of gait based on visual information. PPC neurons estimate the relative location of objects with respect to the body and retain information in working memory to facilitate coordination of the limbs. The contribution of other cortical and subcortical areas to locomotor planning remains little studied.

10. Inputs from the cerebellum and the basal ganglia are used to correct motor errors and select the appropriate patterns of motor activity. The contribution of the basal ganglia to the control of locomotion is complex and is only now being determined.

11. The available evidence suggests that the neural control mechanisms determined from experiments in animals are also used to control locomotion in humans, including the existence of a CPG. Major advances remain to be made in understanding the mechanisms of spinal and supraspinal influences on human locomotor control.

12. Recent technological advances now give us an unparalleled opportunity to investigate the control mechanisms underlying locomotion. Molecular and genetic advances provide the ability to manipulate behavior at both the cellular and systems level and allow detailed study of the contributions of brain stem and spinal circuits to the initiation and regulation of locomotion. Advances in multineuronal recording techniques in animals, as well as the development of high-resolution recordings of human brain activity, will facilitate our understanding of the contribution of cortical structures to the control of locomotion.

<div align="right">Trevor Drew
Ole Kiehn</div>

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34

Voluntary Movement: Motor Cortices

I N T H I S C H A P T E R, W E D E S C R I B E H O W the cerebral cortex uses sensory information from the external world to guide motor actions that allow the individual to interact with the surrounding environment. We begin with a general description of what we mean by the term voluntary movement and some theoretical frameworks for understanding its control, followed by the basic anatomy of the cortical circuits involved in voluntary motor behavior. We then consider how information related to the body, external space, and behavioral goals is combined and processed in parietal cortical regions. This is followed by a discussion of the

role of premotor cortical regions in selecting and planning motor actions. Finally, we examine the role played by the primary motor cortex in motor execution.

Voluntary Movement Is the Physical Manifestation of an Intention to Act

Animals, including humans, have a nervous system not just so that they can sense their world or think about it, but primarily to interact with it to survive and reproduce. Understanding how purposeful actions are achieved is one of the great challenges in neuroscience. We focus here on the cerebral cortical control of voluntary motor behavior, in particular voluntary arm and hand movements in primates.

In contrast to stereotypical fixed-latency reflexive responses that are automatically triggered by incoming sensory stimuli (Chapter 32), voluntary movements are purposeful, intentional, and context-dependent, and are typically accompanied, at least in humans, by a sense of "ownership" of the actions, the sense that the actions have been willfully caused by the individual. Decisions to act are often made without an external trigger stimulus. Moreover, the continuous flux of events and conditions in the world presents changing opportunities for action, and thus voluntary action involves choices between alternatives, including the choice not to act. Finally, the same object or event can evoke different actions at different times, depending on the current context.

Throughout evolution, these features of voluntary behavior have become increasingly prominent in higher primates, especially in humans, indicating that the neural circuits controlling voluntary behavior in primates are adaptive. In particular, evolution has resulted in an increasing degree of dissociation of the physical properties of sensory inputs from their behavioral salience to the individual. Adaptation of the control circuits also enhances the repertoire of voluntary motor actions available to a species by allowing individuals to remember and learn from prior experience, to predict the future outcomes of different action choices, and to adopt new strategies and find new solutions to attain their desired goals. Volitional self-control over how, when, and even whether to act endows primate voluntary behavior with much of its richness and flexibility and prevents behavior from becoming impulsive, compulsive, or even harmful.

Voluntary behavior is the physical manifestation of an individual's intention to act on the environment, usually to achieve a goal immediately or at some point in the future. This may require single nonstereotypical movements or sequences of actions tailored to current conditions and to the longer-term objectives of the individual. The ability to use fingers, hands, and arms independent of locomotion further helps primates, and especially humans, exploit their environment. Most animals must search their environment for food when hungry. In contrast, humans can "forage" by using their hands to cook a meal or simply enter a few numbers on a cellphone to order food for delivery. Because large areas of the cerebral cortex are implicated in various aspects of voluntary motor control, the study of the cortical control of voluntary movement provides important insights into the purposive functional organization of the cerebral cortex as a whole.

