Cortical Motor Control

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R. Chris Miall

Brief History

The localization of motor functions within the cerebral cortex has a long history, dating back to the demonstration in 1870 by Fritsch and Hitzig that weak electrical stimulation of the cortex of the dog could evoke movements of the contralateral limbs. At about the same time, Hughlings Jackson made careful clinical observations of the convolutions of epileptic patients, including his own wife. Epileptics often have a spasm of the muscles that may spread sequentially from, for example, the fingers up the arm to the shoulder. Hughlings Jackson realized that the March of the seizures along the limb (*Jacksonian March*) might reflect some physiological event sweeping across a topographical map of the body within the brain. These ideas were later confirmed by experiments, initially on dogs and monkeys, in which the cortex was stimulated with brief electric shocks. In 1906, Sherrington showed that movements could be evoked most easily from an area now known as the *primary motor cortex*, and this finding was extended by Penfield in the 1950s, who demonstrated during brain surgery on epileptic patients that the body was topographically mapped on the surface of the human motor cortex (Fig. 37.1). More recently, the unknown events that Hughlings Jackson predicted were shown to be waves of neuronal activation which spread across this topographical map.

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The Cerebral Cortex Has Multiple Motor Areas

Penfield in the 1950s demonstrated during brain surgery on epileptic patients that the body was topographically mapped on the surface of the human motor cortex (Fig. 37.1).

It is now clear that there are actually several distinct motor areas (Fig. 37.2). These are the *primary motor cortex*, M1 or Brodmann's area 4, which corresponds to the area stimulated by Fritsch and Hitzig; the *premotor cortex*, PMC or area 6, lying rostral to M1; and the *supplementary motor area* (SMA), lying more medially within area 6 and partly hidden on the medial surface of the longitudinal fissure. Other areas that are less directly involved include the cingulate motor area, further below the SMA on the medial wall; the *posterior parietal cortex*; and, in fact, the somatosensory cortex as well. Voluntary control of the eyes involves separate areas known as the *frontal eye fields* and *supplementary eye fields*, which lie in front of the premotor cortex within area 8.

The remainder of this chapter will discuss these various areas in what is their probable sequence of activations during the generation of movements of the limbs. Control of the eyes will be discussed elsewhere. Control of speech vocalization (but not the interpretation of speech) involves an area of frontal cortex known as Broca's area (Fig. 37.2), which lies in the inferior frontal gyrus, adjacent to the ventral premotor cortex.
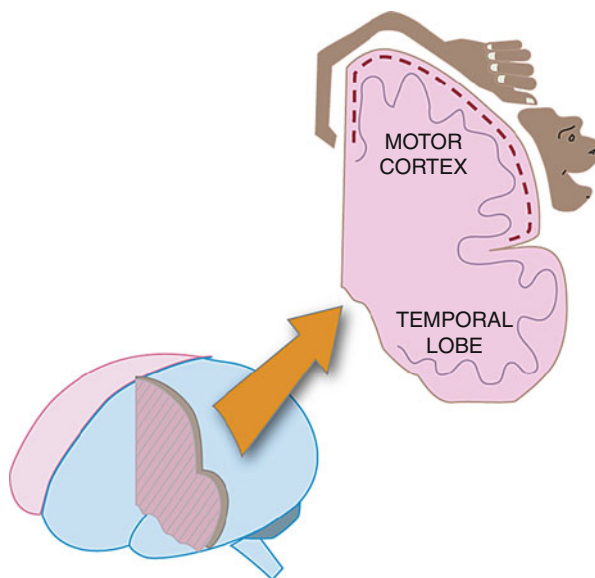

