals using epidural ECoG recordings in the motor cortex of non-human primates (refer to B in Figure 1.1). By using naïve co-adaptive algorithms that iteratively update feature weights, we have demonstrated accurate control of a computer cursor in up to 4-DOF. The primary goals of this work are to study the neural activation patterns resulting from control schemes in both extrinsic and intrinsic reference frames and to directly assess the feasibility of a basic anthropomorphic BCI control signal for use in upper limb control. The three specific aims of this dissertation are:

**Aim I: Identify topographical and frequency-dependent characteristics of directional tuning in ECoG during 2-D kinematic cursor control with a naïve co-adaptive decoder.**

Previous results have suggested that M1 is the most effective cortical region for BCI control. In single neuron directional tuning studies, the cortical topography is rarely discussed. The reasons are that regions that are not tuned to scientific parameters are excluded and the preferred directions have been reported to be uniformly distributed. With virtually stationary chronically implanted grids above the cortical surface, we have an opportunity to examine these properties.

*Hypothesis:* With a large sample size (n = 6 monkeys) we expect to see functional differences between motor and sensory areas, be it in either the strength or direction of encoding or in the control weights assigned to these areas.
Aim II: Compare kinematic control between intrinsic and extrinsic reference frames in a virtual environment using a novel joint angle-based BCI paradigm. To accomplish this aim we will alternate the cursor control between two tasks:

a. Use a simple 2-D center-out closed loop BCI task in which the neural features are used to control the Cartesian coordinates of a cursor in the traditional kinematic velocity fashion.

b. Expand the current 2-D task such that the features are used to control the joint angular velocity of a simple two-link arm to reach the same set of targets with the virtual hand.

Hypothesis: The subjects (n = 2) will be able to learn the new task and perform at a similar level to the Cartesian center-out task. To achieve this, a shift or change in the neural signal modulations between the two control tasks may be required.

Aim III: Investigate the online control of a force-based anthropomorphic control signal in closed-loop ECoG BCI by implementing controllable musculotendon units into the two-link arm model. We wish to address whether a force-based BCI control signal is viable for applications such as functional neuromuscular stimulation of paralyzed limbs. Previously, our lab has implemented force-based control by re-applying kinematic models in effort to reduce the learning curve and smoothly transition the animals to the new scheme. Similarly, we will:

a. Train the animals on a dynamics-based BCI task in a virtual environment simulating simple real-world physics, including Coriolis and joint friction forces.

b. Transition the animals to a muscle force-based control task by using a minimum stress model for intended muscle activations.

c. Quantify movement times, trajectories, and accuracy to compare with results of the kinematic joint angle task to assess the obtainable degree of control.

Hypothesis: Learning the inverse dynamics model of the arm may inherently be difficult. The subjects (n = 3) may need to produce entirely new patterns of neural modulation when learning either the inverse model or the musculoskeletal scheme. The transition from joint torques to individual muscle forces requires the use of coordinated activations of opposing muscles for movement. This entirely new frame of reference may cause a perceivable loss in dexterity of the virtual arm.
1.3 Organization of the Dissertation

This document is divided into six subsequent chapters. Chapter 2 provides relevant background material on basic motor control neurophysiology, current BCI technologies and algorithms, recent developments in ECoG-based research, and current approaches to implementing anthropomorphic control such as functional neuromuscular stimulation of the upper limb. Chapter 3 presents the general experimental formats and methodologies used throughout this work. Further data analyses are introduced separately for Chapters 4 through 6. Chapter 4 addresses the goals outlined in Aim I through post-hoc analysis of 2-D center-out closed-loop BCI experiments with six chronically implanted rhesus monkeys. Chapter 5 presents a series of experiments geared toward addressing Aim II through evaluation of an intrinsic but kinematics-based control signal in a novel joint angle control variation of the center-out task using two monkeys. Chapter 6 accounts for Aim III by implementing a dynamic model of the virtual two-link arm for use in the aforementioned joint angle center-out task. Three monkeys performed the task using control signals mapped to 1) joint angle velocity, 2) joint torque, and 3) muscle forces of six simulated muscle groups on the arm. This chapter also concludes this work with a discussion of the findings presented and their implications as well as several possible paths for additional investigation based upon these results.
2 Background

In 1780, Luigi Galvani established a link between nerve cells and electricity by showing that the muscles of dead frogs’ legs twitched when struck by an electrical spark. This finding is credited with starting the field of bioelectricity; the study of electrical patterns and signals from tissues such as nerves and muscles [12]. 1849 marked the beginning of modern electrophysiology when Hermann von Helmholtz demonstrated the electrical interactions between adjacent nerve cells. At this time, it was believed that electricity flowed (immeasurably fast) from the point of contact through the nerve and to the innervated muscle like a conductor. However, Helmholtz determined this was actually an electrochemical reaction, and that electrons were not flowing through the nerve. Instead, he postulated that the electricity would cause the stimulated cell to emit an action potential (referred to as a “spike”) that would propagate down the length of the axon to the next cell, at which point the next cell may also spike. Using a galvanometer as a sensitive timing device, he electrically stimulated a recently dissected sciatic nerve of a frog and the calf muscle to which it attached. Helmholtz measured this speed as being between 24 and 38 meters per second; much slower than the flow of electrons through a conductive medium.

Over the last two centuries, numerous studies have been carried out to learn more about these electrophysiological relationships, particularly those related to the surface of the brain, the cerebral cortex. This chapter serves to introduce core concepts in motor neurophysiology and engineering algorithms as they pertain to a BCI system for control of an assistive device.
2.1 The Cerebral Cortex

The cerebral cortex is made up of layers containing billions of neurons which communicate by way of binary signals. These neurons are the basic building blocks of information transfer in the brain and corresponding peripheral nervous system. Neurons are nerve cells that process and transmit information through electrical and chemical signals called action potentials or “spikes”. These electrically excitable cells process and transmit information through electrochemical signals to other cells through synapses. The connective network of neurons allows different regions of the cortex the ability to perform various functions. Hence, the cerebral cortex plays a key role in memory, attention, perception, awareness, thought, language, and consciousness.

In humans and other mammals, the cerebral cortex is the outer layer of neural tissue of the cerebrum of the brain. It is separated by the longitudinal fissure that divides the cerebrum into the left and right cerebral hemispheres. In humans the cerebral cortex is 2 to 4 millimeters thick [13] and folded, giving a much greater surface area within the confined volume of the skull. A fold or ridge in the cortex is termed a gyrus (plural gyri) and a groove or fissure is termed a sulcus (plural sulci).

Scientists have constructed maps of cortical areas on the basis of variations in cell types and the appearance of the layers. One of the most widely used maps came from Korbinian Brodmann, who split the cortex into 52 numbered areas [14]. Many of the areas Brodmann defined based solely on their neuronal organization have since been closely correlated to diverse cortical functions. For example, Brodmann areas 1, 2 and 3 are the primary somatosensory cortex (S1); area 4 is the primary motor cortex (M1); area 17 is the primary visual cortex (V1); and areas 41 and 42 correspond closely to primary auditory cortex (A1). Many of the brain areas
Brodmann defined have their own complex internal structures. In a number of cases, brain areas are organized into topographic maps, where neighboring columns of the cortex correspond to adjoining parts of the body (e.g. S1 and M1) [15]–[18], or of more abstract arrangements (e.g. V1 and A1) [19]–[21].

The primary motor cortex is located on the precentral gyrus (e.g. the anterior bank of the central sulcus, while the primary somatosensory cortex is located on the postcentral gyrus, (e.g. the posterior bank). In 1937, Penfield and Boldrey were the first to show the similarities in the maps between primary motor cortex and primary somatosensory cortex through electrical stimulation of human patients suffering from focal epilepsy [18]. While stimulation of the precentral gyrus was known to produce muscle twitches, they discovered that stimulation on the postcentral gyrus would elicit a tingling sensation rather than movement. These somatotopic maps on the motor and sensory cortices are known today as the cortical homunculi (singular homunculus, or “little man inside the brain”). This somatotopic representation is not evenly distributed, however. The head, for example, is represented by a region that is almost three times as large as the portion for the entire back and trunk. The size of any region correlates to the precision of motor control or sensory discriminatory ability. Hence, the areas for the lips, fingers, and tongue, are particularly large, considering the proportional size of their matching anatomical body parts. Figure 2.1 illustrates the topographical arrangement, with hands and face taking up much more of cortical real-estate in the lateral portions of cortex than the legs and trunk do in the more medial locations.
Using electrical stimulation during awake craniotomies in humans, Penfield and Boldrey mapped out several sensorimotor regions. Stimulation of the precentral gyrus (M1) elicited movements of the body, and within M1 different body parts were topographically separated. They deemed this the motor homunculus or “little man”. Similarly, stimulation of the postcentral gyrus (S1) also exhibited topographical separations. This is called the sensory homunculus, and its arrangement is nearly paralleled in the mediolateral direction [22].

The results from these stimulation mapping experiments are indicative of the corticospinal tract, which conducts impulses from the brain to the spinal cord. The cells have their bodies in the cerebral cortex, and the axons form the bulk of the pyramidal tracts [23]. The nerve axons traveling down the tract are referred to as efferent nerve fibers of the upper motor neurons. Upper motor neurons are large layer V pyramidal neurons whose axons extend to the spinal cord for muscle contraction. Most of these fibers arise from the primary motor cortex (about 30%), supplementary motor area and the premotor cortex (together also about 30%), while the somatosensory cortex, parietal lobe, and cingulate gyrus supply the rest [24].

The majority of fibers of the corticospinal tract cross over in the medulla, resulting in muscles on one side of the body being controlled by the opposite (contralateral) hemisphere of the brain. These axons travel down the tracts in the white matter of the spinal cord until they
reach the vertebral level of the muscle that they will innervate [25]. Most axons do not directly synapse with lower motor neurons, but instead synapse with interneurons that then synapse with lower motor neurons. Nerve axons of the lateral corticospinal tract that did not cross over in the medulla do so at the level of the spinal cord in which they terminate [26].

While the majority of nerve axons are small (< 4 μm) in diameter, about 3% have a much larger diameter (16 μm) and arise from Betz cells [24]. Exclusive to primary motor cortex, Betz cells are thought to be some of the largest neurons in the human nervous system and have been recorded to reach over 100 μm in diameter [27] and have the highest signal conduction rates (over 70 m/s) from the brain to the spinal cord [24]. This is due in part to the fact that the axons of these pyramidal neurons must travel a considerable distance to reach their targets, most notably the motor neurons of the spinal cord and the brainstem.

2.2 Cortical Representations of Movement

Movement plays a large role in how we get around in the world and communicate with others. To speak, muscles in the vocal cords must vibrate to modulate airflow. To communicate through text or e-mail; requires the input of combinations of words or numbers via speech or movement of the fingers. For the motor impaired, these simple daily activities are severely hindered or even impossible.

The previously described electrical stimulation studies generated rough movements or sensations artificially by activating subpopulations of neurons in the area. As technology has advanced, the ability to record signals from individual neurons in the cortex has allowed researchers to better understand the role these cortical areas play in motor control. Spiking activity of single neurons can be recorded using intra-cortical electrodes embedded in the parenchyma and is traditionally termed “single unit activity” [28]–[30]. It seems intuitive that a
brain controlled prosthetic device with the goal of reproducing the complex movements natural
to the human body would work best if its operation was appropriately matched to its natural
counterpart in the brain. If a prosthetic arm is tasked with reaching for an object, the brain might
respond most naturally to a BCI system that utilizes brain signals which normally encode arm
movement parameters. Accordingly, much research has been devoted to understanding how
motor-associated areas of cortex naturally act in the production of volitional movements using
non-human primate models.

In the 1960’s, influential work by Evarts demonstrated individual neurons firing in the
primary motor cortex during spontaneous movements such as feeding and grooming in non-
human primates [31]. He and others over the next 20 years established that M1 neurons may
encode various low-level parameters of movement like static and dynamic components of force
by having the animals perform stereotyped wrist movements [32]–[35] and gripping force [36]
trials.

One of the premier debates in motor neurophysiology centers around whether primary
motor cortex encodes low-level (i.e., intrinsic) commands such as individual muscle activations
or forces or whether it encodes higher-level (i.e., extrinsic) commands such as a desired position
or velocity with distal structures in the motor system such as the spinal cord performing the
appropriate transformations to muscle activations. In 1982, Georgopoulos and colleagues
discovered the phenomena known as “cosine tuning” by establishing that the spiking activity of
individual neurons was modulated by the direction of hand movements [37]. Using a novel
center-out reaching task, animals would perform reaching movements from a center position to
one of eight equally spaced radial targets while neuronal activity was recorded from primary
motor cortex. They demonstrated that the firing rate of recorded neurons were cosine tuned with
the direction of motion (i.e., target direction). This refers to the fact that firing rate is highest in a preferred direction (PD), and activity falls off as the cosine of the angle between the PD and movement direction as illustrated in Figure 2.2.

This finding has fueled the debate in favor of primary motor cortex encoding extrinsic features of movement. In the years following, Georgopoulos et al. introduced the population vector algorithm (PVA), in which the population activity can be vector summed to predict the movement direction in both 2- and 3-dimensional space [7], [38]. In their more rigorous experimentation, they found that M1 neurons were distributed uniformly in their PD’s, with a population sample distribution approaching uniformity driving the accuracy of the predicted movement direction [39]–[41]. Schwartz and colleagues expanded this notion to windowed time periods during movement to demonstrate movement direction was temporally encoded by the population vector during sinusoidal tracing movements [42]. A more definitive relationship between neural activity and instantaneous velocity was published by Moran and Schwartz in 1999 [43], [44].

Subsequent studies aimed to correlate this directional-tuning with other parameters such as position, velocity, acceleration, as well as effects of posture [45]–[48]. While neuronal activity was found to be influenced by all of these parameters, the most well represented high-level parameters in motor cortex appear to be position and velocity. In both cases, the encoded parameters were broadly represented and well fit by a cosine function [49].

To date, it is widely accepted that extrinsic kinematics are well represented in primary motor cortex, and that intrinsic representations will coexist when task parameters are correlated. However, some studies have teased these correlations apart, and found that some neurons are still intrinsically motivated, even if to a lesser extent than extrinsic representation [8]. These cortical
representations in motor and sensory areas provided the initial foundation and aspiration for external prosthetic devices that could be controlled directly by the brain. The knowledge acquired from these studies, and their major implications have encouraged and enabled researchers to make tremendous advances in brain computer interface development. Over the past couple of decades BCI systems have been designed using multiple recording methods and decoding algorithms, which are summarized in Section 2.3. This section also demonstrates the prominence that ECoG has gained in the field and the basis for the algorithms used in this dissertation.

Figure 2.2: Cosine Tuning in Primary Motor Cortex
An example of a unit response recorded during the center-out task. A) Shows spike rasters arranged by movement direction. Each row in the raster is a trial aligned to movement onset. The cell fired intensely for upper left movements and slowed for the opposite downward right movements. Firing intensity was graded for movements between these extremes. B) Shows cosine tuning of cortical response. The data from A) are redisplayed as the mean firing rates in each direction and these are fitted with a cosine. The peak of the cosine is near 150 degrees and is termed the ‘preferred direction’. Figure from Georgopoulos et al. [37].
2.3 BCI Implementation

While the previous studies demonstrated the ability to decode several facets of movement information using large populations of neurons (usually hundreds to thousands of individual units), implementation of purposeful movement-based BCI systems requires the ability to extract and decode neural signals in real-time. The extracted neural signals must then be used to produce motor commands for the end effector of the BCI, be it a virtual computer cursor or physical prosthesis. This section provides a brief overview of the recording methods proposed for BCI operation, the design of the control signals for driving artificial movement, and the importance of closed-loop systems.

2.3.1 Recording Methods

To clinically implement a BCI-controlled prosthesis, activity recorded from the brain must be able to balance information content, surgical risk, cost, and durability. Unlike the majority of the studies presented in section 2.2, real-time operation of BCI systems requires instantaneous signal acquisition. The previous studies had animals performing stereotyped reaching task for several repetitions for each isolated neuron. A new neuron was isolated, and the experiment was repeated for several days or months until a significant number of cells were represented.

Several different electrophysiology recording modalities have been proposed and studied as the potential output control signal for brain computer interfaces; the most popular being the aforementioned intracortical, EEG, and ECoG techniques. All of these methods record extracellular microvolt-level potentials from either individual neurons or ensemble activity. However, each of these different recording modalities require trade-offs between surgical
invasiveness and signal fidelity (see Figure 2.3). There are two styles of continuous movement BCI; spike-rate and sensorimotor rhythms. Both can be performed using penetrating electrodes, but surface electrodes are unable to identify individual spikes.

![Figure 2.3: Electrophysiological Recording Modalities](image)

**Figure 2.3: Electrophysiological Recording Modalities**
Drawing depicting the signals for BCI and their locations relative to the brain. Three general categories of signals are used for BCI applications; EEG, ECoG, and intraparenchymal (*i.e.* intracortical). Figure from Leuthardt *et al.* [50].

**Intracortical Recordings**

Intracortical signals have been the most successful modality for implementing BCI. Recording spiking activity from multiple neurons simultaneously gives direct access to the rudimentary building blocks of electrical activity in the brain. Recording individual spikes requires the use of penetrating electrodes in order to get close enough to read extracellular voltages from the cell bodies.

In the last decade, microelectrode arrays of penetrating tips have allowed for simultaneous recording of several channels. Common array sizes are 96 channels, and in some cases, multiple arrays are implanted over desired cortical regions [51]. As a modality for BCI,
these intracortical electrode arrays have proven to yield the highest information rate; some recording over 200 individual units simultaneously [4], [5], [52]. Research groups have used single- and multi-unit activity recorded from arrays of intracortical electrodes to control virtual cursors on a screen [52]–[59] or prosthetic limbs with multiple degrees of freedom. Studies in both humans with motor disabilities [4], [5], [60]–[62] and non-human primates [63], [64] have demonstrated control of external devices such as robotic arms with unmatched levels of accuracy.

However, using penetrating metal electrodes to record from the cortex has its disadvantages. Brain tissue is soft and the penetration of pointed metal electrode tips causes damage to the surrounding vasculature. This process of implantation greatly increases the risk of CNS infections. In addition, the presence of a stiff, foreign body in the cortex leads to tissue response from microglial and astrocyte cells [65]. Accumulation of these cells and their reactive response eventually leads to electrode encapsulation and degradation of signal quality [66]. For these reasons, the use of intracortical recordings for BCI is not a feasible long-term solution. To enable the clinical use of BCI for patients with motor disabilities, researchers need to use recording modalities that are less susceptible to infection and can provide stable and reliable recording of the neural activity.
Local Field Potentials (LFPs)

In addition to spiking activity, another useful tool in studying the relationship between neural activity and behavior is to examine local field potentials (LFPs), which are the summed electrical activity of a sub-population of cortex [67]. The electrical summation from several simultaneously spiking neurons generates field potentials that can be recorded using either intracortical electrodes or surface electrodes such as ECoG [68] or EEG [69].

While the information obtained from single neurons is encoded in the firing rate, field potentials appear to encode information in spectral power (as opposed to raw voltages in the time domain). These power spectra can be obtained via Fourier transforms or similar processes. Several studies have found that these field potentials are tightly coupled with the underlying neural population and show that the power at the higher LFP frequencies: 60-150 Hz [70], 40-90 Hz [71] provide the best estimates of underlying spike activity. Studies examining the high gamma signals of ECoG recordings 60-200 Hz [72] demonstrate that these signals are more specific in their timing and localization than lower frequencies.

In addition to comparisons to underlying firing rates, LFP power changes have also been shown to display many of the same tuning properties that can be observed with single-units. Studies of LFP recordings in motor cortex found that the frequency band of 60-200 Hz had the most predictive power for direction of reaching and that the higher frequency changes were more narrow in time and concentrated around only movement onset [73], [74].
Figure 2.4: Cosine Tuning to Movement Direction in Single-unit and LFP

A) Spike rasters for five repetitions of reaches to each of eight targets in the center-out task. Four inner plots represent reaches to four targets farthest from subject, while the four outer plots represent reaches to the four targets closest to subject. Reaches are aligned by onset of movement. Each black line represents a spike and red lines indicate various task periods. Cell has preferred direction near lower left proximal target. B) Spectral amplitude as percent change from baseline of LFP recorded on same electrode while cell in A) was recorded. White line illustrates the average spectral amplitude of LFP from 60-200 Hz, which has similar tuning properties to the cell recorded simultaneously. Figure from Heldman et al. [73].
A variety of electrode sizes and locations can be used to measure field potentials, and there is an inverse relationship between invasiveness and spatial specificity of the recorded signals. Both intracortical LFPs [73] and surface recording field potentials using ECoG [75] have shown tuning characteristics, with Figure 2.4 illustrating the similarities in tuning between a single neuron and the LFP recorded from the same electrode. These previous experiments seem to point towards the high frequency component of the LFP being highly related to the observable task-related spiking activity of nearby neurons even if it is not a direct surrogate for the instantaneous firing rate of simultaneously recorded multi-unit activity. These findings suggest that field potential recordings such as EEG and ECoG may contain similar tuning information to that of single-units with the benefit being increased safety and reduction of neural tissue damage.

**Electroencephalography (EEG)**

EEG signals are recorded from the surface of the scalp and come with the big benefit of being non-invasive. However, these signals have been observed to exhibit only non-specific modulations with different movement parameters [50]. Given the large distance from an EEG electrode to the brain (~ 2 cm), individual spikes cannot be resolved, and thus a more distant field potential is recorded from the contacts on the scalp. Because of this distance, the spatial resolution is very poor when compared to other neural recording methods [76], [77]. Like LFP, information is encoded in sensorimotor rhythms (*i.e.*, the spectral content), with information encoded in frequencies up to about 50 Hz. This notably misses out on some of the richest LFP content in the aforementioned 60-200 Hz range due to the electrical characteristics of the skull and surrounding tissue to effectively “low-pass filter” the underlying cortical activity [51].
Moreover, the amplitude of EEG signals is very small making them highly susceptible to movement artifacts and electrical noise [50].

Even with all these limitations, EEG is still a highly desired and popular BCI platform due to its low cost and surgically non-invasive nature. EEG-based BCI studies have been used to communicate with ALS patients in the locked-in state [78] and have also demonstrated two [1], [79]–[82] and three [2], [83] dimensional movement control when paired with extensive training sessions.

**Electrocorticography (ECoG)**

The short-comings of EEG and intracortical recordings have led to the interest in ECoG as a recording modality for BCI, as it provides a balance between surgical invasiveness and signal quality. Though semi-invasive, ECoG electrodes are placed on the surface of the cortex, either above (epidural) or beneath (subdural) the dura. Bypassing the thick skull tissue reduces the distance between the electrode and the brain and increases the recordable bandwidth from about 50 Hz in EEG to approximately 200 Hz in ECoG recordings [3], [84]. Like EEG, ECoG signals also exhibit specific modulation with overt and imagined movements. The high gamma frequency bands (>60 Hz) have been popularly theorized to represent synchronous spiking activity from the cortical columns under the recording electrode [85].

Electrocorticography has shown growing promise in the BCI field as an intermediate solution between the two extremes of recording single-unit activity and EEG. Although the signals are not the direct representation of the underlying neural code that can be observed at the single neuron level, the surgical procedure to implant ECoG electrodes is less invasive and has a lower chance of cortical tissue damage, infection, or encapsulation [86]. ECoG provides better
Spatial and spectral resolution than EEG, albeit at the trade-off of being an invasive technique when compared to non-invasive scalp electrodes. Recent studies have also demonstrated the long-term stability and robustness of ECoG recordings in monkeys over primary motor cortex [9]. These results showed that the predictive value of hand position from ECoG signals did not significantly decay over a period of five months. Additionally, the recordings were also stable as cross-day predictions did not differ significantly from the accuracies using same-day coefficient prediction. This long-term stability is a key advantage that ECoG-based BCIs offer compared to BCIs based on single-unit activity.

Subdural ECoG grids have been extensively used by neurosurgeons in the treatment of intractable epilepsy [3], [75], [87]–[93]. A majority of human ECoG-based BCI experiments have been conducted in such patients during the short implantation period. The drawback of such experiments has been that the location of electrodes is governed by the clinical needs of the patients and that the grids can only be implanted for a short duration of a few weeks. However, seeing initial success with ECoG in human BCI [3], [94]–[97] and decoding studies [92], [93], [98], [99], researchers have started using non-human primates to develop ECoG-based BCI [10], [100]–[103] and movement decoding studies [9], [11], [104]–[107].

Components of ECoG signals have been shown to be well-correlated to multiple parameters when subjects perform different motor tasks. Event-related potential (ERP) changes of the raw waveform in the time-domain of the ECoG signal have been used to identify the onset and timing of various motor actions on individual trials [108]. The spectral power is computed over time windows during a given task as well as while at rest. Using this analysis to estimate the power at different frequencies of the signal for the given epochs of data, it is possible to identify different frequency components that increase or decrease in power during the task.
compared to rest. Historically, two bands that have been specifically identified were the alpha (8-13 Hz) and beta (15-25 Hz) bands which tended to show a decrease in power with the onset of motor movement or imagery [68], [109]. Additionally, regions of the gamma band (30-200 Hz) have been identified that show an increase in power during movement [68], [109].

These characteristic spectral features have been used for real time, closed-loop BCI experiments with motor imagery tasks as the training paradigm [3]. By first having patients perform various real and imagined motor movements, recorded ECoG signals were analyzed to identify power spectrum features well-correlated to the motor behavior. These features could then be assigned to control the cursor kinematics during a brain control task and the subject could be instructed on the necessary motor movement or imagery necessary to complete the task (e.g., “Imagine opening and closing your hand to move the cursor to the right”). Successful BCI control with ECoG recordings has been demonstrated with these types of experimental paradigms in several instances [95], [96], [110], [111].

Our lab has investigated the use of ECoG electrodes in the epidural space of non-human primates over the last decade with a lot of success [85], [100]–[102]. Epidural ECoG electrodes are implanted over the surface of the dura as opposed beneath the dura as is the case with subdural electrodes. As the outside layer of the dura is part of the peripheral immune system, these epidural electrodes are even less likely to cause CNS infections. As the electrical conductivity of the dura is similar to that of cerebral spinal fluid, it does not affect the signals like the skull does in the case of EEG. In fact, negligible signal degradation is observed due to its presence of dura between the electrode and the brain [91]. Thus, epidural ECoG provides an ideal balance between the fidelity of recorded signals and the risk of infection for the purpose of BCI systems.
In each of the experiments in this dissertation, non-human primates were chronically implanted with ECoG arrays, with placement of the recording sites spanning from premotor areas to parietal cortex. In most cases the goal was to capture M1 activity with as many electrodes as possible.

### 2.3.2 Control Signals for Movement

While a large portion of BCIs are designed for the purpose of communicating with patients in a locked-in state (usually via neural selection or classification methods), the focus of this dissertation is on restoration of motor function in individuals with varying levels of impairment. Despite the variety of low- and high-level movement parameters that have been correlated with neural activity in motor cortical areas, mainly position and velocity have been used as control signal outputs to drive movement (*i.e.*, non-classification) BCI devices.

Most of the work in the field of movement BCI has been in designing and implementing decoding algorithms that help capture the most information embedded in the recorded signals. The aforementioned Population Vector Algorithm (PVA) proposed by Georgopoulos *et al.* [38] utilized the cosine tuning properties of single M1 neurons to predict the instantaneous velocity of movement by summing the preferred direction vectors scaled by their instantaneous firing rate.

Proposed by Salinas and Abbot [112], the Optimal Linear Estimator (OLE) method assigned directional weights to neural features in a way that minimized the least squares error between the final estimate of the velocity and the true observed velocity. Using neural and behavioral data obtained from Georgopoulos *et al.*, they demonstrated that the predictive power of PVA is dependent on the sampling of recorded units and preferred directions. While PVA accuracy decreases as the number of recorded neurons decreases, OLE remains accurate with smaller neural populations. As such, the OLE method has proven useful for BCI control signal
applications using small, real-time neural populations. A number of studies have successfully extended movement reconstruction algorithms previously used to reconstruct physical movements from neural activity to BCI control of a computer cursor [46], [47], [56].

Marathe and Taylor investigated differences between position and velocity control signals in healthy human subjects using transformations of physical reaching characteristics to control a computer cursor [113]. In these experiments, hand position or velocity were remapped to cursor position or velocity with various amounts of added noise. Subjects had to use these remapped physical movements in order to complete a center-out task. Remapping a given noisy control signal to cursor velocity resulted in much better performance than remapping the same signal to the cursor position. In the cursor position case, all of noise was also remapped to cursor position; while in the velocity case the integration to position acted to low-pass filter this noise. Although this study did not examine whether this result extended to even higher-order time derivatives such as acceleration or force, recent experiments in our lab demonstrated that velocity-based control signals could be re-applied to either acceleration or force control BCI paradigms [114].

2.3.3 Biofeedback and Cortical Plasticity

Though the aforementioned algorithms have been proposed for use in implementing BCI, the most important factor in success appears to be the real-time visual feedback (closed-loop configuration) to the subject and the resulting cortical changes (i.e., neural plasticity). An open-loop BCI for movement occurs when feedback is withheld from the user. This would be real-time decoding of movement, that could be portrayed virtually or by a physical effector. The cortical activity is controlling the actions of this effector, but the user cannot act to change neural activity based on feedback. The loop in BCI experiments is predominantly closed by way of
visual feedback of a physical or artificial effector of brain activity. Several studies have shown clear differences between the performances of various algorithms when used in open-loop versus closed-loop configurations [55], [115]. For instance, Chase et al. demonstrated an equivalent closed-loop performance of OLE and PVA algorithms, despite OLE providing optimal open-loop decoding [116].

Most BCI systems use mapping or screening tasks to determine which features make the most sense for control, but an alternative approach is to map arbitrary neural features to control signals and allow the brain to adapt the feature modulations to complete the task. Fetz and colleagues introduced the idea of biofeedback induced adaptation by allowing animals to see the control signals, coining the term “volitional control of single neurons” [117]–[120]. These M1 neurons could be conditioned to change tuning properties in order to complete the visual control task.