Theoretical Frameworks Help Interpret Behavior and the Neural Basis of Voluntary Control

The neural processes by which individuals acquire information about their environment and the relationship of their body to it, decide how to interact with the environment to achieve short- or long-term goals, and organize and execute the voluntary movement(s) that will fulfill their goals are traditionally partitioned into three analytic components: Perceptual mechanisms generate an internal representation of the external world and the individual within it, cognitive processes use this internal model of the world to select a course of action to interact with its environment, and the chosen plan of action is then relayed to the motor systems for implementation. This serial view of the brain's overall functional organization has long dominated neuroscience; this textbook, for example, has separate sections dedicated to perception, cognition, and movement.

The brain must transform a goal into motor commands that realize the goal. For example, taking a sip of coffee requires the brain to convert visual information about the coffee cup and somatic information about the current posture and motion of your arm and hand into a pattern of muscle contractions that moves your hand to the cup, grasps it, and then lifts it to your mouth. Many behavioral and modeling studies suggest that this could be accomplished by a series of transformations of sensorimotor coordinates that convert the retinal image of the cup into motor commands (Figure 34–1A).

Variants of this sensorimotor transformation model have guided the design and interpretation of many studies on the control of voluntary arm movements. Neural recording studies, including many that will be described here, have found possible neural correlates of the motor parameters and sensorimotor transformations presumed to underlie movement
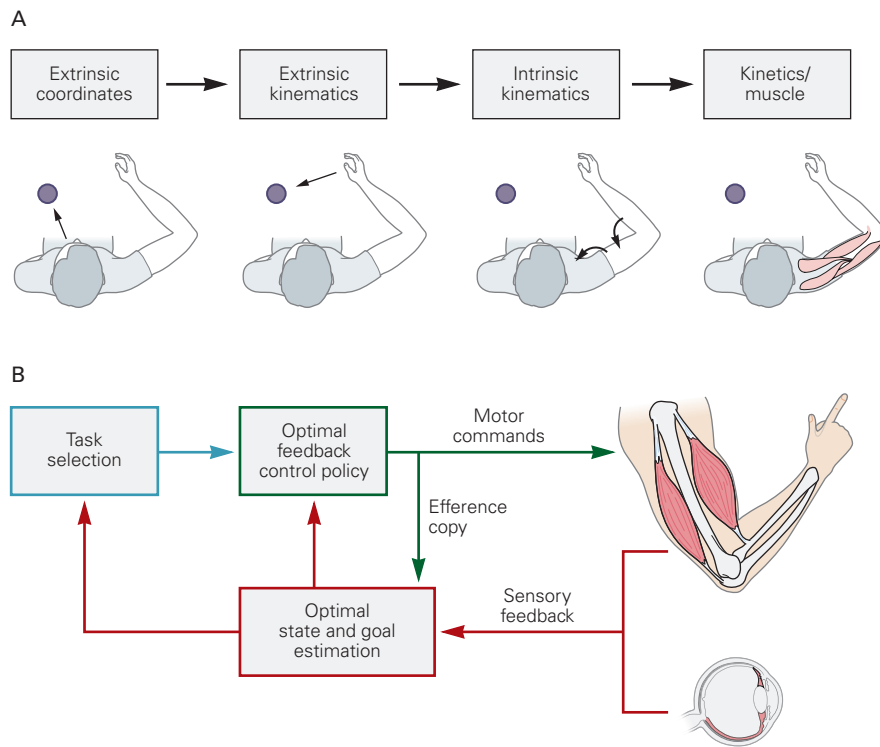
Figure 34–1 Theoretical frameworks for interpreting neural processing during voluntary motor actions.