Fig. 37.1 The motor map in the precentral cortex. Electrical stimulation of the surface of the motor cortex evokes movements in different parts of the body, and from this, a motor "homunculus" can be drawn on the surface of the cortex (Adapted from Penfield and Rasmussen 1950)
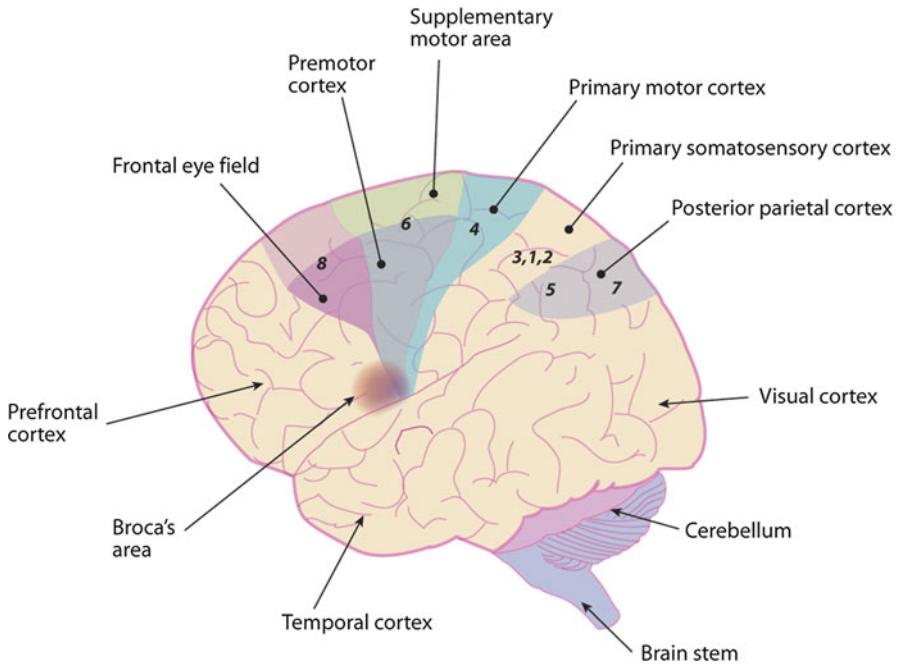
Fig. 37.2 The motor areas of the cerebral cortex. The *numbers* in each area are the Brodmann's area number, for example, BA4 is the primary motor cortex. The posterior parietal cortex (PPC) in monkeys includes BA 5 and 7, but in humans, these two areas are only the superior portion of the PPC, and the exact correspondence between different areas in man and monkey is still being established

The Supplementary Motor Area Is Involved in Planning Complex Movements

The supplementary motor area (SMA) is now known to be made up of two distinct regions, confusingly labeled the SMA proper and the pre-SMA. The SMA proper is closely interconnected with the other motor areas, M1 and PMC, whereas the pre-SMA is more heavily interconnected with prefrontal areas. For the remainder of this chapter, the term SMA will be used to mean SMA proper. The main inputs to the SMA arise from the basal ganglia, via the ventral-anterior thalamus, from the parietal and premotor cortices, and from the contralateral SMA (Fig. 37.3). The pre-SMA receives inputs from the basal ganglia and from non-motor areas of the cortex (prefrontal and temporal). Together, these regions receive a complex set of inputs that have been highly processed by other cortical areas. The main outputs of the SMA are to the adjacent premotor cortex, bilaterally to the motor cortex, and to the basal ganglia, to thalamic nuclei and the brain stem and spinal cord. Thus the SMA's outputs are principally to other motor structures. The pre-SMA sends much of its output forward to the dorsolateral prefrontal cortex but also projects to the basal ganglia.
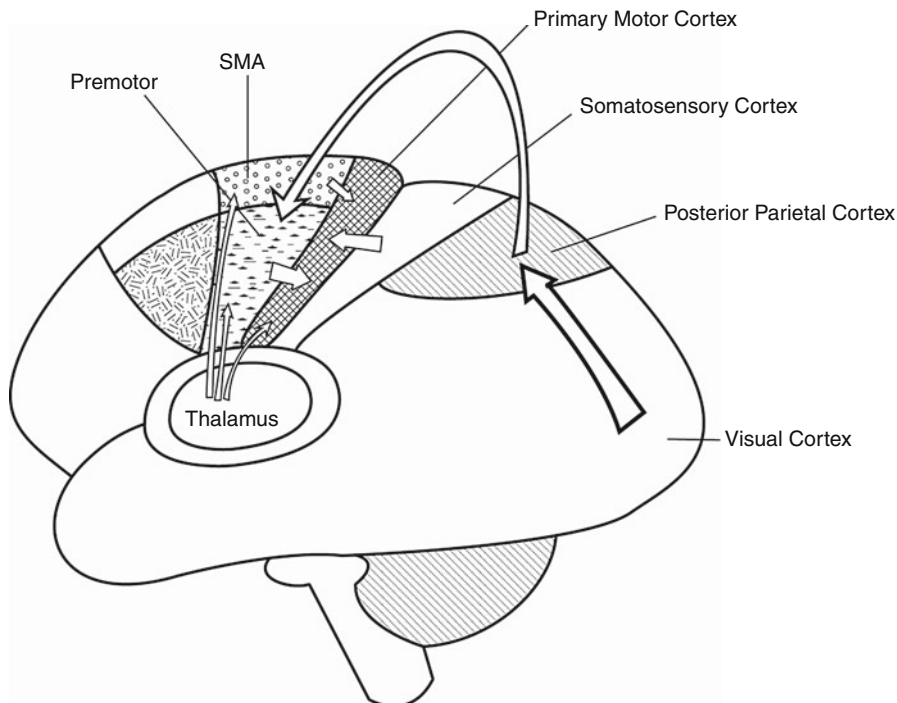
Fig. 37.3 The main cortical and thalamic connections of the motor cortex. Topographically organized sensory information is provided by the thalamus and somatosensory cortex. The main thalamic projections to premotor (PMC and SMA) and motor cortices in the monkey are from the oral ventrolateral (VLo) and ventroposteriolateral (VPLo) thalamic nuclei, respectively; in man, these are known as Vo and Vim, respectively. The input from basal ganglia is mainly to VA and VLo, whereas input from the cerebellum is mainly to Vim (and in monkey, area X). Highly processed sensory and cognitive input to the primary motor cortex is provided by the premotor cortex and supplementary motor cortex; there are also important indirect pathways from the visual cortex via the posterior parietal cortex