Further evidence for widespread BCI induced plasticity was presented by Lebedev and colleagues [121], demonstrating that operation of a closed-loop BCI results in incorporation of artificial actuators into brain representations. Their study showed that modifications in the neuronal representation of the monkey's hand and the actuator that was controlled by the monkey brain occurred in multiple cortical areas while the monkey operated the BCI. In these single day experiments, monkeys initially moved the actuator by pushing a joystick. After mapping out the motor neuron ensembles, control of the actuator was switched to the model of the ensembles so that the brain activity, and not the hand, directly controlled the actuator. The activity of individual neurons and neuronal populations became less representative of the animal's hand movements while representing the movements of the actuator. Presumably as a result of this adaptation, the animals could eventually stop moving their hands yet continue to operate the
actuator. Thus, during BCI control, cortical ensembles plastically adapt within tens of minutes, in order to represent behaviorally significant motor parameters.

Many cells used for closed-loop control become even more cosine tuned to direction in order to better match the control algorithm [51]. Cells also show changes in their preferred direction, but this adaptation is not uniform across a population (i.e., some neurons show great changes while others show hardly any change in preferred direction) [122]. As such, it may be important to update decoding models as these changes take place.

Cunningham et al. demonstrated the difference in time of integration of the recorded signal that produced optimal results and overall smaller errors when the same algorithm was used in closed-loop [123]. Subsequently, Orsborn et al. revealed that using a Kalman filter decoder updated every 1-2 minutes during the experiment induced rapid improvements in closed-loop performance when compared to a static decoding model [124].

These observations have led researchers to believe that algorithms that incorporate feedback and update their parameters iteratively would be more successful in ease and efficiency of control for BCI devices. Previous BCI studies in our lab have demonstrated cortical plasticity through ECoG signals [85], [100], [102], [125]. In the first study, subjects performed a circle drawing task by controlling the vertical movement of the cursor with one electrode and horizontal movement with another. To improve the performance in this task, a decorrelation of the control signals was necessary. A steady decrease in the correlation between the two control electrodes, specifically in the frequency band controlling the cursor was observed, demonstrating targeted changes in the signals to increase performance in the task as seen in Figure 2.5 [100]. Overall, these results suggest that the brain is fairly plastic in terms of adapting to the control algorithm that is implemented, and this may aid in developing a force-based control system.
Figure 2.5: Cortical Plasticity in ECoG Control Band
Utilizing cortical plasticity for device control. To achieve 2-D control, the amplitude of the signal between 65–100 Hz from one epidural ECoG electrode was used as the control for the horizontal velocity of the cursor, and a separate electrode was used for the vertical velocity of the cursor. The 2 sites were ~1 cm apart. For the monkey to improve his performance in a circle-drawing task, it must gain independent control of the 2 signals being used for control. For a perfectly drawn circle, the overall correlation between the 2 signals will be 0. This decorrelation could be done either indiscriminately across all frequencies or only within the frequency band being used for control. To examine what actually occurred during the experiment, the power spectrum was calculated for the 2 recorded signals in 300-ms non-overlapping time bins. The correlation between the powers at each given frequency for the 2 different channels was then calculated for all points in time. Graph showing that the correlation between the recording sites decreased across most frequencies but most dramatically between 65–100 Hz. Therefore, these data clearly show that through biofeedback, motor cortex is quite adaptable to learning and improving BCI control. Figure from Rouse and Moran [100].

2.4 Significance of Anthropomorphic Schemes

While computer cursor control has been a staple of BCI research, some studies have shown BCI control extended to more real-life applications such as controlling a robotic arm [4], [5], [61], [63]. Since a robotic arm has real mass and inertia, an inverse dynamic model is necessary to transform a desired velocity signal into the appropriate forces to produce that trajectory. To date, these calculations have been computed by an external controller in the robotic arm using a
known physical model of the arm and any external forces on it. In this light, control of the robotic arm is still purely kinematic from the user’s point of view.

For conditions such as spinal cord injury in which the motor chain is broken but the remaining nervous system components on either side of the damaged section remain mostly intact, FNS would offer a solution for rerouting motor commands to healthy muscles. Several methods for eliciting muscular activity by an external device have been investigated, ranging from micro-stimulation of the spinal cord [126], activating multiple muscle groups or coordinated movement primitives, to stimulation of individual muscle groups through intramuscular stimulation [127], [128].

With FNS applications in mind, Blana et al. developed a simulated controller for a simple six-muscle, two-joint dynamic musculoskeletal arm model [58]. This controller employed an artificial neural network (ANN) for the inverse-dynamic model of the feed-forward plan muscle stimulations, and a sequential proportional-integral-derivative (PID) controller and ANN as a feedback model for correcting errors due to muscle fatigue and external disturbances. Chadwick et al. showed that a human subject with tetraplegia could control a virtual version of this arm constrained to the horizontal plane with no gravity [57]. In both of these studies however, the input from the subject to the controller was an endpoint velocity command. More recently, a study by Ajiboye et al. [60], utilized a joint angle-based velocity command signal in a human patient with a modified version of the ANN controller used for real-time FNS control. The subject was able to perform multiple tasks, culminating in picking up a cup of water and drinking through a straw under muscle stimulation control. While the results from this study were far from healthy limb control patterns, they demonstrated a significant leap towards restoration of motor function.
2.5 Summary

Intrinsic decoding schemes in BCI systems have yet to be thoroughly investigated as a possible control scheme, especially using ECoG as a recording modality. Control of robotic arms, single muscle groups, and simulated FNS models have been demonstrated using single-unit recordings, but control on the part of the user has been purely kinematic. Due to possible advantages offered by a dynamics-based control signal over higher-level kinematic variables as well as numerous evidence of neural plasticity observed in BCI settings, a force-based control signal may indeed be a feasible alternative strategy for applications such as FNS. With recent advances in ECoG technology, implanted arrays may offer a suitable platform for this type of system with high spatial content, long-term stability, and a relatively decreased risk to the patient compared to more invasive modalities like intracortical recordings. Many BCI studies utilizing ECoG signals to date have used features for control related to pre-screened physical movements, so developing algorithms to exploit neural plasticity will likely be important for implementing a dynamics-based control scheme. Overall, addressing these questions may not only influence important design considerations for future BCI systems, but might also reveal vital neurophysiological phenomena related to BCI operation.
3 General Experimental Methods

The experiments in this dissertation focus on the use of ECoG and its applications towards improving the current state of BCI. This chapter describes the animal protocols, device technologies, signal processing methods, and the behavioral and recording paradigms used for the experiments. Since the goals of each experiment varied, later chapters will describe the behavioral tasks and analyses specific to those experimental paradigms in more detail.

3.1 Subjects

The experiments described in this dissertation utilized a selection of male Rhesus macaques (*Macaca mulatta*, monkeys G, I, K, O, P, R) weighing 6-12 kilograms. Five of the six subjects were chronically implanted with ECoG electrode arrays in the epidural space over the motor and/or sensory cortices. Monkey G, an animal previously studied in single unit physical reaching tasks [129], was implanted with an array of subdural ECoG electrodes over sensory cortex. Monkeys I, K, and R had arrays implanted on both the hemispheres (i.e., bilateral) whereas, monkeys G, P, and O had single left hemisphere implants.

Three of the implanted animals, monkeys K, P, and R, had previous BCI experience [101], [114], [125], [130] and were only involved in the experiments detailed in Chapter 4. Monkey I participated in the experiments described in Chapters 4 and 6 and was well versed in ECoG BCI, previously performing control tasks in 2, 3, and 4 dimensions [131], [132]. Last but not least, monkeys G and O were experimentally naïve to BCI prior to the experiments in Chapters 4, 5, and 6. Unlike single or multi-unit recordings using penetrating electrodes, chronic ECoG recordings are resilient to encapsulation and signal degradation. In support of this, the initial recordings and tasks completed in this dissertation occurred between 11 and 36 months after
array implantation and, and three of the six monkeys performed BCI experiments at a high level for over 5 years.

3.2 Behavioral Setup

Each monkey learned to perform a variety of behavioral tasks through operant conditioning with a liquid reward. The monkey sat in a custom primate chair approximately 20” from an LCD monitor displaying visual feedback of the behavioral task. The monkey’s arms and legs were completely enclosed within the chair but were free to move during experiments. For initial training, a joystick (APEM 9000 Series Joystick, APEM Components Inc.) was attached to the front of the chair with the handle extending into the interior of the chair such that the monkey could move the joystick in the frontal plane at approximately chest level.

The basic behavioral task template used in this dissertation was for each monkey to interact within a virtual 2-dimensional environment displayed on the computer screen through control of a small spherical cursor. This cursor was controlled using either position information relayed from the joystick or a processed control signal extracted from the monkey’s ECoG signals. The animals received their daily water consumption via the liquid reward system. On the rare occurrence the monkey did not meet the daily water intake requirement; they were supplemented in their home cage (after a delay, preventing association of poor behavior with this reward).

3.3 ECoG Arrays

Two different styles of ECoG arrays were implanted in the subjects used in this dissertation. Monkeys G and I were implanted with large contact (≥1500 μm diameter) platinum electrodes encased in a Silastic sheet (i.e., similar to standard clinical ECoG grids used for epilepsy monitoring) [3]. Monkeys K, O, P, and R were implanted with custom designed thin
film polyimide micro-ECoG arrays [103], [133], [134]. The details of these electrodes and their placement are shown in Table 3.1 and are described in detail in the following sub-sections.

<table>
<thead>
<tr>
<th>Hemisphere</th>
<th>Manufacturer</th>
<th>Channels</th>
<th>Diameter (μm)</th>
<th>Spacing (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>G</td>
<td>Left PMT</td>
<td>7</td>
<td>2,000</td>
<td>3.75</td>
</tr>
<tr>
<td>I</td>
<td>Right PMT</td>
<td>14</td>
<td>2,000</td>
<td>3.75</td>
</tr>
<tr>
<td></td>
<td>Left Ad-Tech</td>
<td>14</td>
<td>1,500</td>
<td>3.75</td>
</tr>
<tr>
<td>K</td>
<td>Right UW</td>
<td>32</td>
<td>300-600</td>
<td>3.00</td>
</tr>
<tr>
<td></td>
<td>Left UW</td>
<td>32</td>
<td>300-600</td>
<td>3.00</td>
</tr>
<tr>
<td>O</td>
<td>Left UW</td>
<td>32</td>
<td>300-600</td>
<td>3.00</td>
</tr>
<tr>
<td>P</td>
<td>Left UW</td>
<td>32</td>
<td>300-600</td>
<td>3.00</td>
</tr>
<tr>
<td>R</td>
<td>Right UW</td>
<td>32</td>
<td>300-1,200</td>
<td>3.00</td>
</tr>
<tr>
<td></td>
<td>Left UW</td>
<td>32</td>
<td>300-1,200</td>
<td>3.00</td>
</tr>
</tbody>
</table>

3.3.1 Silastic Arrays

Monkeys G and I were implanted with Silastic electrode arrays manufactured by Ad-Tech Medical (Racine, WI, USA) and PMT Corporation (Chanhassen, MN, USA). Each Silastic array consisted of fourteen platinum (Pt) recording electrodes facing downwards towards the brain and three skull-facing (i.e. upwards) Pt reference electrodes as depicted in Figure 3.1A. The Ad-Tech array comprised of thirteen electrodes with 1.5 mm diameter and one electrode with 3 mm diameter separated by 3.75 mm inter-electrode spacing center-to-center. The PMT arrays included thirteen electrodes with 2 mm diameters and one electrode with 3 mm diameter also separated by 3.75 mm spacing center-to-center. Monkey G was implanted with one modified PMT array on the left hemisphere in the subdural space. This array had seven 2 mm recording electrodes facing downward and in direct contact with pia mater and one 3 mm reference electrode facing upward and in direct contact with the dura mater. Monkey I was implanted bilaterally with one Ad-Tech array on the left hemisphere and one PMT array on the
right hemisphere, both in the epidural space and with all recording electrodes in contact with the top of the dura mater.

![Figure 3.1: Design of Silastic Arrays](image)

**Figure 3.1: Design of Silastic Arrays**

A) ECoG electrode array with 14 Pt electrodes with 3.75 mm spacing (center to center) and 3 skull facing references embedded in Silastic. B) **Left:** Schematic of the stainless steel chamber housing the connecting wires and the PCB. **Right:** Cross-section of the chamber showing the PCB and one male Omnetics connector. (Renderings courtesy of JJ Wheeler).

Each recording electrode and reference on an array was cable bundled and routed together out of the Silastic sheet. In the case of Monkey I, the bundles from the left and the right implants were routed to a central stainless steel chamber secured to the skull with dental acrylic (see Figure 3.1B). The ends of each cable were connected to male Omnetics connectors (18 Position Nano-Miniature Connector, Omnetics Connector Corp., Minneapolis, MN, USA). These connectors were placed on a circular printed circuit board (PCB) that resided securely in the metal chamber. The PCB enabled the choice of any combination of three skull-facing reference electrodes per side during the experiment. The stainless steel chamber was used as ground and connected to externally accessible skull screws. In Monkey G, the bundle from the array was directly connected to a male Omnetics connector potted into a smaller stainless steel
chamber with cap and secured with dental acrylic to the existing head-cap. A skull screw was used as ground and was connected to the ground cable of the connector.

### 3.3.2 Polyimide Arrays

Thin-film polyimide arrays were designed and manufactured in collaboration with the lab of Dr. Justin Williams at the University of Wisconsin (Madison, WI). Each array consisted of thirty-two circular electrode sites ranging in diameter from 300-1200 μm (four distinct sizes per array) and 3 mm center-to-center spacing facing the dura (see Figure 3.2A-B). Electrode sites were made up of gold contacts coated with platinum-black powder. Sites were arranged in a 4-by-8 rectangle with each row consisting of a single electrode size (two rows of each size). These sites were printed on one half of a flexible polyimide ribbon. On the other half, signals were referenced to a large “H” shaped ground pad and similarly sized reference sites sitting above the electrode sites, facing toward the skull. This referencing configuration was accomplished on a single planar printed surface by folding the polyimide ribbon in half before connecting both ends to a ZIF connector (Tucker Davis Technologies, Alachua, FL, USA) as seen in Figure 3.2C. This configuration was chosen such that skull-facing ground and references would remain relatively quiet from cortical signals but still pick up common mode noise or artifact in the local recording area above recording sites for rejection by differential amplifiers. The base of the ZIF connector was secured in dental acrylic within a recording chamber with protective cap, both constructed from Delrin® plastic (DuPont, USA). In addition, the polyimide ribbon cable portion of the array was coated with silicone rubber to provide cushioned relief from movement of the ribbon cable relative to the surrounding skull.

The polyimide electrode arrays implanted in all the monkeys were identical except for the sizes of recording electrodes. Monkeys K, O, and P were implanted with arrays containing
electrodes with 300 μm, 425 μm, 520 μm, and 600 μm in diameter. Monkey R was implanted with electrodes sizes of 300 μm, 600 μm, 900 μm and 1200 μm. Approximate electrode locations on the surface of the brain will be provided in the following chapters.

Figure 3.2: Design of Polyimide Arrays
A) Polyimide thin film ECoG electrode array layout with one half housing 32 channels of four different sizes of exposed electrode surface and separated by 3 mm (center to center). The other half is covered with an “H” shaped ground and reference electrodes. B) Schematic of implanted electrode with its relative position to the skull, dura, and brain. The array was folded at the mark shown in A and placed under the skull with ground and reference facing up. C) Picture of the folded array before implantation. The white Delrin housing contains the Zero Insertion Force (ZIF) connector and is exposed outside the head-cap after implantation.
3.3.3 Surgical Implantation

All surgeries were performed in the primate facility at the Washington University School of Medicine. Epidural surgeries were performed by Dr. Daniel W. Moran with one or more graduate students assisting in the procedure. Surgery for Monkey G, with a subdural implant, was performed by neurosurgeon Dr. Eric C. Leuthardt. Subjects were placed under general anesthesia, and the facility’s veterinary staff was present to assist if necessary. All the surgeries were performed in accordance with the approved set of protocols. The general steps of each surgery after placing the animal under anesthesia were as follows:

1. A 19 mm craniotomy was performed using a hand trephine centered at the point determined using stereotactic maps of the Rhesus macaque brain. The dura mater covering the brain was kept intact, and the bone plug was retained.
2. The chronic array to be implanted was slid through the craniotomy between the skull and the dura. Surgical spatulas were used to separate the dura from the skull as well as to gently depress the dura against the brain to ensure the array remained flat and was placed as desired.
3. With the array positioned and the recording chamber as close to the skull as possible, the bone plug was replaced. Any gaps between the bone plug and skull were filled with moistened Gelfoam® (Pfizer) to provide a scaffold for bone regrowth. The bone plug was secured to the rest of the skull using 2 cm titanium straps and skull screws.
4. If a subject had a bilateral implant, steps 1-3 were repeated on the other side.
5. 4-5 additional 4 cm titanium straps were attached to peripheral sections of skull near temporal level with screws to provide extra stability for an acrylic head-cap.
6. The acrylic head-cap was fabricated by laying thin layers of dental acrylic on top of the exposed skull, titanium straps, and bases of the recording chambers.
7. Metal head-posts were placed at the top of the head-cap to secure the subject's head in a fixed position during the experiments.
Steps were modified or changed according to the requirements of a particular subject with respect to the stereotactic coordinates of the craniotomy, type of recording electrodes and chambers, and presence or absence of external skull screws to be used for ground.

### 3.3.4 Recording and Signal Processing

ECoG signals were recorded using a Tucker-Davis Technologies (TDT) neurophysiology recording system. The raw signals at the connector were transmitted using a short cable (30 cm) to a differential head-stage and pre-amplifier assembly. The head-stage provided an initial 5x amplification gain and then band-pass filtered the raw signals between 3 and 500 Hz. The signals were then routed to a 10x gain pre-amplifier. The pre-amplifier digitized these signals (>17 bit resolution with oversampling) and converted them to optical signals to be delivered to the TDT base-station at a down-sampled rate of 6 kHz. The use of fiber optic cables from the pre-amplifier assembly in the recording room to the adjacent control room prevented any 60 Hz electrical noise from being picked up over the length of the cable between rooms.

In addition to the TDT base-station, the control room housed the host computer (Microsoft Windows-based Dell workstation) used to interface with the TDT system and display the virtual BCI environment to the subject in the recording room. The TDT base-station was programmed to down-sample and store the raw ECoG voltage signals at approximately 2 kHz.

### Digital Signal Processing in Hardware

As mentioned in Chapter 2, initial ECoG BCI experiments carried out in the lab used the 70-115 Hz gamma band for velocity or acceleration based control [85], [100], [102], [114]. More recently, however, we have expanded the bandwidth to encompass four more bands for control
which has improved BCI performance [101], [131]. Weighted voltage amplitude estimates in each of these bands were used as control features in the respective BCI algorithms.

A basic amplitude demodulation technique, using the digital signal processors (DSPs) in the TDT base-station, was used to process the signals into five separate frequency bands. The raw signals recorded from each electrode were separated into alpha (8-15 Hz), beta (15-30 Hz), low-gamma (30-55 Hz), mid-gamma (70-115 Hz), and high-gamma (130-175 Hz) using digital band-pass filters. The standard gamma band (30-200 Hz) was split into three individual bands to avoid noise from the 60 Hz mains power supply and its harmonics (i.e., 120 Hz).

The raw signals were first band-pass filtered using an 8th order Butterworth filter with the desired low and high cutoff frequencies of each band. The output from these filters were then full-wave rectified before low-pass filtering at 2 Hz (1st order Butterworth) to get an amplitude estimate for each particular band. Completing the required signal processing by dedicated DSP hardware enabled fast near real-time computations and reduced the delays in the system. Figure 3.3 shows a comprehensive schematic of all the steps in the TDT hardware signal processing chain. At this point the N (number of channels × 5 frequency bands) features were relayed to the BCI virtual task environment on the host computer.
Following the initial processing steps and digitization, the raw signals are separated into five different frequency bands; 8-15 Hz (alpha), 15-30 Hz (beta), and three gamma bands; 30-55 Hz (low gamma), 70-115 Hz (mid gamma), and 130-175 Hz (high gamma). Band-pass filtering is followed by estimation of the power envelope via full wave rectification and low-pass filtering at 2 Hz. The resulting raw features are then sent to the host computer. All steps shown occur in the DSP hardware, reducing the computational lag time. (Illustration courtesy of JJ Wheeler)

Normalization of Features in Software

Once the raw features were relayed to the host computer they were interpreted and pre-processed by the BCI virtual task environment. As the raw features were positive by definition, the distribution of amplitudes was skewed toward higher amplitudes. That is, the mean of this distribution was greater than the median. The Pearson 2 skewness coefficient, \( Sk_2 \), is a simple measure of a distribution’s skewness and symmetry that works well for unimodal distributions [135]. This coefficient is related to a distribution’s mean (\( \mu \)), median (\( m \)), and standard deviation (\( \sigma \)) by:

\[
Sk_2 = \frac{3(\mu - m)}{\sigma}
\]  
Eq. 3.1

Figure 3.3: Signal Processing Chain Occurring in DSP Hardware

[Diagram showing the signal processing chain with frequency bands and filtering steps]
Positive and negative coefficient values indicate rightward and leftward skewed distributions, respectively, while a coefficient value of zero indicates a symmetric distribution. As seen in the top row of Figure 3.4, a natural log transformation significantly decreases the skewness of the amplitude distribution.

The BCI algorithms used in this dissertation are based on linear regression in order to map the aforementioned features to a BCI control signal. Since the spectral power of ECoG signals fall off at a rate inversely proportional to the frequency as seen in the lower left of Figure 3.4, features from the different frequency ranges need to be standardized for un-biased comparison. These normalized features would then be treated as independent signals and weighted appropriately by the decoding algorithm. Since the features were previously log transformed and near-normally distributed, the z-score was used to achieve this normalization as shown in the lower right of Figure 3.4.

Z-scores of individual features were computed in real-time during the experiments [136]. The means and standard deviations were calculated at every time point using the following equations:

\[
m[k] = m[k-1] + \frac{x[k] - m[k-1]}{k}
\]

Eq. 3.2

\[
y[k] = y[k-1] + \left(x[k] - m[k-1]\right)\left(x[k] - m[k]\right)
\]

Eq. 3.3

\[
s[k] = \sqrt{\frac{y[k]}{k-1}}
\]

Eq. 3.4

Where, \(m[k]\) and \(s[k]\) are the estimated mean and standard deviation of a given feature at time \(k\), \(x[k]\) is the raw feature value at time \(k\), and \(y[k]\) is an intermediate variable for calculation of the
standard deviation. The values of \( m[1], y[1], \) and \( s[1] \) are initialized to \( x[1], 0, \) and \( 0, \) respectively. The z-score for each feature was then calculated as follows:

\[
z[k] = \frac{x[k] - m[k]}{s[k]}
\]

Eq. 3.5

This z-scored value of each feature was then used by the decoder to form the control signal of the BCI task. With each individual feature now having zero mean and unit variance, the decoder could assess and weight the features without being biased by their central tendency.

Figure 3.4: Pre-processing of Neural Features in Software

**Top Row:** Histograms of raw (left) and log transformed (right) amplitude estimates for a feature from Monkey G. Red and green stem plots indicate the mean and median of each distribution, respectively. The Pearson 2 skewness coefficients, \( \text{Sk}_2 \), are indicated for each distribution, showing a clear reduction in skewness after log transformation. **Bottom Row:** Log transformed distributions for all 5 frequency bands on each channel. Error bars represent the mean ± 1 standard deviation. **Left:** Log amplitude estimates lie in different amplitude ranges for different features. **Right:** After z-scoring, each feature has zero mean and unit variance.
3.4 BCI Tasks

Two general types of BCI tasks were used during the course of the experiments in this thesis: a classic center-out task and a novel two-link arm reaching task. Experiments in Chapters 4 and 5 had the subjects performing a classic 2-D Center-out task [7]. The center-out task is a well-known behavioral task often used in both non-human primate and human reaching studies to explain possible movement parameter representations in neural data as well as act as a test bed for BCI applications. In this thesis, the center-out task was used to assess BCI performance as would be applied for reaching movements. In Chapters 5 and 6, subjects completed variations of a novel “2-D Joint Angle Center-out” task. The joint angle center-out task is an extension of the classic center-out task designed around an intrinsic control scheme. Instead of applying an extrinsic velocity to the cursor, the control signal was mapped to the joint angles of a two-link arm model instead. These two basic tasks are defined in the following sub-sections, with further distinctions described in the corresponding chapters.

3.4.1 Classic Center-out Task

A classic 2-D Center-out task with eight targets was used for most of the experiments carried out during this study. The target for each individual trial was selected pseudo-randomly from an initial pool of sixteen. If a trial was incorrect, the chosen target was replaced in the pool of possible targets and a new target from the pool was selected. Each trial started with the cursor auto-centered to the center of the screen. One of the eight randomly chosen targets appeared on the screen after a 500 ms hold period (Hold A). The subject then had to move the cursor from the center to the presented target within the allotted maximum movement time. If the subject was successful in contacting the cursor and target spheres and completing a short 400 ms hold
period (Hold B), the trial was marked as correct and a small liquid reward was given. In any other case, the trial was marked incorrect and no reward was given.

### 3.4.2 Joint Angle Center-out Task

The joint angle task consisted of a two-link arm where the subject again performed center-out with the hand initialized to the center of the screen and the eight targets placed in the same locations as in the classic center-out task. Using a right arm orientation in which rotation at the shoulder and elbow joints were restricted resulted in a one-to-one mapping between the extrinsic (Cartesian) position of the cursor and the intrinsic joint angles of the arm as shown by:

\[
x = S_x + L_1 \cos \theta_1 + L_2 \cos(\theta_1 + \theta_2) \quad \text{Eq. 3.6}
\]
\[
z = S_z + L_1 \sin \theta_1 + L_2 \sin(\theta_1 + \theta_2) \quad \text{Eq. 3.7}
\]

Where \(L_1\) is the length of the upper arm segment and \(L_2\) is the length of the forearm segment. The shoulder angle, \(\theta_1\), is measured relative to the x-axis and the elbow angle, \(\theta_2\), is measured relative to the upper arm segment. The shoulder position, \(S_x\) and \(S_z\) in Cartesian coordinates, remained static throughout the task and did not change during any of the experiments. As in the classic center-out task, the subject had to move the spherical cursor (i.e., the “hand” of the two-link arm) from the starting center position to the presented target within the maximum allotted time. Upon completion of the hold at the target, a small liquid reward was given. If the monkey did not come in contact with the target or failed to hold for 400 ms, the trial was marked incorrect and no reward was given.
Figure 3.5: Novel 2-D Joint Angle Task
A) At the start of the trial, the cursor (hand) is moved to the center of the screen with the two-link arm in a resting position and a peripheral target appears. B) The monkey then has 5-10 seconds (depending on the subject) to bring the cursor to the target. C) The monkey must hold the cursor in contact with the target for 400ms. Once the hold time is complete or the maximum movement time has been reached, the trial is over; a one second inter-trial interval occurs, and the monkey is rewarded if the Hold time was completed.

3.5 BCI Control Scheme

The BCI experiments examined in this dissertation utilized ECoG derived control signals to move a spherical cursor in two dimensions on a computer screen. As each task made use of eight equally spaced radial targets (from $0^\circ$ to $315^\circ$), a block was defined as sixteen correct reaches; two to each of the eight targets. This block structure was chosen to allow a decoding algorithm to update every few minutes while recording neural data from reaches sampling the
movement space. While more than two trials per target would aid in reducing localized overfitting, we found that updating the decoder more frequently allowed the subject to make changes in neural control strategy that might otherwise be washed out by longer periods between decode updates. In all experiments, the decoder was naïve in that it started each day with zeroed out weights and learned throughout the day. It did not use any knowledge from previous sessions. Small changes to the decoding algorithm were made between experiments, so the algorithm for each experiment will be further explained in the respective chapter.

For kinematic control tasks, the monkeys controlled the velocity of the cursor in either extrinsic space (classic center-out) or intrinsic space (joint angle center-out). After translating the ECoG signal to the desired control signal and integrating appropriately on the host computer, the cursor position and the rest of the virtual task scene was relayed to the monkey’s monitor for display as depicted in Figure 3.6. Observing the visual feedback of the cursor’s movement, the monkey is able to adjust his cortical output to produce a desired movement toward completing the BCI task.

In Chapters 4 and 5, the neural control signal was mapped to the extrinsic (Cartesian) velocity of the cursor, while in Chapters 5 and 6, the control signal was mapped to the intrinsic (joint angular) velocity of the two-link arm. The final experiments involved mapping the control signal to the joint torque (2-dimensional control signal) or the muscle forces (6-dimensional control signal) associated with a dynamic model of the arm described in Chapter 6.
Figure 3.6: BCI Control Schematic

Raw signals are first recorded from the monkey’s ECoG electrodes, amplified, and digitized. Digital signal processors produce spectral estimates for each channel of the amplitude within five frequency bands using an envelope detection method. Spectral estimates are sent to a host computer for feature normalization. A decoding model transforms the normalized features into a 2-dimensional control signal, which is subsequently transformed into either a velocity or force variable depending on the experiment the monkey is performing (experiments and control schemes lasted several weeks before switching). The kinematic or dynamic variable is then integrated appropriately to a cursor position, which is displayed on an LCD screen along with the rest of the behavioral task.
3.5.1 Decoding Algorithm

The ECoG derived control signal was conceptualized as a weighted linear sum of the neural features used to elicit movement of the cursor. The decoding algorithm is used to build the neural control signals by determining this optimal set of weights through linear regression. With this in mind, the neural control signal, \( y(t) \), was defined as the transposed decoding weights matrix, \( W^T \), multiplied by the instantaneous vector of z-scored features, \( x(t) \).

\[
\vec{y}(t) = W^T \vec{x}(t) , \quad \text{where} \quad \vec{x}(t) = \begin{bmatrix}
f_1 \\
f_2 \\
\vdots \\
f_N 
\end{bmatrix}
\]

Eq. 3.8

In all experiments, the decoder was naïve in that it started each day with the weights initialized to an empty matrix (zeroed out). It did not use any knowledge from previous sessions. The assumption was made that at each point during the movement, the goal of the animal was to produce a movement in the direction of the target. We call this assumed directional intent \( u(t) \), which is the normalized vector of the target position (e.g., \( [T_x, T_z]^T \)) minus the cursor position at time ‘\( t \)’.

