and across movement-related cortical areas, with stronger correlations to causal movement kinetics in M1 and to higher-order motor parameters in premotor and parietal cortex. However, these experimental findings have not yet led to a single unifying hypothesis about how cortical motor circuits control voluntary movements. Part of this uncertainty may result from inadequacies in experimental task design.

Representational motor-control models have interpreted these complex results as evidence of the transformations between different levels of representation of intended movements performed by neural populations distributed across different cortical motor areas. In contrast, nonrepresentational motor-control models such as optimal feedback control argue that these same results can only be interpreted as evidence of when and where neural correlates of different motor output parameters emerge in the dynamical activity distributed across cortical motor areas but do not shed much insight into the underlying neural computations. This illustrates the experimental challenges still confronting researchers as they try to reverse engineer the cortical motor circuitry to reveal its internal computational organization.

Sensory Feedback Is Transmitted Rapidly to the Primary Motor Cortex and Other Cortical Regions

Postcentral and posterior parietal cortex provide much of the sensory information related to the position and motion of the body and the location of spatial goals that is important in voluntary motor control, although the cerebellum is likely another important source (Chapter 37).

The type of afferent information transmitted to M1 differs between the proximal and distal portions of the limb. Afferent input from cutaneous and muscle sensory neurons is equally prevalent for hand-related neurons, reflecting the importance for both sources of sensory feedback when grasping and manipulating objects with the hand. Muscle afferents provide the major source of feedback from the proximal limb. Information from muscles is more prevalent in the rostral M1, whereas cutaneous input is more common in the caudal M1. Muscle afferent feedback to M1 is surprisingly rapid as it takes as little as 20 ms for M1 neurons to respond following a mechanical disturbance to the limb. Analogous to reaching, neural activity is broadly tuned to the direction of the mechanical disturbance.

Sensory feedback supports our ability to make rapid goal-directed corrections for motor errors that arise during movement planning and execution or are caused by unexpected disturbances of the limb. When a perturbing mechanical load is applied to the limb, the motor system generates a multipeaked compensatory electromyographic response, beginning with a short-latency stretch response (20–40 ms after the perturbation), followed by a long-latency response (50–100 ms) and then a so-called "voluntary" response (≥100 ms). The short latency of the initial response indicates that it is generated at the spinal level. The response is relatively small and stereotyped, and its intensity scales with the magnitude of the applied load. In contrast, motor corrections beginning in the long-latency epoch (50–100 ms) are modulated by a broad range of factors necessary to attain a behavioral goal, including the physics of the limb and environment, the presence of obstacles in the environment, the urgency of the goal, and properties of the target, including alternate goals. These context-dependent features suggest the long-latency feedback epoch is an adaptive process in which the control policy (ie, feedback gains) is adjusted based on the behavioral goal, as predicted by the optimal feedback control model.

The ability of the motor system to rapidly generate these goal-directed long-latency motor responses is supported by a transcortical feedback pathway. Neural activity across frontoparietal circuits responds rapidly to mechanical disturbances to a limb, and the pattern of activity across the cortex depends on the behavioral context. Perturbation-related activity is observed in all cortical regions beginning at approximately 20 ms after the disturbance even if the monkey is distracted by watching a movie and does not have to respond to the disturbance (Figure 34–23A,B). If the monkey is actively maintaining its hand at a spatial goal, there is an immediate increase in the neural response in parietal area PE following the disturbance, followed shortly thereafter by changes in activity in other cortical regions (Figure 34–23A,B). If the disturbance is a cue that instructs the monkey to move to another spatial target, then M1 activity reflects the need for a more vigorous response if the disturbance knocks the hand away from the target compared to knocking the hand into the target (Figure 34–23C). In contrast, perturbation-related activity in PE remains similar regardless of target location.