The SMA is topographically arranged. Electrical stimulation at different sites can therefore evoke movement in different parts of the body – the legs more caudally and the arms more rostral. The threshold for evoking movement is higher than in the primary motor cortex, however, and the topography is less clear – see later. Movements are not easily stimulated from the pre-SMA, suggested a separate role for this area. The movements evoked from the SMA proper also tend to be quite complex, for example, a grasping motion involving the whole hand. This and the large projection from the SMA to the primary motor cortex suggest that the SMA precedes the primary motor cortex in generating movement.

In monkeys, activity in single cells within the SMA has been recorded during complex motor tasks. For example, both SMA and pre-SMA cells may respond to a pull or push hand action, but only if that action is in a particular sequence of other actions, responding differently for twist-pull-push compared to twist-push-

Fig. 37.4 Neurons in the
premotor cortex can be
classified into three groups.
A monkey was trained to wait
without moving after the
presentation of a priming
stimulus until a second light
switched on. The *upper graph*
in each panel shows the
activity of a single cell in the
premotor cortex, averaged
over many trials. The *lower
graphs* are *raster plots* in
which the activity is shown
trial by trial. The cells are
grouped by correlating their
activity with the time of the
"get set" or "go" stimuli
(Adapted from Weinrich et al.
1984)
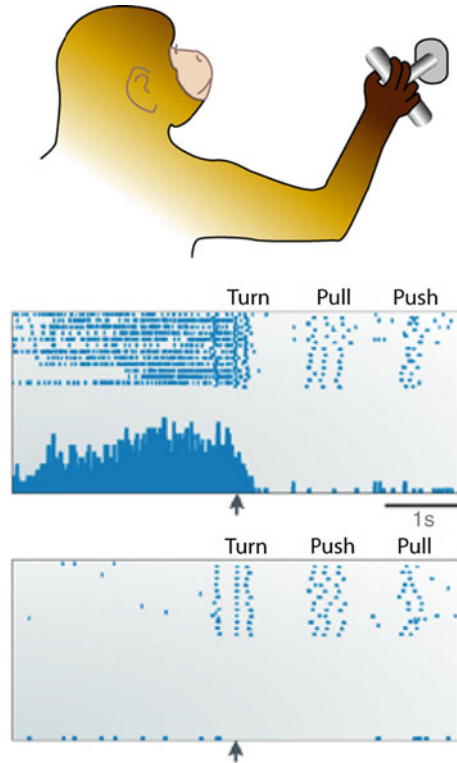
pull (Fig. 37.4). In general, the SMA is active well before any movement occurs and seems particularly to respond to the sensory cues used to trigger the monkey's movements. The SMA cells tend to be less clearly related to the time or direction of arm movements that the monkey performed. The SMA seems therefore to be concerned with the preparation to make complex voluntary movements and with the sensory cues triggering movement. In man, the SMA is thought to be the main cortical area that generates the *Bereitschaftspotential*, a potential recorded in the scalp EEG that precedes voluntary planned actions by up to a second. One suggestion is that the SMA may also play a role in adjusting posture before limb movement. Part of this involves stabilizing the proximal musculature to support the moving limb, and therefore, it is not surprising that the spinal projections of the SMA tend to be onto motor neurons of the proximal and axial muscles. There is also evidence that the SMA and especially the pre-SMA have important roles in learning movement sequences.