The decoding algorithm was designed with the intention of updating the weights based on the modulation of features, at the end of each block of trials. The act of the subjects adapting to the control scheme through biofeedback and the decoding algorithm updating the weights to become optimal has led us to call this a co-adaptive algorithm. The algorithm is adaptive in that it is always running and calculating new weights at the end of every 16 trial block.

To avoid contaminating the decoder with neural signals unrelated to efforts towards completing the task, only neural data from correct reaches was saved for regression. Although incorrect trials could occur while the animal was trying to complete the task, errors were usually
a sign of distraction, boredom, or frustration. The data during the movement period of the correct trials in the block was used to calculate each new set of weights. The desired direction vectors from correct trials were placed into a matrix $U$, and the neural features from correct trials were placed into a matrix $X$.

$$U = \begin{bmatrix} \vec{u}(t_0), \vec{u}(t_1), \ldots, \vec{u}(t_f) \\ \text{movement #1} \\ \ldots, \quad \vec{u}(t_0), \vec{u}(t_1), \ldots, \vec{u}(t_f) \\ \text{movement #16} \end{bmatrix}$$  \text{Eq. 3.9}

$$X = \begin{bmatrix} \vec{x}(t_0), \vec{x}(t_1), \ldots, \vec{x}(t_f) \\ \text{movement #1} \\ \ldots, \quad \vec{x}(t_0), \vec{x}(t_1), \ldots, \vec{x}(t_f) \\ \text{movement #16} \end{bmatrix}$$  \text{Eq. 3.10}

Where $X \in \mathbb{R}^{N_{\text{features}} \times N_{\text{samples}}}$, and $U \in \mathbb{R}^{N_{\text{dimensions}} \times N_{\text{samples}}}$. 

In order to determine the weights, the instantaneous unit vector in the desired movement direction was used as the response variable ($U$) and the modulation of features ($X$) during the movement period was used as the independent variable that predicted the desired movement direction.

$$W_{\text{regressed}}X = U$$  \text{Eq. 3.11}

The regressed decoding weights, $W_{\text{regressed}}$, were chosen with the aim of minimizing the squared error of the prediction. The least squares solution to the regression problem can be obtained by multiplying each side of Equation 3.11 by the right-sided inverse of the neural features matrix, $X^+$, where “$+$” denotes the Moore-Penrose pseudoinverse.

$$W_{\text{regressed}} = UX^+$$  \text{Eq. 3.12}
To reduce the effects of local overfitting and the possibility of large sudden changes from one block to another, a weight matrix smoothing technique was implemented. This procedure is similar to those previously described in intracortical BCI studies [55], [124], [137]. An update smoothing factor $\alpha$ (a value between 0 and 1) was used to blend the new weights with the previously used weights.

$$W = \alpha W_{\text{regressed}} + (1 - \alpha)W_{\text{previous}}$$  \hspace{1cm} \text{Eq. 3.13}

Where $W_{\text{previous}}$ is the matrix of weights used in the previous block, and $W$ is the matrix of weights to be used for the upcoming block. Setting the value of $\alpha$ to 0 results in the weights remaining locked to the previous setting, essentially turning off the decoder adaptation. On the other hand, a smoothing factor of 1 means that only the regressed weights are used and no smoothing occurs. Most of the experiments in this dissertation utilized a smoothing factor of 0.2, as we found this to work well in previous studies [131].

### 3.5.2 Training Paradigm

To initially train the subjects to both understand and perform the tasks, we used an additive directional bias on the cursor [85]. The bias signal was calculated as the scaled instantaneous unit vector pointing from the cursor to the target. This bias signal was then added to the current cursor velocity. If the monkey was not actively moving the cursor, the bias signal would cause the cursor to drift towards the target. For velocity control tasks, the velocity applied to the cursor was defined as:

$$\vec{v}(t) = \underbrace{G_y \cdot \vec{y}(t)}_{\text{neural control signal}} + \underbrace{\text{Assistance} \cdot G_{\text{Bias}} \cdot \vec{u}(t)}_{\text{constant speed bias signal}}$$  \hspace{1cm} \text{Eq. 3.14}
Where the terms $G_y$ and $G_{Bias}$ refer to the gain applied to the control signals and bias signals respectively and $u(t)$ is the aforementioned instantaneous unit vector pointing from the cursor to the target.

Each day, the experiment began with a block of “watch” trials, a technique first introduced by Wahnoun and colleagues [138]. During this block, the decoding weights were zero, meaning the subject had no control over the cursor and it was completely controlled by the assistive bias signal. The monkey received feedback of trial completion with a reward at the end of each trial. In each successive block, the assistance was slowly reduced causing the monkey to gain relatively more control of the cursor. This assistance helped to keep the monkey from becoming frustrated while still allowing the opportunity to identify a neural state that made the cursor travel in the direction of the target faster and therefore be rewarded more often. As the monkey identified productive cortical modulations over blocks, the additive bias velocity was gradually decreased until the cursor was under complete brain control (see Figure 3.7).

This training paradigm together with the adaptive decoding algorithm resulted in complete control of a 2-dimensional cursor in 20-45 minutes for all subjects on day one of experiments. Although this is not surprising for the monkeys with past BCI experiences, even the naïve monkeys were able to fully control the cursor in this short time period. By day two and beyond, each animal was able to attain full control of the cursor within 5 minutes. We have previously used watch tasks to train our subjects in multi-dimensional BCI experiments in which the goal state may have been inevitably difficult to understand [131]. In previous BCI experiments without the biased adaptive decoding paradigm, it could take weeks before a respectable level of control could be achieved in a naïve subject [100].
A. Watch Task

B. Desired Direction Vectors

Figure 3.7: Daily Training Protocol
A) Computer controlled cursor assistance for each block. Each monkey began the day with a watch task (100% computer control, with 0% brain control). During the next few blocks the bias velocity was scaled down until zero assistance was supplied from the fifth block onward. B) Example trajectories are shown to each of the 8 targets, with the desired direction vector, $u(t)$, illustrated at each point in the trajectory.

3.5.3 Virtual Task Environment

Each of the tasks used in this dissertation were programmed using an in-house application construct pioneered by former lab members JJ Wheeler and TM Pearce. NERVE (Neuroscience and Engineering Reconfigurable Virtual Environment), was designed using Visual Studio and C++ and allowed subsequent users to design, customize and run tasks for experiments by providing a basic framework for the virtual task environment.

The virtual task environment incorporated a Graphical User Interface (GUI) created in Qt Designer (The Qt Company), to modify the current task and its operational parameters. Two graphical windows were created by the GUI at the beginning of each experiment. One window was presented to the subject in full-screen mode on a 20-inch monitor with 4:3 aspect ratio. The second window was for the convenience of the experimenter and replicated what was presented.
in the subject’s window. Graphical objects presented to the subject during the task, such as the cursor, targets, and virtual arm, were programmed with OpenSceneGraph using OpenGL.

The state sequence of the task was programmed in a collection of C++ scripts that interacted with the described virtual environment. These scripts read the parameters defined in the GUI and controlled the displayed objects in the virtual world accordingly. They received the raw features from the TDT base-station in order to normalize the features in real-time as designated in section 3.3.4. A MATLAB runtime engine was utilized in order to implement a MATLAB script executing the decoding algorithm between blocks during the BCI task. The decoding algorithm was only performed during the short rest period between blocks, and a visual representation of the decode weights and regression statistics were generated for the experimenter. The C++ script relayed the data required by the algorithm and used the output decoding weights to combine the different features into the control signal. The control signal was then used to move the elements in the virtual environment based on the rules of the task.

The virtual environment operated at 100 Hz, both reading the amplitude estimates from the TDT base-station and updating the virtual environment. The feature means, standard deviations, and z-scores were recorded and stored at a down-sampled rate of 20 Hz in a text file (individual band features were found to modulate at a maximum rate of 3-5 Hz). Other details of the task, such as the specific parameters used and results of each trial were written to a separate text file. The TDT base-station stored the raw ECoG signals received from the head-stage and pre-amplifier assembly, the current state of the task, and movement of the element controlled in the task in a data tank for further analysis.
4 Directional Tuning in ECoG BCI with a Naïve Co-Adaptive Decoder

4.1 Introduction

In general, motor neurophysiological decoding experiments involve a subject performing a stereotypical task (e.g., physical reaching tasks, saccade based decision making tasks) and the neural activity is compared to the physical actions; typically attempting to reproduce one or more aspects of the task using only these neural codes. In this work however, the neural signals were causal to movements of the cursor and explain the act perfectly. The two central themes of this chapter are to determine: 1) what directional information is encoded by the neural features whilst performing ECoG BCI, and 2) how and where this information is encoded by cortical surface potentials. Movement decoding has been observed using ECoG during voluntary movements [9], [11], [75], [106], but what kind of tuning structure exists (if any) under BCI control versus those found during physical movements?

We have previously demonstrated control of a cursor in a 2-D kinematic task using ECoG by splitting the raw signals into five separate frequency control bands [101]. This chapter aims to gain further understanding of how these control features modulate individually as well as together in the population. Like tuning experiments of the single unit variety, we will be identifying preferred directions and cosine tuning strength of these control features, while the animals perform center-out BCI tasks.
The remainder of this chapter is divided into three different sections. Section 4.2 describes the background and methodology used for the experiments and analyses performed. Post-hoc analysis of the collected data was used to determine variations in the BCI control, distributions of neural features, and changes in modulation of individual features during closed-loop control. Section 4.3 demonstrates the results obtained from this set of experiments. Finally, Section 4.4 concludes the chapter with a discussion of the observed results and their overall implications moving forward in the field of ECoG BCI.

4.2 Methods

4.2.1 Subjects

The experiments in this chapter utilized all six rhesus macaques introduced in Chapter 3, monkeys G, I, K, O, P, and R. Monkeys K and P had roughly eight months of 2-D center-out BCI control experience under different decoding schemes before using the co-adaptive scheme implemented in this chapter [114]. Monkey I had participated in several BCI tasks before being subject to this particular experiment, as he was well versed in 2-D, 3-D, and 4-D kinematic BCI [131] as well as 2-D feature pruning experiments [125] with the decoding algorithm used here. Monkey R had learned to modulate the beta and mid gamma bands individually in order to control the cursor velocity in a one dimensional task [125]. The last two subjects’ previous experiences were with physical reaching [129] and joystick center-out tasks and were relatively naïve to BCI experiments. A summary of each animal’s BCI experience can be seen in the first three columns of Table 4.1.
Table 4.1: Subjects Background
Each subject with prior BCI experience is listed with the maximum degree of freedom (DOF) control achieved, the number of months successfully performing BCI control tasks prior to these experiments, and the implant duration in months at the time these experiments began. In addition, the numbers of physical electrodes presumed to be placed over the motor or sensory cortex are listed, followed by the percentage of total electrodes in parenthesis. There are a total of 5 control features for each electrode.

<table>
<thead>
<tr>
<th>Subject</th>
<th>DOF Control Accomplished</th>
<th>BCI Experience (months)</th>
<th>Implant Duration (months)</th>
<th>Motor Contacts</th>
<th>Sensory Contacts</th>
<th>Total Features, N_{feats}</th>
</tr>
</thead>
<tbody>
<tr>
<td>G</td>
<td>2</td>
<td>1</td>
<td>16</td>
<td>0 (0%)</td>
<td>7 (100%)</td>
<td>35</td>
</tr>
<tr>
<td>O</td>
<td>2</td>
<td>1</td>
<td>33</td>
<td>19 (59%)</td>
<td>13 (41%)</td>
<td>160</td>
</tr>
<tr>
<td>R</td>
<td>1</td>
<td>2</td>
<td>24</td>
<td>28 (58%)</td>
<td>20 (42%)</td>
<td>240</td>
</tr>
<tr>
<td>I</td>
<td>4</td>
<td>34</td>
<td>36</td>
<td>17 (61%)</td>
<td>11 (39%)</td>
<td>140</td>
</tr>
<tr>
<td>K</td>
<td>2</td>
<td>10</td>
<td>11</td>
<td>51 (81%)</td>
<td>12 (19%)</td>
<td>315</td>
</tr>
<tr>
<td>P</td>
<td>2</td>
<td>10</td>
<td>11</td>
<td>19 (61%)</td>
<td>12 (39%)</td>
<td>155</td>
</tr>
</tbody>
</table>

As noted previously (see Table 3.1) the electrode arrays differed in manufacturing technique, number of channels, size of individual contacts, and even in their location on the cortical surface. The right columns of Table 4.1 list the number of contacts presumed to reside in motor and sensory areas and their corresponding percentage in the population. Each subject’s total number of features, N_{feats}, is referenced in the last column, with each channel producing five control features.

The location and orientation of the arrays varied on a case-by-case basis. Silastic arrays were implanted on both hemispheres of monkey I through a single center craniotomy with the goal of encompassing large parts of primary motor and sensory cortices. Array orientation was paralleled across the hemispheres as seen in Figure 4.1A-B. Monkey G received a single subdural Silastic array positioned over sensory cortex on the left hemisphere. This subdural array was implanted through the previously created single unit recording chamber and positioned
Figure 4.1: Overview of Implanted ECoG Arrays
A) 1.5mm Ad-Tech array implanted in monkey I.  B) 2mm PMT array implanted in monkey I.  C) 2mm PMT array implanted in the subdural space of monkey G.  D) 300-1200μm UW array implanted in monkey R.  E) 300-600μm UW array implanted in monkeys P, K, O and R* (monkey R used a UW 300-1200μm array shown here).  F) 300-600μm UW array implanted in monkey K.
across the central sulcus from the previous penetrating electrode locations in dorsal premotor cortex (see Figure 4.1C). Polyimide arrays implanted on the left hemisphere of monkeys K, O, P, and R were all oriented in the rostral-caudal direction spanning approximately from premotor areas to S1/Parietal Area 5 as shown in Figure 4.1E. This placement and orientation was chosen to provide coverage of arm and shoulder motor areas spanning from abstract planning (parietal areas near the posterior boundary of the array) to areas closer to physical movement execution (premotor and primary motor cortex at the anterior half of the array). The two remaining implants were the right hemisphere implants on monkeys K and R. Monkey K’s right hemisphere array was oriented medial-laterally to approximately follow the pre- and primary motor strips (Figure 4.1F). Monkey R’s implant was placed mirroring the array on the left hemisphere (Figure 4.1D).

### 4.2.2 Behavioral Task and Experimental Protocol

Prior to performing the BCI task, the monkeys were trained to perform the 2-D center-out task with a joystick. Once the animals were proficient and understood how the task functioned, the joystick was removed and the animal began training on the BCI task. In each daily recording session, the animal began with the watch task, during which the computer controlled the movement of the cursor and the monkey was rewarded upon trial completion for the first block. During the next 4-6 blocks, the additive bias was reduced from 100% to 0% and the monkey gained exclusive control of the cursor. All blocks with additive bias were removed from the data set, and only blocks completed without bias were included for analysis.

All animals performed the standard 2-D center-out task with equally spaced targets using kinematic velocity BCI control. Eight radially spaced targets were possible for selection in the pseudorandom block design, with each target requiring two correct reaches per block. The
monkeys were split into two groups, Group A was given an “easy task” with large targets and short target distances. Monkeys G, O, and R had the least previous BCI experience and were placed into group A. Alternatively, monkeys I, K, and P, who were more experienced, were placed into group B and assigned to the “hard task” with smaller cursors and targets and longer target distances. The additional task parameters for each monkey are shown in Table 4.2.

**Table 4.2: Task Related Parameters for 2-D Center-out BCI**
Target and cursor measurements are listed in the first three columns. The smoothing factor, $\alpha$, represents the memory for regression weights from one block to the next. A value of 1.0 means there is no memory of the previous regression weights, while a value of 0.0 means the previous weights are unaffected during regression updates. The maximum movement time allotted from target onset before timing out is shown for each subject. The translational gain was set individually for each monkey.

<table>
<thead>
<tr>
<th></th>
<th>Target Distance (cm)</th>
<th>Cursor Radius (cm)</th>
<th>Target Radius (cm)</th>
<th>Smoothing Factor, $\alpha$</th>
<th>Max Movement Time (sec)</th>
<th>Translational Gain, $G_T$ (au)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Group A</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>7.5</td>
<td>1.25</td>
<td>1.25</td>
<td>0.2</td>
<td>5</td>
<td>14</td>
</tr>
<tr>
<td>O</td>
<td>7.5</td>
<td>1.25</td>
<td>1.25</td>
<td>0.2</td>
<td>10</td>
<td>13</td>
</tr>
<tr>
<td>R</td>
<td>7.5</td>
<td>1.25</td>
<td>1.25</td>
<td>1.0</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td><strong>Group B</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>10</td>
<td>0.80</td>
<td>0.80</td>
<td>0.2</td>
<td>8</td>
<td>11</td>
</tr>
<tr>
<td>K</td>
<td>10</td>
<td>0.80</td>
<td>0.80</td>
<td>0.1</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>P</td>
<td>10</td>
<td>0.75</td>
<td>0.75</td>
<td>0.1</td>
<td>8</td>
<td>6</td>
</tr>
</tbody>
</table>

**4.2.3 BCI Psychophysics and Metrics**

Correct trials that satisfied the hold and movement time criteria were included for analysis. First, the movement time was calculated as the time between the end of the Hold A period ($t_0$) and the beginning of the Hold B period ($t_f$). While this metric gives an idea of how fast a subject could touch a peripheral target after it was presented, it does not give any additional information about the cursor trajectory or level of control during a single trial. A slow but straight and steady cursor trajectory could yield similar results to a fast but meandering path.
To supplement this measure, the maximum speed and average speed during the Hold B period were determined.

Two metrics were used to quantify the cursor trajectory itself. A normalized path length metric, $d_{path}$, was calculated as the path-dependent distance traveled by the cursor over the movement period by integrating the absolute speed and dividing by the distance between the start and end cursor positions over the same period:

$$d_{path} = \frac{1}{\|\bar{p}(t_f) - \bar{p}(t_0)\|} \int_{t_0}^{t_f} \|\vec{v}(t)\|\,dt$$  \hspace{1cm} \text{Eq. 4.1}

As the shortest path from the center target to the peripheral target is a straight line, path lengths greater than this value indicate the degree of deviation from a straight line trajectory. However, perfectly straight reaches towards the far edge of a target would result in a minimum value of 1.

To account for how well the subject was aiming towards the center of the target, a dot product metric, $d_{vel-tar}$, between the instantaneous cursor velocity vector and the cursor-to-target vector was calculated:

$$d_{vel-tar} = \frac{1}{t_f - t_0} \int_{t_0}^{t_f} \frac{\vec{v}(t) \cdot \vec{u}(t)}{\|\vec{v}(t)\|\|\vec{u}(t)\|}\,dt$$  \hspace{1cm} \text{Eq. 4.2}

where $\vec{v}(t)$ is the instantaneous velocity vector and $\vec{u}(t)$ is the instantaneous vector pointing from the cursor to the target. The integrand of this metric has an advantage in that it can assess the subject’s ability to correct the cursor’s trajectory as a function of time and will be used in later chapters of this dissertation.
The last metric, \( R_{B/\text{max}} \), was calculated as the ratio of the average speed during the Hold B period to the maximum speed during the movement period:

\[
R_{B/\text{max}} = \frac{|v_{\text{Hold B}}|}{|v_{\text{max}}|}
\]  

Eq. 4.3

This ratio portrays the subject’s ability to accelerate towards and then hold at a target. Since these two speeds are not necessarily independent (e.g., a trial with a higher maximum velocity is likely to have a higher Hold B velocity as it requires more deceleration to come to a complete stop), this metric moreover acts as a way to compare subjects.

4.2.4 Neural Data Analyses

Cosine Tuning

The firing rate response of motor and premotor cortical neurons can be described via “tuning curves” - functions that relate neural activity to various parameters. The classic description in the literature is one of broad tuning to movement direction, with maximal firing rate in the “preferred direction” (PD), minimal in the anti-preferred direction, and a smooth transition in between. This relationship can be fit with a cosine function and visualized by plotting neural activity as a function of angle. Although the experiments documented here were accomplished using local field potentials, not individual neuron spike rates, the goal of the analysis is the same; identifying tuning characteristics in neural activity. While a cosine may not necessarily the best function to describe all cortical activity, it has three benefits. It a) has the advantage of being a simple least-squares linear regression model; b) is widely used in the literature making comparisons to previous studies possible; and c) does a reasonable job at describing the response properties of neural signals.
In this chapter, multilinear least-squares regression models (cosine tuning) are fit to the z-scored features during movements to the different peripheral targets (denoted by the direction, $\phi$). Statistically significant correlations were determined using the F-test ($\alpha = 0.05$) on the residuals of the least-squares model fit.

\[ z(\phi) = b_0 + b_1 \cos(\phi) + b_2 \sin(\phi) \]  

Eq. 4.4

\[ d = \sqrt{b_1^2 + b_2^2} \]  

Eq. 4.5

\[ \theta = \tan^{-1} \frac{b_2}{b_1} \]  

Eq. 4.6

\[ z(\phi) = b_0 + d \cos(\phi - \theta) \]  

Eq. 4.7

The offset, or mean of the modulation, is given by $b_0$. The peak-to-peak amplitude, or depth of modulation, is given by two times $d$. The tuning preferred direction is given by $\theta$. Cosine fits were determined for every recorded feature, using the trial data from every block, for all sessions (i.e. days). Figure 4.2 shows the distributions and cosine fits for two such representative features from a single electrode of monkey G. The mid gamma feature pictured had very large $R^2$ values (measure of the percentage of variance explained) while the low gamma feature had very low $R^2$ values. Both features were from the same recording electrode.
Figure 4.2: Cosine Tuning Example

**Top** Cosine fits for a low gamma feature (green) and a mid-gamma feature (orange) from Channel 3 of monkey G on day 26 of BCI control. **Bottom** Histograms show the same two features over all recording days (n = 31 days). Left plot displays the difference in regression $R^2$'s between the two features. Plot legend indicates the median regression $R^2$ with the percentage of regressions reaching significance at $p < .05$, $p < .01$, and $p < .001$ for each feature. Right plot shows mean tuning angle and the mean vector length (“MVL”) of the circular distribution for each respective feature.
Circular Statistics

A very important cosine tuning characteristic is preferred direction. In this work, there is a preferred direction, \( \theta \), for each of the \( N_{\text{feat}} \) features and for every completed block in the BCI task. Since this large aspect of the data set is directional, we must first familiarize ourselves with some tools from circular statistics.

The elementary but also fundamental property of circular data is that the beginning and end of the scale coincide: for example, \( 0^\circ = 360^\circ \). An immediate implication is that the arithmetic mean is likely to be a poor summary: the mean of \( 1^\circ \) and \( 359^\circ \) cannot sensibly be \( 180^\circ \). The solution is to project the angular data onto the unit circle and use the vector mean direction as the circular mean. This is analogous to the Taylor expansion of a complex exponential which projects the angle \( \theta \) onto the unit circle in the complex plane:

\[
e^{i\theta} = \cos \theta + i \sin \theta, \quad i = \sqrt{-1}
\]

Eq. 4.8

The real part (\( \cos \theta \)) corresponds to the \( x \)-coordinate on the circle, and the imaginary part, \( \sin \theta \), is the \( y \)-coordinate on the circle. By projecting each sample \( \theta \) to the complex plane, the mean of \( \theta \) can be determined like any other complex number. The circular mean consists of two parts: 1) the magnitude and 2) the direction. In this work we commonly refer to the magnitude of the circular mean as the “Mean Vector Length” as it is literally the length of the mean vector in the complex plane. For \( N \) samples, with each individual sample denoted by the index \( k \), the circular mean is calculated as follows:

\[
MVL = \frac{1}{N} \sqrt{\left( \sum_{k=1}^{N} \cos \theta_k \right)^2 + \left( \sum_{k=1}^{N} \sin \theta_k \right)^2}
\]

Eq. 4.9
\[ \theta_{circ} = \tan^{-1} \left( \frac{\sum_{k=1}^{N} \sin \theta_k}{\sum_{k=1}^{N} \cos \theta_k} \right) \]

Eq. 4.10

Figure 4.3 illustrates the preferred directions of two features over time. On the left in Figure 4.3A we see a feature that is sporadic in its preferred direction with a high spread of \( \theta \) values. Although the feature visibly prefers 50°, it also has a tendency to wander around and be tuned in other directions. In contrast, Figure 4.3B demonstrates a less sporadic feature that is more consistently tuned to 88°. This consistency is reflected in the length of the mean vector.

**Figure 4.3: Mean Vector Length Example**

A) Feature with a high circular spread of regressed cosine tuning preferred directions. B) Feature with a low circular spread of assigned preferred directions. Each blue dot represents the preferred direction from regression on a unit circle. The red line in each plot is the mean resultant vector calculated using all the points on the unit circle. The length of this resultant vector was used to quantify how “consistent” each feature was and is referred to as the Mean Vector Length or “MVL”. (Figure courtesy of P Karande)
4.3 Results

4.3.1 Task Performance and Psychophysics

Each subject executed the task over the course of several days and achieved respectable error rates. The daily recording sessions routinely lasted between 1 and 2 hours with each subject averaging over 600 correct trials per day and five of the six subjects completing the task at over 90% accuracy. The number of sessions each monkey completed and a summary of the data collected is shown in Table 4.3.

Table 4.3: General Task Performance

<table>
<thead>
<tr>
<th>Group</th>
<th>Days</th>
<th>Blocks</th>
<th>Trials</th>
<th>Percent Correct</th>
<th>Blocks (Daily Average)</th>
<th>Trials (Daily Average)</th>
</tr>
</thead>
<tbody>
<tr>
<td>G</td>
<td>31</td>
<td>3,231</td>
<td>52,115</td>
<td>99.2 %</td>
<td>104.2 ± 20.3</td>
<td>1,681 ± 322</td>
</tr>
<tr>
<td>O</td>
<td>25</td>
<td>2,051</td>
<td>33,300</td>
<td>98.5 %</td>
<td>82.0 ± 22.2</td>
<td>1,332 ± 339</td>
</tr>
<tr>
<td>R</td>
<td>6</td>
<td>318</td>
<td>5,528</td>
<td>92.0 %</td>
<td>53.0 ± 17.6</td>
<td>921 ± 210</td>
</tr>
<tr>
<td>I</td>
<td>7</td>
<td>877</td>
<td>14,107</td>
<td>99.5 %</td>
<td>125.3 ± 20.3</td>
<td>2,015 ± 328</td>
</tr>
<tr>
<td>K</td>
<td>9</td>
<td>509</td>
<td>8,332</td>
<td>97.7 %</td>
<td>56.6 ± 9.3</td>
<td>926 ± 142</td>
</tr>
<tr>
<td>P</td>
<td>10</td>
<td>307</td>
<td>6,692</td>
<td>73.4 %</td>
<td>30.7 ± 10.3</td>
<td>669 ± 143</td>
</tr>
</tbody>
</table>

The performance in a 2-D center-out task can be quantified by the movement times to target and the trajectories taken to reach it. In order to maximize liquid rewards over the course of the day, subjects had incentive to complete trials as fast as possible. Deviations from straight line reaches would increase overall trial times and thus not be preferred by the subjects. The performance metrics introduced in 4.2.3 were calculated for these 2-D center-out experiments and are shown in Table 4.4.
These metrics included the movement time, normalized path length ($d_{path}$), dot product between the velocity and cursor-target vectors ($dp_{vel-targ}$), peak cursor speed, cursor speed during the hold period, and the Hold B-to-maximum velocity ratio ($R_{B/max}$). These metrics were calculated only for correct trials in which the peripheral target was touched and the Hold B satisfied and serve to summarize the “reaching” characteristics and performance of each monkey. Additionally, they provide a standard for comparison for the intrinsic BCI control tasks introduced later.

Table 4.4: Single Trial Performance Metrics

<table>
<thead>
<tr>
<th></th>
<th>Movement Time (sec)</th>
<th>$d_{path}$</th>
<th>$dp_{vel-targ}$</th>
<th>Peak Speed (cm/s)</th>
<th>Hold Speed (cm/s)</th>
<th>$R_{B/max}$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>1.21 ± 0.42</td>
<td>1.42 ± 0.33</td>
<td>0.68 ± 0.16</td>
<td>10.25 ± 2.15</td>
<td>5.64 ± 1.89</td>
<td>0.57 ± 0.21</td>
</tr>
<tr>
<td>O</td>
<td>1.29 ± 0.57</td>
<td>1.40 ± 0.48</td>
<td>0.66 ± 0.21</td>
<td>10.33 ± 2.14</td>
<td>6.91 ± 2.47</td>
<td>0.68 ± 0.23</td>
</tr>
<tr>
<td>R</td>
<td>1.51 ± 0.89</td>
<td>1.58 ± 0.66</td>
<td>0.64 ± 0.22</td>
<td>9.95 ± 2.09</td>
<td>5.60 ± 2.01</td>
<td>0.57 ± 0.21</td>
</tr>
<tr>
<td><strong>B</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>1.43 ± 0.39</td>
<td>1.20 ± 0.19</td>
<td>0.70 ± 0.17</td>
<td>11.42 ± 1.79</td>
<td>6.32 ± 1.88</td>
<td>0.56 ± 0.17</td>
</tr>
<tr>
<td>K</td>
<td>2.45 ± 0.47</td>
<td>1.12 ± 0.09</td>
<td>0.79 ± 0.12</td>
<td>5.74 ± 1.26</td>
<td>3.97 ± 0.94</td>
<td>0.70 ± 0.16</td>
</tr>
<tr>
<td>P</td>
<td>2.97 ± 1.14</td>
<td>1.19 ± 0.15</td>
<td>0.76 ± 0.12</td>
<td>6.0 ± 1.90</td>
<td>3.45 ± 1.50</td>
<td>0.59 ± 0.21</td>
</tr>
</tbody>
</table>

During physical reaching (and even joystick movements) a 400ms hold time is sufficient for stopping at the target. However, under this BCI control paradigm, the 400 ms hold only requires the animals to slow down enough such that the cursor remains in contact for the 400ms duration. In effect, this does not make the task a “reach and hold” but rather a “reach and slow” directive.

