those for more proximal parts of the arm. The terminal of a CM cell axon often branches and terminates on spinal motor neurons for several different agonist muscles and can also influence the contractile activity of still more muscles through synapses on spinal interneurons (Figure 34–17B,C). This termination pattern is organized to produce coordinated patterns of activity in a *muscle field* of agonist and antagonist muscles. Most frequently, a CM cell axon directly excites the spinal motor neurons for several agonist muscles and indirectly suppresses the activity of some antagonist muscles through spinal inhibitory interneurons (Figure 34–17C). The fact that CM cells are more prominent in humans than in other species may be one of the reasons why lesions of M1 in humans have a more profound effect on voluntary motor control compared to other mammals (Box 34–3).

The complexity of the motor map in M1—as revealed by short trains of electrical stimuli and anatomical and neurophysiological studies of direct and indirect M1 descending outputs targeting single muscles and small muscle groups—shows how motor commands from M1 to the spinal motor apparatus are able to control movements of every part of the body, with special focus on the fingers, hand, arm, face, and mouth in primates.

Activity in the Primary Motor Cortex Reflects Many Spatial and Temporal Features of Motor Output

As already noted, a given action such as reaching for an object can be described on many levels, ranging from the hand's spatial trajectory and velocity to its joint-centered causal forces and muscle activity (Figure 34–1A). Representational models assume that the motor system directly plans and controls specific parameters of movement. They predict that different neural populations encode the intended movement in a parameter space (ie, hand or joint motion or joint muscular torque) and perform the transformations between them. Dynamical models predict that neural circuits control movements through changes in their activation state from its current state to the desired final state. As their activity changes across time, correlates of various parameters and properties of the intended movement can be observed in the activity

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Box 34–3 Lesions in Primary Motor Cortex Lead to Impairments in Motor Execution

The effects of primary motor cortex (M1) lesions differ across species. Large lesions in cats do not cause paralysis; the animals can move and walk on a flat open surface. However, they have severe difficulties using visual information to navigate within a complex environment, avoid obstacles, or climb the rungs of a ladder. In cats, the pyramidal tract neurons in M1 are much more strongly activated when an animal must modify its normal stepping motion to clear an obstacle under visual guidance than during normal unimpeded locomotion over a flat, featureless surface (Chapter 33).

Large M1 lesions in monkeys have more drastic consequences, including initial paralysis and usually the permanent loss of independent movements of the thumb and fingers. Monkeys nevertheless recover some ability to make clumsy movements of the hands and arms and to walk and climb.

More focal lesions of M1 typically result in muscle weakness, slowing and imprecision of movements, and discoordination of multi-joint motions, perhaps as a result of selective perturbations of the control circuitry for specific muscles or muscle groups. Lesions limited to part of the motor map, such as the contralateral arm,

leg, or face, lead to paralysis of that body part. There is diminished use of the affected body part, and movements of the distal extremities are much more affected than those of the proximal arm and trunk.

The severity of the deficits also depends on the level of required skill. Control of fine motor skills, such as independent movements of the fingers and hand and precision grip, is abolished. Any residual control of the fingers and the hand is usually reduced to clumsy, claw-like, synchronous flexion and extension motions of all fingers, not unlike the unskilled grasps of young infants. Remaining motor functions, such as postural activity, locomotion, reaching, and grasping objects with the whole hand, are often clumsy.

In humans, large motor cortex lesions are particularly devastating, resulting in severe motor deficits or complete paralysis of affected body parts, usually with limited potential for recovery. This presumably reflects the increased importance in humans of descending signals from M1 onto spinal interneuronal circuits and spinal motor neurons and a diminished capacity of other cortical and subcortical motor structures to compensate for the loss of those descending M1 signals.

of single neurons and neural populations. However, the activity of most neurons reflects a combination of parameters that does not correspond to any identifiable parameter in any specific coordinate framework.

Despite their different assumptions, both perspectives suggest that one can infer the possible contribution of different neurons and different neural structures to motor control by studying how their activity correlates with different parameters of movements. The activity of M1 neurons has been intensively studied since the 1960s to try to reveal, for instance, whether M1 generates a high-level signal about the hand motion or a lower-level kinetic signal more related to the causal forces and muscle activity.

Knowledge about the nature of the control signals generated by M1 also helps to clarify the role of other motor structures, notably the spinal cord. If M1 encodes specific information about muscle activity patterns, less computational processing would be necessary at the spinal level. In contrast, if M1 mainly encodes higher-level information about the intended movement, the spinal cord would have to perform the processes that convert this global signal into detailed patterns of muscle activity.

However, one of the major experimental challenges in identifying how M1 controls movement is the fact that virtually all movement-related parameters are intercorrelated through the laws of motion. As a consequence, a particular muscular force (kinetics) will cause a specific motion (kinematics) given an initial condition (posture, movement) of the body. As a result, if one recorded neural activity while a monkey makes reaching movements in different directions, a neuron that theoretically signals the spatial direction of movement will also inevitably show a correlation with the direction of causal forces. Likewise, the contractile activity of a muscle will co-vary systematically with the spatial direction of movement even though it is clearly generating the causal forces. Unless the task design adequately dissociates these different classes of parameters, it will yield ambiguous information about the functional role of each neuron.