The Primary Motor Cortex Is Dynamic and Adaptable

One of the most remarkable properties of the brain is the adaptability of its circuitry to changes in the environment—the capacity to learn from experience and to store the acquired knowledge as memories. When human subjects practice a motor skill, performance improves.
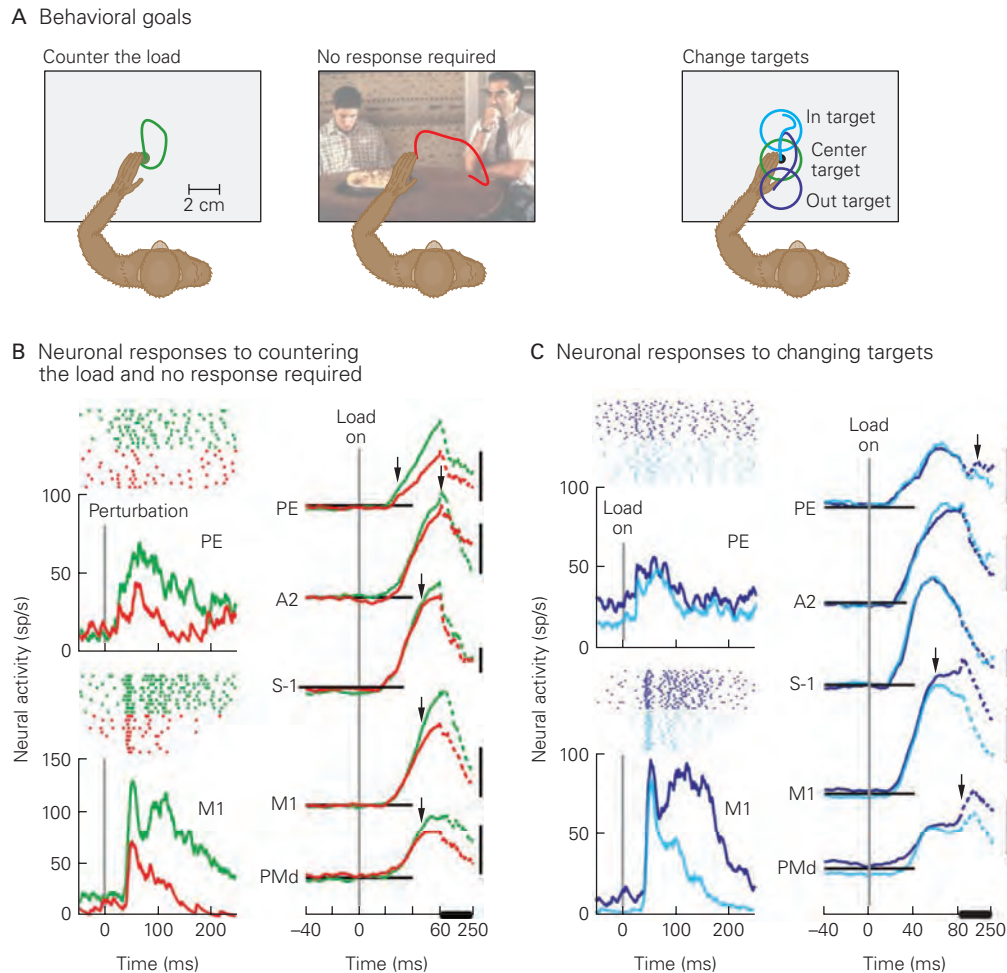
Figure 34–23 Changes in behavioral goals alter rapid sensory feedback to parietal and frontal motor cortices. (Reproduced, with permission, from Omrani et al. 2016. Part A photo is from the film American Pie and is reproduced, with permission, from Universal Studios. © 1999, Universal Pictures, All Rights Reserved.)

A. In the experiment described here, the responses of cortical regions to mechanical loads randomly applied to the arm are compared. In the *left* panel, motor corrections return the hand to the spatial goal following the disturbance (**green hand trajectory**). In the *middle* panel, the monkey watches a movie and does not have to respond to the disturbance, leading to the hand remaining to the right following the disturbance (**red hand trajectory**). In the *right* panel, the monkey places its hand at a central start target, and one of two other targets is also presented. The disturbance applied to the limb is a cue for the monkey to move to this second target with its position being either in the direction of the disturbance (**cyan** "in target" trajectory) or away from the disturbance (**blue** "out target" trajectory).