Further analyses of cursor trajectories were performed to visualize the degree of control each monkey attained. Each correct trial was segmented into 40 time bins starting from center position to the target and a mean cursor position in this time bin was calculated. This produced
40-point trajectories for all correct trials during the experiment. Trials were grouped by the target presented and averaged over the 40-point trajectories. Standard deviations in the cardinal directions were calculated at each time point and illustrated in Figure 4.4. Trajectories were colored by the z-score of the average movement time for the trials for each given target (means and standard deviations for each subject shown in Table 4.4). All subjects, with the exception of monkey I, showed a strong preference for completing trials quickly in a cosine tuned fashion, with clear preferred and anti-preferred targets. Subjects in Group A exhibited “thicker” trajectories as a result of greater deviations from trial to trial in the path taken.

![Figure 4.4: Average Movement Trajectories](image)

Trajectories are shown for a sample day of 2-D Center-out BCI control with colored areas representing the position mean ± 1 standard deviation to each target. Colors represent the normalized movement time in number of standard deviations above (red, slower) or below (green, faster) the mean shown in Table 4.4. **Top Row**, Group A: A) Monkey G, N = 2,033 trials, B) Monkey O, N = 1,445 trials, C) Monkey R, N = 1,056 trials, **Bottom Row**, Group B: D) Monkey I, N = 2,447 trials, E) Monkey K, N = 1,056 trials, F) Monkey P, N = 822 trials.
Taking a step back from individual reaches to each of the eight targets, the daily averages for movement times, average cursor speed, normalized path length, blocks per day, and error rates, were calculated. Figure 4.5 illustrates the variations in these parameters each subject experienced for each day of recording.

Declaring which animal performed “the best” is a tough decision to make. Right away it can be seen that subjects in Group A were faster on average than those in Group B, but the trade-off for being faster is generally an increase in deviation from a straight line path. If each of these characteristics of control were an event in a competition weighted equally, we could grade each subject as the summation of performance in each event, a “BCI Pentathlon”. The competition results are shown in Table 4.5.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Group A</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>4</td>
<td>4</td>
<td>17</td>
</tr>
<tr>
<td>O</td>
<td>3</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td>14</td>
</tr>
<tr>
<td>R</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td>9</td>
<td>9</td>
<td>3</td>
<td>8</td>
<td>8</td>
<td>37</td>
</tr>
<tr>
<td><strong>Group B</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>5</td>
<td>5</td>
<td>4</td>
<td>5</td>
<td>5</td>
<td>24</td>
</tr>
<tr>
<td>K</td>
<td>1</td>
<td>1</td>
<td>5</td>
<td>2</td>
<td>2</td>
<td>11</td>
</tr>
<tr>
<td>P</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td>6</td>
<td>6</td>
<td>12</td>
<td>7</td>
<td>7</td>
<td>38</td>
</tr>
</tbody>
</table>

Table 4.5: BCI Pentathlon Scoring Chart
Each event is scored as the “number of participants beaten” resulting in a maximum of 5 points per event. The “Time” event refers to the average movement time (faster being better), “Speed” refers to the average tangential velocity, or cursor path length divided by movement time (faster being better), “Deviation” refers to the normalized path length, \(d_{path}\) (smaller being better), “Blocks” is a measure of stamina (i.e., average number of blocks performed per day, where more is better), and “Errors” is the average daily error rate (lower is better). Data from individual days can be seen in Figure 4.5.
Figure 4.5: Daily Task Psychophysics

A) Movement Time is the measure of how quick the subject can complete the trial on average. B) Average Cursor Speed is the average speed at which the cursor moved during the trial, and is the quotient of total path length and movement time. C) Normalized Path Length is the measure of deviation from straight line path as outlined in Section 4.2.3. D) Completed Blocks per session is the number of blocks completed without any computer aid during training or otherwise. E) Percent Error is the rate at which errors are made on a trial by trial basis. Data points are shown for each training day, with the average per day displayed as a solid line. Monkeys 1-3 are from Group A and are G, O, and R respectively. Monkeys 4-6 are from Group B and are I, K, and P.
Monkey I, who won four of the five events and claimed the silver in the fifth for a nearly perfect score of 24/25 possible points was the clear winner. Monkeys G and O, both from Group A produced respectable scores of 17/25 and 14/25 for Silver and Bronze. In the competition between Groups A and B, Group B was carried across the finish line by monkey I by a final margin of 38 to 37. Essentially, Group A was faster and made fewer errors, but Group B exhibited straighter reaches and had the MVP, most valuable primate.

4.3.2 Tuning Relationships

For each complete block of trials performed by the subjects, features were assigned a two-dimensional decode weight for control of the cursor as well as a regressed cosine fit. The decode weights were implemented immediately after block completion and used for control in the next block. After the day’s experimental session had ended, the multilinear regressions were performed to produce a cosine fit for each feature/block combination. The numbers of blocks completed by each subject were shown previously in Table 4.3 and range from the low 300’s to over 3,000 in the case of monkey G. The size of the data set is N regressions and weights for each individual feature. Taking each feature as an independent variable with N discrete time measurements, relationships between regression coefficients and statistics were observed.

Encoding Relationships

The results of the cosine fit regressions represent directional encoding of each feature. The depth of modulation (peak-to-peak amplitude of the cosine fit) is a measure of how much the feature can modulate between preferred and anti-preferred targets. The coefficient of determination, \( R^2 \) is a measure of how similar the data is to a cosine function. In addition, the
mean vector length (MVL) speaks to the consistency and repeatability of the tuning angle \( \theta \) (i.e. preferred direction) across blocks and days of experiments.

The left column in Figure 4.6 represents the relationships between the three encoding characteristics mentioned above. The depth of modulation is linearly related to the cosine fit regression \( R^2 \) as shown in Figure 4.6A. This is consistent with an additive noise common to all features, and the ones that modulate more (higher depth of modulation) have larger signal to noise ratios and thus fit a cosine in a superior way. There were slight variations between subjects, but the linear fit when using all subjects was still significant as noted in the first major column of Table 4.6. When observing the relationship between regression strength and preferred direction consistency, we find that the consistency measure is largely explained by a bounded growth function of \( R^2 \) (see Figure 4.6D) of the type:

\[
y = 1 - e^{ax+b}, \quad ax + b \leq 0 ,
\]

Eq. 4.11

Where \( y \) is the mean vector length, \( x \) is the regression \( R^2 \), and \( a \) and \( b \) are constants. We can determine a linear relationship in the linear growth function as shown in Figure 4.6B using the following linear equation:

\[
\ln(1 - y) = ax + b
\]

Eq. 4.12

Using least squares regression the constants \( a \) and \( b \) can be determined. Thus it appears that the consistency (MVL), depth of modulation, and \( R^2 \) are highly linearly related and contain mutual information. For this reason, \( R^2 \) will be the primary measure used for characterizing encoding as it is the simplest for comparison between subjects by nature of representing the statistical
significance of the regressions. As the term \((1 - \text{MVL})\) is defined as the circular variance, we are finding that the circular variance decreases exponentially as \(R^2\) increases linearly.

Figure 4.6: Feature Tuning Relationships
Each feature is represented by an open circle and colored by subject. A) The mean \(R^2\) for each feature’s cosine fit is plotted vs. the mean depth of modulation for that feature. B) The mean \(R^2\) is plotted against the natural logarithm of 1 minus the MVL of that feature. The fit of mean \(R^2\) vs. MVL is shown in D). C) The mean percentage weight of each feature is plotted against the natural logarithm of 1 minus the MVL of that decode weight. The fit of mean percentage weight vs. MVL is shown in E).
Table 4.6: Feature Tuning Relationship Regression Statistics
The regression statistics for the linear fit of all features for each individual subject are shown below. The bottom row (denoted Σ) shows the statistical fit across all subjects which is depicted as the black linear fits in Figure 4.6. All regression slopes are significant at $p < 10^{-35}$.

<table>
<thead>
<tr>
<th></th>
<th>A. Depth of Modulation vs. Cosine Fit $R^2$</th>
<th>B. Tuning Circular Mean vs. Cosine Fit $R^2$</th>
<th>C. Weight Circular Mean vs. Weight Magnitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slope</td>
<td>$\alpha$</td>
<td>$\beta$</td>
<td>$\gamma$</td>
</tr>
<tr>
<td>G</td>
<td>1.49</td>
<td>-6.23</td>
<td>-0.58</td>
</tr>
<tr>
<td>O</td>
<td>1.63</td>
<td>-5.70</td>
<td>-0.46</td>
</tr>
<tr>
<td>R</td>
<td>1.83</td>
<td>-5.96</td>
<td>-0.51</td>
</tr>
<tr>
<td>I</td>
<td>2.19</td>
<td>-5.96</td>
<td>-0.59</td>
</tr>
<tr>
<td>K</td>
<td>2.04</td>
<td>-5.64</td>
<td>-1.51</td>
</tr>
<tr>
<td>P</td>
<td>1.83</td>
<td>-5.39</td>
<td>-0.67</td>
</tr>
<tr>
<td>Σ</td>
<td>1.86</td>
<td>-5.78</td>
<td>-0.64</td>
</tr>
</tbody>
</table>

Decoding Relationships

Decoding relationships are represented by the decode weights and their consistency between days and blocks (i.e. decode updates). The relationship between weight magnitude and weight consistency appears to reflect the encoding relationship with a bounded growth function as shown in Figure 4.6E. Thus, weights that are consistently pointing in the same direction are likely to have the largest weights. It is worth noting that the correlations in decoding are noisier than in encoding as noted by the $R^2$ values in the right major column of Table 4.6. Decoding weight magnitudes are not correlated to cosine tuning strength, because the weights are a sparse representation of the encoding space. For example, if all features had strong cosine tuning but the same preferred direction, most weights would be low, with the largest weights being assigned to the features that differed from the rest of the pack, resulting in a poor correlation between the two. The smoothing factor $\alpha$ can play a role in the consistency metric, as the smoothing acts as a
low pass filter on preferred direction rotation, increasing the consistency of all features. However, even using the raw regression weights produced extremely similar results.

4.3.3 Frequency Band Distributions

The idea behind normalizing the features and using a naïve decoder was to give each feature an equal chance at control. As seen previously in Figure 3.4, the decoder was introduced to $N_{feat}$ (number of features = number of channels × 5 frequency bands) unlabeled control features with zero mean and unit variance. Despite the summary statistics being the same for each feature, the temporal profiles were very different. We observed differences in encoding strength, decoding strength, range of modulation, and preferred direction among the different frequency bands.

Encoding Strength

Strength of tuning/encoding is the cosine fit $R^2$ measure. As discussed in the previous subsection, $R^2$ is linearly related to the depth of modulation and also related to the consistency or MVL. Thus, high $R^2$ values associate to higher depths of modulation and consistency measures. Using the F-test ($\alpha=0.05$) we can look at the total number of regressions reaching significance in each frequency band. Table 4.7 details this percentage in each frequency band for each subject. The higher gamma bands (70-115 Hz and 130-175 Hz) produce a much higher percentage of significantly cosine tuned channels, with the beta band (15-30 Hz) generating a larger percentage than the alpha (8-15 Hz) and low gamma (30-55 Hz) bands. Appendix Figure A.1 illustrates the percentage of significant regressions (y-axis) vs. the $R^2$ cutoff value for significance.
Table 4.7: Percent Significant Tuning by Band
The percentages of cosine fit regressions reaching significance for each band are shown below for each subject. Significance determined using the F-test ($\alpha = 0.05$) resulting in a cutoff of $R^2 > 0.3695$. See Appendix Figure A.1 for a visual representation of these values for each subject at all $R^2$ cutoff levels.

**Feature Population:**

<table>
<thead>
<tr>
<th></th>
<th>Alpha (8 – 15 Hz)</th>
<th>Beta (15 – 30 Hz)</th>
<th>Low Gamma (30 – 55 Hz)</th>
<th>Mid Gamma (70 – 115 Hz)</th>
<th>High Gamma (130 – 175 Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>G</td>
<td>12.1 %</td>
<td>50.5 %</td>
<td>26.8 %</td>
<td>97.2 %</td>
<td>95.4 %</td>
</tr>
<tr>
<td>O</td>
<td>19.9 %</td>
<td>21.8 %</td>
<td>20.3 %</td>
<td>87.4 %</td>
<td>65.8 %</td>
</tr>
<tr>
<td>R</td>
<td>11.9 %</td>
<td>16.8 %</td>
<td>12.5 %</td>
<td>70.8 %</td>
<td>68.8 %</td>
</tr>
<tr>
<td>I</td>
<td>13.4 %</td>
<td>37.0 %</td>
<td>18.5 %</td>
<td>85.4 %</td>
<td>84.5 %</td>
</tr>
<tr>
<td>K</td>
<td>23.4 %</td>
<td>71.2 %</td>
<td>25.4 %</td>
<td>82.4 %</td>
<td>76.5 %</td>
</tr>
<tr>
<td>P</td>
<td>18.9 %</td>
<td>56.7 %</td>
<td>43.9 %</td>
<td>95.8 %</td>
<td>92.1 %</td>
</tr>
<tr>
<td>$\mu$</td>
<td>16.6 %</td>
<td>42.3 %</td>
<td>24.6 %</td>
<td>86.5 %</td>
<td>80.5 %</td>
</tr>
</tbody>
</table>

**Median Feature Only:**

<table>
<thead>
<tr>
<th></th>
<th>Alpha (8 – 15 Hz)</th>
<th>Beta (15 – 30 Hz)</th>
<th>Low Gamma (30 – 55 Hz)</th>
<th>Mid Gamma (70 – 115 Hz)</th>
<th>High Gamma (130 – 175 Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>G</td>
<td>10.1 %</td>
<td>43.0 %</td>
<td>17.1 %</td>
<td>99.3 %</td>
<td>98.0 %</td>
</tr>
<tr>
<td>O</td>
<td>17.8 %</td>
<td>20.2 %</td>
<td>15.7 %</td>
<td>90.3 %</td>
<td>67.7 %</td>
</tr>
<tr>
<td>R</td>
<td>9.4 %</td>
<td>15.4 %</td>
<td>10.7 %</td>
<td>68.6 %</td>
<td>72.0 %</td>
</tr>
<tr>
<td>I</td>
<td>9.0 %</td>
<td>25.0 %</td>
<td>15.2 %</td>
<td>97.9 %</td>
<td>94.1 %</td>
</tr>
<tr>
<td>K</td>
<td>22.8 %</td>
<td>75.2 %</td>
<td>16.9 %</td>
<td>100 %</td>
<td>99.6 %</td>
</tr>
<tr>
<td>P</td>
<td>9.4 %</td>
<td>51.5 %</td>
<td>40.1 %</td>
<td>100 %</td>
<td>99.3 %</td>
</tr>
<tr>
<td>$\mu$</td>
<td>13.1 %</td>
<td>38.4 %</td>
<td>19.3 %</td>
<td>92.7 %</td>
<td>88.5 %</td>
</tr>
</tbody>
</table>

**Best Feature Only:**

<table>
<thead>
<tr>
<th></th>
<th>Alpha (8 – 15 Hz)</th>
<th>Beta (15 – 30 Hz)</th>
<th>Low Gamma (30 – 55 Hz)</th>
<th>Mid Gamma (70 – 115 Hz)</th>
<th>High Gamma (130 – 175 Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>G</td>
<td>26.1 %</td>
<td>75.8 %</td>
<td>50.9 %</td>
<td>99.9 %</td>
<td>99.7 %</td>
</tr>
<tr>
<td>O</td>
<td>50.4 %</td>
<td>55.1 %</td>
<td>62.5 %</td>
<td>97.8 %</td>
<td>91.5 %</td>
</tr>
<tr>
<td>R</td>
<td>34.3 %</td>
<td>31.8 %</td>
<td>31.4 %</td>
<td>95.3 %</td>
<td>94.7 %</td>
</tr>
<tr>
<td>I</td>
<td>42.8 %</td>
<td>88.0 %</td>
<td>40.4 %</td>
<td>99.9 %</td>
<td>99.9 %</td>
</tr>
<tr>
<td>K</td>
<td>84.9 %</td>
<td>100 %</td>
<td>95.9 %</td>
<td>100 %</td>
<td>100 %</td>
</tr>
<tr>
<td>P</td>
<td>75.2 %</td>
<td>99.7 %</td>
<td>95.4 %</td>
<td>100 %</td>
<td>100 %</td>
</tr>
<tr>
<td>$\mu$</td>
<td>52.3 %</td>
<td>75.1 %</td>
<td>62.8 %</td>
<td>98.8 %</td>
<td>97.6 %</td>
</tr>
</tbody>
</table>
Figure 4.7: \( \text{R}^2 \) and Weight Magnitudes by Frequency Band
The mean ± 1 standard deviation calculated across all 6 monkeys is shown for each band. The black line represents the 0.05 significance level for: a) cosine fit regression \( \text{R}^2 \) (F-test) on the left, and b) the expected value of weight distribution given random chance weights (0.2 or 1/5) on the right.

In Figure 4.7 we see the mean and standard deviation of regression \( \text{R}^2 \) across subjects in each band. The significance level (p < 0.05) is denoted by the black horizontal line at \( \text{R}^2 = 0.3695 \). The beta band hovers around this range, and is split with three subjects having mean \( \text{R}^2 \) reaching significance and three subjects not. The higher gamma bands are well above this mark for all six subjects while the alpha and low gamma bands do not reach significance in any subject.

Decoding Strength

The BCI naïve decoding scheme in this work is based on the population vector algorithm (more specifically the Optimal Linear Estimator, OLE) for reproducing the kinematics of physical movements from cosine tuned neural firing rates. Thus our expectation would be that features that are cosine tuned would have a superior impact on the decoding by having larger
decode weights. In the perfect scenario, the preferred directions of the neural features are well spread and span the directional space. Features with the best cosine tuning and signal to noise ratio would be assigned the largest weights. In a scenario in which features are correlated however, the large weights are divided between the correlated features and orthogonal features are assigned the remaining weights. The right panel in Figure 4.7 illustrates that the rank ordering observed in $R^2$ is carried over into the magnitude of the decoding weights.

**Range of Modulation**

What are the limits of neural modulation and what governs a spectral features ability to modulate? The regression offset term, $b_0$, represents the mean feature modulation during movement. Means greater than zero demonstrate a positive modulation of the feature whilst moving the cursor. We previously published that animals only modulate the mid gamma band above the baseline [85] and for most subjects this statement remains true. As seen in Appendix Figure A.2, all subjects have a mean modulation greater than zero. However, the subjects also show a decrease in activity to anti-preferred targets. In some subjects, there is a correlation between the mean and the depth of the modulation in a given frequency band (see Appendix Figure A.3). Monkey P is highlighted in Figure 4.8 due to the fact that all frequency bands show significant correlations between the mean and depth of modulation.

Correlations and significance are shown for each subject in Table 4.8. It is interesting to note that the three animals that show very significant ($p < .001$) correlations in individual bands (Monkeys R, K, and P) are the three worst performing subjects in terms of movement time, percent correct, and trials per day. Monkey P is the only animal that shows significant positive correlations in the alpha and low gamma bands. The three best performing subjects did not show highly significant single band correlations (apart from the alpha band of monkey O). Monkey G
with only seven electrodes demonstrated no correlation in a single band or as a whole, while the other five animals all showed strong positive correlation when including all control bands by nature of gamma having a higher mean than alpha and beta.

Figure 4.8: Mean vs. Depth of Modulation in Monkey P
A) Range of modulation, rank ordered by each feature’s mean modulation for Monkey P. Shaded region is the depth of modulation centered at the mean for each feature. B) The depth of modulation is plotted against the absolute value of the mean of modulation for each feature from Monkey P. Linear fits are shown for each band and are colored appropriately, with the black line representing the fit on all features. (* denotes significance with p < .05, ** denotes p < .01 and *** denotes p < .001). See Appendix Figure A.2 for each animal’s individual breakdown of A) and Appendix Figure A.3 for B).
Table 4.8: Significant Relationships between Mean and Depth of Modulation
The table below shows the significance of the correlation between mean modulation and depth of modulation in each band for each subject. It is a summary of the data presented in Figure A.2. The final two rows sum the number of animals with either positive ($\Sigma_+$) or negative ($\Sigma_-$) significant correlations. (* denotes significance with $p < .05$, ** denotes $p < .01$ and *** denotes $p < .001$, “+” denotes a positive correlation and “–” denotes a negative correlation)

<table>
<thead>
<tr>
<th></th>
<th>Alpha</th>
<th>Beta</th>
<th>Low Gamma</th>
<th>Mid Gamma</th>
<th>High Gamma</th>
<th>All Features</th>
</tr>
</thead>
<tbody>
<tr>
<td>GO</td>
<td>---</td>
<td>-</td>
<td>+</td>
<td></td>
<td>+++</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>+++</td>
<td>-</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
</tr>
<tr>
<td>I</td>
<td></td>
<td>-</td>
<td></td>
<td></td>
<td>+++</td>
<td></td>
</tr>
<tr>
<td>K</td>
<td>---</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
</tr>
<tr>
<td>P</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
</tr>
<tr>
<td>$\Sigma_+$</td>
<td>1 / 6</td>
<td>3 / 6</td>
<td>1 / 6</td>
<td>3 / 6</td>
<td>4 / 6</td>
<td>5 / 6</td>
</tr>
<tr>
<td>$\Sigma_-$</td>
<td>2 / 6</td>
<td>1 / 6</td>
<td>2 / 6</td>
<td>0 / 6</td>
<td>0 / 6</td>
<td>0 / 6</td>
</tr>
</tbody>
</table>

Preferred Directions

When talking about preferred directions, we must make a distinction between the two types: a) encoding directions, or results of the cosine fit, and b) decoding directions, or the weighted direction assigned to each feature in the decode model. Encoding directions are tightly grouped by band affiliation as shown in Figure 4.9A, with mid and high gamma being most similar, and beta generally being anti-correlated.

The distribution of preferred decoding directions is not as cleanly separated as the encoding directions were (see Figure 4.9B). In most cases, the decoding weight directions for a feature are different from the encoding direction. This is due to the sparse weighting of correlated features as mentioned previously. Although the individual features in the band appear to group, the preferred tuning directions are organized topographically within each band.
A. Preferred Directions

B. Mean Weight Vectors

Figure 4.9: Overview of Encoding and Decoding Directions
A) The circular mean of the cosine tuning preferred directions for each monkey. B) The average decoding weights for each monkey. Frequency bands are denoted by color.
4.3.4 Spatial Distributions

Motor vs. Sensory

Five of the subjects had electrode grids spanning over both motor and sensory areas. Monkey G’s implant did not cover a portion of motor cortex and was not used for comparison in this subsection. Encoding strength, decoding strength and preferred directions of encoding and decoding will be compared. To quantify differences in these measures, the sensitivity index or d’ metric used in detection theory will be employed. It provides the separation between the means of two distributions compared against their standard deviations.

\[ d' = \frac{\mu_{motor} - \mu_{sensory}}{\sqrt{\frac{1}{2}(\sigma^2_{motor} + \sigma^2_{sensory})}} \]  \hspace{1cm} \text{Eq. 4.13}

When looking at regression R² in each band, we find that although small differences can be seen across the group of subjects, these differences are not significant (t-test, α = .05). Some monkeys (K, P) show very large differences in tuning strength between motor and sensory areas when averaging across all 5 bands (see Figure 4.10B). As summarized in the left major column of Table 4.9, individual subjects had different tuning characteristics between the motor and sensory cortices. However, taken as a whole, we do not see these differences be consistent across animals.
Figure 4.10: Regression $R^2$ differences between motor (Red) and sensory (Blue) electrodes
A) Average feature $R^2$ for each frequency band from all subjects. B) Average feature $R^2$ across all features for individual subjects. (Significant d’ values greater than 1 are shown above with an * denoting significance with $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$)

Table 4.9: Significant differences between motor and sensory
The table below consists of d’ values for the distributions of $R^2$ on the left and Proportional Weight Magnitude on the right. Positive d’ values demonstrate the mean of the motor distribution is higher than that of the sensory distribution. Values of $|d’| < 1$ have been omitted, all d’ values shown are significant ($p < .001$). (* denotes significance with $p < 0.05$, ** denotes $p < 0.01$ and *** denotes $p < 0.001$, “+” denotes motor dominates and “-” denotes a sensory dominates) See Appendix Figure A.4 for individual subject $R^2$ distributions and Figure A.5 for individual subject Weight distributions.

<table>
<thead>
<tr>
<th>Regression $R^2$</th>
<th>Proportional Weight Magnitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha$ $\beta$ $\gamma_{low}$ $\gamma_{mid}$ $\gamma_{high}$</td>
<td>$\alpha$ $\beta$ $\gamma_{low}$ $\gamma_{mid}$ $\gamma_{high}$</td>
</tr>
<tr>
<td><strong>G</strong></td>
<td>NO MOTOR ELECTRODES FOR COMPARISON</td>
</tr>
<tr>
<td>O</td>
<td>1.70 -1.13 1.38 -</td>
</tr>
<tr>
<td>R</td>
<td>++</td>
</tr>
<tr>
<td>I</td>
<td>+</td>
</tr>
<tr>
<td>K</td>
<td>-1.04 --- 2.04 2.04</td>
</tr>
<tr>
<td>P</td>
<td>-1.09 --- --</td>
</tr>
<tr>
<td><strong>M1</strong></td>
<td>2 / 5 0 / 5 1 / 5 2 / 5 1 / 5</td>
</tr>
<tr>
<td><strong>S1</strong></td>
<td>2 / 5 3 / 5 2 / 5 1 / 5 0 / 5</td>
</tr>
</tbody>
</table>
When comparing decoding weights between cortical regions, we must consider the discrepancy of number of electrodes in each cortical region. In most cases, there are more motor electrodes than there are sensory electrodes for a given animal, as shown previously in two columns of Table 4.1. If weights were completely random, more cumulative weight would be assigned to motor electrodes (~80% for monkey K and ~60% for the others). The cumulative weight distributions for each monkey are shown in Figure 4.11A. We see that motor is given more cumulative weight in all subjects except for monkey O, and there is a significant difference in cumulative weight distribution between the cortical regions.

If we account for the discrepancy in number of contacts and instead consider and compare the average motor electrode to the counterpart sensory electrode we find a more jumbled picture. Comparing the average weight given to a motor cortex feature vs. the average weight given to a sensory cortex feature, we see that monkeys I, O, and P have significantly higher weights on the sensory cortex than on the motor cortex (see Figure 4.11B). Monkey K has significantly larger motor cortex weights, and monkey R has slightly larger motor cortex weights. On average, there is no clear winner across all animals, but each animal has a clear preference.

Some patterns emerge when these weights are broken down by frequency band (see Appendix Figure A.5). We generally see the beta band is preferred by sensory cortex (4/5 subjects), and the gamma bands are preferred by motor cortex (3/5 subjects). Our lab has previously shown that motor areas are better than pre-motor and sensory areas when it comes to BCI control using the 70-115 Hz band. And while this data confirms (4/5 subjects) more decoding weights attributed to motor areas, it also shows that the average motor electrode is not
significantly higher in weight than the average sensory electrode, with 3 subjects preferring sensory over motor areas.

As the beta and gamma frequency bands demonstrated the most changes, Figure 4.12 investigates differences in preferred directions between motor and sensory areas. In the beta band, differences emerge in monkeys O and P. In the gamma band of monkey R, preferred directions originating in sensory cortex are more tightly grouped than those in motor; but these characteristics are not reflected in the decoding weights. For the most part, it appears the only differences between motor and sensory electrodes are on an individual subject level when concerned with 2-D BCI tasks using a naïve co-adaptive decoder.

![Figure 4.12](image)

**Figure 4.11: Decoding weight differences between motor (Red) and sensory (Blue) electrodes**

A) Percentage of total weight by magnitude from motor and sensory electrodes for each subject.

B) Proportional weight for a single meta electrode from motor or sensory cortex on average for each subject. (Significant d' values greater than 1 are shown above with an * denoting significance with p < .05, ** p < .01 and *** p < .001)
Figure 4.12: Motor vs. Sensory Preferred Directions. With the exception of a few cases, the motor/sensory division of the cortex does not separate into different preferred directions. Monkey O and P demonstrate some separate preferred directions in the beta band, while monkey R shows some degree of separation in the gamma band. This separation is also accompanied by lower tuning strength ($R^2$, depth of modulation, and MVL) in sensory areas.
**Left vs. Right Hemisphere**

Three subjects (monkeys R, I, and K) were implanted in both hemispheres. Intra-hemispheric preferred directions were correlated within each frequency band in monkeys R and K. For instance, monkey R’s gamma band preferred directions tended to cluster around 240° in the left hemisphere and 310° in the right hemisphere. Their corresponding beta band preferred directions tended to be anti-correlated with their gamma band preferred directions (see Figure 4.13). The preferred directions in the gamma band offer insights into how the features are topographically organized. In monkeys R and K, the preferred encoding directions are tightly

<table>
<thead>
<tr>
<th>Electrode Configuration</th>
<th>Beta Band</th>
<th>Gamma Band</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Tuning</td>
<td>Weights</td>
</tr>
<tr>
<td>R</td>
<td><img src="image1" alt="Diagram" /></td>
<td><img src="image2" alt="Diagram" /></td>
</tr>
<tr>
<td>I</td>
<td><img src="image5" alt="Diagram" /></td>
<td><img src="image6" alt="Diagram" /></td>
</tr>
<tr>
<td>K</td>
<td><img src="image9" alt="Diagram" /></td>
<td><img src="image10" alt="Diagram" /></td>
</tr>
</tbody>
</table>

**Figure 4.13: Left vs. Right Hemisphere Preferred Directions**
Electrodes from the opposing hemispheres have unique tuning properties. In each of the three bilaterally implanted monkeys, the preferred directions of the features in the beta and gamma bands are separable.
grouped, but still completely distinguishable. Likewise, the weights split and rotate as a group away from the corresponding tuning directions. In contrast, monkey I appears to have three groups of preferred directions with matching decode weight directions. Although the hemispherical split into two groups yields separable encoding and decoding directions, we should investigate the possibility of a third spatial group.