Edward Evarts was the first to examine this issue in the 1960s, in pioneering single-neuron recordings in monkeys while they made simple flexion/extension movements of the wrist. Using a system of pulleys and weights, he applied a load to the wrist of the monkey that pulled the wrist in either the direction of flexion or extension in different trials. This required the monkey to alter the level of wrist muscle activity to compensate for the load while making the movements. As a result, the kinematics (direction and amplitude) of wrist movements remained constant, but the kinetics (forces and muscle activity) changed with the load.

Using a microelectrode, he located single neurons in the M1 motor map that modulated their activity when the monkey made movements of the wrist without the external load. In some neurons, their discharge increased during wrist flexion (*preferred movement direction*) and was suppressed during extension, whereas others displayed the opposite pattern. This movement-related activity typically began 50 to 150 ms before the onset of agonist muscle activity, supporting a causal link between M1 neural activity and movement. When a load was applied, many M1 neurons increased their activity when the load resisted movement in their preferred direction and decreased activity when the load assisted the movement (Figure 34–18). These changes in neural activity paralleled the changes in muscle activity required to compensate for the external load.

Subsequent studies have confirmed that the activity of many M1 neurons varies systematically with the magnitude of muscle force output. This is best shown in tasks in which monkeys generate isometric forces against immovable objects that prevent movement. The activity of many M1 neurons, including CM cells, varies with the direction and level of static isometric output forces generated across a single joint, such as the wrist or elbow, as well as during precise pinches using the thumb and index finger (Figure 34–19A). At least over part of the tested range, these responses vary linearly with the level of static force.

Most natural behaviors involve multi-joint, multi-muscle actions. For instance, reaching movements of the arm in different directions requires different patterns of coordinated motions at the shoulder and elbow. Proximal limb muscle activity during reaching shows a roughly cosine pattern of activity with maximal activity in a specific movement direction, its preferred movement direction, that gradually diminishes as the angle between the desired direction of reach and the muscle's preferred direction increases (Figure 34–20A). Like the proximal arm muscles, single neurons related to shoulder and elbow movements respond in a continuously graded fashion during movements in different reach directions centered on a preferred direction of maximal activity (Figure 34–20B). Different neurons have different preferred directions that cover the entire directional continuum around the circle, and during any given movement, neurons with a wide range of preferred directions discharge at different rates.