B. *Left:* Response of a neuron in PE and in M1 when a mechanical load was applied to the limb and the monkey had to counter the load and return the hand to a spatial target (**green**) or was not required to respond to the disturbance (**red**). *Right:*

Population signals in each cortical region in response to perturbations. Note how all cortical areas show an increase in activity approximately 20 ms after the applied load. **Arrows** denote when activity was different when the monkey had to respond to the disturbance (**green curve**) as compared to not being required to respond to the disturbance (**red curve**). Note that PE is the first to show a difference in activity between the two conditions. Other cortical areas show changes at 40 ms or later. A2 is a subregion of S-I. (For B and C: Vertical scale bars, 20/spikes/s; Activity between 60–250 ms (**thick horizontal line**) compressed for visualization purposes.)

C. *Left:* Responses of single neurons in PE and M1 when a mechanical load was a cue and instructed the monkey to move to another target. The disturbance either pushed the hand toward the target (**cyan**) or away from it (**blue**). *Right:* Population signals based on perturbation-related activity in each cortical region for the "in target" and "out target" conditions. The initial responses are similar for both "in target" and "out target" disturbances across all cortical areas, and **arrows** denote when there is a difference in activity between conditions. M1 is the first to display an increase in activity for the "out target" disturbance just prior to changes in muscle activity moving the hand to the spatial target.

Motor experience can also modify the motor map. In monkeys trained to use precise movements of the thumb, index finger, and wrist to extract treats from a small well, the area of the motor map in which intracortical microstimulation (ICMS) could evoke movements at these joints was larger than before training (Figure 34–24). If a monkey did not practice the task for a lengthy period, its skill level decreased, as did the cortical area from which the trained movements could be elicited by ICMS. Similar modifications of the
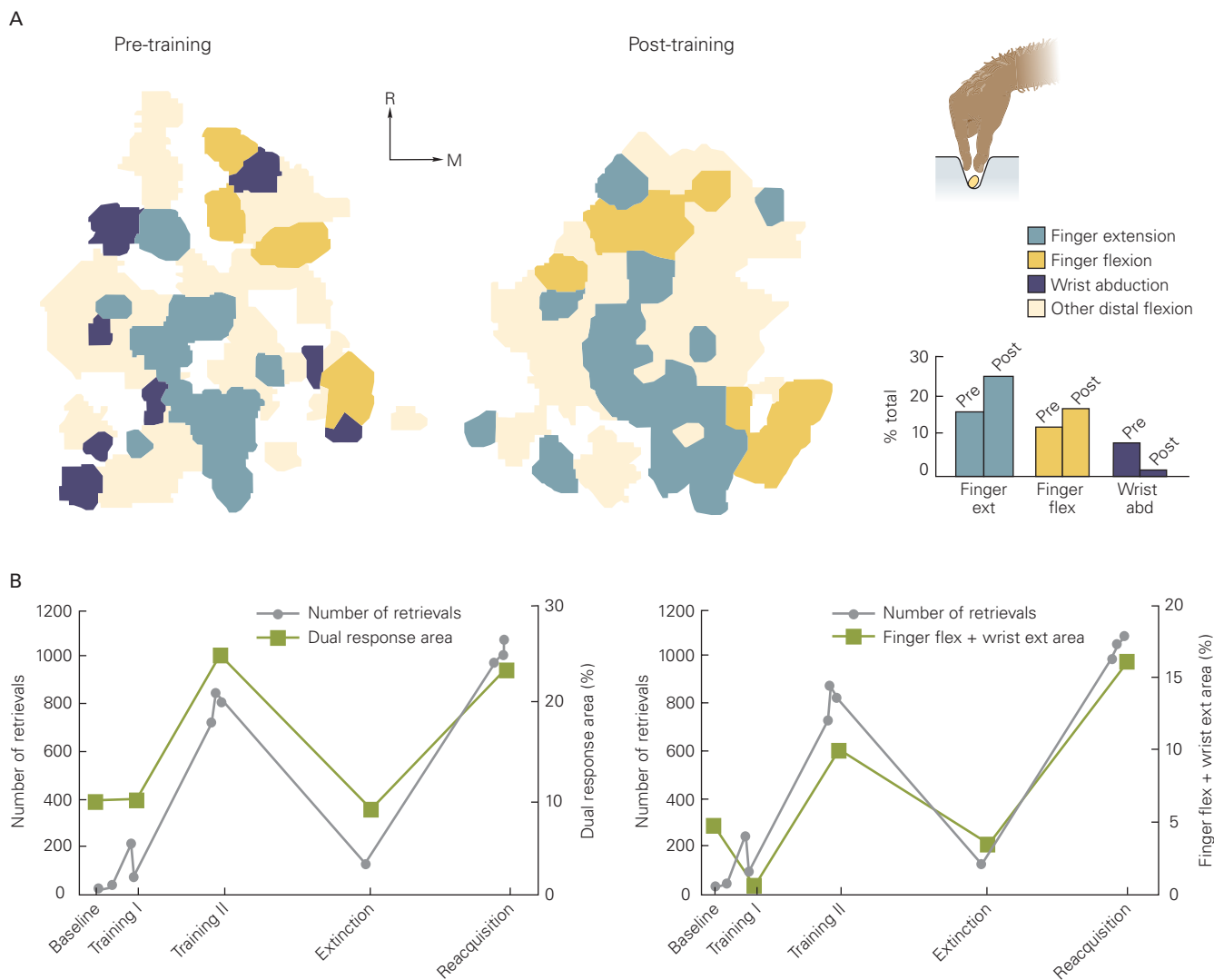
Figure 34–24 Learning a motor skill changes the organization of the M1 motor map. (Reproduced, with permission, from Nudo et al. 1996. Copyright © 1996 Society for Neuroscience.)