Three Control Columns

Monkey I appeared to use three equally spaced (120º apart) tuning columns (each tuning column is composed of multiple adjacent electrode sites) in the higher two gamma bands for control. Clustering by preferred direction, these three columns were arranged spatially on the cortex (one column in the left hemisphere and two in the right hemisphere). K-means clustering (see below) yielded identical results in the mid and high gamma bands, so the features from the two bands were grouped together. Using three principal control columns allows for positive modulations to push in any direction desired. However, using just two principal columns (e.g., the x and y cardinal directions) requires both positive and negative modulations to achieve the same effect. Monkey I using a three column modulation scenario demonstrated great control of the BCI cursor as presented earlier in section 4.3.1.

We used K-means clustering to identify independent cortical control columns (composed of multiple adjacent electrode sites) as well as outlier electrode sites in each monkey. Observing the mean vector lengths of the tuning of the two gamma features revealed a group of “less consistent” control columns in monkeys R and K. Although it is common practice to use z-scores to identify possible outliers, this can be misleading for small sample sizes. A recommended method for small sample sizes for identification of outliers is to use the modified z-score using the median absolute deviation [139].
\[ \text{MAD} = \text{median}(|x_i - \bar{x}|) \quad \text{Eq. 4.14} \]

where \( \bar{x} \) is the median of the data and \(|x|\) is the absolute value of \( x \). This is a variation of the average absolute deviation that is even less affected by extremes in the tail because the data in the tails have less influence on the calculation of the median than they do on the mean. The modified z-score for each sample \( x_i \) is given by:

\[ z_{\text{modified}} = \frac{0.6745(x_i - \bar{x})}{\text{MAD}} \quad \text{Eq. 4.15} \]

Modified z-scores with an absolute value greater than 5 were labeled as outliers and placed into a fourth cluster irrespective of tuning direction. Clustering of the circular data was performed by initializing each feature to a unique cluster. The distances between each feature and cluster circular mean were calculated. The feature with the shortest distance was iteratively added to the nearest cluster and the circular mean was updated. Each iteration the total number of clusters was reduced until three clusters remained.

The results from the clustering algorithm obtained from monkey I are shown in Figure 4.14. The plot in panel A depicts the spatial organization of the three clusters on the cortical surface. All electrodes on the left hemisphere were assigned to a single cluster with the exception of two electrodes being assigned to the fourth “inconsistent” cluster. On the right hemisphere, there was a topographical organization of two clusters with the fourth cluster acting to separate the two. The chart in B shows the proportional weight assigned to an electrode in each cluster and frequency band. The polar plot in panel C displays the preferred cosine tuning directions from the mid and high gamma bands, colored by cluster affiliation. Histograms of tuning directions for all blocks are shown in D, illustrating the consistency of each cluster. Unlike the other five animals, monkey I demonstrated decode weights closely aligned to the same directions the features were tuned to as shown in panels E and F.
Figure 4.14: Three Control Columns
Mid and high gamma bands cluster in their preferred directions for monkey I. A) Result of clustering by tuning direction. Contacts illustrated at 150% the actual size for visualization. Features with significantly lower MVL’s were placed in a fourth cluster regardless of tuning direction (shown here in grey). B) The proportional weights in each cluster by frequency band. Error bars represent standard deviations. C) Circular means of all mid and high gamma features with N = 877 regressions performed. D) Histograms representing the probability of direction in which a feature in each cluster is tuned. E) Average weights of all mid and high gamma features. F) Histograms representing the probability of direction of decoding weights in each cluster.
K-means Clustering by Mid Gamma Band Preferred Directions

Using the K-means clustering method for circular data discussed in the preceding subsection, the five remaining animals’ electrodes were divided into clusters in the same fashion. Although none of the remaining five animals exhibited more than two distinct clusters in the same manner that monkey I displayed, clustering with two and three clusters revealed the effective spatial gradient of tuning angles on the cortical surface. The first pass of clustering using $K=2$ clusters yielded the results shown in Figure 4.15.

It is immediately apparent that monkeys K and R, the two animals with an implant on each hemisphere, have a primary separation between the hemispheres as demonstrated previously. Although monkey K appears to have a small cluster on the right hemisphere with the remaining electrodes being attributed to the larger cluster, the weights shown in the right column associated with the larger cluster lie entirely on the left hemisphere. Since no large decoding weights exist on the right hemisphere of the larger cluster, it is interesting to note that the encoded tuning directions remain strong while not being actively used to move the cursor. Monkey R clearly separates the right from left hemisphere in both encoded tuning directions and decode weights.

The remaining three animals with single implants form less distinct clusters in the tuning direction space, but remain tightly grouped physically on the surface of the cortex. Monkeys G and O appear to form a divide along the sensory/motor strip while monkey P has a small cluster surrounded by the larger cluster on three sides. This could be consistent with the homunculus, with clusters being assigned to different somatotopic regions with little regard to motor vs. sensory mapping.
Figure 4.15: K-means clustering with $K = 2$

The result of the K-means clustering by mid-gamma preferred directions. For the bilateral implant monkeys, this separation occurred between the hemispheres, while in unilateral implant monkeys the separations appear to be in the medio-lateral direction.
Increasing the number of clusters to $K = 3$, as shown in Appendix Figure A.6, provides a clearer picture of the topographic separations that can be seen just by clustering the encoded tuning angle in the mid gamma band. In the remaining bilaterally implanted animals, we still only see the presence of two groups of decode weights. In monkey R, the addition of the third cluster in encoding directions was not accompanied by a third cluster in decoding weights. Instead, the features assigned to the new cluster were ones that were minimally contributing to movements of the cursor. In monkey K the aforementioned region that remained highly tuned while not contributing to cursor movement shifted into the third cluster along with a portion of the left hemisphere. Interestingly, this leaves both hemispheres with a divide along the sensory/motor strip as seen in the three single implant animals.

Essentially what we have learned is that when two implants are present, there is a tendency to cluster across the hemispheres/implants first. This was also true in the case of monkey I as shown in Figure 4.14A. Unlike monkey I however, the addition of the third clusters for Monkeys K and R did not result in a separate grouping of decode weights. Instead, this third cluster was assigned very little weight at all, as if they were not needed to control the cursor accurately in 2-D space.

Clustering in animals with single implants behaves in much the same way as creating additional clusters in an animal with two implants; divide up the cortical region into different parts of the homunculus. All three single implant animals show a clear gradient of encoded tuning directions spatially on the sensory/motor strip. As observed in the “Motor vs. Sensory” subsection, encoding and decoding directions in the mid gamma band were not affected by which side of the central sulcus in which the control features reside. Instead, the somatotopic
region, such as “left arm”, “right arm”, “right leg”, appears to be the more accurate correlate behind the gradient of encoded tuning directions observed.

### 4.3.5 Inferred Strategies

The previous results have illustrated target specific differences in power modulation during movement as well as the directional weight vectors used for BCI control of the cursor. We can observe the product of these two to infer the strategies used for control. Each individual feature moves the cursor along its weight vector scaled by the power estimate.

Two clear strategies were revealed: 1) the strategy that monkey I used, and 2) the strategy that every other monkey used. As shown previously, the weight vectors had the largest magnitudes in the mid and high gamma bands. The preferred directions for the other five subjects were tightly clustered in two groups in a small $90^\circ$ window. Unsurprisingly, the weight vectors were scaled the most in that $90^\circ$ window, and had very little scaling in the other directions. Figure 4.16 illustrates these scaled weight vectors during movement for monkey G. During reaches to the upper three ($45^\circ$-$135^\circ$) targets, the summed weight vectors are greater than the other targets. Thus the monkey was actively increasing power in the mid and high gamma bands during reaches to those three targets, and decreasing power in order to reach the opposing targets. We refer to this strategy as “push and relax”, and it was also displayed by the remaining four monkeys.
Figure 4.16: Push and relax strategy, monkey G
Feature modulated weights to all 8 targets. Red resultant vectors are the scaled sum of all modulated weights toward each target. The single blue resultant vector is the sum of all 8 target resultant vectors. For this subject the sum of all 8 target resultant vectors was heavily biased towards 100°. The animal would modulate more (“PUSH”) in this direction than in the opposite direction (“RELAX”).
Figure 4.17: Push, push, and push strategy, monkey I
Feature modulated weights to all 8 targets. Red resultant vectors are the scaled sum of all modulated weights toward each target. The single blue resultant vector is the sum of all 8 target resultant vectors. For this subject the 8 resultant vectors summed to zero indicating a balance of the weighted modulation to the 8 targets.
As monkey I demonstrated a different distribution of preferred directions, using three finely tuned and equally spaced preferred directions versus the tightly grouped clusters, he did not “relax” to any of the targets. This notion is illustrated in Figure 4.17, in which the weighted modulation to each of the 8 targets is equal. It is unclear if this was a previously learned and reinforced strategy (as mentioned, this monkey previously achieved control of 2, 3, and even 4 dimensions) or just the easiest for the monkey. The fact that the remaining five monkeys all demonstrated similar tuning properties and did not previously participate in BCI control with greater than 2 degrees of freedom may suggest that the natural progression from naivety to learning 2-DOF control would be to de-correlate tuning directions across the ECoG electrodes as little as required and not more. In bilaterally implanted monkeys, this separates the hemispheres, and in unilaterally implanted monkeys the separation appears to mimic the homunculus.

4.4 Discussion

It is possible that due to the z-scoring system used, mid and high gamma features are unable to “pull” in the weight direction as the z-score is positive to all 8 targets on average. This is because the z-score is taken over all time, rest, movement, and otherwise. The mid and high gamma features modulate positively for movement in all directions. It is unclear whether an adjustment in the z-scoring process allowing the features to modulate above and below the “movement mean” rather than the overall mean could abolish this strategy in favor of a “push and pull” scenario.

In the “push and relax” monkeys, it almost appears as if the upper gamma bands all tune in the same preferred direction, and through cortical plasticity and learning by visual feedback, spread those preferred directions as much as is required for the task. In each of the monkeys, be it unilateral or bilateral, the gradient of PD’s is in one direction. For the bilateral monkeys, this
gradient is largely defined by the hemisphere. In the single implant monkeys the preferred directions predominantly arrange in a mediolateral orientation (like the homunculus) rather than an anterior-posterior one (which might be suggestive of motor vs. sensory regions).

However, post-hoc analyses of motor and sensory electrodes do not paint the entire picture. In the experiments conducted here, all electrodes were used. Several single/multi-unit studies have compared cortical regions for control or decoding, and nearly all have determined that M1 neurons clearly have the strongest relationship to the motor variables of interest. This was assumed to carry over to ECoG recordings, but in this task setting it did not appear to transfer. Future work can be carried out that explicitly uses either motor or sensory electrodes, but from the data presented here I would not suspect to see any differences in a 2-D center-out task.

Monkey G was one of the best performing subjects in spite of his low channel count and lack of motor representation.

The results shown here do not suggest any wide-spread tuning differences in the local field potentials recorded from ECoG electrodes above motor or sensory areas, or even any spatial relationships in the anterior-posterior (rostral-caudal) direction. On the contrary, the directional information appears to be laid out primarily in the medio-lateral direction, similar to the arrangement of the homunculus. The following chapters will explore whether these findings translate to control in an intrinsic reference frame as well, and the results from this chapter can provide a benchmark for which to compare these intrinsic BCI tasks.
5 Comparison of Extrinsic and Intrinsic Kinematic BCI Control in Naïve Subjects

5.1 Introduction

While there are examples of movement BCI systems in which the neural control signals are mapped directly to 1-dimensional muscle stimulation [120], [140], [141], the overwhelming majority of systems employ an extrinsic, kinematic control signal for control of anthropomorphic robotic limbs with multiple degrees of freedom [4], [5], [10], [57], [58], [61], [63], [111]. Although the majority of these closed-loop BCI experiments were performed in the intracortical domain, recent open-loop neuroscientific studies have described the ability to decode intrinsic factors such as joint angles and muscle forces using electrocorticography (ECoG) [9], [11], [104], [106].

This work involves alternative control schemes for ECoG-based brain computer interfaces. State of the art BCI systems have grown to incorporate as many as 10-DOF [5]. As more degrees of freedom become possible for BCI, it could be beneficial to move to a more anthropomorphic scheme for dexterous control of robotic or re-animated limbs. The experiments in this chapter are designed to assess the use of ECoG signals as applied to 2-D kinematic BCI control in an intrinsic (i.e. joint angle space) in comparison to the standard kinematic control in the Cartesian (extrinsic) space. We hope to determine how easily the subject can adapt to the new control paradigm, how dexterous the movements can be, and what neural changes are required to do so.

This chapter is organized in three different sections. Section 5.2 describes the experimental and analytical methodology used in this study as well as the design of the novel
intrinsic BCI task. Results from the post-hoc analysis of the experimental data have been outlined in Section 5.3 as they pertain to both performance and tuning properties. Finally, section 5.4 discusses the observations and draws conclusions that lead in to the experiments presented in Chapter 6.

5.2 Methods

5.2.1 Novel Joint Angle Velocity BCI Task

In addition to the classic 2-D center-out BCI task implemented in the previous chapter, subjects were trained on a novel joint angle center-out BCI task to model the intrinsic (kinematic) features of a virtual arm. As humans, we spend time controlling devices with a multitude of control schemes. We control a computer mouse differently than operating a car or heavy machinery. Although we can simplify these controls into extrinsic goals such as “move left, right, down”, the physical motor movements our bodies must make in order to achieve these goals differ for each task. In much the same manner, control of an artificial, robotic, or prosthetic limb can be approached in multiple ways. As mentioned previously, most BCI studies which focus on control of these limbs use the extrinsic goal of where the hand or end-point of the arm is desired, to move. This method puts a computational load on the controller to move each degree of freedom of the arm to achieve the desired movement. The driving motivation for the following experiments is to give the end-user the ability to control an artificial limb not by extrinsic kinematic parameters, but by controlling the actual anthropomorphic forces acting on the limb itself. As a first step towards reaching this goal, we have designed a 2-dimensional task and limited the control signal to the kinematics in the joint angle space to more directly compare to classic extrinsic BCI control.

With a rotationally constrained two-link arm, there is a one-to-one mapping between the hand
location and joint angles. Thus, the difference between joint space and Cartesian space is a non-linear transformation, allowing for this one-to-one correspondence. The virtual arm consisted of two links (upper arm and forearm) with a fixed shoulder position. This simplified model of the arm has been utilized for examination of the shoulder and elbow joints in several physical reaching studies [144]–[150]

Even with extensive use in motor neurophysiology, this model has not been used in a BCI paradigm. The task parameters in this study were slightly modified from the typical task in which the resting state of the arm has the upper arm in a horizontal position and the elbow at 90°. Arm parameters (segment lengths and shoulder position) were selected in such a way that during average reaches to each of the eight targets the elbow would remain visible, allowing for constant visual feedback of both joints. The task parameters determining the target locations in joint space are displayed in Table 5.1. Although the eight center-out targets are equally spaced on the circumference of a circle in Cartesian space, the angular distance in joint space from the center position of the arm to the target states are neither equally spaced nor equidistant as illustrated in Figure 5.1.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper arm length</td>
<td>L₁</td>
<td>10 cm</td>
</tr>
<tr>
<td>Forearm length</td>
<td>L₂</td>
<td>10 cm</td>
</tr>
<tr>
<td>Shoulder position</td>
<td>(S₁, S₂)</td>
<td>(-9, -5) cm</td>
</tr>
<tr>
<td>Shoulder angle</td>
<td>θ₁</td>
<td>-115° ≤ θ₁ ≤ 115°</td>
</tr>
<tr>
<td>Elbow angle</td>
<td>θ₂</td>
<td>0° ≤ θ₂ ≤ 170°</td>
</tr>
<tr>
<td>Cartesian Center Position</td>
<td>(cₓ, cᵧ)</td>
<td>(0, 0) cm</td>
</tr>
<tr>
<td>Joint Center Position</td>
<td>(cθ₁, cθ₂)</td>
<td>(-30, 118°)</td>
</tr>
<tr>
<td>Cartesian Target Distance</td>
<td>Dtar₂D</td>
<td>7.5 cm</td>
</tr>
<tr>
<td>Mean Joint Target Distance</td>
<td>Dtar_JA</td>
<td>53°</td>
</tr>
</tbody>
</table>
Figure 5.1: Joint Angle Task Overview
A) Target locations in Cartesian space. The visible outer ring shown illustrates the target +
cursor size (not visible to the subject), while the inner circle represents the true target size. B) Target locations in joint space (i.e., the data from A transformed into joint space using Equation 5.6). C) Visual representation of the two-link arm model defining $\theta_1$ and $\theta_2$ (drawing adapted from Li [149]). D) In Cartesian space, the targets are equidistant from the center. In joint space however, the average distance is ~0.92 radians (or 53°). By normalizing the target distances by the mean, we see that the 45° and 225° targets are 30-40% further than the average, while the 135°, 180° and 315° targets are roughly 15% shorter than the average. E) The difference in the target angle directions for each frame of reference (i.e., the Cartesian target angle minus the joint space target angle). The average angular difference is shown as approximately 104°.

Modified Decoding Algorithm and Control Signal
For the classic 2-D center-out BCI task (the extrinsic task), the same decoding methodology described in section 3.5 and executed in Chapter 4 was implemented using the desired movement direction as the unit vector pointing from the current cursor position to the target position. The control signal was assigned to the x- and z-velocity of the cursor. During the transition to joint angle velocity control, the peripheral target positions were unchanged from the 2-D center-out task (8 targets spaced 45° in a circle of radius 7.5 cm). However, the monkey now had control over the joint angular velocities. This joint angle space became the new control space for the subjects. Given this and the one-to-one mapping between Cartesian and joint angle spaces, the joint angle positions of the target were no longer equal in distance and angle from the center position. As such, the desired movement direction supplied to the decoder, \( u_\theta \), was the unit vector pointing from the current state of the arm \( \theta = [\theta_1, \theta_2]^T \) to the desired state of the arm.

\[
\vec{v}_\theta(t) = \frac{G_y \cdot \vec{y}(t)}{\text{neural control signal}} + \frac{\text{Assistance} \cdot G_{Bias} \cdot \vec{u}_\theta(t)}{\text{constant speed bias signal}},
\]

Eq. 5.1

where \( \vec{y}(t) \) is unchanged from Equation 3.8. Although the visual feedback was that of the arm itself in Cartesian space, the monkey had to transform that knowledge to know when a joint needed to be flexed or extended. The joint space desired direction vector is depicted graphically within the reach region in Figure 5.2. This graphical representation aids in understanding the curvature that straight reaches in joint space produce. As illustrated in the figure, the arm is able to leave the field of view. However, this is not beneficial for receiving the liquid reward, and occurs rarely when the monkey is paying attention and working. When the subject is bored, satiated, or agitated, this instance happens more regularly.
Figure 5.2: Joint Space Error Direction Represented in Cartesian Space

The “comma-shaped” areas represent the region in which the hand can physically reach during the joint angle task, while the dotted rectangular outlines depict the viewable area on the computer screen. **Center** The arm position at each of the 8 target locations and center location. Movements to each of the target positions cause the majority of the arm to reside within the viewable area for maximum visual feedback of the joints at all times. **Outside** The error direction vectors in joint space ($u_\theta$) are denoted by color in Cartesian coordinates for each target. The curved contours converge on the target for any given Cartesian position, and these curves signify straight line reaches in joint space (**i.e.,** $u_\theta$ is constant).
5.2.2 Subjects

Two male Rhesus Macaques (*Macaca mulatta*, monkeys G and O), weighing 12 and 10 kilograms respectively, were used as subjects in the experiments described in this chapter. Each monkey was implanted with a single chronic ECoG array on the left hemisphere. Monkey G was implanted with a 7-channel large contact array in the subdural space. This low channel count array featured contacts 2 mm in diameter over a sizeable portion of parietal cortex (including primary somatosensory cortex and parietal area 5; for visual reference see Figure 4.1C). Of noteworthy importance, Monkey G did not have any electrodes directly over motor cortex. Monkey O was implanted with a 32-channel thin-film array in the epidural space, with contacts spanning from dorsal premotor (PMd) to primary motor (M1) and over the sulcus into parietal cortex. This particular array orientation was depicted in Figure 4.1E.

Both subjects had been implanted in excess of a year’s time before attempting the BCI control experiments outlined in this chapter. Prior to BCI control experiments, each subject had previously been trained in both the classic center-out task and joint angle center-out task with a joystick mapped to velocity. Neither subject had prior experience in a BCI task. Additional details of each animal’s implant were covered previously in Chapters 3 (section 3.3) and 4 (section 4.2.1).

5.2.3 Experimental Protocol

Prior to performing any BCI task, the two monkeys were trained to perform the classic 2-D center-out task with a joystick by mapping position of the joystick to the x- and z-velocities of the cursor. Once the animals were adept at the task and understood how it functioned, they were transferred to the joint angle center-out task. In this version of the task the x-position of the joystick was mapped to the joint angle velocity at the shoulder ($\theta_1$) and the z-position was
mapped to the joint angle velocity at the elbow ($\theta_2$). Clearly, the physical movements of the joystick required to reach the targets in the joint angle space were distinct from those in the Cartesian space during the 2-D center-out task (see Figure 5.1B). A transformation had to be made in the way the animals moved and interpreted the visual feedback. Early on, the two-link arm waivered chaotically, so a weak bias signal was applied (not strong enough to complete the trials in the absence of user control) and slowly diminished. In the matter of a few days the subjects became proficient in each of these joystick control tasks with comparable performance. Knowing that the animals had to control the joystick differently in the “extrinsic” task vs. the “intrinsic” task, we continued to use both BCI tasks.

At the conclusion of joystick training, monkey G was scheduled to begin BCI training on the joint angle center-out task while monkey O was slated to begin BCI training on the classic 2-D center-out task. During BCI training, the joystick was removed, and the animal began each day with a watch task. Over the course of the first block (16 trials, 2 trials to each of 8 targets in a pseudorandom order), the computer controlled the movement of the cursor to each target and the subject was rewarded upon trial completion. During the cursor’s movements the neural features and the desired direction vectors were logged. At the completion of each 16 trial block, the recorded neural features during the movement time were regressed onto the desired movement directions in order to calculate the weights for the next block. The additive bias was gradually reduced block by block. While the total assistance applied to the bias gain, $G_{Bias}$, was still greater than zero, the animal had limited control of the cursor via the regression weights. Over the course of several blocks the additive bias was reduced to zero and the monkey gained exclusive control of the cursor. The translational gain on the cursor movement, $G_y$, was incrementally increased or decreased based on the animal’s performance. If a higher gain was
reasoned to benefit the monkey it was increased, and if the animal struggled and moved the
cursor beyond the target or erratically, the gain was decreased. The decoding smoothing factor $\alpha$
was set to 0.2 for all experiments.

BCI training was deemed complete when the animal was able to achieve full control by
the fifth recording block (refer to Figure 3.7A) on a daily basis. The translational gain achieved,$G_y$, was held relatively constant within recording sessions moving forward. As long trial times
meant longer periods between rewards, the animals had incentive to move the cursor as quickly
and accurately as possible and their performance was expected to improve over the following
weeks.

Based on previous experiments, we decided three weeks (15 days) on a task would be
sufficient for the monkey to hone in on his preferred control methods and master the craft from
day to day. The subjects alternated between extrinsic control (cursor velocity in Cartesian space)
and intrinsic control (joint angle velocity of the virtual arm). Monkey G began with an
approximately three week session of intrinsic BCI control and monkey O began with three weeks
of extrinsic BCI control. After three weeks, the subjects were switched to the opposite task. At
the conclusion of the first six weeks of BCI control (termed “early” control sessions), the
subjects completed an additional three weeks of the extrinsic task followed by three weeks of the
intrinsic task (termed “late” control sessions). The experimental timeline for each subject is
outlined in Figure 5.3A. The parameters chosen for the BCI gain terms, both the control signal
gain and the bias gain, are listed in Figure 5.3B. The average distance to each target in joint
angle space was mentioned previously to be approximately 0.92 radians or 53°, compared to the
7.5 cm in the Cartesian space. Normalizing the gains between the two tasks by the average
target distance reveals larger gains were used during the joint angle sessions. These control
gains were chosen on the first day of each session as the largest gain that did not negatively affect performance in terms of accuracy and movement times, resulting in a mismatch of normalized gains between the control sessions.

A. Experimental Timeline

<table>
<thead>
<tr>
<th>Session</th>
<th>Control Gain, ( G_y )</th>
<th>Normalized Gain, ( G_y/D_{tar} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>JA1</td>
<td>1.45 rad/s</td>
<td>1.56 s(^{-1})</td>
</tr>
<tr>
<td>2D1</td>
<td>11.20 cm/s</td>
<td>1.49 s(^{-1})</td>
</tr>
<tr>
<td>2D2</td>
<td>12.80 cm/s</td>
<td>1.71 s(^{-1})</td>
</tr>
<tr>
<td>JA2</td>
<td>2.00 rad/s</td>
<td>2.15 s(^{-1})</td>
</tr>
<tr>
<td>2D1</td>
<td>12.62 cm/s</td>
<td>1.68 s(^{-1})</td>
</tr>
<tr>
<td>JA1</td>
<td>1.72 rad/s</td>
<td>1.85 s(^{-1})</td>
</tr>
<tr>
<td>2D2</td>
<td>10.53 cm/s</td>
<td>1.40 s(^{-1})</td>
</tr>
<tr>
<td>JA2</td>
<td>2.05 rad/s</td>
<td>2.21 s(^{-1})</td>
</tr>
</tbody>
</table>

B. BCI Gain Parameters for Each Session

Figure 5.3: Experimental Protocol
A) Experimental timelines for each monkey. An initial training period was followed by four 3-week sessions of experiments during which the subjects controlled the cursor with alternating control schemes in either the Cartesian space (2D) or joint angle space (JA). Effort was made to keep the animal’s weekly work schedule consistent, so the task was not changed from one scheme to the other during the week; only after a weekend break.
B) The gain applied to the cursor, \( G_y \), is shown for each session alongside the normalized gain. This gain was normalized by dividing by the average target distance \( D_{tar} \) in the control space. The bias gain is also listed for each control scheme along with the average movement time during the watch task (i.e., 100% bias; at 50% bias the cursor would move half as fast).
5.2.4 Trajectory Analyses

Neural features as well as cursor and joint kinematics were binned into 52 equal sizes bins for each trial movement. Each movement period was divided into 40 equal time bins spanning from movement onset (bin 7) to target acquisition (bin 46). This period was then preceded and followed by 6 equal length time bins for a total of 52 bins per trial. These extra-movement bins represent 15% of the total movement time on either side.

The performance metrics introduced in Chapter 4 were also calculated for BCI center-out experiments in both Cartesian and joint angle spaces. These metrics included the normalized path length ($d_{\text{path}}$), dot product between the velocity and cursor-target vectors ($dp_{\text{vel-target}}$), peak and hold B speeds, as well as the trial by trial Hold B-to-maximum velocity ratio ($R_{B/\text{max}}$). These metrics were only calculated for correct trials. To transform the Cartesian control data into the joint angle space, the following process was used. As defined previously, the “hand” position of the two-link arm (i.e., $x$ and $z$) is given by:

\[ x = S_x + L_1 \cos \theta_1 + L_2 \cos(\theta_1 + \theta_2) \]  \hspace{1cm} \text{Eq. 5.2}

\[ z = S_z + L_1 \sin \theta_1 + L_2 \sin(\theta_1 + \theta_2) \]  \hspace{1cm} \text{Eq. 5.3}

These are non-linear equations, but given the restraints placed on $\theta$ and having $L_1 = L_2$, (see Table 5.1) there are some geometric shortcuts to solve the inverse equations for $\theta_1$ and $\theta_2$ using triangles. For any $x$ and $z$, both the hand and shoulder positions are known. The distance from the shoulder to the hand uniquely defines the elbow angle, $\theta_2$, as the shoulder-hand-elbow form the vertices of a triangle. First let us define both the length and direction of the vector from the shoulder to the hand:
\[ R = \sqrt{(x - S_x)^2 + (z - S_z)^2}, \quad \tan \theta_R = \frac{z - S_z}{x - S_x} \tag{Eq. 5.4} \]

Given the task parameters \( L_1 = L_2 \), the formed triangle is isosceles, and the interior angle at the elbow, which is equivalent to \( \pi - \theta_2 \), can be obtained via the Law of Cosines:

\[ \pi - \theta_2 = \cos^{-1} \left( 1 - \frac{R^2}{2L^2} \right) \tag{Eq. 5.5} \]

The other interior angles are each equal to \( \theta_2 / 2 \) by nature of the isosceles triangle, and this interior angle at the shoulder is equal to \( \theta_R - \theta_1 \). Thus, for any point \((x, z)\) within the reach region, the closed-form solutions for \( \theta_1 \) and \( \theta_2 \) are given by:

\[ \theta_2 = \pi - \cos^{-1} \left( 1 - \frac{R^2}{2L^2} \right), \quad \theta_1 = \theta_R - \frac{\theta_2}{2} \tag{Eq. 5.6} \]

Equation 5.6 was used to make the plot shown in Figure 5.1B and to transform Cartesian movement data into joint angle data for trajectories and calculation of psychophysical metrics.

### 5.3 Results

#### 5.3.1 Task Performance and Psychophysics

General task performance in the center-out BCI task can be quantified by movement times and percent accuracy. In addition, the number of completed trials and blocks performed act to convey the robustness of the BCI system. Table 5.2 summarizes these statistics over each of the four sessions in the study. Each animal performed well over 60,000 correct BCI “reaches” to the targets without any assistance from the decoding bias signal. Approximately 15 days were spent performing each session of the experiment, with some variance due to either electrical
recording or behavioral malfunctions. Noteworthy items in this summarization table are the trends seen in both the percent correct and the movement times.

As mentioned previously, the control gains, $G_y$, for each session were chosen on the first recording day as the largest gain that did not negatively affect performance in terms of movement times and error rates. In this selection process the psychophysical reach metrics $d_{\text{path}}$ and $d_{\text{vel-tar}}$ were not considered. Given this, the movement times for each animal progressively got faster from one session to the next. Notably, monkey O was given a smaller gain in the third session (2D$_2$), yet performed with equal movement times and better accuracy in terms of the error rate. In addition, the accuracy of each animal also increased over time; although this effect was not large given the animals were already operating at a percentage correct rate of greater than 97.5% to begin with.