As Ed Evarts had shown in single-joint tasks, much of the M1 activity during reaching is closely related to the causal kinetics. For instance, in monkeys trained to make reaching movements in eight directions while compensating for external loads that pulled the arm in different directions, the reach-related activity of both
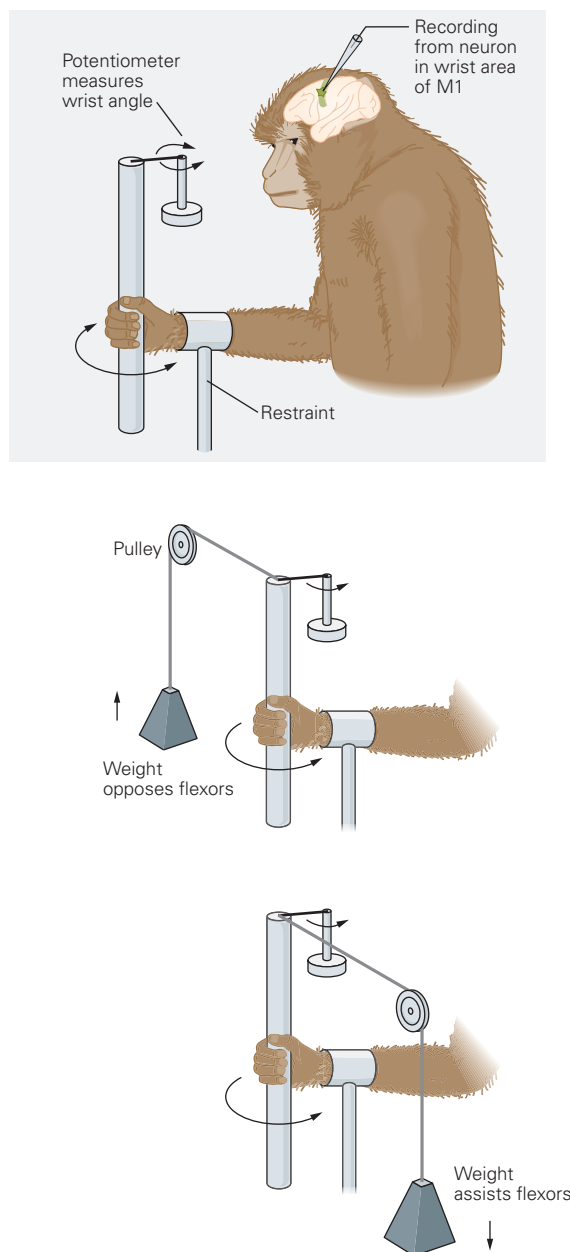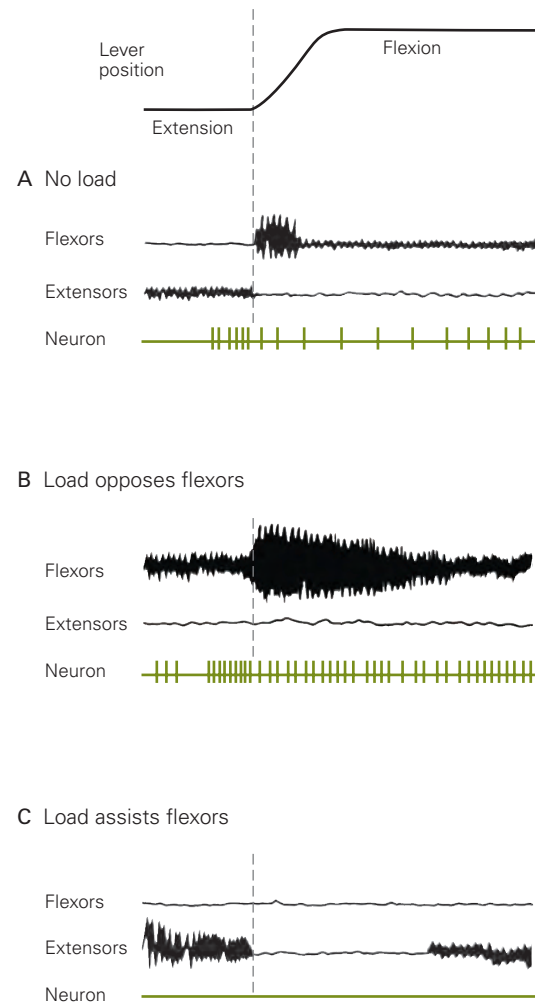
Figure 34–18 Activity of a motor cortex neuron correlates with changes in the direction and amplitude of muscle forces during wrist movements. The records are from an M1 neuron with an axon that projected down the pyramidal tract. The monkey flexes its wrist under three load conditions. When no load is applied to the wrist, the neuron fires before and during flexion (**A**). When a load opposing flexion is applied, the activity of the flexor muscles and the neuron increases (**B**). When a load assisting wrist flexion is applied, the flexor muscles and neuron fall silent (**C**). In all three conditions, the wrist displacement is the same, but the neural activity changes as the loads and compensatory muscle activity change. Thus, the activity of this motor cortex neuron is better related to the direction and level of forces and to muscle activity exerted during the movement than to the direction of wrist displacement. (Adapted from Evarts 1968.)

proximal-arm muscles and many M1 neurons changed systematically with the direction of the external loads and the corresponding corrective forces that the monkeys had to generate for each reach direction. Both muscle and neural activity increased when the load resisted movements in their preferred directions and decreased when the loads assisted those movements. In addition, when a monkey uses its whole arm to exert constant isometric force levels in different directions at the hand, the activity of many M1 neurons varies
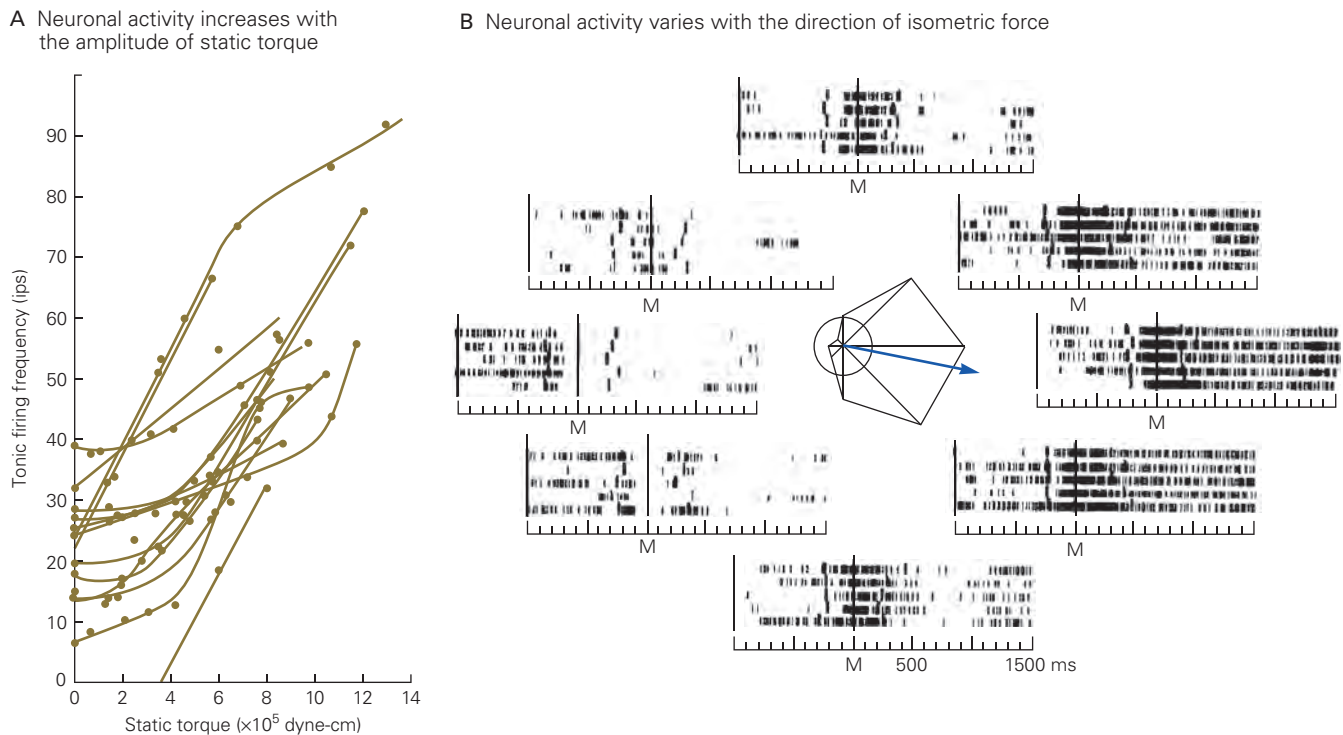
A Neuronal activity increases with
the amplitude of static torque