A. Motor maps for the hand in a monkey before and after training on retrieval of treats from a small well. Before training, areas of the motor map that generate index finger and wrist movements occupy less than half of a monkey's motor map. After training, the area from which the trained movements can be evoked by intracortical microstimulation expands substantially. The area of the map from which one could elicit individuated movements such as finger extension and flexion has expanded considerably, while the areas controlling wrist abduction, which this monkey used less in the new skill, became less prominent. (Abbreviations: **M**, medial; **R**, rostral.)

B. The areas of the motor output map parallel the level of performance (number of successful pellet retrievals) during acquisition of the motor skill and extinction (due to lack of practice). Two areas were tested: a "dual response" area (*left plot*), from which any combination of finger and wrist motions could be evoked, and an area from which the specific combination of finger flexion and wrist extension could be evoked (*right plot*). Both areas increased as the monkey's skill improved with practice and decreased as the monkey's skill was extinguished through lack of practice. These data are from a different monkey than the one in part **A** but trained for same task.

cortical representation of practiced actions in humans have been demonstrated by functional imaging and transcranial magnetic stimulation.

At least some of the processes contributing to these changes to the motor map are local to M1 itself. One of the mechanisms contributing to the cortical reorganization underlying improved reach-to-grasp performance in rodents involves changes in synaptic strength similar to long-term potentiation and depression within the local horizontal connections linking different parts of the arm motor map. It has been shown that spike-triggered ICMS could cause specific alterations to the M1 motor output map even without specific training. For instance, one study first identified two different cortical sites (A and B) that caused contractions of different muscles (muscle A and muscle B, respectively) when electrically stimulated. They then recorded the activity of a neuron at site A; whenever that neuron fired, they stimulated site B. Within a day or two of this ICMS conditioning at site B, electrical stimulation of site A was able to cause simultaneous contractions of both muscles A and B. The change likely resulted from a spike-timing dependent increase in synaptic strength that was limited to the horizontal cortical projection from site A to site B. Electromyographic responses elicited by ICMS at a third site that did not receive similar conditioning did not change, confirming that the effect was not generalized.

Motor adaptation to visual or mechanical disturbances has been studied extensively in human subjects (Chapter 30). Neural-recording studies have demonstrated that these alterations lead to changes in the activity of M1 neurons in monkeys as the animals adapt to the perturbations. For instance, when monkeys make reaching movements in a predictable external force field that pushes on the arm in a direction perpendicular to the direction of movement, their initially curved reach trajectories get straighter. As this adaptation evolves, large increases gradually arise in the activity of M1 cells whose preferred directional tuning is opposite to the applied force field. The magnitude of such adaptation-dependent changes in activity diminishes progressively as the angle between the force direction and cell preferred direction increases, following a cosine-like function. This shows that the adaptive changes were specific to the neurons that would make the greatest contribution to compensate for the external force field.

