MOTOR CORTEX IN VOLUNTARY MOVEMENTS

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EDITED BY
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Methods & New Frontiers in Neuroscience

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Preface

Voluntary movement is undoubtedly the overt basis of human behavior. Without movement we cannot walk, nourish ourselves, communicate, or interact with the environment. This is one of the reasons why the motor cortex was one of the first cortical areas to be explored experimentally. Historically, the generation of motor commands was thought to proceed in a rigidly serial and hierarchical fashion. The traditional metaphor of the piano presents the premotor cortex “playing” the upper motoneuron keys of the primary motor cortex (M1), which in turn activate with strict point-to-point connectivity the lower motoneurons of the spinal cord. Years of research have taught us that we may need to reexamine almost all aspects of this model. Both the premotor and the primary motor cortex project directly to the spinal cord in highly complex overlapping patterns, contradicting the simple hierarchical view of motor control. The task of generating and controlling movements appears to be subdivided into a number of subtasks that are accomplished through parallel distributed processing in multiple motor areas. Multiple motor areas may increase the behavioral flexibility by responding in a context-related way to any constraint within the environment. Furthermore, although more and more knowledge is accumulating, there is still an ongoing debate about what is represented in the motor cortex: dynamic parameters (such as specific muscle activation), kinematic parameters of the movement (for example, its direction and speed), or even more abstract parameters such as the context of the movement. Given the great scope of the subject considered here, this book focuses on some new perspectives developed from contemporary monkey and human studies. Moreover, many topics receive very limited treatment.

Section I, which includes the first two chapters, uses functional neuroanatomy and imaging studies to describe motor cortical function. The objective of Chapter 1 is to describe the major components of the structural framework employed by the cerebral cortex to generate and control skeletomotor function. Dum and Strick focus on motor areas in the frontal lobe that are the source of corticospinal projections to the ventral horn of the spinal cord in primates. These cortical areas include the primary motor cortex (M1) and the six premotor areas that project directly to it. The results presented lead to an emerging view that motor commands can arise from multiple motor areas and that each of these motor areas makes a specialized contribution to the planning, execution, or control of voluntary movement. The purpose of Chapter 2 is to provide an overview of the contribution of functional magnetic resonance imaging (fMRI) to some of the prevailing topics in the study of motor control and the function of the primary motor cortex. Kleinschmidt and Toni claim that in several points the findings of functional neuroimaging seem to be in apparent disagreement with those obtained with other methods, which cannot always be attributed to insufficient sensitivity of this noninvasive technique. In part, it may
reflect the indirect and spatio-temporally imprecise nature of the fMRI signal, but these studies remain informative by virtue of the fact that usually the whole brain is covered. Not only does fMRI reveal plausible brain regions for the control of localized effects, but the distribution of response foci and the correlation of effects observed at many different sites can assist in the guidance of detailed studies at the mesoscopic or microscopic spatio-temporal level. A prudently modest view might conclude that fMRI is at present primarily a tool of exploratory rather than explanatory value.