B Neuronal activity varies with the direction of isometric force

Figure 34–19 Activity in many primary motor cortex neurons correlates with the level and direction of force exerted in an isometric action.

A. The activity of many primary motor cortex neurons increases with the amplitude of static torque generated across a single joint. The plot shows the tonic firing rates of several different corticomotoneuronal cells at different levels of static torque exerted in the direction of wrist extension. Other motor cortex neurons show increasing activity with torque exerted in the direction of wrist flexion, and so would show response functions with the opposite slope (not shown). (Reproduced, with permission, from Fetz and Cheney 1980.)

B. When a monkey uses its whole arm to push on an immovable handle in its hand, the activity of some primary motor cortex neurons varies with the direction of isometric forces. Each of the eight raster plots shows the activity of the same primary motor cortex neuron during five repeated force ramps in one direction. Each row shows the pattern of spikes during a single trial of the task. The position of each raster of activity corresponds to the direction in which the monkey is generating isometric forces on the handle. The onset of the force ramp is indicated by the vertical line labeled **M**. The **thick ticks** on the left of that line in each row indicate when the target appeared on a computer monitor, telling the monkey the direction in which it should push on the handle. The central polar plot illustrates the directional tuning function of the neuron as a function of the direction of isometric forces. (Reproduced, with permission, from Sergio and Kalaska 2003.)

systematically with force direction, and the directional tuning curves for isometric force resemble those for activity during reaching movements (Figure 34–19B).

The complex and nonlinear properties of multisegmented limbs present a major control problem for the motor system. For instance, one can make reaching movements with similar hand trajectories but different arm geometries that require changes in the causal joint-centered torques and muscle activity. In one experiment, when monkeys made horizontal reaching movements along the same planar spatial hand trajectories while holding the arm in different spatial orientations (ie, elbow raised versus lowered), the activity of proximal-arm muscles and many M1 neurons showed corresponding changes in the strength and directional

tuning of their reach-related activity. This indicates that the M1 neurons generate signals that take into account the changes in intrinsic limb biomechanics during the reaching movements.