Lesions of the SMA have few obvious long-term effects unless they are bilateral. Then the patient often displays difficulties in using both hands simultaneously and may also exhibit rather few spontaneous movements and also reduced speech. Actions that require different movements from each hand (e.g., doing up buttons) are particularly affected. The SMA therefore seems to have a particular role in the
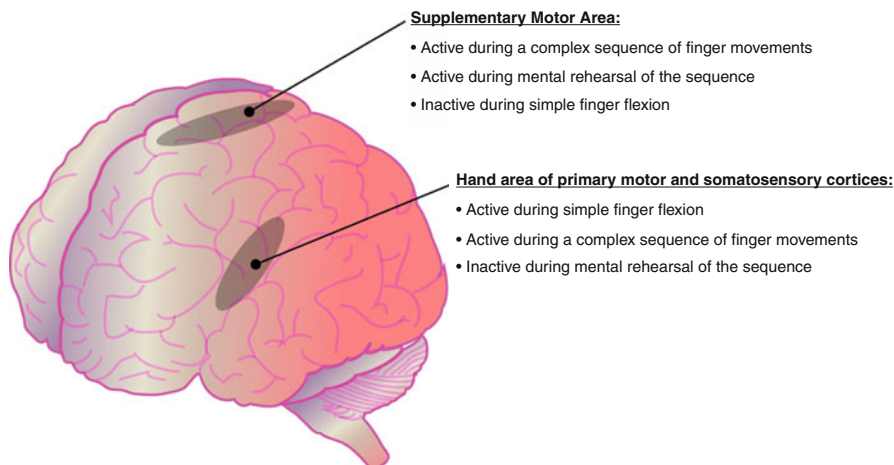
Supplementary Motor Area:

• Active during a complex sequence of finger movements

• Active during mental rehearsal of the sequence

• Inactive during simple finger flexion

Hand area of primary motor and somatosensory cortices:

• Active during simple finger flexion

• Active during a complex sequence of finger movements

• Inactive during mental rehearsal of the sequence

Fig. 37.5 The supplementary motor area is active during the planning of complex movements. A single neuron in the SMA of a monkey is shown activated when the animal prepared to turn a handle, but only if the turning action is followed by a pull and a push. If the sequence is turn-push-pull, the neuron is not active. The *upper panel* in each part of the figure is a raster plot, in which each action potential of the neuron is marked by a *dot* and each row represents one trial. Trials are aligned at the moment the animal turned the handle. The *lower panel* shows the combined activity over all the trials (Adapted from Tanji and Shima 1994)

planning and organization of bimanual activity. Recently, these aspects have been demonstrated in man by monitoring cerebral blood flow during various tasks. Such positron emission tomography (PET) scans show increased SMA activity during sequential movement of all fingers when compared with simply squeezing together the thumb and forefinger. This enhanced activity is maintained even if the subject only *thinks* of making the movements (Fig. 37.5). The SMA activity is particularly high when the subject performs difficult bimanual movements, for example, when musicians tap out different rhythms with each hand. Curiously, some patients display "alien-limb" syndrome in which the limb makes movements the patient denies controlling; others may show utilization responses in which they repeatedly pick up a tool, for example, a pen placed in front of them, even if instructed not to.

These various facts therefore place the SMA near to the top of the "motor hierarchy," at the interface between sensation and action. The pre-SMA is even higher and is concerned with the cognitive aspects of motor planning, learning, and execution of complex sequences of actions. As yet the full roles that the SMA and pre-SMA perform are still uncertain.

The Premotor Cortex Is Involved in Sensory Initiation of Movement

The premotor cortex (PMC) occupies a large area in front of the primary cortex and is only poorly distinguished from the neighboring SMA. In man, the SMA and
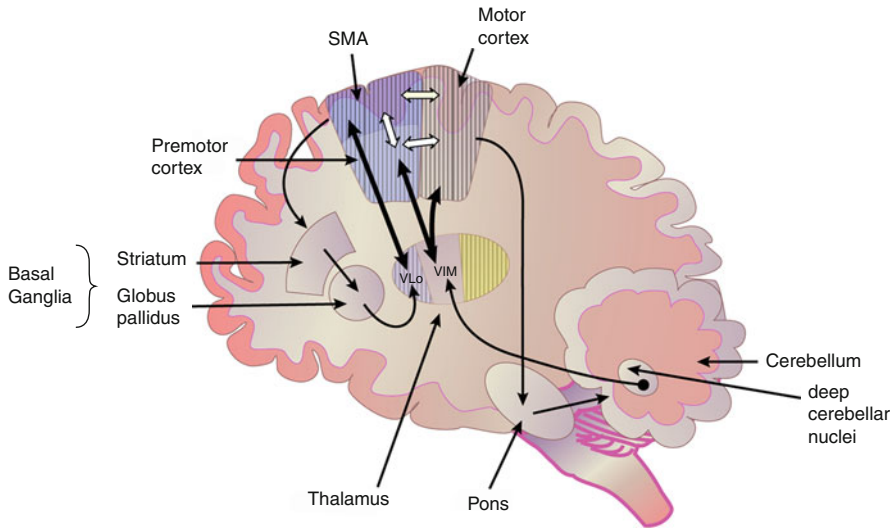
Fig. 37.6 There are two major subcortical loops that connect the motor areas with the basal ganglia and with the cerebellum. These are discussed in more detail in other chapters. The cerebellum receives input from the motor areas (and other cortical areas) via the pontine nuclei in the brainstem and sends projections from the deep cerebellar nuclei via the ventral intermediate thalamus to the same cortical areas (especially the ventral PMC). The basal ganglia receive inputs into the striatum and again provide feedback to the motor areas (especially the SMA) via the ventral-anterior thalamus