Tables 5.3 and 5.4 further breakdown the summary results in terms of the average day and the average block respectively. Monkey G appeared to have a slight preference for the final Cartesian control session (2D$_2$) in terms of completed blocks and percentage correct. Monkey O got progressively better in both blocks per day and percentage correct over the entirety of the experiment. Although monkey G performed better overall in each of these statistical categories, monkey O was sometimes noted to take breaks after long strings of correct trials; sometimes not attending to the task for the duration of 3 to 4 trials timing out. Although each one of these breaks were not tracked and recorded, this attribute likely played a role in why monkey O performed worse than monkey G who continuously appeared to be attending to the task at hand. The final, incomplete, block on each day was not included for analysis as this block contained several incorrect trials as the animals indicated they were done for the day.
### Table 5.2: General Task Performance / Data Collection Summary

<table>
<thead>
<tr>
<th>Session</th>
<th>Days</th>
<th>Blocks</th>
<th>Trials</th>
<th>Percent Correct</th>
<th>Movement Time (msec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>JA1</td>
<td>11</td>
<td>1,006</td>
<td>16,349</td>
<td>98.45%</td>
<td>1,685 ± 898</td>
</tr>
<tr>
<td>2D1</td>
<td>15</td>
<td>1,397</td>
<td>22,692</td>
<td>98.50%</td>
<td>1,529 ± 452</td>
</tr>
<tr>
<td>2D2</td>
<td>16</td>
<td>1,840</td>
<td>29,527</td>
<td>99.71%</td>
<td>1,251 ± 357</td>
</tr>
<tr>
<td>JA2</td>
<td>15</td>
<td>1,649</td>
<td>26,588</td>
<td>99.23%</td>
<td>1,179 ± 372</td>
</tr>
<tr>
<td>2D1</td>
<td>13</td>
<td>983</td>
<td>16,116</td>
<td>97.59%</td>
<td>1,519 ± 590</td>
</tr>
<tr>
<td>JA1</td>
<td>11</td>
<td>912</td>
<td>14,949</td>
<td>97.61%</td>
<td>1,428 ± 542</td>
</tr>
<tr>
<td>2D2</td>
<td>12</td>
<td>1,072</td>
<td>17,337</td>
<td>98.93%</td>
<td>1,433 ± 473</td>
</tr>
<tr>
<td>JA2</td>
<td>13</td>
<td>1,261</td>
<td>20,332</td>
<td>99.23%</td>
<td>1,264 ± 435</td>
</tr>
</tbody>
</table>

### Table 5.3: General Task Performance / Daily Averages ± Standard Deviation

<table>
<thead>
<tr>
<th>Session</th>
<th>Blocks</th>
<th>Trials</th>
<th>Percent Correct</th>
<th>Movement Time (msec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>G</td>
<td>JA1</td>
<td>91.46 ± 37.28</td>
<td>1,486 ± 574</td>
<td>97.54 ± 4.90 %</td>
</tr>
<tr>
<td></td>
<td>2D1</td>
<td>93.13 ± 17.56</td>
<td>1,513 ± 283</td>
<td>98.45 ± 1.71 %</td>
</tr>
<tr>
<td></td>
<td>2D2</td>
<td>115.00 ± 16.73</td>
<td>1,845 ± 269</td>
<td>99.71 ± 0.25 %</td>
</tr>
<tr>
<td></td>
<td>JA2</td>
<td>109.93 ± 11.54</td>
<td>1,773 ± 185</td>
<td>99.23 ± 0.87 %</td>
</tr>
<tr>
<td>O</td>
<td>2D1</td>
<td>75.62 ± 22.27</td>
<td>1,240 ± 318</td>
<td>96.39 ± 9.51 %</td>
</tr>
<tr>
<td></td>
<td>JA1</td>
<td>82.91 ± 17.40</td>
<td>1,359 ± 275</td>
<td>97.58 ± 7.37 %</td>
</tr>
<tr>
<td></td>
<td>2D2</td>
<td>89.33 ± 20.36</td>
<td>1,445 ± 319</td>
<td>98.81 ± 1.44 %</td>
</tr>
<tr>
<td></td>
<td>JA2</td>
<td>97.00 ± 18.41</td>
<td>1,564 ± 296</td>
<td>99.25 ± 1.08 %</td>
</tr>
</tbody>
</table>

### Table 5.4: General Task Performance / Block Averages ± Standard Deviation

<table>
<thead>
<tr>
<th>Session</th>
<th>Trials</th>
<th>Percent Correct</th>
<th>Movement Time (msec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>G</td>
<td>JA1</td>
<td>16.25 ± 2.58</td>
<td>99.21 ± 5.19 %</td>
</tr>
<tr>
<td></td>
<td>2D1</td>
<td>16.24 ± 1.52</td>
<td>98.90 ± 4.64 %</td>
</tr>
<tr>
<td></td>
<td>2D2</td>
<td>16.05 ± 0.35</td>
<td>99.74 ± 1.76 %</td>
</tr>
<tr>
<td></td>
<td>JA2</td>
<td>16.12 ± 1.06</td>
<td>99.40 ± 2.91 %</td>
</tr>
<tr>
<td>O</td>
<td>2D1</td>
<td>16.40 ± 2.74</td>
<td>98.56 ± 6.47 %</td>
</tr>
<tr>
<td></td>
<td>JA1</td>
<td>16.39 ± 2.78</td>
<td>98.50 ± 5.88 %</td>
</tr>
<tr>
<td></td>
<td>2D2</td>
<td>16.17 ± 1.16</td>
<td>99.26 ± 4.57 %</td>
</tr>
<tr>
<td></td>
<td>JA2</td>
<td>16.12 ± 0.75</td>
<td>99.37 ± 3.14 %</td>
</tr>
</tbody>
</table>
Cursor Path Trajectories

The next step in evaluating BCI performance is to look at the path trajectories of the cursor. Figure 5.4 shows the center-out cursor trajectories for each monkey and control scheme. In panels A and B the cursor trajectories during the Cartesian velocity control tasks (2D1 and 2D1) are mostly straight to the target. Panels C and D show the trajectories during joint velocity control sessions (JA1 and JA2) and appear to be more curved in nature. As discussed in section 5.2.1, straight reaches in Cartesian space are necessarily curved in joint space and vice versa. Panels E and F display the cursor trajectories overlaid in order to better dissect these differences in curvature. These results of straight reaches during Cartesian control and curved reaches with joint angle control are consistent with the idea of the monkeys performing straight reaches in the control space, a sign of path optimization.

To visually investigate this possibility of path optimization in the control space, the same cursor path trajectories are plotted in joint angle space in Figure 5.5. Although the skewed nature of the targets in joint space makes visual inspection of path curvature difficult to judge, it appears that the trajectories in joint space during Cartesian control curve in the opposite direction from their corresponding trajectories during joint angle control. This suggests that reaches during joint control were not as optimized for control as they were during Cartesian velocity control tasks. Given that all visual feedback was relayed to the animals in a Cartesian frame of reference, visual error correction would likely be better optimized when controlling the cursor in the same reference frame.
Figure 5.4: Cursor Path Trajectories in Cartesian Space
Panels A-B show extrinsic cursor path trajectories to all 8 targets using the Cartesian velocity control scheme for each monkey. Panels C-D show cursor trajectories for joint velocity control movements, and panels E-F show the trajectories for each control scheme overlaid on top of each other, with the Cartesian velocity movements shown in green, and the joint velocity movements shown in blue. Total trial numbers for each monkey/control scheme combination are indicated by N, and targets are grouped by color. (For plotting purposes, the daily average trajectories are shown)
Figure 5.5: Cursor Path Trajectories in Joint Space
Panels A-B show intrinsic cursor path trajectories to all 8 targets using the Cartesian velocity control scheme for each monkey. Panels C-D show cursor trajectories for joint velocity control movements, and panels E-F show the trajectories for each control scheme overlaid on top of each other, with the Cartesian velocity movements shown in green, and the joint velocity movements shown in blue. Total trial numbers for each monkey/control scheme combination are indicated by N, and targets are grouped by color. (For plotting purposes, the daily average trajectories are shown)
BCI Psychophysics

The psychophysical metrics introduced in Chapter 4 are shown for each session of these experiments in Table 5.5. These statistics summarize the “reaching” characteristics and performance of each monkey during center-out BCI control. The path length and dot product metrics were longer and smaller, respectively, during the joint angle task when compared to the Cartesian task. This finding is consistent with the cursor trajectories in Figures 5.4 and 5.5 showing more deviation from a straight line trajectory.

During joint angle control, reaches were more efficient in joint space than in Cartesian space. The path lengths were shorter and the dot products were greater. This finding demonstrates that some optimization was being performed in the control space. Both animals were given greater control gains in the final joint angle session versus the first and consequently had faster movement times. However, monkey G demonstrated improvements in both path length and dot product metrics, while monkey O got worse in each of these categories. It is possible the control gain was either too great to achieve efficient movements, or the increased speed allowed the monkey to sloppily complete the task within his desired movement time (i.e., perhaps the monkey was happy with 1.2s movements and did not feel the need to do quicker).

Throughout joint angle control, both monkeys had the shortest movement times to the lower right (315°) target and this coincides with the target distance in joint space (this particular target was only 62% of the average target distance). As the targets were equally spaced during Cartesian control sessions, the shortest movement times corresponded to the preferred directions of the mid gamma features as seen previously in Chapter 4.
Table 5.5: BCI Trajectory Metrics in each Reference Frame
Summary of the psychophysical results from correct movements made during each control session. The ratio, $R_{B/\text{max}}$, was calculated from the trial-by-trial ratio of the average speed during the Hold B period to the maximum cursor speed during the movement period. Values are shown as mean $\pm$ 1 standard deviation for each trial block. Metrics calculated in the Cartesian space are printed in red, while metrics calculated in the joint angle space are in blue.

<table>
<thead>
<tr>
<th>Session</th>
<th>$d_{\text{path}}$</th>
<th>$d_{\text{vel-tar}}$</th>
<th>Peak Speed (cm/s), (rad/s)</th>
<th>Hold Speed (cm/s), (rad/s)</th>
<th>$R_{B/\text{max}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>JA1</td>
<td>1.64 ± 0.17</td>
<td>0.57 ± 0.03</td>
<td>9.64 ± 1.64</td>
<td>5.58 ± 1.27</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.49 ± 0.18</td>
<td>0.62 ± 0.04</td>
<td>1.00 ± 0.06</td>
<td>0.55 ± 0.13</td>
</tr>
<tr>
<td></td>
<td>2D1</td>
<td>1.36 ± 0.07</td>
<td>0.66 ± 0.04</td>
<td>8.39 ± 0.42</td>
<td>4.92 ± 0.33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.37 ± 0.07</td>
<td>0.64 ± 0.04</td>
<td>1.08 ± 0.06</td>
<td>0.67 ± 0.06</td>
</tr>
<tr>
<td></td>
<td>2D2</td>
<td>1.31 ± 0.05</td>
<td>0.69 ± 0.03</td>
<td>9.45 ± 0.42</td>
<td>5.59 ± 0.20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.33 ± 0.05</td>
<td>0.66 ± 0.03</td>
<td>1.23 ± 0.06</td>
<td>0.79 ± 0.03</td>
</tr>
<tr>
<td></td>
<td>JA2</td>
<td>1.60 ± 0.08</td>
<td>0.56 ± 0.04</td>
<td>13.30 ± 1.03</td>
<td>7.58 ± 0.78</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.44 ± 0.07</td>
<td>0.62 ± 0.04</td>
<td>1.37 ± 0.10</td>
<td>0.80 ± 0.07</td>
</tr>
<tr>
<td>O</td>
<td>2D1</td>
<td>1.53 ± 0.12</td>
<td>0.59 ± 0.04</td>
<td>10.06 ± 0.73</td>
<td>6.76 ± 0.50</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.62 ± 0.14</td>
<td>0.57 ± 0.04</td>
<td>1.37 ± 0.09</td>
<td>0.99 ± 0.08</td>
</tr>
<tr>
<td></td>
<td>JA1</td>
<td>1.86 ± 0.11</td>
<td>0.50 ± 0.02</td>
<td>13.99 ± 0.69</td>
<td>9.16 ± 0.33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.73 ± 0.10</td>
<td>0.55 ± 0.02</td>
<td>1.44 ± 0.07</td>
<td>0.94 ± 0.03</td>
</tr>
<tr>
<td></td>
<td>2D2</td>
<td>1.36 ± 0.05</td>
<td>0.65 ± 0.04</td>
<td>9.09 ± 0.43</td>
<td>5.96 ± 0.40</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.42 ± 0.06</td>
<td>0.63 ± 0.03</td>
<td>1.17 ± 0.06</td>
<td>0.87 ± 0.07</td>
</tr>
<tr>
<td></td>
<td>JA2</td>
<td>1.94 ± 0.10</td>
<td>0.46 ± 0.03</td>
<td>16.60 ± 1.32</td>
<td>11.11 ± 1.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.79 ± 0.08</td>
<td>0.53 ± 0.02</td>
<td>1.66 ± 0.12</td>
<td>1.11 ± 0.10</td>
</tr>
</tbody>
</table>

Peak cursor speeds were higher on average under joint angle control for both subjects. The translational gain was chosen such that the average reach time under each control scheme was similar rather than the average maximum velocity. Consequently, the average peak speeds (in cm/s) were highly correlated to the normalized control gain for each session ($R^2 = 0.94$ for monkey G and 0.92 for monkey O). Mean speed during the hold period was always correlated to the maximum speed during the movement, remaining steady across control sessions. Each animal appeared to have an innate “slowing rate”, with monkey G slowing to ~58% of the maximum speed while monkey O averaged the target hold period at a more brisk ~66% of the max speed.
Although many of these measures exhibit mean statistical differences between control schemes based on the standard error of the mean (SEM), trial-by-trial comparison yields substantial overlap of parameter distributions based on each metric’s standard deviation. In previous experiments, we found that the animals will slow down considerably when the task is difficult [125], and in the process their trajectories are more direct (to minimize time between rewards). It may be possible that with the gain reduced, we would see straighter reaches in the control space, as this would be the best way to minimize time between rewards.

5.3.2 Movement and Control Signal Profiles

Observing the cursor velocity profiles shown in Figure 5.6, two things become clear; a) velocities are sharper and faster during joint angle control, and b) the timing profiles are more irregular. In the Cartesian task, the 2-dimensional cursor velocity, $v_x$ and $v_z$, is the product of the neural control signal and the control gain. As each of the targets are equally difficult, it makes sense that the temporal profiles of the velocity curves would be similar to each of the eight targets.

It is well established that the end-point (in this case the cursor or “hand”) velocity in natural reaching movements of humans and non-human primates follows a bell-shaped trajectory consistent with a “minimum jerk” control policy [150]. The velocity profiles during Cartesian control approach a bell-shape, but appear to have a more drawn-out plateau of constant maximum velocity from about 40% through the movement until the target is touched (100%). If the short 400 ms hold time was removed, we may not see the animals slow down at all (shown here they didn’t even begin to slow down until the target was touched). Both the plateaued velocity profile and minimal slowing of the cursor help to explain the rather high $R_{B/max}$ ratios shown previously in Table 5.5.
Figure 5.6: Cursor Velocity Profiles
A) Cursor velocity profiles for monkey G, and B) for monkey O, colored by target. For the “2D” tasks, the Cartesian velocity of the cursor was given by $v(t) = \mathbf{G}_x \cdot p(t)$, where $p(t)$ is the control signal defined previously. During the “JA” tasks, the relationship between the Cartesian velocity and the control signal is represented by the Jacobian of the system (see Equation 5.8). As the target distances in joint space are not equal, the velocities during joint angle control sessions peak at different times for different targets. During Cartesian control the velocity peaks in the same manner to each of the targets, and this difference in the velocity profiles between sessions is prominent.
This distinguishable characteristic is not seen in the velocity profiles during the joint angle control tasks; instead, the velocity profiles are both more peaked and more varied in their peak timings. Movements to some targets peak in velocity just as the target is reached, and others follow more traditional bell-shaped profiles and peak half-way through the movement. Although a wide range of peak velocities and peak times are observed during joint angle control tasks, averaged over all targets, the $R_B/\max$ ratio is not meaningfully different than during the Cartesian control task. The differences in the velocity profiles in effect average out over the eight targets.

One trait common to both animals, is that velocities to the downward target (i.e., $270^\circ$, depicted in red) always peak earlier (about 50% through the movement) than velocities to the lower right target (i.e., $315^\circ$, depicted in brown, peaking as the target is reached). This late peak in velocity is likely because this target is the closest in joint space (see Figure 5.1D) and by the time the cursor reaches peak velocity the target has already been attained.

When controlling the cursor velocity in extrinsic space, the speed of the cursor is proportional (via the gain term) to the magnitude of the control signal vector, $y(t)$. However, when controlling the intrinsic joint angle velocity of the two-link arm, the extrinsic speed of the cursor is no longer proportional to the magnitude of the control signal vector, but instead also dependent on the current arm configuration. Thus, differences can arise in the hand velocities between the two tasks even with identical neural control signals. The actual value of the speed and direction in Cartesian space can be approximated by the Jacobian of the space transformation, which changes in magnitude and direction depending on the current position of the arm.
\[ J = \frac{\partial (F_1, F_2, \ldots, F_m)}{\partial (x_1, x_2, \ldots, x_n)} = \begin{bmatrix} \frac{\partial F_1}{\partial x_1} & \ldots & \frac{\partial F_1}{\partial x_n} \\ \vdots & \ddots & \vdots \\ \frac{\partial F_m}{\partial x_1} & \ldots & \frac{\partial F_m}{\partial x_n} \end{bmatrix} \]  
\text{Eq. 5.7}

The Jacobian matrix represents the partial derivative in Cartesian space (e.g. \(x\)- and \(z\)-velocity) with respect to joint space (e.g. joint angular velocity). Starting with equations 5.2 and 5.3 for \(x\) and \(z\) respectively, the Jacobian for this system is given by:

\[
J = \begin{bmatrix} \frac{\partial x}{\partial \theta_1} & \frac{\partial x}{\partial \theta_2} \\ \frac{\partial z}{\partial \theta_1} & \frac{\partial z}{\partial \theta_2} \end{bmatrix} \approx \begin{bmatrix} -\sin \theta_1 - \sin(\theta_1 + \theta_2) & -\sin(\theta_1 + \theta_2) \\ \cos \theta_1 + \cos(\theta_1 + \theta_2) & \cos(\theta_1 + \theta_2) \end{bmatrix} \quad \text{Eq. 5.8}
\]

This matrix approximates the \(x\) and \(z\)-velocity of the cursor in the vicinity of the point \((\theta_1, \theta_2)\):

\[
\vec{v}(t) = J(\theta_1, \theta_2) \vec{v}_\theta(t) \quad \text{Eq. 5.9}
\]

The magnitude of this change in speed is given by the determinant of the Jacobian matrix, which has been graphically recreated in Appendix Figure A.7. This illustrates the determinant is solely a function of the elbow angle, \(\theta_2\), and is maximum at \(90^\circ\) and approaches zero in close proximity to the shoulder (i.e. \(180^\circ\)). Thus, even large angular velocities near the shoulder result in small Cartesian velocities.

Figure 5.7 shows the average control signals projected onto the center-to-target vector for each of the eight targets in both subjects. Positive values indicate a net increase on this vector resulting in movement towards the target, and negative values indicate moving away from the target. For each subject, the average control signals were larger during the Cartesian control task to most targets. Movements to the lower left target, which is nearest the shoulder,
Figure 5.7: Control Signals Projected onto the Center-Target Line
Control signal projections for each target during the second Cartesian velocity control session ($2D_2$, shown in red) and the second joint angle velocity control session ($JA_2$, shown in blue). The velocity in the control space is the neural control signal scaled by the control gain, $G_v$.

A) Control signal projections for monkey G, with normalized gains of $1.71 \text{s}^{-1}$ and $2.15 \text{s}^{-1}$ for Cartesian and joint control respectively. B) Control signal projections for monkey O with normalized gains of $1.40 \text{s}^{-1}$ and $2.21 \text{s}^{-1}$. Daily averages ± 1 standard deviation are shown.
demonstrated increases in the control signals during joint angle control in both subjects. We postulate the animals increased the modulation of the neural control signal to traverse through this “dead-spot” due to the Jacobian. Although this target represents the largest region in joint space (see Figure 5.1B), the other aspects make this target the most difficult to reach. Even though the normalized control gains were higher during joint velocity control (2.15s\(^{-1}\) vs. 1.71s\(^{-1}\) and 2.21s\(^{-1}\) vs. 1.40s\(^{-1}\)), both animals had to modulate the neural control signal stronger for reaches to this target.

**Figure 5.8: Dot Product Temporal Profiles for Cartesian and Joint Angle Control**
The instantaneous normalized dot product between the velocity vector \(v(t)\) and the error direction vector \(u(t)\) is depicted for each monkey/task combination. Dashed lines denote the dot product in joint space (i.e., using \(v_\theta(t)\) and \(u_\theta(t)\)) while solid lines denote the dot product in Cartesian space. The temporal dot products were averaged across all correct trials on each day; the means ± standard deviations of the daily averages are shown.
Dot Product Profiles

As shown in Figure 5.8, the dot product during Cartesian control is greater than the dot product during joint control for each monkey and frame of reference. This measure of the directional agreement of the cursor velocity and the desired direction acts as an efficiency measurement of the movement at each point in time. We hypothesized that the dot product would be maximized in the control space (i.e., straighter reach in the control space). This hypothesis is in agreement with both the average dot product over the movement and the temporal profiles. However, the results shown here also suggest the primary differences in dot products primarily occur during the first 40% of the movement time, after which the movements become more direct.

5.3.3 Decoding Model Stability

The adaptive decoder has played a large role in both the training and the robust performance in our BCI subjects. Transitioning between Cartesian and joint angle velocity schemes requires a change or shift in either the weights or the neural modulation patterns for successful control. Using the co-adaptive operation, the assumption was that both the weights and the subject would adapt towards this goal. The aforementioned BCI performance results speak for themselves in that the subjects were successful in controlling the cursor using both control schemes. However, these results also revealed that movements were considerably less path-efficient during the joint control tasks. The decoding algorithm began each day with the weights initialized to zero, and these weights were updated on a block-by-block basis as outlined in section 3.5.1. As each of the subjects began these experiments in a state naïve to BCI, it was possible that their control strategies could change and the decoder would be able to adapt to these changes.
One of our initial enquiries into decoding model stability was if the percent contribution from each of the individual frequency bands would change between control schemes. As in the previous chapter, we calculated the sum of the weight magnitudes in each frequency band for each completed block. For each session, the mean and standard deviations of these distributions were attained for each frequency band. Figure 5.9 shows these distributions for each subject. As can be seen in the figure, both subjects show consistency in their percent contributions between control sessions. Although very small differences in the mean are observed, there is significant overlap in the overall sample distributions. Of these small differences, monkey G displayed slight preferences towards Cartesian control in the alpha and upper gamma bands, while the beta and lower gamma band was slightly more impactful during joint angle control. For monkey O, the only control task dependent changes were found in the upper gamma bands, with mid gamma contributing more during Cartesian control and high gamma skewed towards joint angle control.
Figure 5.9: Percentage Weight Contributed by each Frequency Band

The percent contributions of the total weight vector remained consistent between sessions. The horizontal line at 20% indicates what would be equal contributions from each of the five frequency bands. Error bars represent 1 standard deviation from the mean, with each distribution consisting of $N_{\text{blocks}}$ samples.
We next turned our attention to the decoding weights from day to day. Figure 5.10 depicts the time course of decoding model weights for monkeys G and O. From this figure, clear differences can be seen when transitioning between Control schemes, as the weights change from \((x, z)\) to \((\theta_1, \theta_2)\). However, the weights within a given control scheme are highly consistent from day to day. The average weight during a control session appears to be a good estimate for each other day within that scheme.

These average weights were plotted as vectors in the control space to visualize the changes between control sessions in Appendix Figure A.8. Inspection of these polar plots revealed what looked to be a global rotation of the weights between control scheme changes. To investigate this possibility further, we calculated the Pearson correlation coefficient between the daily weight matrices depicted in Figure 5.10 to measure their directional agreement across days.

Correlations of the weight matrices from day to day are illustrated in Figure 5.11. Panels A and B show the correlation coefficients between days using the average weights, while panels C and D show the correlations of the weights when the joint space weights are rotated by an angle \(\theta\). It is easily seen that the correlations for monkey O are much lower than those for monkey G both before and after this rotation is performed. In both cases, the rotation brings the day to day correlation values in line with those seen between days on the same task. These rotations yielding the maximum correlations were 92° and 121° for monkeys G and O respectively. Given that the mean difference in target angles between the reference frames was approximately 104° (see Figure 5.1D), these rotations are not very surprising. For example, if the neural signals were unchanged, but the regression response vectors were changed to that of the targets in joint space, we would expect a rotation of 104° for straight reaches. Since the reaches were not extremely straight, some variation would be expected.
Figure 5.10: Daily Decoding Weights over Time
The average decoding weights for each day are plotted. The y-axis denotes the feature number, and the x-axis is each recording day. The switch from one control scheme to the other can clearly be seen in the weights, as they are consistent from day to day within the control scheme session. As the control scheme changes from Cartesian to joint angle, the weights change from $(x, z)$ to $(\theta_1, \theta_2)$ by construction.
Additionally, this correlation analysis shows that the weights from early sessions are highly correlated to later sessions. Reproducibility of control weights given the decoder started every day without prior knowledge of previous decoding weights is a testament to each monkey’s consistent strategy. This is an important finding, in that the adaptive decoder may only need to be used to train the subject initially, and then could be turned off indefinitely, as evident by the correlations between the first and last control sessions for a given task. An end-user of such a BCI system would not want to be hampered by the need to train a decoder continuously.
Figure 5.11: Correlation of Decoding Weights
Panels A and B depict the Pearson correlation coefficient of the linearized weight vector on each day which was correlated to the weight vectors from every other day. Panels C and D illustrate the same method of correlation, but all weight matrices decoded during the joint angle task were rotated by an angle $\theta$ before linearization and correlation. The angle $\theta$ was chosen such that the average correlation coefficient over all days was maximized. Weights for monkey G were rotated counter-clockwise by 92°, and the weights for monkey O were rotated by 121°.
5.3.4 Changes in Neural Signal Modulation

Chapter 4 demonstrated the existence of strong cosine tuning in the cortical field potentials recorded from the surface of the brain. The preferred directions were organized in what appears consistent with the motor homunculus (even in animals limited to sensory electrodes). We hope to address how this tuning changes, if at all, during the change to joint angle-based control. These results are a first step in testing the feasibility of an intrinsic-based BCI control paradigm.

Because the decoding scheme for monkeys G and O adapted on a daily basis from the beginning of their experiments, it is difficult to firmly decipher who/what was adapting to whom. Although it is possible for the neural modulations not to change between control schemes (the only alteration could be that of the weights), it is unlikely that small error corrections could be made without accounting for the new control scheme (i.e., the Jacobean). It was clear that the BCI movements were not all straight toward the target as evident by the path length and dot product metrics in Table 5.5, and that both of these were worse during joint controlled movements. Given that constant error corrections were being made, we would expect some changes manifest in the neural signals themselves. Figure 5.12 shows the cosine tuning $R^2$'s for each frequency band over the four control sessions. For both monkeys, the tuning strength was reduced in joint angle control sessions.

The increased error corrections during the joint angle task are the likely reason for the decrease in cosine tuning strength in the majority of features. As the movements deviate more and more from straight paths, regressing on the target direction gets further from the actual movements performed.
A. Monkey G

B. Monkey O

Figure 5.12: Cosine Tuning $R^2$ by Frequency Band
The average regression $R^2$ for each band over the four sessions. The horizontal line at 0.3695 indicates significance at the $p = 0.05$. 
We found that tuning $R^2$’s were related to both the path length and dot product metrics, with greater deviations from straight paths correlating to lower $R^2$ values in each subject.

Monkey O demonstrated poor cosine tuning in the lower three frequency bands, yet a sizable portion of the weights were assigned to these bands for control. The “optimal linear estimator” nature of the decoder likely made use of these features on a block-by-block basis as they were most dissimilar from the gamma bands. Due to the noise in the tuning of these bands, different beta features were likely weighted heavily from block to block and the daily weight correlations were strongly affected.

The tuning relationships discussed in Chapter 4 between the regression $R^2$, depth of modulation, and the mean vector length (MVL) remained consistent during each control session. As such, the $R^2$ of the cosine tuning regression can be viewed as a group representation of all three. Although directional tuning changes were also small, they did exist for several features between control schemes. Appendix Figure A.9 graphically depicts these small directional rotations between sessions.

*Exemplar Feature*

Figure 5.13 examines a highly-tuned feature from monkey G in which the preferred direction remained constant throughout the first three sessions and then clearly shifted between the final Cartesian and joint angle sessions. Looking at the temporal modulations to the eight targets in panel A, it is seen that the modulation patterns to each of the targets has shifted. Panel C displays the histograms of the preferred directions captured from each individual block regression (smoothed with a unit Gaussian with 2° standard deviation). This session-wide shift of ~31° was very consistent. This shift in preferred direction was transferred to the decoding weights as well as shown in panel D. The difference in weight directions was initially 104°,
Figure 5.13: Exemplar Feature from Monkey G
A) Neural modulation z-scores to all eight targets for a high-gamma (130-175 Hz) feature from monkey G over all four control sessions. The non-directional activations have been subtracted such that the overall mean from the eight targets is zero. B) Location of the electrode from which this feature resides; feature #34 on Channel 6. C) Histograms of cosine tuning preferred directions of this feature for each session. D) Histograms of the preferred directions of the decoding weights.
mirroring the target angle differences between the spaces. After the 31° change in tuning preferred directions, the new assigned weights were only 76° rotated from their Cartesian control equivalents.

The average feature modulations across targets (i.e., the non-directional activations) were subtracted in order to better observe the directional tuning properties. Although not shown here, the temporal dynamics of the features themselves resemble step functions. Both the constant speed bias used during the watch task and regressing on unit direction vectors may contribute to this phenomenon, as that is essentially how the subjects were trained to complete the task. It should be noted that the step-like nature is two-fold: First, each feature “turns on” during movement, regardless of target direction. Then, when the target has been “desired” the cosine tuned activity is revealed, as seen easily in the mean-subtracted neural features.