Similarly, arm movements toward or away from the body require much larger angular motion at the shoulder and elbow joints compared to movements to the right or left. In contrast, muscular torques tend to be larger for movements to the right and left. Both of these factors influence the amount of muscle activity required to move the limb, which can be quantified by a single term, joint muscular power (joint angular velocity multiplied by net muscular torque about that joint). With the limb in the horizontal plane, joint power is greatest for movements away from the body and slightly to the left,
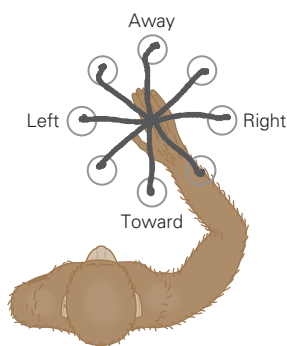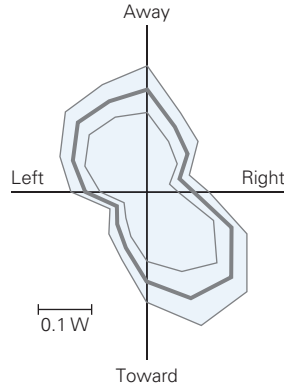
A Posterior deltoid EMG activity
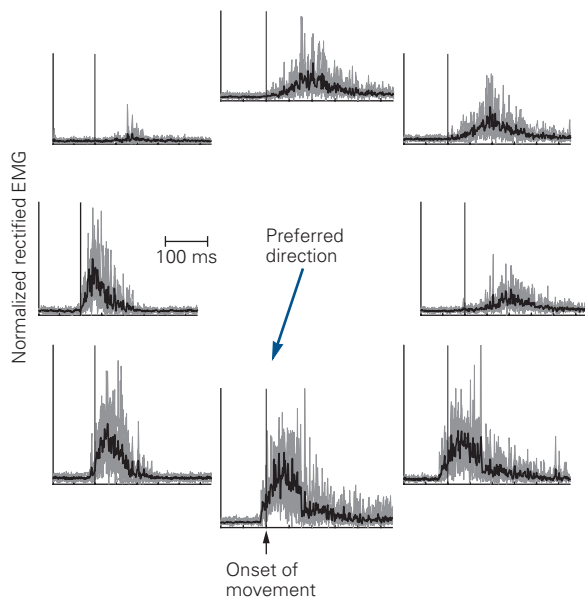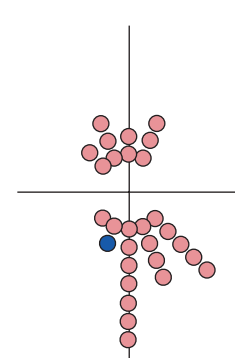

B Primary motor cortex cell activity
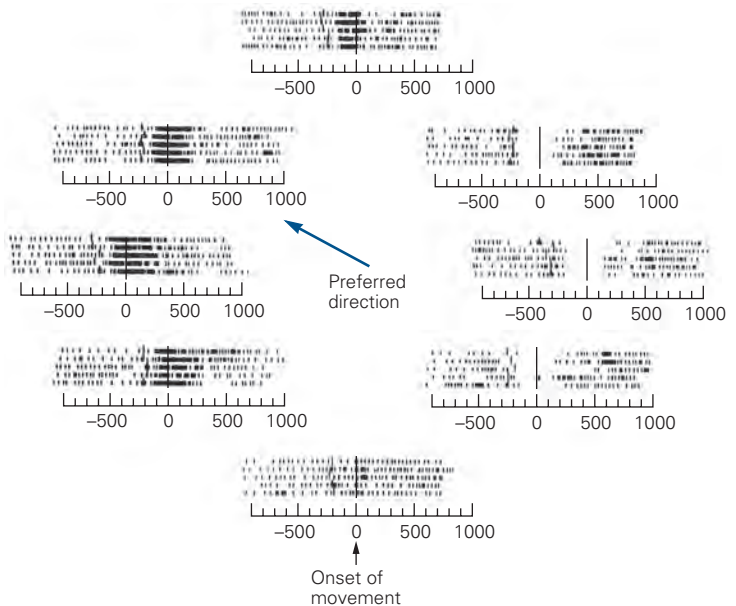
C Hand motion

D Joint power
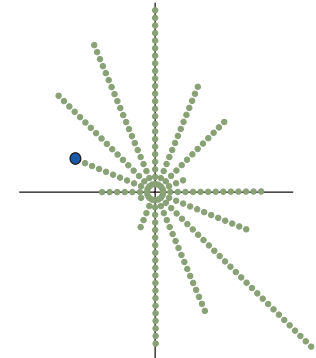

E Muscle activity

F M1 Activity

Figure 34–20 Limb muscles and primary motor cortical neurons are broadly tuned to the direction of reaching.

A. Plots show the activity of posterior deltoid of the right arm, a shoulder extensor, during arm movements in eight directions (see panel C) (central panel displays mean hand trajectories). The muscle is initially maximally active for movements at 270° (towards the body, preferred direction = 250°) and diminishes for movements in other directions. **Black lines** denote the mean activity of the muscle across multiple trials, and data are aligned on movement onset (**vertical thin line**). (Abbreviation: EMG, electromyography.)

B. Raster plots show the firing pattern of a single primary motor cortex neuron during whole-arm movements in eight directions. The neuron discharges at the maximal rate for movements near 135° and 180° and at lesser intensities for movements in other directions. The cell's lowest firing rate is for movements opposite the cell's preferred direction. Each row of **thin tics** in each raster plot represents the activity in a single trial, aligned at the time of movement onset (time 0); **thick tics**, time of target appearance. (Reproduced, with permission,

from Georgopoulos et al. 1982. Copyright © 1982 Society for Neuroscience.)

C. Hand trajectories when reaching from a central position in the horizontal plane.

D. Peak joint power (joint muscular torques multiplied by joint velocity) for movements performed in different spatial directions (shoulder and elbow power added together). A large amount of power is required to reach away from the body and to the upper left and to reach toward the body and to the lower right. (Right X-axis is at 0°.)