A. The concept of sensorimotor transformations addresses the basic problem that tasks such as reaching to a visual target require the brain and spinal cord to convert sensory information about the spatial location of the target, initially represented in retinal coordinates, into patterns of muscle activity to move the limb to the target object. It is assumed that this sensorimotor transformation involves the use of intermediary representations—representation of the location of the target object relative to the body, the spatiotemporal trajectory of the hand (extrinsic kinematics), and motion of the joints (intrinsic kinematics) necessary to reach and grasp the object—before

generating the patterns of neural activity that specify the causal forces (kinetics) or muscle activity.

B. Optimal feedback control recognizes three key processes for control. Optimal state and goal estimation (**red box**) integrates sensory feedback from various modalities along with an efference copy of motor commands to estimate the present position and motion of the body and objects in the world. Task selection (**blue box**) involves processes that identify behavioral goals based on internal desires and information about the state of the body and the world. Control policy (**green box**) determines the feedback gains, operations, and processes necessary to generate motor commands to control movement.

planning and execution. This conceptual framework is an example of a *representational model* of brain function. Just as the activity of neurons in primary sensory areas appears to encode specific physical properties of stimuli, the sensorimotor transformation model assumes that the activity of neurons in the motor system explicitly encodes or represents specific properties and parameters of the intended movement.

However, the sensorimotor transformation model has important limitations. Among them, the parameters and coordinate systems typically used in such models were imported from physics and engineering, rather than derived from the physiological properties of biological sensors and effectors. Furthermore, the model places all emphasis on strictly serial feedforward computations and relegates feedback circuits

primarily to the detection and correction of performance errors after they are committed. The model also requires that every temporal detail of a movement be explicitly calculated before the motor system can generate any motor commands. Another limitation is its rigidity; it assumes that the same sequence of computations controls every movement in every context. Finally, this approach has not addressed how the proposed sensorimotor transformations could be implemented by neurons.

In recent years, theoretical studies of the motor system have been moving away from strictly representational models to more dynamical causal models. This approach begins with the premise that the functional architecture of motor control circuits evolved to generate movements, not to represent their parameters.

These circuit properties were acquired by evolutionary changes in neural circuitry and by experience-dependent adaptive processes during postnatal development that produce the patterns of synaptic connectivity within the neural circuits that are necessary to generate the desired movements. Spinal and supraspinal motor circuits ensure that spinal motor neurons generate the appropriate muscle contraction signals across task conditions without relying on computational formalisms such as coordinate transformations.

One such theoretical framework is optimal feedback control (Figure 34–1B; and see Chapter 30). There are many different forms of optimal control, and each captures important aspects of control. Optimal feedback control, as the name implies, emphasizes the importance of feedback signals for the planning and control of movements. It is optimal in the sense that it emphasizes the importance of the behavioral goal and the current context in determining how best to plan and control movements. This flexibility can explain how human motor performance can be both highly variable and yet successful.

The optimal feedback control framework also divides the control of voluntary movements into three key processes: state estimation, task selection, and control policy (Figure 34–1B). State estimation involves forward internal models that use efference copies of motor commands and external sensory feedback to provide the best estimate of the present state of the body and the environment (Chapter 30). Task selection involves the neural processes by which the brain chooses a behavioral goal in the current context and what motor action(s) might best attain that goal. This selection can be based on the sensory evidence supporting alternative actions and alternate options to attain the goal, and on other factors that influence the optimal response such as motivational state, task urgency, preferences, relative benefits versus risks, the mechanical properties of the body and environment, and even the biomechanical costs of different action choices. Finally, the control policy provides the set of rules and computations that establish how to generate the motor commands to attain the behavioral goal given the present state of the body and the environment. Importantly, the control policy process in optimal feedback control is not a series of pure feedforward computations to calculate every instantaneous detail of a desired movement trajectory and associated muscle activity patterns before movement onset. Instead, it involves context- and time-dependent adjustments to feedback circuit gains that allow the spatiotemporal form of muscle activity to emerge dynamically in real time as part of the control process underlying movement generation.