5.4 Discussion

These studies have demonstrated that naïve monkeys can quickly learn to control a cursor using kinematic control variables in either a Cartesian or joint angle-based reference frame. This result represents a first step towards the design of an intrinsic, limb-centered BCI system. As noted before, joint angle control is not truly intrinsic control, but this experimental setup would be akin to monkeys producing the appropriate joint torques in a highly viscous environment to complete the task.

We have analyzed basic parameters of dexterous control, such as movement times, path efficiency, accuracy (percent correct) and cursor speed. We have also looked at differences in cosine tuning between control paradigms as well as decode weight differences. It seems clear that in the completion of the center-out task in either Cartesian or joint angle coordinates, the similarities outweigh the differences. Small differences could be detected in the neural signal
modulations, yet not the large differences that we would expected in the case of a visuomotor
transformation due to a) the adaptive decoder and b) the similarity between the reference frames.

The two naïve subjects were initially trained in opposite tasks in order to see if the starting
task would bias the learning of the second task. However, monkey G made no discernible
changes when transitioning from joint angle control to Cartesian control, yet improved
significantly. This behavioral improvement was similar to that demonstrated by monkey O when
going from joint angle to Cartesian; however, his improvements were accompanied by tuning
changes. This might suggest that monkey G was using a Cartesian control strategy during the
initial joint angle task. Upon monkey G’s final transition from Cartesian to joint angle, a large
shift in the neural signatures was seen.

The differences in the two subjects with respect to frequency bands with the most weight
contributions are an interesting observation (see Figure 5.9). While monkey G had a strong bias
toward the mid gamma frequency band for control, monkey O had a split-bias between the beta
and mid-gamma bands. This was in contrast to the trial averaged cosine tuning results,
illustrating very weak cosine tuning in the lower three frequency bands (Figure 5.12). One
possible explanation could be due to the noise in the recorded ECoG signals. ECoG signals from
monkey O were recorded from much smaller electrodes resulting in a higher noise floor. Since
the higher frequency signals have much lower power, they are more easily affected by noise, and
leading the monkey chose to use a lower frequency band that was more reliable. This could have
resulted in the divided preference towards both mid gamma and beta band features in the
decoding weights. However, a more in-depth analysis of the noise in the signals would be
required to test this hypothesis.
While the experiments performed in this Chapter aimed to discern if BCI subjects could adapt from one control scheme to another, the simplistic way in which control was regained in the joint space implies the animals had to do very little in the way of adapting to a new scheme. Instead, the animals could use a gross rotation (supplied by the decoding weights) and make minimal adjustments on the fly; for the most part preserving the directional tuning of individual features from Cartesian control tasks. In both monkeys, a rotation of the joint space weights brought the day-to-day weight matrix correlation values from cross-control comparisons into agreement with those made during the same control scheme.

Knowing just how consistent the weights were, it would be interesting in a future study to lock the weights to what they were during the Cartesian control task, and then re-apply them in joint space for the joint angle task. As the weights would be locked, the adaptive algorithm would not be able to account for the “rotation” and the monkey would instead have to modulate the features in a new manner in order to complete the task. Previous studies in our lab have shown animals’ ability to adapt to locked weight decoding schemes over long periods of time. Adaptation could occur by global rotation, or the monkey could choose another strategy. The primary benefit of using the co-adaptive decoder is the ease and speed at which naïve subjects can learn BCI control. In the future, this may be a viable training structure to induce learned cosine tuning, which can then be massaged or shaped to the will of the experimenter through biofeedback and neural plasticity.

Although the results demonstrated here do show the animals controlling a two-link arm in joint space with considerable dexterity, it is not clear that this ability would transfer to a different type of task. In the center-out task, the rotation does an adequate job at estimating the optimal control pattern. A more difficult assignment such as a circle drawing task would require the
animals to de-correlate velocities in the $x$ and $z$ directions. This would not correspond to a perfect anti-correlation in joint space, but if the animal was able to perform both the center-out and circle-drawing tasks with the same decoding weights we could more confidently state the animal was controlling the actual two-link arm rather than the end-point in Cartesian coordinates.
6 Cortical Control of Simulated Muscles for an Intrinsic, Dynamics-based BCI

6.1 Introduction

The results from the previous chapter provided an initial assessment of the feasibility of a kinematic BCI system based in an intrinsic frame of reference. Although these kinematic control signals are satisfactory for control of simulated objects, they may not be ideal for the control of real-world prosthetic devices that are subject to external and unexpected forces.

State of the art implementations of these devices employ complex controllers to estimate the current and future states of the mechanical system. These controllers have been used to translate kinematic control signals into either robotic joint torques (for robotic limb control) or muscle stimulation patterns (for FNS paradigms). These controllers are designed on case by case bases as they need to contain accurate internal models of the controlled limb dynamics.

If subjected to a BCI system in which the physical model is unknown or incomplete, then using an inverse dynamics model to calculate joint torques or muscle stimulations from the user’s kinematic control signal can result in very large errors and unproductive movements. In order to eliminate these large errors, it might be more effective to map brain activity to muscle stimulation directly and allow the brain to develop its own transfer function between muscle stimulation and limb movement. Given this, we sought to expand on the results of the previous chapter by applying ECoG signals as a muscle force-based control signal in a virtual environment with simple, real-world physics.
6.2 Methods

6.2.1 Applied Models for Arm Dynamics and Muscle Forces

The inverse dynamics for a planar arm with two joints (shoulder and elbow) moving in the horizontal plane without gravity (the “table-top model” as illustrated previously in Figure 5.1 and with the musculoskeletal model in Figure 6.1) is given by Equation 6.1 below:

\[ \mathbf{M}(\theta)\ddot{\theta} = \tau - \mathbf{C}(\theta, \dot{\theta})\dot{\theta} - \mathbf{B}\dot{\theta}, \quad \text{Eq. 6.1} \]

\[ \theta = \begin{bmatrix} \theta_1 \\ \theta_2 \end{bmatrix}, \quad \tau = \begin{bmatrix} \tau_1 \\ \tau_2 \end{bmatrix}, \quad \text{Eq. 6.2} \]

where \( \theta \in \mathbb{R}^2 \) is the joint angle vector (shoulder: \( \theta_1 \), elbow: \( \theta_2 \)), \( \mathbf{M}(\theta) \in \mathbb{R}^{2 \times 2} \) is a positive definite symmetric inertia matrix, \( \mathbf{C}(\theta, \dot{\theta}) \in \mathbb{R}^{2 \times 2} \) is a matrix of centripetal and Coriolis forces, \( \mathbf{B} \in \mathbb{R}^{2 \times 2} \) is a joint friction matrix, and \( \tau \in \mathbb{R}^2 \) is the applied joint torque. \( \dot{\theta} \) and \( \ddot{\theta} \) refer to the first and second derivative of \( \theta \) with respect to time (\( d\theta/dt \) and \( d^2\theta/dt^2 \), i.e. joint angular velocity and acceleration). Here we consider direct torque control where \( \tau \) is the control signal.

![Musculoskeletal Model](image_url)

**Figure 6.1: Musculoskeletal Model**

Using a 2-DOF planar arm, the six muscles are attached in such a way that four of them induce torques about single joints (two at the shoulder and two at the elbow) and the remaining two actuate both joints simultaneously (Figure adapted from Katayama et al. [151] and Fagg et al. [152]).
We model the arm segments as rigid rods which rotate about the connected end (the upper-arm to the shoulder and the forearm to the elbow). Thus, the moments of inertia for each segment are given by:

\[ I_1 = \frac{M_1 L_1^2}{3}, \quad I_2 = \frac{M_2 L_2^2}{3}, \quad \text{Eq. 6.3} \]

where \( M_1 \) and \( M_2 \) are the masses of the upper-arm and forearm and \( L_1 \) and \( L_2 \) are their respective lengths. The corresponding expressions for the remaining terms in Equation 6.1 are given by:

\[
\mathbf{M} = \begin{bmatrix}
I_1 + I_2 + \frac{M_2 L_1^2}{3} + 2M_2 L_1 L_{g2} \cos \theta_2 & \frac{I_2 + M_2 L_1 L_{g2} \cos \theta_2}{2}
\end{bmatrix}, \quad \text{Eq. 6.4}
\]

\[
\mathbf{C} = M_2 L_1 L_{g2} \sin \theta_2 \begin{bmatrix}
-2\dot{\theta}_1 \\
-\dot{\theta}_2
\end{bmatrix}, \quad \mathbf{B} = \begin{bmatrix}
b_{11} & b_{12} \\
b_{21} & b_{22}
\end{bmatrix}, \quad \text{Eq. 6.5}
\]

where \( L_{g2} \) is the center of mass for the forearm. The joint friction term \( \mathbf{B} \) was simplified such that the friction terms at each joint were equal \((b_{11} = b_{22})\) and the interaction terms between the joints \((b_{12} \text{ and } b_{21})\) were absent. This reduces the joint friction matrix to a scalar value, which we refer to as the joint viscosity, \( b \), in units of N·m/(rad/s). The values used for the masses and lengths of the segments as well as the joint viscosity are summarized in Table 6.1.

Table 6.1: Dynamic Model Parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper arm / Forearm mass</td>
<td>( M_1, M_2 )</td>
<td>0.4 kg</td>
</tr>
<tr>
<td>Upper arm / Forearm length</td>
<td>( L_1, L_2 )</td>
<td>10 cm</td>
</tr>
<tr>
<td>Forearm center of mass</td>
<td>( L_{g2} )</td>
<td>5 cm</td>
</tr>
<tr>
<td>Joint viscosity at ( \theta_1 ) and ( \theta_2 )</td>
<td>( b )</td>
<td>3.33 N·mm/(rad/s)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Constant Moment Arms</th>
<th>a1</th>
<th>15 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>monoarticular shoulder</td>
<td>a2</td>
<td>5 mm</td>
</tr>
<tr>
<td>biarticular shoulder</td>
<td>a3</td>
<td>8 mm</td>
</tr>
<tr>
<td>biarticular elbow</td>
<td>a4</td>
<td>10 mm</td>
</tr>
</tbody>
</table>
Arm stiffness and viscosity are caused by the combined effects from muscle intrinsic properties and low-level neural reflexes. Bennett et al. measured the elbow joint viscosity during a single-joint cyclic movement with amplitude of 1 rad and a period of 750 ms [153]. In this experiment, small pseudorandom force disturbances were applied to the wrist with an airjet actuator. The measured viscosity values ranged from 0 to 0.7 N·m/(rad/s) during movements.

**Muscle Model**

We have chosen to implement a 6-muscle model featuring flexor and extensor muscles at each joint (monoarticular) as well as across the joints (biarticular). These 6 muscles are illustrated in Figure 6.1, and represented as \( m_1 \) (shoulder flexor), \( m_2 \) (shoulder extensor), \( m_3 \) (elbow flexor), \( m_4 \) (elbow extensor), \( m_5 \) (biarticular flexor), and \( m_6 \) (biarticular extensor). The torque applied by these muscles is equivalent to the muscle tension vector times a matrix describing the moment arms.

Amis et al. examined the moment arm for each muscle around the elbow joint and found a nonlinear relationship between the moment arm and the joint angle [154]. For our study, we have used a simple muscle model in which the moment arms are constant with respect to joint angle and there are no force-length and force-velocity properties in the muscles. Likewise, each muscle had the same strength (physiological cross-sectional area). Complex muscle models also implement activation dynamics which generally act to introduce a time lag to the system. For our initial experiments of controlling this type of system we chose to start off with a simpler form. As such, the torque at each joint is given by Equation 6.6:
\[ \tau = A^T T, \quad A = \begin{bmatrix} a_1 & 0 \\ -a_1 & 0 \\ 0 & a_2 \\ 0 & -a_2 \\ a_3 & a_4 \\ -a_3 & -a_4 \end{bmatrix}, \quad T = \begin{bmatrix} m_1 \\ m_2 \\ m_3 \\ m_4 \\ m_5 \\ m_6 \end{bmatrix}, \quad \text{Eq. 6.6} \]

where \( A \in \mathbb{R}^{6 \times 2} \) is the matrix of constant moment arms for each muscle unit, and \( T \in \mathbb{R}^6 \) is the tensile force exerted by the contraction of each muscle \((m_1, m_2, ..., m_6)\). Superscript \( "^T" \) denotes the matrix transpose.

6.2.2 Dynamic BCI Task Implementation

Our lab’s previous attempts to utilize dynamics-based control were limited to reassigning the decoding weights used for velocity control, and applying them as an acceleration or force signal on the cursor itself. This methodology inherently requires a set of decoding weights in order to begin the dynamics-based task. Using our co-adaptive algorithm, we sought to improve upon this technique by building the decoding model over the course of a few minutes while continuing to update and improve it as time passed.

For the point mass (cursor) we used previously, accelerating and decelerating forces had to be applied to start and stop the cursor respectively. Akin to applying the gas or brake pedals in an automobile, the time at which these applications are made can widely vary between users. Some will apply the brakes late, others early. Building a decoder requires some assumption of the user’s intent. In the previous chapters, this assumption has been that the user wished to move the cursor in the direction pointing directly to the target.

In the described dynamic model of the arm, the viscous term, \( b \), acts to dampen the applied torques. Because of this, the torque required to make the hand move towards the target is largely in the same direction as the error vector, \( u(t) \), for a large range of movement speeds.
(see Appendix Figure A.12). Rather than try to infer when the animals wanted to accelerate or decelerate, we chose to use a unit torque vector pointing towards the target as our reference for regression. Thus, for joint torque control, the control signal $y(t)$ was constructed in the same manner as during joint velocity control (defined in Equation 3.8).

For muscle force control, we chose to again utilize the unit torque directional decoding model. As previously defined in Equation 6.6, the applied torque at each joint, $\tau$, is equivalent to the transpose of the moment arms matrix $A$ times the muscle tension vector $T$. As the number of muscles (6) is greater than the physical DOF (2), there are an infinite number of muscle tension vectors that satisfy the relationship, which is a redundant problem in biomechanics. While the least squares solution can be solved using the pseudoinverse technique, this unique solution typically requires some muscles to push (exhibit a negative tensile force). Using a minimum muscle stress criterion (or force since the modeled muscles have the same physiological cross-sectional areas), Yamaguchi, Moran, and Si proposed an iterative pseudoinverse regression process [155]. First, the elements in $T$ are searched to find those which had values less than a negligible negative value $\varepsilon$ ($e.g. \varepsilon = -0.01$). The muscle $j$ having the largest negative stress is identified, and its corresponding column ($i.e.$ column $j$) in $A^T$ is then divided by a large positive number $Z$ ($e.g. Z = 1000$) in order to essentially eliminate that muscle from consideration without reducing the rank of $A^T$. The pseudoinverse algorithm is then repeated and rechecked until all the negative stresses in $T$ are serially eliminated.
To determine the decode weights, the 2-dimensional unit error vector $u(t)$ is replaced with the optimal 6-dimensional muscle tension vector from Equation 3.9 as follows:

$$U_{\text{muscle}} = \left[ T(t_0), T(t_1), \ldots, T(t_f), \ldots, T(t_0), T(t_1), \ldots, T(t_f) \right] \quad \text{Eq. 6.7}$$

$$X = \left[ \ddot{x}(t_0), \ddot{x}(t_1), \ldots, \ddot{x}(t_f), \ldots, \ddot{x}(t_0), \ddot{x}(t_1), \ldots, \ddot{x}(t_f) \right] \quad \text{Eq. 6.8}$$

Where the feature z-scores from the trial block, $X \in \mathbb{R}^{N_{\text{features}} \times N_{\text{samples}}}$, and the desired muscle forces, $U_{\text{muscle}} \in \mathbb{R}^{N_{\text{dimensions}} \times N_{\text{samples}}}$. The resulting decode weights are thus:

$$W_{\text{regressed}} = U_{\text{muscle}}X^+ \quad \text{Eq. 6.9}$$

And the control signals used to drive movements are attributed to the applied joint torque:

$$\tau(t) = G_yy(t) = G_yW^T\ddot{x}(t) = A^T f \left( G_yW^T\ddot{x}(t) \right) \quad \text{Eq. 6.10}$$

Where $f(x)$ is a threshold-linear function used to ensure all muscle forces are positive:

$$f(x) = \begin{cases} 0, & x < 0 \\ x, & x \geq 0 \end{cases} \quad \text{Eq. 6.11}$$

The last term is the instantaneous tension forces, $T$, produced by each muscle (in Newtons).

When multiplied by the matrix of moment arms in meters yields units of N·m. The control gain term, $G_y$, is mathematically equivalent between joint torque control and muscle force control aside from the units, as the scalar term can be applied outside the matrix multiplication and threshold-linear function.

Although the construction of the control signals remains similar to the kinematic decoding tasks, the application of the control signal is now very different. First, using the current state of the system ($\theta$ and $\dot{\theta}$), we compute the acceleration resulting from the applied
joint torque, \( \tau \). As the mass matrix is positive definite symmetric, it is invertible, and the resulting angular acceleration can easily be solved by multiplying both sides of Equation 6.1 by this inverse:

\[
\ddot{\theta} = \mathcal{M}^{-1}(\tau - \mathcal{C}\dot{\theta} - \mathcal{B}\dot{\theta}) \tag{Eq. 6.12}
\]

The joint velocity is determined via Euler integration of the joint acceleration as follows:

\[
\dot{\theta}_{\text{new}} = \dot{\theta}_{\text{old}} + \ddot{\theta}\Delta t \tag{Eq. 6.13}
\]

This velocity is then integrated to position in the same manner; as done in each of the previous experiments.

### 6.2.3 Subjects and Experimental Protocol

At the end of the experiments in Chapter 5, Monkey I began training on the same joint angle velocity task that monkeys G and O had just performed. Monkey I had years of previous BCI experience in 2-4 dimensional control, and easily transitioned to the joint angle velocity task introduced in Chapter 5. All three animals were trained for a long period of time on the joint angle velocity task. During this period, several BCI parameters were adjusted such as the weights smoothing factor and the required hold time. Three to five weeks prior to attempting dynamic control tasks, all BCI parameters were returned to the original values for a more direct comparison of control.

The task structure of 16 blocks per trial remained unchanged from the previous experiments. As far as BCI parameters were concerned, the weight smoothing factor, \( a \), was set to 0.2 for all experimental sessions. The maximum allowed movement time was 8 seconds and the hold time remained at 400 ms throughout the experiments. The base bias gain was set to 0.52 rad/s and acted as a bias velocity in all control tasks. Thus, the watch task (first block of each
day) resulted in movements being approximately 1200 ms for each monkey/control combination. For this study, a contiguous sampling of joint angle velocity task data was collected from each animal before transitioning to the dynamics-based tasks. Monkeys G and I then ran for an extended period of six weeks on the joint torque task, while Monkey O was put on the fast track to the muscle force task.

To begin training on dynamic control, the viscosity term, $b$, was set very high such that the control signal mapped to joint torque was mostly converted to velocity. To maintain similar velocities to the previous task, the gain was also greatly increased. In this way, the task was very similar to the velocity control task. Over a period of 5-10 training days the viscosity and gain were slowly reduced to the lowest amount the monkeys could perform without becoming too frustrated with the newfound difficulty of the task. This viscosity was $b = 3.33 \text{ N}\cdot\text{mm}/(\text{rad/s})$ (a value of 2.00 N\cdot mm/(rad/s) was found to be too difficult).

At this point, although the monkeys could control the arm with a viscosity of 3.33, they still needed to be “eased” into it. Each day during the first five blocks in which the computer assistance went from 100% to 0%, the viscosity was set at 26.67 N\cdot mm/(rad/s) (8 times the base value of 3.33). The control gain was set appropriately high to allow the animals to move at reasonable speeds. Thus, during the watch task and bias trials, the task more closely resembled velocity control. After the bias was turned off, both the gain and viscosity were decreased after each block until the viscosity was down to 3.33 and the gain was the value shown in Table 6.2.

In the same way, the bias signal acts as “training wheels”, the high gain and viscosity terms acted to minimize the dynamic aspects of the task. While these were being reduced, the decoding model was generating weights similar to those used during velocity control.
6.3 Results

6.3.1 General Task Performance

General task performance in the center-out BCI task can be quantified by movement times and percent accuracy. In addition, the number of total trials and blocks completed act to convey the robustness of the BCI system. Table 6.3 summarizes these statistics over each of the three sessions in the study. Each animal performed over 60,000 correct BCI “reaches” to the targets without any assistance from the decoding bias signal. Each animal completed a minimum of 26 days on the dynamic control tasks, with monkey O spending only 7 days on joint torque control and monkey I completing only 10 days on muscle force control. Noteworthy items in this summarization table are the trends seen in blocks completed per day, percent correct, and movement times.

Monkey G was the only animal to perform more trials per day under muscle force control than joint torque control, while all subjects completed the highest number of trials per day under joint velocity control (see Table 6.4). All three animals performed with the greatest accuracy in the joint velocity task, and saw a considerable decrease in the transition to dynamic control.

<table>
<thead>
<tr>
<th>Control</th>
<th>Gain, G_y</th>
</tr>
</thead>
<tbody>
<tr>
<td>Joint Velocity</td>
<td>2.2 rad/s</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>7.3 N·mm</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>6.7 mN</td>
</tr>
<tr>
<td>Joint Velocity</td>
<td>1.8 rad/s</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>6.7 N·mm</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>8.0 mN</td>
</tr>
<tr>
<td>Joint Velocity</td>
<td>2.2 rad/s</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>6.0 N·mm</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>7.3 mN</td>
</tr>
</tbody>
</table>
Both monkeys G and O demonstrated an uptick in accuracy when transitioning to the muscle force task from the joint torque task, while monkey I showed a decrease in performance. Notably, monkey I suffered severe signal degradation in six channels from the left hemisphere just prior to muscle force control due to an electrical failure. These six channels were not used for control during this session.

Movement errors were clustered in time, as monkeys were observed to take breaks when they were momentarily satiated, bored, or fatigued. Although we did not label individual errors (errors were simply the trial timing out after 8 s), very rarely was an unsuccessful attempt made towards reaching the target. As a preliminary metric for determining if the monkey was motivated or not, we looked at the number of blocks with at least one error. This is a gross underestimate of motivation, as there were likely blocks in which the animals made one tiny mistake in an otherwise perfect block. The occurrences of these blocks with 1 or more error are listed in Table 6.5 as “Error Blocks”. Calling these 1-trial-or-more error blocks “lapses in motivation”, we found that the lowest motivation rate was still greater than 86% across all sessions. The worst monkey/control combination (monkey I, muscle force control) still completed 86.6% of the blocks with perfect 16/16 accuracy. Thus, the true accuracy rate, including only trials in which the monkey was motivated to complete the trial, is likely greater than the block average estimates shown in Table 6.5. These block estimates list the percent correct for monkey I during muscle force control to be approximately 94.7%, much greater than the overall percent correct of 89.5% including all trials.
Table 6.3: General Task Performance / Data Collection Summary

<table>
<thead>
<tr>
<th>Control</th>
<th>Days</th>
<th>Blocks</th>
<th>Trials</th>
<th>Percent Correct</th>
<th>Movement Time (msec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>G</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Joint Velocity</td>
<td>28</td>
<td>2,880</td>
<td>47,462</td>
<td>97.09 %</td>
<td>1,131 ± 306</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>29</td>
<td>1,760</td>
<td>30,232</td>
<td>93.15 %</td>
<td>2,122 ± 703</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>17</td>
<td>1,214</td>
<td>20,715</td>
<td>93.77 %</td>
<td>2,131 ± 498</td>
</tr>
<tr>
<td>O</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Joint Velocity</td>
<td>33</td>
<td>2,995</td>
<td>48,496</td>
<td>98.11 %</td>
<td>1,498 ± 566</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>7</td>
<td>408</td>
<td>6,764</td>
<td>95.51 %</td>
<td>2,091 ± 721</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>19</td>
<td>1,016</td>
<td>16,619</td>
<td>97.82 %</td>
<td>2,120 ± 709</td>
</tr>
<tr>
<td>I</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Joint Velocity</td>
<td>19</td>
<td>1,641</td>
<td>26,784</td>
<td>98.03 %</td>
<td>1,005 ± 375</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>23</td>
<td>1,518</td>
<td>25,448</td>
<td>95.44 %</td>
<td>1,870 ± 562</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>10</td>
<td>450</td>
<td>8,044</td>
<td>97.82 %</td>
<td>2,126 ± 610</td>
</tr>
</tbody>
</table>

Table 6.4: General Task Performance / Daily Averages ± Standard Deviation

<table>
<thead>
<tr>
<th>Control</th>
<th>Blocks</th>
<th>Trials</th>
<th>Percent Correct</th>
<th>Movement Time (msec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>G</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Joint Velocity</td>
<td>102.86 ± 14.59</td>
<td>1,695 ± 231</td>
<td>97.07 ± 2.98 %</td>
<td>1,127 ± 73</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>60.69 ± 11.85</td>
<td>1,043 ± 191</td>
<td>92.82 ± 3.45 %</td>
<td>2,114 ± 208</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>71.41 ± 8.48</td>
<td>1,219 ± 128</td>
<td>93.72 ± 3.81 %</td>
<td>2,134 ± 121</td>
</tr>
<tr>
<td>O</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Joint Velocity</td>
<td>90.76 ± 13.04</td>
<td>1,470 ± 196</td>
<td>98.69 ± 3.01 %</td>
<td>1,502 ± 134</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>58.29 ± 10.52</td>
<td>966 ± 152</td>
<td>96.17 ± 3.44 %</td>
<td>2,081 ± 109</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>53.47 ± 8.17</td>
<td>875 ± 113</td>
<td>97.46 ± 4.80 %</td>
<td>2,126 ± 96</td>
</tr>
<tr>
<td>I</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Joint Velocity</td>
<td>86.37 ± 19.68</td>
<td>1,410 ± 323</td>
<td>97.80 ± 2.32 %</td>
<td>1,003 ± 139</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>66.00 ± 17.14</td>
<td>1,106 ± 254</td>
<td>94.80 ± 5.67 %</td>
<td>1,872 ± 152</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>45.00 ± 16.56</td>
<td>804 ± 281</td>
<td>89.03 ± 7.96 %</td>
<td>1,688 ± 63</td>
</tr>
</tbody>
</table>

Table 6.5: General Task Performance / Block Averages ± Standard Deviation

<table>
<thead>
<tr>
<th>Control</th>
<th>Trials</th>
<th>Percent Correct</th>
<th>Error Blocks</th>
<th>Movement Time (msec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>G</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Joint Velocity</td>
<td>16.48 ± 3.10</td>
<td>98.27 ± 7.16 %</td>
<td>5.76 %</td>
<td>1,131 ± 142</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>17.18 ± 5.63</td>
<td>96.37 ± 10.75 %</td>
<td>10.57 %</td>
<td>2,122 ± 308</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>17.06 ± 7.73</td>
<td>97.86 ± 10.48 %</td>
<td>4.86 %</td>
<td>2,131 ± 210</td>
</tr>
<tr>
<td>O</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Joint Velocity</td>
<td>16.19 ± 2.29</td>
<td>99.39 ± 4.69 %</td>
<td>1.67 %</td>
<td>1,498 ± 254</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>16.58 ± 2.48</td>
<td>97.66 ± 7.99 %</td>
<td>5.88 %</td>
<td>2,091 ± 296</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>16.36 ± 2.36</td>
<td>98.57 ± 5.80 %</td>
<td>4.43 %</td>
<td>2,120 ± 318</td>
</tr>
<tr>
<td>I</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Joint Velocity</td>
<td>16.32 ± 1.85</td>
<td>98.69 ± 6.12 %</td>
<td>4.39 %</td>
<td>1,005 ± 217</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>16.76 ± 4.34</td>
<td>97.53 ± 9.14 %</td>
<td>7.18 %</td>
<td>1,870 ± 244</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>17.88 ± 6.61</td>
<td>94.68 ± 14.76 %</td>
<td>13.33 %</td>
<td>1,683 ± 272</td>
</tr>
</tbody>
</table>
Monkey I demonstrated the quickest movement times across each control paradigm, just as in the Cartesian velocity control task in Chapter 4. All animals were considerably slower to complete trials during dynamic control tasks compared to the kinematic task. The increased movement times likely played some role in these lapses in motivation. Whereas monkeys G and O completed trials with similar movement times between joint torque and muscle force control, monkey I improved from approximately 1.87s to 1.68s. Despite this improvement in terms of movement times during muscle force control, monkey I completed fewer trials overall and had an increased error rate while the other two subjects demonstrated decreased error rates. This finding with monkey I could also be related to the removal of six channels during muscle force control.

6.3.2 Movement Trajectories

In addition to the general task performance metrics, we were interested in the movement trajectories themselves and how they were affected by the transition from kinematic to dynamic control. Figures 6.2 and 6.3 illustrate the cursor path trajectories in the Cartesian and joint angle spaces respectively for all monkey/control combinations. As seen from these figures, the direction of curvature of the trajectories changes for some of the targets between the control schemes. The largest changes can be seen in the 45° target (blue) and the 225° target (orange). During joint velocity control, reaches that are the straightest, most direct reaches in the Cartesian space occurred to the 45° target. When moving to dynamic control, the curvatures of these path trajectories were greatly increased in the Cartesian space, while a relatively small change was observed in the joint angle space. Perhaps more interesting, the reaches to the 225° target completely flipped the direction of curvature in all three subjects when transitioning to dynamic control. This directional flip in curvature in the Cartesian space corresponded to an increase in
curvature in the joint angle space. These two targets happen to also be the most distant targets in joint angle space with the smallest Jacobian determinants caused by heavy flexion (225° target) or extension (45° target) of the elbow (see Appendix Figure A.7).