E. Preferred directions of proximal-limb muscles tend to be for movements that require greater muscular power, reflecting the obvious link between muscle use and the physical requirements of the motor task. Each **dot** represents an individual muscle binned into 22.5° sectors; the **blue dot** represents the preferred direction of the muscle displayed in panel **A**.

F. Distribution of preferred directions of neurons in primary motor cortex (**M1**). Each **dot** represents an individual neuron, and the **blue dot** represents the preferred direction of the neuron displayed in panel **B**. (Adapted, with permission, from Scott et al. 2001.)

and toward the body and to the right (Figure 34–20C,D). This bias in the physics of limb movement leads to a bias in the preferred directions of shoulder and elbow muscles, which tend to be maximally active in these same directions (Figure 34–20E). Correspondingly, the distribution of preferred directions of neurons in M1 also parallels this bias, with neurons tending to have preferred directions either away and slightly to the left or toward and to the right (Figure 34–20F). Thus, the physics of the limb dictates the pattern of muscle activity needed to generate movement, and this in turn is reflected in the pattern of neural activity in M1.

The impact of limb physics on M1 activity extends to the level of muscle-related signals. The activity of some single M1 neurons, including CM cells, can be correlated with specific components of the contraction patterns of different muscles during such diverse tasks as isometric force generation, precision pinching of objects between the thumb and index finger, and complex reaching and grasping actions (Figure 34–21). These findings highlight how M1 contributes to the specification of muscle activity patterns for motor actions, including onset times and magnitudes. Nevertheless, the final pattern of muscle activity will only be generated by the spinal motor neurons since they alone take into account the additional influence of other descending supraspinal inputs and local spinal interneuronal processes.

All the studies described so far related the activity of single M1 neurons to motor output. However, voluntary motor control is implemented by the simultaneous coordinated activity of many neurons throughout the motor system. Their activity is noisy, varying stochastically between repetitions of the same movement. Furthermore, their broad symmetrical movement-related tuning curves introduce a high level of uncertainty as to what the limb should do in response to the ambiguous signal generated by each neuron.

A simple computational approach was developed to extract a unique signal about each reaching movement by pooling the heterogeneous single-neuron activity of the recorded M1 population. The activity of each neuron is represented by a vector pointing in its preferred direction; the length of the vector varies as a function of its mean discharge rate during reaches in each direction. This vector notation implies that an increase in the activity of a given M1 neuron evokes changes in activity in the spinal motor apparatus and muscles that causes the arm to move along a path corresponding to the neuron's task-related preferred direction; the strength of that single-neuron influence varies systematically with the difference between the neuron's preferred direction and the desired movement (Chapter 39, Figure 39–6). When the reach-related
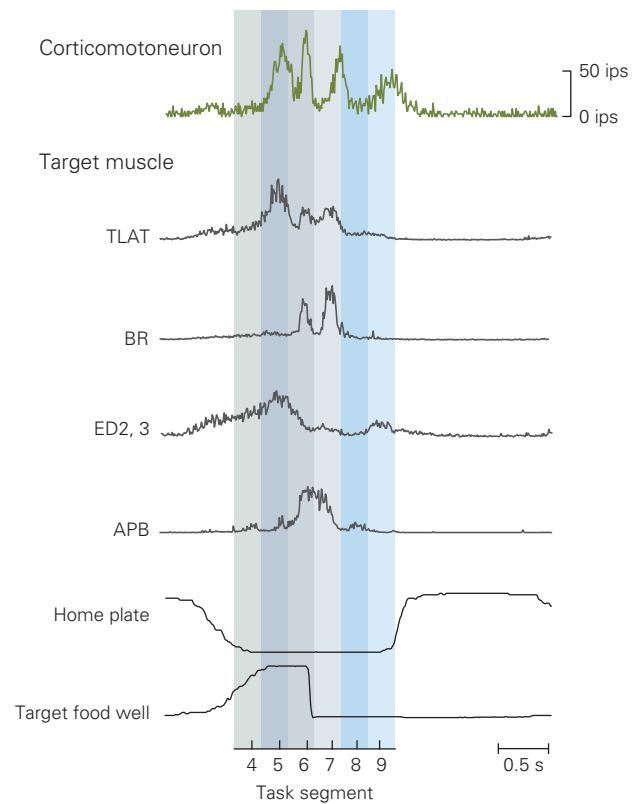

Figure 34–21 The activity of some primary motor cortex neurons can be correlated with particular patterns of muscle activity. Bursts of activity in a single corticomotoneuron during a reach-and-grasp movement to retrieve food pellets from a small well are correlated with bursts of contractile activity in several of its target muscles at different times during the movement. (Abbreviations: **APB**, abductor pollicis brevis; **BR**, brachioradialis; **ED2, 3**, extensor digitorum 2, 3; **ips**, impulses per second; **TLAT**, lateral triceps.) (Reproduced, with permission, from Griffin et al. 2008.)

activity of about 250 M1 neurons was represented by variable-length vectors for each of the eight reach directions and summed, the direction of the net resultant *population vectors* varied systematically with the actual reach directions (Figure 34–22A).