Another example of selective changes in M1 activity during motor learning comes from a visuomotor learning study in which visual feedback from a computer monitor is rotated 90° clockwise such that movements of a monkey's arm to the right result in downward movement of the cursor. Initially, the monkeys make arm movements in the original direction aimed at the visual target location, with corrections made online after movement onset. However, with practice, the monkeys begin to move in a new direction rotated counterclockwise to the visual target so that the cursor moves directly to the target. When training occurs for only one direction, learning generalizes poorly to other directions, suggesting that the adaptive changes occur only in neurons that evoke the adapted movement. The tuning curves of neurons with preferred directions near the learned direction were altered during training, whereas neurons with other preferred directions were not affected by the training. This confirmed that the adaptation was local, consistent with the findings of the force-field adaptation study, and explained why adaptation to the visuomotor rotation in one direction generalized poorly to other directions.

Motor-error signals in the precentral cortex also play an important role in trial-by-trial motor adaptation based on feedback learning. In one study with monkeys, an adjustable prism was used to displace the apparent location of the reach target in the environment. Visual feedback of the target and arm were blocked during the reaching movements, leading to systematic errors in touching the target. The monkeys were allowed to see visual feedback of the position of the hand relative to the target for a brief period of time at the end of movement (Figure 34–25). Activity in M1 and PMd during that brief period of visual feedback after movement reflected the direction of reach end-point errors and could be involved in adapting reaching movements to correct these errors. To test that hypothesis, ICMS was then used in M1 and PMd to simulate those error responses and showed that the monkeys began to make adaptive changes in their reaching movements to compensate for the simulated errors even though no reaching error was actually made.

Some motor skills are relatively easy to learn, such as compensation for a visuomotor rotation. Others, however, are very difficult to learn. Recent studies examined this discrepancy by first measuring the activity of a population of M1 neurons as the monkey moved a cursor on a computer screen using a brain–machine interface and a neural activity decoder. This population-level mapping between M1 activity and cursor motion was then altered by changing the association between the directional tuning of each neuron and cursor motion in the decoder. When the altered decoder mapping retained the normal co-modulation structure of neural activity, as would be the case for instance if the mapping between the activity of all

Figure 34–25 (right) **Error signals in the primary motor cortex drive adaptation.** After a movement is complete, M1 activity reflects the error between the spatial target and final hand position. (Reproduced, with permission, from Inoue, Uchimura, and Kitazawa 2016. Copyright © 2016 Elsevier Inc.)

A. Monkeys made reaching movements to spatial targets on a touch screen. On each trial, adjustable prism goggles shifted the viewed position of the spatial target by a variable amount during the movement, while a shutter blocked vision of the monkey's hand and the target. Feedback of the final hand position was only provided for 300 ms after contact with the touch screen at the end of movement.
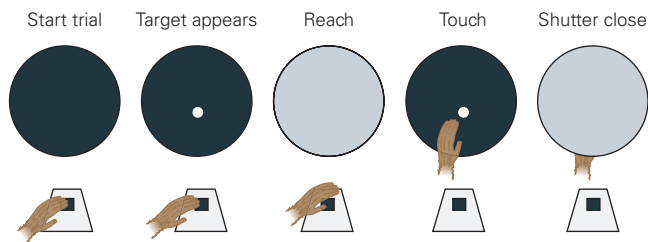
B. Top: Discharge response of a typical M1 neuron. Raster plots and spike-timing histograms are aligned with the initial screen contact (touch).