Table 6.6 summarizes the BCI psychophysical metrics introduced in Chapter 4 characterizing the movement trajectories. The normalized path lengths ($d_{path}$, a measure of path efficiency) were as efficient or better in the joint angle space than they were in the Cartesian space across all monkey/control combinations. Perhaps indicating a difference in task difficulty, the $d_{path}$ measures were worse during the joint torque control task versus the joint velocity task for all animals. Movements performed during muscle force control resulted in large improvements in this metric for monkeys G and I, with monkey O showing a very minor improvement. Interestingly, all monkeys demonstrated the straightest reaches in Cartesian space during the muscle force control task. While the path length metric references the straightness and efficiency from the starting position to the final position, it does not depend on the target direction itself. A perfectly straight path that just grazes the outside edge of the target yields a perfect 1.0 measure while a slightly more meandering path that quickly approaches the target center results in a worse measure. To dissect whether the subjects were making corrections towards the true center of the target, the dot product metric, $dp_{vel-tar}$, was used to measure the average directional agreement between the velocity vector and the vector pointing towards the center of the target. For the most part, the dot product metric mirrored the trends seen in the path lengths, albeit with less consistent statistical differences. For all three subjects $dp_{vel-tar}$ was worst during joint torque control, but improved during muscle force control. It is unclear if this was due to learning and experience or simply an effect of thresholding the control signals such that the muscles could not produce negative tensile (i.e. pushing) forces.
Figures 6.2: Cursor Path Trajectories in Cartesian Space
Panels A-C show the daily cursor path trajectories to all eight targets using the joint velocity control scheme for each monkey. Panels D-F show cursor trajectories for joint torque control movements, and panels G-I show the trajectories for muscle force control. The total numbers of correct trials performed for each monkey/control scheme combination are indicated in parenthesis. For plotting purposes, the daily average trajectories are shown and movements to the eight targets are specified by color.
Figure 6.3: Cursor Path Trajectories in Joint Angle Space
Panels A-C show cursor path trajectories to all eight targets using the joint velocity control scheme for each monkey. Panels D-F show cursor trajectories during joint torque control movements, and panels G-I show the trajectories for muscle force control. The total numbers of correct trials performed for each monkey/control scheme combination are indicated in parenthesis. For plotting purposes, the daily average trajectories are shown and movements to the eight targets are specified by color.
Table 6.6: BCI Trajectory Metrics in each Reference Frame
Summary of the psychophysical results from correct movements made during each control session. The ratio, $R_{B\text{max}}$, was calculated from the trial-by-trial ratio of the average speed during the Hold B period to the maximum cursor speed during the movement period. Values are shown as mean ± 1 standard deviation for each trial block. Metrics calculated in the Cartesian space are printed in red, while metrics calculated in the joint angle space are in blue.

<table>
<thead>
<tr>
<th>Control</th>
<th>$d_{\text{path}}$</th>
<th>$d_{\text{vel-tar}}$</th>
<th>Peak Speed (cm/s)</th>
<th>Hold Speed (cm/s)</th>
<th>$R_{B\text{max}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>G Joint Velocity</td>
<td>1.46 ± 0.05</td>
<td>0.60 ± 0.05</td>
<td>11.99 ± 0.43</td>
<td>6.83 ± 0.32</td>
<td>0.57 ± 0.01</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>1.49 ± 0.13</td>
<td>0.54 ± 0.04</td>
<td>7.91 ± 0.93</td>
<td>5.53 ± 0.63</td>
<td>0.70 ± 0.03</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>1.19 ± 0.03</td>
<td>0.62 ± 0.03</td>
<td>6.45 ± 0.37</td>
<td>4.60 ± 0.32</td>
<td>0.71 ± 0.02</td>
</tr>
<tr>
<td>Joint Velocity</td>
<td>1.64 ± 0.08</td>
<td>0.57 ± 0.04</td>
<td>11.64 ± 0.83</td>
<td>6.60 ± 0.50</td>
<td>0.57 ± 0.02</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>1.52 ± 0.07</td>
<td>0.63 ± 0.03</td>
<td>1.17 ± 0.08</td>
<td>0.70 ± 0.04</td>
<td>0.59 ± 0.02</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>1.63 ± 0.08</td>
<td>0.54 ± 0.03</td>
<td>8.01 ± 0.65</td>
<td>6.29 ± 0.39</td>
<td>0.79 ± 0.02</td>
</tr>
<tr>
<td>Joint Velocity</td>
<td>1.45 ± 0.13</td>
<td>0.62 ± 0.07</td>
<td>14.13 ± 1.45</td>
<td>7.72 ± 1.01</td>
<td>0.55 ± 0.03</td>
</tr>
<tr>
<td>Joint Torque</td>
<td>1.47 ± 0.10</td>
<td>0.55 ± 0.03</td>
<td>8.32 ± 0.92</td>
<td>6.33 ± 0.52</td>
<td>0.76 ± 0.03</td>
</tr>
<tr>
<td>Muscle Force</td>
<td>1.34 ± 0.09</td>
<td>0.63 ± 0.04</td>
<td>8.18 ± 0.45</td>
<td>6.35 ± 0.41</td>
<td>0.78 ± 0.01</td>
</tr>
</tbody>
</table>

All path-related metrics were skewed in favor of the joint angle space across all other conditions, with the lone exception being monkey G performing the joint torque control task, with the dot product in Cartesian space being slightly larger than in the joint angle space. As the switch was made to joint torque, and later muscle force control, this gap was closed between the spaces. Perhaps the longer duration movements allowed them to make more visual corrections (in Cartesian space) on the fly, versus possibly relying on an internal model of the joint angle space. We proceeded to look at the temporal dynamics of the instantaneous dot products to get
better idea of how online error corrections were made. For each day, the eight target temporal profiles of the dot product were averaged, and the resulting daily averages are presented in Figure 6.4. For each monkey, the largest difference between control schemes was observed prior to 40% of the normalized movement time. After this point, the dot products were extremely similar between control paradigms. The stability or plateau of the dot products in the joint angle space may suggest the subjects were more “locked in” in that space and not making minor adjustments on the fly. In contrast, as the cursor gets closer to the target, the dot product spikes in the Cartesian space. Additionally, monkeys G and O demonstrated a faster climb in the dot product during muscle force control, whereas Monkey O did not exhibit any meaningful differences between joint torque and muscle force control schemes.

By far the most drastic differences for all monkeys between kinematic and dynamic control sessions were related to the speed of the cursor. Both peak and hold cursor speeds were much lower during dynamic control sessions, corresponding with the increase in movement times seen in the previous section. The ratio of peak-to-hold speeds was not constant between kinematic and dynamic control, but each monkey exhibited similar trends of ~0.6 during kinematic control and an increased 0.7-0.8 during dynamics-based control. Hold speeds did get significantly slower for monkeys G and I, but given that the animals only had to slow enough to satisfy the 400 ms hold time, they were not incentivized to stop completely. Therefore, it is unclear if their increased velocity ratios were due to an inability to slow down.
Figure 6.4: Temporal Profiles of the Dot Product for Each Control Scheme
The instantaneous normalized dot product between the velocity vector \( \vec{v}(t) \) and the error direction vector \( \vec{u}(t) \) is depicted for each monkey/control combination. Dashed lines denote the dot product in joint angle space, while solid lines denote the dot product in Cartesian space. The mean ± standard deviation of the daily averages is shown for each condition.
Average cursor velocity profiles to each of the eight targets during the three control sessions for monkey G are shown in Figure 6.5. As noted in Table 6.6, these profiles demonstrate similar hold speeds but highly reduced peak speeds during dynamic control sessions, resulting in a much higher ratio of the hold to peak speeds. Although the additional velocity profiles are not shown here, these trends were also observed for monkeys O and I. The consistent speeds seen during the hold period between control tasks suggests the animals were not trying to stop at the target, but rather just slow down enough to receive their liquid reward.

**Figure 6.5: Cursor Velocity Profiles from Monkey G**
Average cursor velocity profiles for each control scheme from monkey G, colored by target location. Top row depicts $x$-velocities and bottom row shows $z$-velocities. The means ± standard deviations of the daily averages are shown.
6.3.3 Control Signal Profiles and Properties

Although the control signals for the three tasks were applied in different ways, each of them could be broken down into two directional components (either joint velocity or joint torque). For the purpose of this analysis, the control signal, $y(t)$, is a dimensionless variable (prior to being scaled by the gain term, $G_y$). For the three tasks, the 2-dimensional control signals are defined as follows:

Velocity and Torque: \[ \vec{y}(t) = W^T \vec{x}(t) \]  
Muscle Force: \[ \vec{y}(t) = A^T \cdot f \left( W^T \vec{x}(t) \right), \]

where $f(\cdot)$ is the threshold-linear function defined in Equation 6.11, $W^T \in \mathbb{R}^{N_{\text{dimensions}} \times N_{\text{features}}}$ is the weights matrix and $\vec{x}(t) \in \mathbb{R}^{N_{\text{features}}}$ is the instantaneous vector of z-scored features. In the muscle force condition with the control signal being in 6-dimensions, the weighted features were thresholded at zero to ensure the individual muscles were not contributing a negative or pushing force. The matrix of moment arms, $A$ serves to sum the torques produced by each individual muscle to create the 2-dimensional control signal.

As the regressions were performed such that the weighted features would best estimate the unit vector pointing towards the target, the expected range of observed magnitudes of the control signal should be $[0, 1]$. This makes for a standard comparison that doesn’t require correcting for units and is thus a suitable measure of the neural modulation. We focused on two particular aspects of the control signals; 1) the temporal profiles to each target, and 2) the dynamic range in which these signals could operate.

Figure 6.6 depicts the temporal profiles of the control signal magnitude (i.e., the root sum of the squared components) to each target/control condition for monkey G. As evident from this figure, the average temporal magnitudes between control schemes were similar to most targets.
Figure 6.6: Magnitudes of the Control Signals for Monkey G
The magnitudes of the 2-dimensional control signals are plotted as a function of time from movement onset. Average movement times for each condition are denoted with vertical lines to better illustrate the time scales of activation between control tasks. Thick lines indicate trial hold periods. Shown are the means ± 1 standard deviations of the daily averages.
As the average movement times vary widely between joint velocity control and dynamic control (from 1.1s to 2.1s for monkey G), the control signals were plotted as a function of time from the onset of movement. What is most interesting in this figure is that the timescale of neural modulation appears to be the same for all movements other than those to the three targets at the lower-left (i.e., 180°, 225° and 270°). This may suggest the animals were trying to complete the trials in the same amount of time as during the velocity tasks. Although the larger average control signals seen during velocity control to the lower-left targets may suggest the animals had the ability to utilize larger magnitude control signals to all targets, we did not see corresponding differences in the dynamic range of individual features between control tasks that would suggest this might be possible.

The overall difference in magnitudes between targets exhibits the same phenomenon that was seen between the joint angle and Cartesian velocity tasks presented in Chapter 5. Lower left targets yielded the largest control signals in order to maintain speed while travelling through the “dead spot” observed in the Jacobian determinant. This increase in magnitude was not seen during Cartesian control tasks, and the effect was also lessened in the intrinsic dynamic tasks. As illustrated in Figure 6.7, all three subjects demonstrated a uniform decrease in the observed range of the control signal between joint torque and muscle force control sessions. This was likely caused by the co-contraction of opposing muscles. All of monkey G’s neural features increased in modulation during muscle force control when compared to both joint velocity and joint torque tasks. Although the individual features did not modulate less during muscle force control on average, due to the weights these neural features could generate cancelling torques. Monkeys O and I on the other hand had a mixture of small feature modulation changes, with both the means and medians being near zero across the population.
For each block, the 2-dimensional control signal was averaged for each target. The range of the control signal magnitudes (dynamic range) across all eight targets was accumulated across all blocks using 31 equally spaced bins centered from 0-3 (bin width = 0.1). The means of the distributions are denoted with solid vertical lines, and medians are denoted with dashed vertical lines. For plotting purposes, the histograms were smoothed using a Gaussian function ($\sigma = 0.2$).
Despite these differences, all three subjects saw similar decreases of 25-30% (of the median) in the range of observed control signals between joint torque and muscle force.

As the control signals for both the joint torque and muscle force tasks were applied as joint torques, the decrease in dynamic range of the control signals could be countered by increasing the gain on the control signal such that the resulting torques resided in the same range. However, increasing the dynamic range for application of larger torques (and similarly muscle forces) likely comes at the cost of decreased sensitivity in the production of smaller torques.
Cortical Muscle Activations

Breaking down the 2-dimensional control signal into the 6 muscle components, we find that the muscle activation profiles for the biarticular muscles more closely resemble those of the elbow muscles than the shoulder muscles. The average temporal muscle activation profiles for monkey G are shown in Figure 6.8. From this figure we see that some muscles are more active during the acceleration phase of movement, while others activate later while slowing down. This is evidence that the animals were not purely relying on the viscous damping force to slow the cursor when approaching the target.

![Figure 6.8: Muscle Activation Profiles for Monkey G](image)

Temporal profiles of the six muscle activations, $y(t)$, during muscle force BCI control, colored by target location. Top row displays the three flexor muscles while the bottom row shows the three extensor muscles. The means ± standard deviations of the daily averages are depicted.
A. Temporal Profiles of Muscle Activation

B. Day by Day Muscle Correlations

Figure 6.9: Muscle Activation Profiles and Correlations for all Subjects
A) Daily average temporal profiles of the 6 muscle activations during muscle force BCI control.
B) Correlations between each muscle/day combination. Calculation of the Pearson correlation coefficient subtracts the means of the 2 distributions, resulting in negative muscle values, which then result in negative correlations. A normalized dot product (without subtracting the mean) accompanies the correlation values for each of the antagonistic muscle pairs in Figure 6.10.
Figure 6.9A illustrates the temporal activation profiles observed for each of the subjects. The daily activation profiles are grouped on the y-axis by the muscle of interest, and the temporal profiles are concatenated for each of the eight targets on the x-axis. From these plots it can be seen that the elbow muscle activations are highly correlated with biarticular muscle activations. For each of the individual rows of the activation matrices plotted in A, the Pearson correlation coefficient \( r \) was calculated to quantify these relationships, shown in panel B. Of these correlations, the lowest observed values are between the antagonistic muscle pairs (i.e., the shoulder, elbow, and biarticular flexor/extensor pairs).

We quantified the co-activation of antagonistic pairs as the ratio of the weaker muscle to the stronger one. At any point in time, this distinction between the weaker and stronger muscle could change (e.g. at the beginning of movement the extensor is active, and when slowing the flexor activates). The observed co-activation levels are shown in Figure 6.10. Panels A-C show the activation patterns for the 3 antagonistic pairs for each monkey. All monkeys demonstrated fairly consistent co-activation levels across muscle groups, with the shoulder appearing to be slightly smaller. Panel D illustrates the activation patterns assumed by the minimum stress muscle model used by the decoding algorithm, denoted as the “Optimal Case”.

A. Monkey G

B. Monkey O

C. Monkey I

D. Optimal Case

Figure 6.10: Co-activation of Antagonistic Muscle Pairs
The co-activation of all three antagonistic pairs (shoulder, elbow, biarticular) are plotted for the three subjects (A-C) as well as in the optimal case (D) where $T = ([A^T + \tau], with [ ] denoting the minimum squares solution with all positive forces. In the optimal case which is used to assign the regression weights, there is zero co-activation.
Torque Distributions and Minimum Jerk Comparisons

We wished to quantify the contributions of torque attributed to the mass and configuration of the arm, \( M \), inertial Coriolis forces, \( C \), and viscous forces, \( V \). Re-arranging these terms in Equation 6.1 yields:

\[
\tau_{Muscles} = M(\theta)\ddot{\theta} + C(\theta, \dot{\theta})\dot{\theta} + B\ddot{\theta} = M + C + V
\]

Eq. 6.16

With the animals performing such slow movements (1600-2100ms) during the dynamic control task, we pondered if the animals were carefully avoiding the non-linear interaction torques (\( C \)). We were able to quantify these torques during control sessions, however we did not have a baseline for comparison. For comparisons, we elected to use simulated movements using the minimum jerk criterion established by Flash and Hogan [150]. The minimum jerk trajectory is commonly used to model primate reaching kinematics, and is defined by:

\[
x(t) = x_i + (x_f - x_i)\left(10\left(\frac{t}{d}\right)^3 - 15\left(\frac{t}{d}\right)^4 + 6\left(\frac{t}{d}\right)^5\right)
\]

Eq. 6.17

Where \( x(t) \) is the position at time \( t \), \( x_i \) is the initial position, and \( x_f \) is the final position at time \( d \). The minimum jerk trajectory comes to a smooth, complete stop at time \( d \). We simulated minimum jerk reaches to all eight targets with movement times ranging from 500 to 3000 ms. From these trajectories, we solved for \( M \), \( C \), and \( V \), with the sum equaling the applied joint torque, \( \tau \). The magnitude of each term is plotted in Figure 6.11. As the peak torque values for \( \tau \) increase exponentially with faster movement times, the terms for each movement time were normalized by the peak applied torque. From this figure, we can see that faster movements yield the largest contributions of mass (\( M \)) and inertial (\( C \)) components, while the slower movements become more attributed to the viscous term (\( V \)). Peak Coriolis torques reach a maximum of 0.28
of the sum of peak torques using the fastest (500 ms) movements, and bottom-out at 0.08 for 3s movements. Thus, the peak Coriolis torques experienced during minimum jerk reaches range from 0.28-0.08 of the peak applied torque across all eight targets and movement times between 500 and 3000 ms.

Figure 6.11: Proportional Torque Contributions for Simulated Reaches
The proportional torque distributions (i.e., scaled by the peak torque, $\tau$) are shown for minimum jerk simulated reaches to all eight targets. Six different movement speeds are illustrated; 500 ms, 1000 ms, 1500 ms, 2000 ms, 2500 ms and 3000 ms; with the slower movements plotted in lighter shades.
The peak proportional contributions of torque are plotted in Figure 6.12 accompanied by the average torque contributions from each monkey during muscle force control. While some monkey/target combinations exhibited lower Coriolis torques than expected in the case of minimum jerk, if animals were carefully avoiding these non-linear torques, we would expect to see the majority of these blue markers residing below the blue lines. We suspected the animals may be moving slowly in order to best mimic velocity control, but there were only a few instances in which the viscous term was more impactful than in the minimum jerk simulations.
The peak torques for mass (M), Coriolis (C), and viscous (V) components are scaled by the maximum torque, $\tau$, observed for the set of targets at each movement time. Clearly, M and C approach zero as movements get longer and longer, while the viscous term V approaches the peak torque (i.e., 1.0). Experimental data was calculated in the same manner for each subject, with each component being scaled by the peak applied torque observed during control.
6.4 Discussion

Compared to the kinematic control task, we found that movement times and percent correct were longer and lower during dynamic control tasks. Conversely, the metrics characterizing the movement trajectories were generally as good or better during the muscle force task. This might suggest that a large factor in the animals performing longer movements with lower peak speeds was the use of an insufficiently large gain term (as evident by equally large signal modulations, assumed to be at the limit of the dynamic range of the control signal). Initially we expected slower reaches as we had previously found that when the task gets difficult the monkeys will deliberately slow down in order to make fewer errors. As the animal’s performance improved throughout the day, we reduced the joint viscosity in order to transform from kinematic control to kinetic control. However, with practice, the animals did not get faster in their reaches as they had in kinematic control. One possible future solution would be to also iteratively increase the gain based on performance throughout the day.

Co-activation of Muscles

Without the co-activation of muscles, each muscle has to be used to modulate joint torque in both directions. By co-activating, one muscle can have a constant activation level (no modulation), while the other modulates above or below this value. In this case, only one muscle is responsible for the magnitude and direction of the applied torque. Even using extrinsic kinematic control schemes, we observed this co-activation phenomenon in a previous ECoG BCI study (see Figure 6.13). Utilizing the difference in spectral power (75-105 Hz) between two electrodes as the control signal, (positive difference moves the cursor in the positive direction, negative difference in the negative direction), it was found that some control feature pairs would
modulate in a push/pull fashion, while others demonstrated high levels of co-activation. Three types of strategies were observed: 1) push vs. pull (see “M,Y” and “N,X”), 2) push-pull vs. rest (“M,X” and “J,Y”), and 3) push vs. push harder (“J,X” and “N,Y”).

Figure 6.13: Co-activation of opposed control signals during extrinsic kinematic control
A) d’ metric measuring the difference in the average control feature modulations using two directionally opposed features and targets. B) Locations of the electrodes for these control features, utilizing the 75-105 Hz band for control. (from Rouse et. al. [85])

During motor learning of a novel task or environment, co-contraction of antagonistic pairs is found to decrease over time [156]. This co-contraction increases limb stiffness and stability. This change in limb stiffness and stability could be implemented into our model by scaling the joint viscosity by the level of co-contraction and/or incorporating the viscoelastic properties of muscles.

One could imagine the animals neglecting the biarticular muscles in favor of two muscles controlling each dimension in a push/pull fashion. Interestingly, deviations from the optimal muscle activations were always positive in magnitude. This positive deviation was highly correlated to the co-activation of antagonistic muscle pairs. Had we turned off the adaptive
decoder and locked the weights, we may have seen some muscles become more or less favored over time with experience. In future experiments, we could attempt to quantify the co-activation levels of the muscle pairs as a function of task difficulty (using the d’ metric referenced in Figure 6.13).

**Non-linear Interaction Torques (Coriolis)**

The results in section 6.3.3 demonstrated that the magnitudes of the observed Coriolis torques were in a similar range to those we would expect during minimum jerk trajectory reaches. This is interesting in that up until this intrinsic dynamic task, we had never utilized non-linear systems with BCI control. While the joint velocity task used a non-linear mapping from the control space (joint angles) to the visible feedback space (Cartesian), the system itself was linear in the control space. In the intrinsic dynamics tasks however, there are non-linear terms interacting directly with the control signal. In this task, these were the inertial, centripetal and Coriolis torques.

These interaction torques have been found to be the difficult to model internally in patients with cerebellar deficits [157], [158]. They found that with cerebellar deficits, the interaction torques were reduced by decomposing the movements (*i.e.*, by focusing on a single joint at a time, rather than a fluid movement). Looking at the cursor path trajectories in joint angle space (Figure 6.3), it is possible we see some evidence of this for the lower left (orange) and upper right (blue) targets. During velocity control, these reaches were relatively straight in joint space, while under dynamic control they became more similar to moving one joint at a time. During initial dynamic task training, the contributions of these non-linear torques could be the reason the animals struggled with lower viscosity values.
In all sessions, the decoding scheme applied was that of a unit vector pointing towards
the target in the control space. This was possible because the torque vector $\tau$ and the velocity
vector are closely aligned for the duration of most reaches. A simple change in the dynamic
model such as reducing the joint viscosity or increasing the gain however, can cause severe
changes in directional agreement of these vectors (i.e., the direction pointing to the target is not
the direction a torque needs to be applied in order to move in that direction). The point at which
the decoding model fails may not be the same point at which the monkeys become unable to
complete the task (due to the resulting non-linear torques). To test this hypothesis, we could lock
the decoding weights so they do not update and reduce the joint viscosity or increase the gain.
We could then compare the temporal stability of the regression weights for periods of control
using different values. This would allow us to tease apart how much the animal is able to adapt
vs. how well the decoder is working. When the adaptive decoder remains online, a failure in
either part leads to an indiscernible reduction in performance. As the handling of these
interaction torques for control are naturally performed by subcortical structures (e.g. cerebellum),
this could be a useful tool in characterizing the plasticity of sensorimotor cortex for BCI control.

Final Thoughts

The results presented here provide a novel demonstration of an intrinsic, force-based BCI
control system. Rather than using brain-derived signals to simply point to or select a target as
has been commonly demonstrated in most BCI studies to date, subjects in this study were
required to interact with and account for non-linear inertial forces using muscles organized in a
push/pull configuration. Although the task and range of conditions was relatively simple
compared to those experienced in the real-world, the results do present a promising first step towards the ability to control an upper limb intrinsically.

In our dynamic model, we had complete control over the simulated system, most importantly, the joint viscosity term. In a physical limb however, these values are an intrinsic property of the arm, induced by the viscoelastic properties of muscles and neural reflexes. Thus, our initial training protocol using a bias velocity and high viscosity would not be achievable in the same manner using a physical system. The main goal of the physical model was not how to best describe a complete realistic system, but rather to show that subjects can adapt and learn an internal model of the control system when using ECoG signals recorded above sensorimotor cortex.

In future studies, perhaps the weights assigned using this virtual training protocol could later be applied to BCI systems incorporating the physical limb. Due to the consistency of the decoding weights and the inferred neural control strategies, a static decoding model could be used. Choosing this decoding model based on previous decode weights could allow the subject to interact with the BCI system immediately, without the need for an additional training session.
References


A. Supplemental Figures

Figure A.1: Percentage of Features Recruited as a function of mean R²
Figure A.2: Individual Monkey Range of Modulation
Figure A.3: Individual Monkey Mean vs. Depth of Modulation Relationships
Figure A.4: Regression $R^2$ distributions for motor and sensory electrodes
Figure A.5: Decoding weight distributions for motor and sensory electrodes
Clustering the mid gamma preferred directions into three groups yielded a more graded insight into the spatial separations of the preferred directions.
Table A.1: Cosine Tuning of Kinematics vs. Frequency Bands

Red text indicates significance on average (p < 0.05) and green text indicates the frequency band tuning direction that most closely relates to the tuning direction of average speed. (Frequency bands that reached significance were shown in Table 4.7) These data suggest the “push and relax” strategy is accompanied by near cosine tuning in cursor speed (and understandably so in movement time for straight movements), and that the “push, push, and push” strategy does not exhibit a similar directional bias in movements.

<table>
<thead>
<tr>
<th>Blocks Reaching Significance</th>
<th>Tuning Direction, θ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>Distance</td>
</tr>
<tr>
<td>G</td>
<td>14.36%</td>
</tr>
<tr>
<td>O</td>
<td>19.75%</td>
</tr>
<tr>
<td>R</td>
<td>17.30%</td>
</tr>
<tr>
<td>I</td>
<td>9.24%</td>
</tr>
<tr>
<td>K</td>
<td>70.14%</td>
</tr>
<tr>
<td>P</td>
<td>91.86%</td>
</tr>
</tbody>
</table>
Figure A.7: Jacobian Determinant from Joint Angle Space to Cartesian Space
The Jacobian (see Equation 5.8) determinant is maximum when $\theta_2 = \pi/2$, and minimum when it approaches $\pi$; large changes in $\theta$ near the shoulder result in very small deviations in $x$ and $z$. This shows the Jacobian determinant is not in fact a function of both shoulder and elbow angles, but just of the elbow angle.
Figure A.8: Mean Decoding Weight Vectors, from Chapter 5
Average decoding weights are depicted as vectors for each control session. Weights during the joint control tasks appear to simply be rotated (~92° for monkey G, ~121° for monkey O) from their Cartesian control task counterparts. For plotting purposes, the weight vector magnitudes for each monkey were normalized by the largest average weight vector from the respective subject (i.e., the same scaling as shown in Figure 5.10).
Figure A.9: Cosine Tuning Preferred Directions, from Chapter 5
Preferred directions (scaled by MVL) show little deviation from one task session to the next. Monkey G features do not change until “JA_2” at which point they rotate almost uniformly by 31°. Monkey O’s features also rotate between each session, with average rotations of -12°, +20°, and -5°. Notably, the rotations occur in opposite directions for each subject.
Table A.2: Percent correct with single worst block removed from each day, from Chapter 6

Percent correct is listed for each monkey/task combination when removing the worst performing block each day. The absolute change from inclusion of all blocks is shown in parenthesis. Removing a single block can have significant changes on the percent correct, with monkey G improving by 4.2 overall percentage points and monkey I by 3.4.

<table>
<thead>
<tr>
<th>Control</th>
<th>Overall</th>
<th>Day</th>
<th>Block</th>
</tr>
</thead>
<tbody>
<tr>
<td>G</td>
<td>Joint Velocity</td>
<td>98.09 % (+1.00)</td>
<td>98.05 % (+0.97)</td>
</tr>
<tr>
<td></td>
<td>Joint Torque</td>
<td>96.33 % (+3.18)</td>
<td>96.47 % (+3.63)</td>
</tr>
<tr>
<td></td>
<td>Muscle Force</td>
<td>97.97 % (+4.20)</td>
<td>97.92 % (+4.19)</td>
</tr>
<tr>
<td>O</td>
<td>Joint Velocity</td>
<td>99.28 % (+0.47)</td>
<td>99.17 % (+0.48)</td>
</tr>
<tr>
<td></td>
<td>Joint Torque</td>
<td>97.46 % (+0.94)</td>
<td>97.22 % (+1.03)</td>
</tr>
<tr>
<td></td>
<td>Muscle Force</td>
<td>98.68 % (+0.86)</td>
<td>98.40 % (+0.93)</td>
</tr>
<tr>
<td>I</td>
<td>Joint Velocity</td>
<td>98.67 % (+0.63)</td>
<td>98.79 % (+0.97)</td>
</tr>
<tr>
<td></td>
<td>Joint Torque</td>
<td>97.11 % (+1.66)</td>
<td>96.52 % (+1.71)</td>
</tr>
<tr>
<td></td>
<td>Muscle Force</td>
<td>92.90 % (+3.38)</td>
<td>92.69 % (+3.65)</td>
</tr>
</tbody>
</table>
Figure A.10: Magnitudes of the Control Signals for Monkey O, from Chapter 6
The magnitude of the 2-dimensional control signals as a function of time from movement onset. Average movement times for each condition are denoted with vertical lines to better illustrate the time scales of activation between control tasks. Shown is the mean ± 1 standard deviation of the daily averages.
Figure A.11: Magnitudes of the Control Signals for Monkey I, from Chapter 6
The magnitude of the 2-dimensional control signals as a function of time from movement onset. Average movement times for each condition are denoted with vertical lines to better illustrate the time scales of activation between control tasks. Shown is the mean ± 1 standard deviation of the daily averages.
Figure A.12: Dot products between the applied torque and velocity vectors
Using the minimum jerk trajectories with movement times from 500-2500ms, only 3 targets required a true “braking” torque, with the straight down target requiring the brakes prior to hold at the 500ms, and during the hold for 1000ms and 1500ms. The straight up and upper-left targets required a braking torque during the hold period at 500ms only. Given these findings, we would not expect the animals to exhibit braking torques at the observed movement times.
Figure A.13: Torque-velocity dot products in the absence of joint friction

The same dot products between torque and velocity as Figure A.12, but without joint viscosity (*i.e.* $b = 0$). Without joint viscosity, the direction of applied torque flips by 180° when slowing to most targets. As such, using the direction vector as the desired torque vector proves contrary to what the animal actually desires to do.