The novel insights of this analysis were that the control of a given reach movement involves coordinated changes in the activity of M1 neurons distributed throughout the M1 arm motor map and that their pooled activity clearly distinguishes the unique identity of each of the reach actions generated by the eight different distributed patterns of population activity. Subsequent studies demonstrated that "instantaneous" population vectors extracted from the pooled activity of large populations of M1 neurons during sequential 20-ms time bins from the start to the end of movement predicted the continually changing trajectory of the
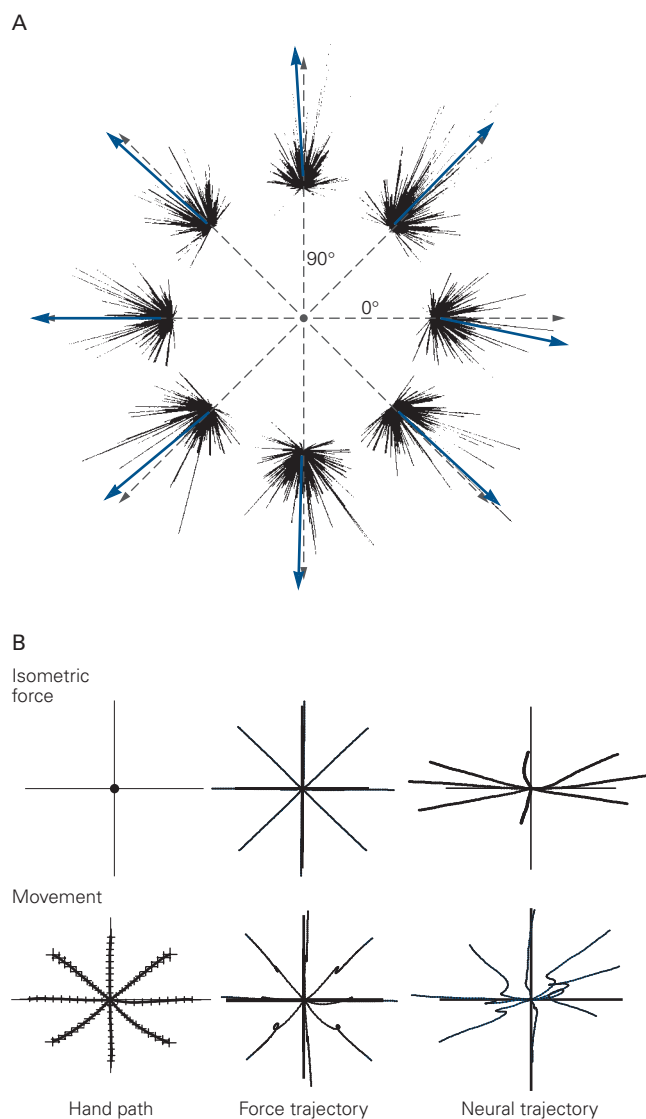
A

B

Isometric
force

Movement

Hand path   Force trajectory   Neural trajectory

Figure 34–22 Population codes relate M1 activity to different properties of movement.

A. The eight single-neuron vector clusters (**thin black lines**) and the population vectors (**blue arrows**) represent the activity of the same population of cells during reaching movements in eight different directions. Each single-neuron vector points in the neuron's preferred movement direction, and its length is proportional to the discharge of the neuron during that movement. The population vectors were calculated by vectorial addition of all the single-cell vectors in each cluster; **dashed arrows** represent the direction of movement of the arm. (Reproduced, with permission, from Georgopoulos et al. 1983.)

B. Comparison of hand kinematics and kinetics and neural population activity in an isometric task and when moving a handle with a large mass. Force and neural trajectories were generated by linking sequences of 20-ms output force vectors or neural population vectors tip-to-tail for each direction of force or movement output. (Reproduced, with permission, from Sergio et al. 2005.)

arm motions 100 to 150 ms into the future while monkeys made reaching movements or traced spirals on a computer monitor. This showed that the simple vector notation could be used to extract from the activity of populations of neurons a signal about intended motor output even on a moment-to-moment basis. These findings were anticipated by a prescient study in 1970 by Donald Humphrey and colleagues, who showed that the appropriately summed activity of three to five M1 neurons was better correlated to the temporal patterns of motor output during single-joint movements than was the signal of any of the single neurons.

Subsequent studies used the population-vector decoder algorithm to provide further insight into neural processing in M1. In one study, the activity of proximal arm–related M1 neurons was recorded while monkeys performed two tasks (Figure 34–22B). In the first task, they generated isometric force ramps in eight different spatial directions uniformly distributed at 45° intervals in a horizontal plane against a rigid handle that they held in their hand, without arm movements. A 20-ms population-vector decoder was used to extract the net directional bias of the pooled activity of many M1 neurons, and the result showed that these pooled signals varied systematically with the direction of output forces throughout the duration of the force-ramp generation, even though there were no movements. However, unlike the actual uniformly distributed directions of the forces generated by the monkey at the hand, the decoded population-vector signals were skewed toward the *x*-axis. This showed that the M1 activity reflected the nonlinear relationship between causal shoulder muscle torques and measured isometric forces at the hand resulting from the complex biomechanical properties of the arm (see Figure 34–20).