The sensorimotor transformation and optimal feedback control models are not mutually incompatible hypotheses. Optimal feedback control explains certain features of motor behavior but is largely agnostic as to the neural implementation for control. It assumes that motor circuits are dynamical systems that attain desired goals under varying task constraints. As a result, a given neuron may contribute to sensorimotor control in different task conditions, but its activity may not correspond to a specific movement parameter in a definable coordinate framework. In contrast, sensorimotor transformation models do not fully explain how real-time movement control is implemented by motor circuits, but emphasize the need to convert information from sensory signals to motor commands.

Even if the neural control system is dynamical, the system it controls—the musculoskeletal plant—is a physical object that must obey the universal physical laws of motion. Thus, neural activity should show correlations with those physical parameters and laws that will help to infer how those neurons are contributing to voluntary motor control, even if they are not attempting to encode those terms. Indeed, experimental tasks that dissociate different types of movement-related information have revealed important differences in how neural activity in different cortical motor regions correlates with different movement properties and different aspects of movement planning and execution. Finally, we can impose arbitrary volitional control on how we move. For example, we can choose to make an unobstructed reaching movement efficiently along a straight path to the target or whimsically along a complex curved path even though there is no obstacle to avoid and the movement is energetically costly. The experimental challenge is to reveal how the brain can implement this willful control with neurons and neural circuits.

Many Frontal and Parietal Cortical Regions Are Involved in Voluntary Control

Here we describe the regions of frontal and parietal cortex that convert sensory inputs into motor commands to produce voluntary movement. We then examine the neural circuits involved in the voluntary control of arm and hand movements that are prominent components of the motor repertory of primates. We focus on studies in the rhesus monkey (*Macaca mulatta*), as much of our knowledge of the cortical control of the arm and hand comes from this species and the neural circuity underlying human voluntary control appears to have a similar organization. Many other neural structures, including the prefrontal cortex, the basal ganglia, and

cerebellum, also play critical roles in the global organization of goal-directed voluntary behavior (Chapters 37 and 38).

Several different nomenclatures have been used in partitioning the precentral, postcentral, and parietal cortex, based on regional differences in cytoarchitectonic and myeloarchitectonic details, cortico-cortical connectivity, the distribution of different marker molecules, and regional differences in neural response properties. Here we will use some of the more widely accepted terminology without describing approximate homologies among the various nomenclatures.

Based on the pioneering cytoarchitectonic studies of humans by Brodmann, the different lobes of the monkey's cerebral cortex were divided into smaller regions, including two in precentral cortex (areas 4 and 6), four in the postcentral cortex (areas 1, 2, 3a, and 3b), and at least two in the superior and inferior parietal cortex (areas 5 and 7). While these cytoarchitectonic divisions persist in the literature, subsequent anatomical and functional studies have radically changed the view of how the precentral and parietal cortices are organized (Figure 34–2).

Current maps usually place the *primary motor cortex* (M1), the cortical region most directly involved in motor execution in primates, in Brodmann's area 4. Brodmann's area 6 is now typically divided into five or six functional areas that are principally involved in different aspects of the planning and control of motor actions of different parts of the body. Arm-control regions include the *dorsal premotor cortex* (PMd) and *predorsal premotor cortex* (pre-PMd), in the caudal and rostral parts of the dorsal convexity of lateral area 6, respectively. Hand-control regions include the *ventral premotor cortex* (PMv), found on the ventral convexity of area 6, which has been further divided into two or three smaller subregions. A variety of functions related to motor selection, sequencing, and initiation have been found in medial premotor cortical regions. These include a region on the medial surface of the cortical hemisphere that was originally called the secondary motor cortex by Woolsey and colleagues, who discovered it, but is now called the *supplementary motor area*. This region is in turn split into two regions, a *supplementary motor area proper* (SMA) in the caudal part and a *presupplementary motor area* (pre-SMA) in the rostral part. Outside of Brodmann's area 6, three additional motor areas, the dorsal, ventral, and rostral cingulate motor areas (CMAd, CMAv, and CMAr, respectively), are also involved in motor selection but have not been as well studied as more lateral premotor areas.