1. Distribution of reach endpoint errors (**black dots**) where the origin represents the center of the target. **Diameters of green circles** denote the firing rate of the neuron during each movement (**green bar** in **B**); the firing rates were unrelated to the subsequent endpoint error. The numbers in each quadrant indicate the summed spike activity during movements that ended in the corresponding quadrant; they are all nearly equal.
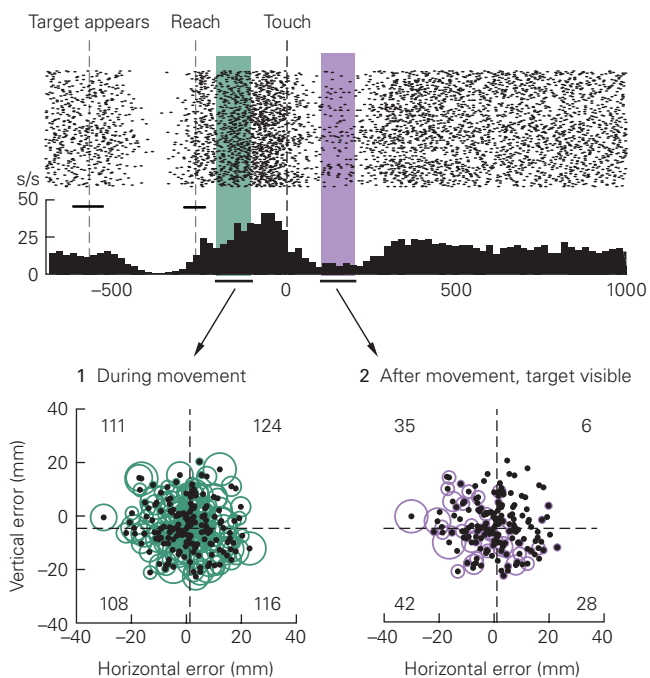
2. Same as in part **B** except **purple circles** denote firing rate 100 to 200 ms after movement while the monkey can see its hand while touching the screen (**purple bar** in part **B**). The circles and spike counts show that the firing rate is greatest for endpoint errors down and to the left relative to the position of the target (0,0), revealing that that the neural activity during this postmovement period is strongly modulated by visual feedback of reach endpoint error.

A Experiment

B Activity of an M1 neuron

1 During movement

2 After movement, target visible

neurons and cursor motions was rotated clockwise by 45°, the monkeys showed significant adaptation to the perturbation within a few hundred trials during a single recording session. In contrast, when the perturbation required the monkeys to learn a more complex "unnatural" remapping, for instance, random clockwise and counterclockwise rotations of the apparent directional tuning of neurons by different amounts, the monkeys showed little ability to recover proficient cursor control over several hundred trials in a single recording session. Importantly, another study found that monkeys could eventually master an "unnatural" change in an M1 neural activity decoder mapping if they could practice with the same altered decoder over several days, indicating that they could learn a new neural co-modulation structure if allowed enough experience with it. These studies reinforce how neural circuits in these cortical motor regions are critical for motor skill learning.

The studies just described used brain–machine interfaces and neural decoders to explore how single neurons and neural populations contribute to motor skill learning. This technology promises to be an increasingly important research tool for developing new insights into the neural mechanisms of voluntary motor control and motor skill learning (Chapter 39).

Highlights

1. Voluntary motor behavior implements an individual's intentional choice or decision to move within, and to interact physically with objects in, the environment. A hallmark of human motor action is the breadth of skills we possess and, when highly practiced, the ease and automaticity of these actions.

2. Voluntary motor control has long been separated into two stages—planning and execution—that

can be dissociated in time. Neural recording studies have found correlates of these two stages differentially distributed across many movement-related cortical areas.

3. The overall computational problem that the motor system must resolve to control voluntary movement is to convert sensory information about the current state of the world and the body into plans for action and ultimately into patterns of muscle activity that generate the causal forces required to execute the desired movement(s), while avoiding or correcting for errors.

4. Representational models of voluntary motor control such as the sensorimotor coordinate transformation hypothesis assume that the motor system directly plans and controls specific features or parameters of intended movements. Single neurons and neural populations express those parameters in their activity and perform definable computations to effect the transformations between the controlled movement parameters in corresponding coordinate frameworks.

5. Dynamical systems models of voluntary motor control, in contrast, assume that motor circuits find empirical solutions for the computations underlying the planning and execution of movements by evolutionary and individual adaptive processes. One recent theory, optimal feedback control, proposes that planning and execution of voluntary movements involve three functional processes, namely, state estimation, task selection, and a control policy. Single neurons and neural populations contribute to voluntary motor control by participating in the computations underlying these three processes.