Section II provides a large overview of studies about neural representations in the motor cortex. Chapter 3 focuses on the neuromuscular evolution of individuated finger movements. Schieber, Reilly, and Lang demonstrate that rather than acting as a somatotopic array of upper motor neurons, each controlling a single muscle that moves a single finger, neurons in the primary motor cortex (M1) act as a spatially distributed network of very diverse elements, many of which have outputs that diverge to facilitate multiple muscles acting on different fingers. This biological control of a complex peripheral apparatus initially may appear unnecessarily complicated compared to the independent control of digits in a robotic hand, but can be understood as the result of concurrent evolution of the peripheral neuromuscular apparatus and its descending control from the motor cortex. Chapter 4 deals with simultaneous movements of the two arms, as a simple example of complex movements, and may serve to test whether and how the brain generates unique representations of complex movements from their constituent elements. Vaadia and Cardoso de Oliveira present evidence that bimanual representations indeed exist, both at the level of single neurons and at the level of neuronal populations (in local field potentials). They further show that population firing rates and dynamic interactions between the hemispheres contain information about the bimanual movement to be executed. In Chapter 5, Ashe discusses studies with respect to the debate as to whether the motor cortex codes the spatial aspects (kinematics) of motor output, such as direction, velocity, and position, or primarily controls, muscles, and forces (dynamics). Although the weight of evidence is in favor of M1 controlling spatial output, the effect of limb biomechanics and forces on motor cortex activity is beyond dispute. The author proposes that the motor cortex indeed codes for the most behaviorally relevant spatial variables and that both spatial variables and limb biomechanics are reflected in motor cortex activity. Chapter 6 starts with the important issue of how theoretical concepts guide experimental design and data analysis. Scott describes two conceptual frameworks for interpreting neural activity during reaching: sensorimotor transformations and internal models. He claims that sensorimotor transformation have been used extensively over the past 20 years to guide neurophysiological experiments on reaching, whereas internal models have only recently had an impact on experimental design. Furthermore, the chapter demonstrates how the notion of internal models can be used to explore the neural basis of movement by describing a new experimental tool that can sense and perturb multiple-joint planar movements. Chapter 7 deals with the function of oscillatory potentials in the motor cortex. MacKay notes that from their earliest recognition, oscillatory EEG signals in the sensorimotor cortex have been associated with stasis: a lack of movement, static postures, and possibly physiological tremor. It is now established that
10-, 20-, and 40-Hz motor cortical oscillations are associated with constant, sustained muscle contractions, again a static condition. Sigma band oscillations of about 14 Hz may be indicative of maintained active suppression of a motor response. The dynamic phase at the onset of an intended movement is preceded by a marked decrease in oscillatory power, but not all frequencies are suppressed. Fast gamma oscillations coincide with movement onset. Moreover, there is increasing evidence that oscillatory potentials of even low frequencies (4–12 Hz) may be linked to dynamic episodes of movement. Most surprisingly, the 8-Hz cortical oscillation — the neurogenic component of physiological tremor — is emerging as a major factor in shaping the pulsatile dynamic microstructure of movement, and possibly in coordinating diverse actions performed together. In Chapter 8, Richle discusses the main aspects of preparatory processes in the motor cortex. Preparation for action is thought to be based on central processes, which are responsible for maximizing the efficiency of motor performance. A strong argument in favor of such an efficiency hypothesis of preparatory processes is the fact that providing prior information about movement parameters or removing time uncertainty about when to move significantly shortens reaction time. The types of changes in the neuronal activity of the motor cortex, and their selectivity during preparation, are portrayed and compared with other cortical areas that are involved in motor behavior. Furthermore, linking motor cortical activity directly to behavioral performance showed that the trial-by-trial correlation between single neuron firing rates and reaction time revealed strong task-related cortical dynamics. Finally, the cooperative interplay among neurons, expressed by precise synchronization of their action potentials, is illustrated and compared with changes in the firing rate of the same neurons. New concepts including the notion of coordinated ensemble activity and their functional implication during movement preparation are discussed. In the last chapter of Section II, Chapter 9, Jeannerod poses the question of the role of the motor cortex in motor cognition. The classical view of the primary motor cortex holds that it is an area devoted to transferring motor execution messages that have been elaborated upstream in the cerebral cortex. More recently, however, experimental data have pointed to the fact that the relation of motor cortex activity to the production of movements is not as simple as was thought on the basis of early stimulation experiments. This revision of motor cortical function originated from two main lines of research, dealing first with the plasticity of the somatotopic organization of the primary motor cortex, and second with its involvement in cognitive functions such as motor imagery.