The *primary somatosensory cortex* (S-I; including areas 1, 2, 3a, and 3b) is located in the anterior postcentral gyrus. It processes cutaneous and muscle mechanoreceptor signals from the periphery and transmits that information to other parietal and precentral cortical regions (Chapter 19). Like area 6, Brodmann's parietal areas 5 and 7 are now divided into several regions within and adjacent to the intraparietal sulcus (IPS), each of which integrates various types of sensory information about the body or spatial goals for voluntary motor control. These include parietal lobe areas PE and PEc on the rostral or superior bank, and PF, PFG, PG, and OPT on the caudal, inferior bank. Areas inside the IPS include the anterior, lateral, medial, and ventral intraparietal areas (AIP, LIP, MIP, and VIP, respectively) as well as intraparietal area PEip and higher visual area V6A.

These precentral, postcentral, and parietal cortical regions are interconnected by complex patterns of reciprocal, convergent, and divergent projections. The SMA, PMd, and PMv have somatotopically organized reciprocal connections not only with M1 but also with each other. Both the SMA and M1 receive somatotopically organized input from S-I and the dorsorostral parietal cortex, whereas PMd and PMv are reciprocally connected with progressively more caudal, medial, and lateral parts of the parietal cortex. These somatosensory and parietal inputs provide the primary motor and caudal premotor regions with sensory information related to behavioral goals, target objects, and the position and motion of the body that is used to plan and guide motor acts.

In contrast, pre-SMA and pre-PMd project to SMA and PMd but do not project to M1 and are only weakly connected with the parietal lobe. They instead have reciprocal connections with prefrontal cortex and so may impose more arbitrary context-dependent control over voluntary behavior. Prefrontal cortex is also connected with other premotor cortical regions.

The control of hand and arm motor actions is implemented by partially segregated parallel circuits distributed across several parietal and precentral motor areas. Hand motor function is generally supported by frontoparietal circuits that are located more laterally, notably AIP and PMv. In contrast, proximal arm motor function is supported by circuits that are more medial, notably parietal areas PE and MIP and precentral areas PMd, SMA, and pre-SMA.

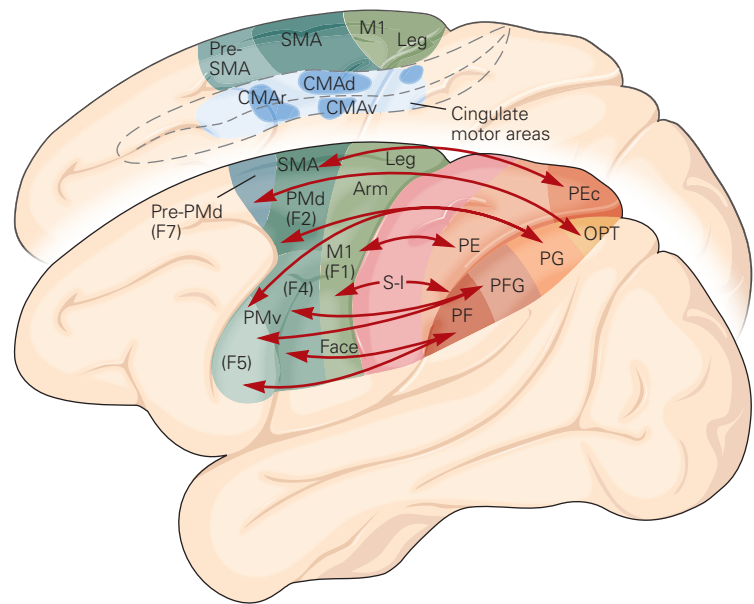## Descending Motor Commands Are Principally Transmitted by the Corticospinal Tract