In the second task, the monkeys made reaching movements of the arm in the same eight directions to move a heavy handle. This required an initial accelerative force in the direction of movement and then a transient reversal of the direction of forces to decelerate the movement of their arm and the mass as it approached the target. The decoded M1 population-vector signals in this task varied dramatically through time. They were directed initially toward the target but then transiently reversed just before the peak of hand velocity. This showed once again that the M1 activity was more closely correlated with the time course of causal forces generating the reaching movements, including their transient directional reversal, than to the uninterrupted motion of the hand toward the target. They also found that correlates of the forces to generate reaching were strongest in M1, weaker in PMd, and largely absent in PE/MIP. This indicated that, unlike M1,

reach-related neurons in area PE/MIP generated a reliable signal about stable arm postures and the kinematics of arm movements independent of the underlying causal forces and muscle activity.

Finally, one study has shown that reliable signals about the time-varying activity of proximal-arm muscles during reaching movements can be extracted from the activity of a population of simultaneously recorded M1 neurons. Another study found that the pooled activity of M1 neurons that fire selectively in connection with either shoulder or elbow movements can predict the changes in onset times and levels of contractile activity of the shoulder or elbow muscles during reaches in different directions.

These studies showed that the pooled activity of many M1 neurons is a rich and reliable source of signals about different time-varying attributes of whole-arm movements. This provided an important conceptual foundation for the development of more sophisticated decoder algorithms in brain–machine interfaces that make use of the movement-related information available in the simultaneous activity of many M1 neurons to allow subjects to control the actions of neuroprosthetic devices by covert modulations of M1 neuron activity without overt limb movements (Chapter 39).

Primary Motor Cortical Activity Also Reflects Higher-Order Features of Movement

Activity in M1 is not correlated only with causal forces and muscle activity. Many studies, beginning with those of Ed Evarts, that have attempted to dissociate kinematic from kinetic properties of motor outputs have found that the activity of some M1 neurons varies with the direction of movement but is only weakly influenced or not influenced at all by changes in output forces. Such neurons appear to preferentially signal the kinematic aspects of limb motion.

Changes in behavioral task can influence the relationship between M1 activity and motor output. One study has highlighted how contextual changes in an isometric force task altered the coding of force magnitude by M1 neurons. Either the order of forces or the range of expected forces results in changes in the activity in M1. They suggested that M1 neurons could dynamically adjust their relationship to output forces to optimize precision of control as a function of the range of forces that would be encountered in a given context. Another study found that many CM neurons may discharge intensely when monkeys performed precisely controlled force tasks with low force levels but are relatively inactive when the monkeys generate powerful contractions of the same muscles to make

brisk, back-and-forth movements of the handle. Likewise, a study demonstrated that CM cells in M1 could be very active when monkeys generated a precision-pinch grip of the thumb and index finger with relatively low force output, but were much less active or nearly silent when the animals generated much larger forces with a power grip involving the entire hand.

Still another study has shown that some M1 neurons that respond to loads applied to the limb during postural control can lose this load sensitivity as soon as the monkey makes a reaching movement to another spatial target, and vice versa. That is, those neurons can reflect output forces during postural control, but reflect only kinematics during movement. This change in the cell's response occurs quite abruptly, about 150 ms before the onset of movement. Importantly, any neurons that are sensitive to loads during both posture and movement will retain the same motor field across behaviors; that is, if the neuron responds only to shoulder flexor loads during postural control, it will respond only to shoulder flexor loads during reaching.

Even a simple change in the metrics of limb movement can have a large influence on M1 activity. In a study of monkeys making slow or fast reaching movements in different directions from a central target to peripheral targets, proximal limb muscles displayed relatively simple scaling of their activity patterns, reflecting increased forces for faster and longer reaches. In contrast, M1 neurons displayed a broad range of changes in their activity patterns that rarely paralleled the pattern of changes observed for muscles.

Activity in neurons can also correlate with higher-level features of movement such as the nature of an upcoming motor action. This was demonstrated in a study in which monkeys were trained to make wrist movements to three targets in a row starting from one extreme, stopping at a central position, and then finishing at the other extreme. Visual cues instructed the monkeys when to make each movement. Because the task used a predictable sequence of wrist movements, the monkeys knew before the visual cues appeared what would be the next direction of movement. While many M1 neurons signaled the current wrist posture or the direction of each movement while they were being performed, some M1 neurons reliably signaled the next movement in the sequence before the visual cue appeared. Many subsequent studies have confirmed that M1 neurons can signal impending intended movements, although these planning-like signals are not as prominent in M1 as in premotor cortical areas.

In summary, neural recording studies have revealed a diverse range of response properties within

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.