Section III is mainly concerned with motor learning. Chapter 10 explores various conditions of mapping between sensory input and motor output. Brasted and Wise claim that studies on the role of the motor cortex in voluntary movement usually focus on standard sensorimotor mapping, in which movements are directed toward sensory cues. Sensorimotor behavior can, however, show much greater flexibility. Some variants rely on an algorithmic transform between the location of the cue and that of the target. The well-known “antisaccade” task and its analogues in reaching serve as special cases of such transformational mapping, one form of nonstandard mapping. Other forms of nonstandard mapping differ strongly: they are arbitrary. In arbitrary sensorimotor mapping, the cue’s location has no systematic spatial relationship with the response. The authors explore several types of arbitrary mapping,
with emphasis on the neural basis of learning. In Chapter 11, Shadmehr, Donchin, Hwang, Hemminger, and Rao deal with internal models that transform the desired movement into a motor command. When one moves the hand from one point to another, the brain guides the arm by relying on neural structures that estimate the physical dynamics of the task. Internal models are learned with practice and are a fundamental part of voluntary motor control. What do internal models compute, and which neural structures perform that computation? The authors approach these questions by considering a task where the physical dynamics of reaching movements are altered by force fields that act on the hand. Many studies suggest that internal models are sensorimotor transformations that map a desired sensory state of the arm into an estimate of forces; i.e., a model of the inverse dynamics of the task. If this computation is represented as a population code via a flexible combination of basis functions, then one can infer activity fields of the bases from the patterns of generalization. Shadmehr and colleagues provide a mathematical technique that facilitates this inference by analyzing trial-by-trial changes in performance. Results suggest that internal models are computed with bases that are directionally tuned to limb motion in intrinsic coordinates of joints and muscles, and this tuning is modulated multiplicatively as a function of static position of the limb. That is, limb position acts as a gain field on directional tuning. Some of these properties are consistent with activity fields of neurons in the motor cortex and the cerebellum. The authors suggest that activity fields of these cells are reflected in human behavior in the way that we learn and generalize patterns of dynamics in reaching movements. In the last chapter of Section III, Chapter 12, Padoa-Schioppa, Bizzi, and Mussa-Ivaldi address the question of the cortical control of motor learning. In robotic systems, engineers coordinate the action of multiple motors by writing computer codes that specify how the motors must be activated for achieving the desired robot motion and for compensating unexpected disturbance. Humans and animals follow another path. Something akin to programming is achieved in nature by the biological mechanisms of synaptic plasticity — that is, by the variation in efficacy of neural transmission brought about by past history of pre- and post-synaptic signals. However, robots and animals differ in another important way. Robots have a fixed mechanical structure and dimensions. In contrast, the mechanics of muscles, bones, and ligaments change in time. Because of these changes, the central nervous system must continuously adapt motor commands to the mechanics of the body. Adaptation is a form of motor learning. Here, a view of motor learning is presented that starts from the analysis of the computational problems associated with the execution of the simplest gestures. The authors discuss the theoretical idea of internal models and present some evidence and theoretical considerations suggesting that internal models of limb dynamics may be obtained by the combination of simple modules or “motor primitives.” Their findings suggest that the motor cortical areas include neurons that process well-acquired movements as well as neurons that change their behavior during and after being exposed to a new task.

The last section, Section IV, is devoted to the reconstruction of movements using brain activity. For decades, science fiction authors anticipated the view that computers can be made to communicate directly with the brain. Now, a rapidly expanding science community is making this a reality. In Chapter 13, Carmena and Nicolelis
present and discuss the recent research in the field of brain–machine interfaces (BMI) conducted mainly on nonhuman primates. In fact, this research field has supported the contention that we are at the brink of a technological revolution, where artificial devices may be “integrated” in the multiple sensory, motor, and cognitive representations that exist in the primate brain. These studies have demonstrated that animals can learn to utilize their brain activity to control the displacements of computer cursors, the movements of simple and elaborate robot arms, and, more recently, the reaching and grasping movements of a robot arm. In addition to the current research performed in rodents and primates, there are also preliminary studies using human subjects. The ultimate goal of this emerging field of BMI is to allow human subjects to interact effortlessly with a variety of actuators and sensory devices through the expression of their voluntary brain activity, either for augmenting or restoring sensory, motor, and cognitive function. In the last chapter, Chapter 14, Pfurtscheller, Neuper, and Birbaumer deal with BMIs, which transform signals originating from the human brain into commands that can control devices or applications. BCIs provide a new nonmuscular communication channel, which can be used to assist patients who have highly compromised motor functions, as is the case with patients suffering from neurological diseases such as amyotrophic lateral sclerosis (ALS) or brainstem stroke. The immediate goal of current research in this field is to provide these users with an opportunity to communicate with their environment. Present-day BCI systems use different electrophysiological signals such as slow cortical potentials, evoked potentials, and oscillatory activity recorded from scalp or subdural electrodes, and cortical neuronal activity recorded from implanted electrodes. Due to advances in methods of signal processing, it is possible that specific features automatically extracted from the electroencephalogram (EEG) and electrocorticogram (ECoG) can be used to operate computer-controlled devices. The interaction between the BCI system and the user, in terms of adaptation and learning, is a challenging aspect of any BCI development and application.