Older textbooks often referred to the primary motor cortex (M1) as the "final common path." Other
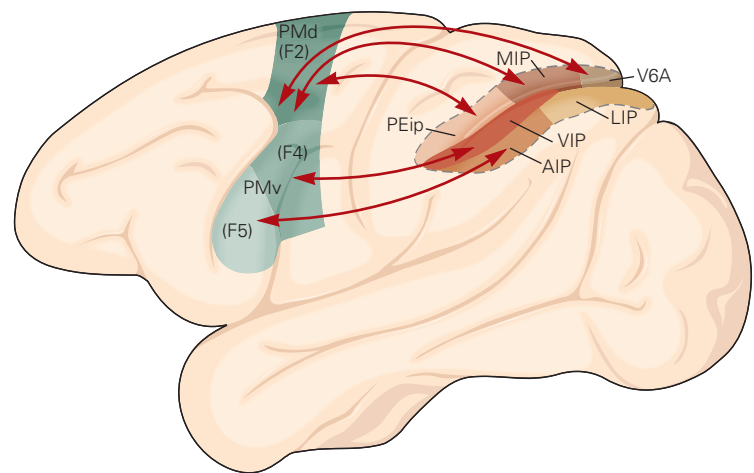
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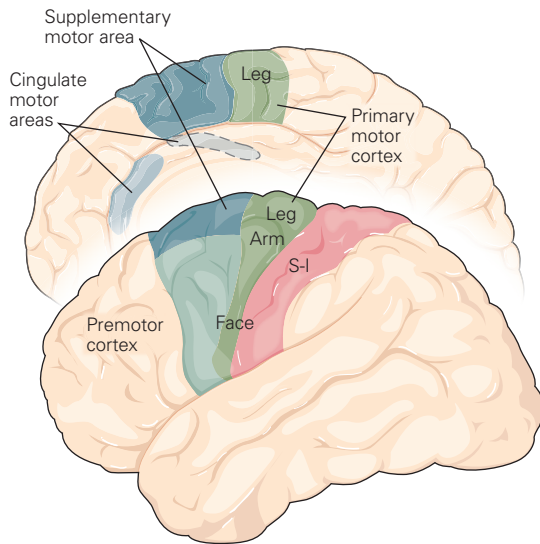
B Macaque monkey

Figure 34–2 Parietal and frontal motor areas that support voluntary control. For illustration purposes, the intraparietal sulcus is opened in the bottom panel. The parietal areas are designated in Constantin von Economo's terminology by the letter **P** (parietal), followed by letters instead of numbers to indicate the cytoarchitectonically different areas. Areas PF and PFG roughly correspond to Brodmann's area 7b, and areas PG and OPT to Brodmann's area 7a. Areas inside the intraparietal sulcus include the anterior, lateral, medial, and ventral intraparietal areas (**AIP, LIP, MIP, VIP,** respectively), as well as the PE intraparietal area (**PEip**) and visual area 6A (**V6A**). **Arrows** show the patterns of the principal reciprocal connections between functionally related parietal and frontal motor areas. (Abbreviations: **CMAr,** rostral cingulate motor area; **CMAv,** ventral cingulate motor area; **CMd,** dorsal cingulate motor area; **F,** frontal; **M1,** primary motor cortex; **OPT,** occipito-parieto-temporal; **P,** parietal; **PE, PF,** and **PFG** are parietal areas according to the nomenclature of von Economo; **PMd,** dorsal premotor cortex; **PMv,** ventral premotor cortex; **Pre-PMd,** predorsal premotor cortex; **S-I,** primary somatosensory cortex; **SMA,** supplemental motor area.)

cortical motor areas were thought to influence voluntary movements via their projections to M1, which then formulated the descending motor command that was transmitted to the spinal cord. This is not correct.

Several cortical motor regions outside of M1 project to subcortical areas of the brain as well as to the spinal cord in parallel with the descending projections from M1. The key descending pathway for