6. Distributed frontoparietal circuits in cerebral cortex play a pivotal role in voluntary control. There are substantial reciprocal axonal interconnections between frontal and parietal cortical regions, partially segregated based on body part (eg, hand, arm, eye). Frontal motor and parietal cortical regions both directly influence spinal processing through the corticospinal tract and indirectly through brain stem descending pathways.

7. Posterior parietal cortex plays a prominent role in identifying potential goals and objects in the environment, state estimation of the body, and sensory guidance of motor actions. Important sources of sensory signals are transmitted from visual cortex through the dorsal visual pathway and from primary somatosensory cortex. Behavioral goals and objects are represented in many parietal subregions, but how they are represented (relative to the orientation of the eye, head, or arm) varies across subregions. The presence of multiple representations provides a rich basis for defining the movement-relevant properties and the locations of objects in the world and relative to the body that can be used to select and guide movement.

8. Premotor and prefrontal cortices play a prominent role in task selection and motor planning. The dorsal and ventral premotor regions are often implicated when external sensory information plays a dominant role in selecting motor actions. In contrast, more medial premotor regions, such as the supplementary and cingulate motor areas, may play a more dominant role when internal desires are more critical in selecting and initiating a motor action. However, this dichotomy is not absolute, and multiple premotor and prefrontal cortical areas all contribute to the control of voluntary behavior in a broad range of contexts and conditions.

9. Primary motor cortex in primates has a representation of the entire body along its mediolateral axis, with larger cortical territories associated with the hand and face relative to other body parts. This cortical region also provides a large component of the corticospinal tract and has projections to both interneurons and alpha motor neurons in the spinal cord.

10. Neural activity that reflects the causal forces and the spatiotemporal features of muscle activity necessary to move the limb is particularly prominent in the primary motor cortex and can be rapidly altered to correct movement errors or to compensate for displacements of the limb away from the desired movement if the limb is perturbed. However, neural activity in primary motor cortex can also show more complex properties, reflecting changes based on the behavioral context, performance goals and constraints, and features such as movement kinematics. These properties of primary motor cortex activity may reflect the formation of a task-specific control policy within the motor system.

11. Although parietal, premotor, and primary motor cortical regions play prominent roles in state estimation, motor planning, and motor execution, respectively, they are not uniquely responsible for any one aspect; they are instead distributed to some degree across most or all of these cortical regions.

12. The cortical motor system is adaptive and can undergo changes in its functional architecture to adapt to long-term changes in the physical

properties of the world and the body, as well as acquire, retain, and recall new motor skills.

13. New technologies such as large-scale multi-neuron recording and imaging methods, enhanced multi-neuron activity decoding algorithms, and optogenetic control of the activity of specific neural populations will lead to deeper insights into the functional architecture of cortical motor circuits.

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John F. Kalaska

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35

The Control of Gaze

I N PRECEDING CHAPTERS, WE LEARNED about the motor systems that control the movements of the body in space. In this and the next chapter, we consider the motor systems that control our gaze, balance, and posture as we move through the world around us. In examining these motor systems, we will focus on three biological challenges that these systems resolve: How do we visually explore our environment quickly and efficiently? How do we compensate for planned and unplanned movements of the head? How do we stay upright?

In this chapter, we describe the oculomotor system and how it uses visual information to guide eye movements. It is one of the simplest motor systems, requiring the coordination of only the 12 evolutionarily old muscles that move the two eyes. In humans and other primates, the primary objective of the oculomotor system is to control the position of the fovea, the central point in the retina that has the highest density of photoreceptors and thus the sharpest vision. The fovea is less than 1 mm in diameter and covers less than 1% of the visual field. When we want to examine an object, we must move its image onto the fovea (Chapter 22).

The Eye Is Moved by the Six Extraocular Muscles

Eye Movements Rotate the Eye in the Orbit

To a good approximation, the eye is a sphere that sits in a socket, the orbit. Eye movements are simply rotations of the eye in the orbit. The eye's orientation can be defined by three axes of rotation—horizontal, vertical, and torsional—that intersect at the center of the eyeball, and eye movements are described as rotations