It is the increased understanding of neuronal mechanisms of motor functions, as reflected in this book, that led to the success of BCI. Yet, the success in tapping and interpreting neuronal activity and interfacing it with a machine that eventually executes the subject's intention is amazing, considering the limited understanding we have of the system as a whole.

Perhaps ironically, the proof of our understanding of motor cortical activity will stem from how effectively we, as external observers of the brain, can tap into it and make use of it.

Alexa Riehle
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Dedication

—to Hanns-Günther Riehle
Editors

Alexa Riehle received a B.Sc. degree in biology (main topic: deciphering microcircuits in the frog retina) from the Free University, Berlin, Germany, in 1976, and a Ph.D. degree in neurophysiology (main topic: neuronal mechanisms of temporal aspects of color vision in the honey bee) from the Biology Department of the Free University in 1980.

From 1980 to 1984, she was a postdoctoral fellow at the National Center for Scientific Research (CNRS) in Marseille, France (main topic: neuronal mechanisms of elementary motion detectors in the fly visual system). In 1984, she moved to the Cognitive Neuroscience Department at the CNRS and has been mainly interested since then in the study of cortical information processing and neural coding in cortical ensembles during movement preparation and execution in nonhuman primates.

Eilon Vaadia graduated from the Hebrew University of Jerusalem (HUJI) in 1980 and joined the Department of Physiology at Hadassah Medical School after postdoctoral studies in the Department of Biomedical Engineering at Johns Hopkins University Medical School in Baltimore, Maryland.

Vaadia studies cortical mechanisms of sensorimotor functions by combining experimental work (recordings of multiple unit activity in the cortex of behaving animals) with a computational approach. He is currently the director of the Department of Physiology and the head of the Ph.D. program at the Interdisciplinary Center for Neural Computation (ICNC) at HUJI, and a director of a European advanced course in computational neuroscience.
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Table of Contents

SECTION I  Functional Neuroanatomy and Imaging

Chapter 1  Motor Areas in the Frontal Lobe: The Anatomical Substrate for the Central Control of Movement
Richard P. Dum and Peter L. Strick

Chapter 2  Functional Magnetic Resonance Imaging of the Human Motor Cortex
Andreas Kleinschmidt and Ivan Toni

SECTION II  Neuronal Representations in the Motor Cortex

Chapter 3  Motor Cortex Control of a Complex Peripheral Apparatus: The Neuromuscular Evolution of Individuated Finger Movements
Marc H. Schieber, Karen T. Reilly, and Catherine E. Lang

Chapter 4  Neuronal Representations of Bimanual Movements
Eilon Vaadia and Simone Cardoso de Oliveira

Chapter 5  What Is Coded in the Primary Motor Cortex?
James Ashe

Chapter 6  Conceptual Frameworks for Interpreting Motor Cortical Function: New Insights from a Planar Multiple-Joint Paradigm
Stephen H. Scott

Chapter 7  Wheels of Motion: Oscillatory Potentials in the Motor Cortex
William A. MacKay

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Chapter 8  Preparation for Action: One of the Key Functions of the Motor Cortex  
Alexa Riehle

Chapter 9  Is the Motor Cortex Only an Executive Area? Its Role in Motor Cognition  
Marc Jeannerod

SECTION III  Motor Learning and Performance

Chapter 10  The Arbitrary Mapping of Sensory Inputs to Voluntary and Involuntary Movement: Learning-Dependent Activity in the Motor Cortex and Other Telencephalic Networks  
Peter J. Brasted and Steven P. Wise

Chapter 11  Learning Dynamics of Reaching  
Reza Shadmehr, Opher Donchin, Eun-Jung Hwang, Sarah E. Hemminger, and Ashwini K. Rao

Chapter 12  Cortical Control of Motor Learning  
Camillo Padoa-Schioppa, Emilio Bizzi, and Ferdinando A. Mussa-Ivaldi

SECTION IV  Reconstruction of Movements Using Brain Activity

Chapter 13  Advances in Brain–Machine Interfaces  
Jose M. Carmena and Miguel A.L. Nicolelis

Chapter 14  Human Brain–Computer Interface  
Gert Pfurtscheller, Christa Neuper, and Niels Birbaumer