premotor cortex together (Brodmann's area 6) are about six times the area of the primary cortex (area 4). The premotor cortex sends a large output to both SMA and the primary motor cortex; it also provides a large output to the brain stem. These descending fibers mainly contribute to the reticulospinal system, but a small number also project to the spinal cord. The direct spinal influence of PMC is onto the proximal muscles, like that of the supplementary motor cortex.

Like the SMA, the PMC is subdivided into several regions: a ventral (lateral) region, known as PMv, and a dorsal region (PMd), which is itself subdivided into rostral and caudal zones. The functional differences between these zones are not fully understood.

Cortico-cortical inputs to the premotor cortex arise from the prefrontal association cortex, from SMA, the posterior parietal cortex. There are also inputs from the basal ganglia and the cerebellum via the thalamus (Fig. 37.6). The cerebellar and posterior parietal inputs provide an important pathway for visual information to reach the motor cortex, especially via the PMv. The PMv is therefore particularly involved in visually guided movements. Like the SMA, it also seems to be situated above the motor cortex in the general hierarchy of movement control, but because of its rather different connections presumably processes rather different information.

Electrical stimulation of the premotor cortex yields movements rather like those evoked from SMA. Movements often require long trains of stimulating pulses, with

relatively high stimulus thresholds. The PMC is not obviously topographically arranged, however, and the evoked movements often involve muscles around several joints.

Single cell recording experiments have in fact demonstrated three main forms of activity within the PMC. Neurons can be classified as stimulus-related, set-related, or movement-related (Fig. 37.7). Set-related activity is the most common in PMd. Here, the cells are often active continuously between presentation to the monkey of a "get set" stimulus and the onset of movement triggered by a second "go" signal. The cells do not fire if no movement is required. They may therefore be presetting the activity patterns of other motor areas in preparation to move. They may also be involved in suppressing immediate reflex responses to stimuli. PMd thus appears important in linking conditional cues to behaviors – as an example, a car driver has to learn that red traffic lights are a stop signal, and the required action is not directed toward the stimulus itself. In fact, experienced drivers will sometimes press the foot against the floor, as if to press the brake pedal, even when sitting in the passenger seat!

Finally, there has been huge interest in recent years following the discovery of "mirror neurons" in the ventral premotor cortex, PMv. These cells respond both during the execution of actions – in monkeys reaching movements toward food – but also during the observation of the same actions performed by others, including the scientists in the room. Some are responsive to the sight of objects toward which a goal-directed action is made, others to the sight (or sound) of goal-directed actions even in the absence of a target object. They provide a mechanism to link visually observed actions to execution of related actions, for example, in imitation tasks, and may also provide a representation of the intention or goal behind an observed action. Evidence is accumulating that very similar cells are in the human premotor cortex. The co-location of these cells with Broca's area (Fig. 37.2) has lead to the suggestion that understanding observed actions could have lead to communication through gesture, as a precursor to spoken language.

The Posterior Parietal Cortex Provides Spatial Information for Motor Planning

The posterior parietal cortex (PPC) is discussed more fully elsewhere. It is sufficient here to mention that it has a major role in providing information to the other motor areas about the spatial relationships between objects and about the spatial position of the body in relationship to the external world.

The anterior part of the superior parietal lobe provides a link between the somatosensory cortex and premotor areas; it is particularly important in tactile guidance and in the representation of the current state and posture of the body. The superior parietal lobe also provides a powerful link between visual cortex and premotor cortex, and also a large indirect link via the lateral hemispheres of the cerebellum. Hence, movements that are aimed toward objects in the near
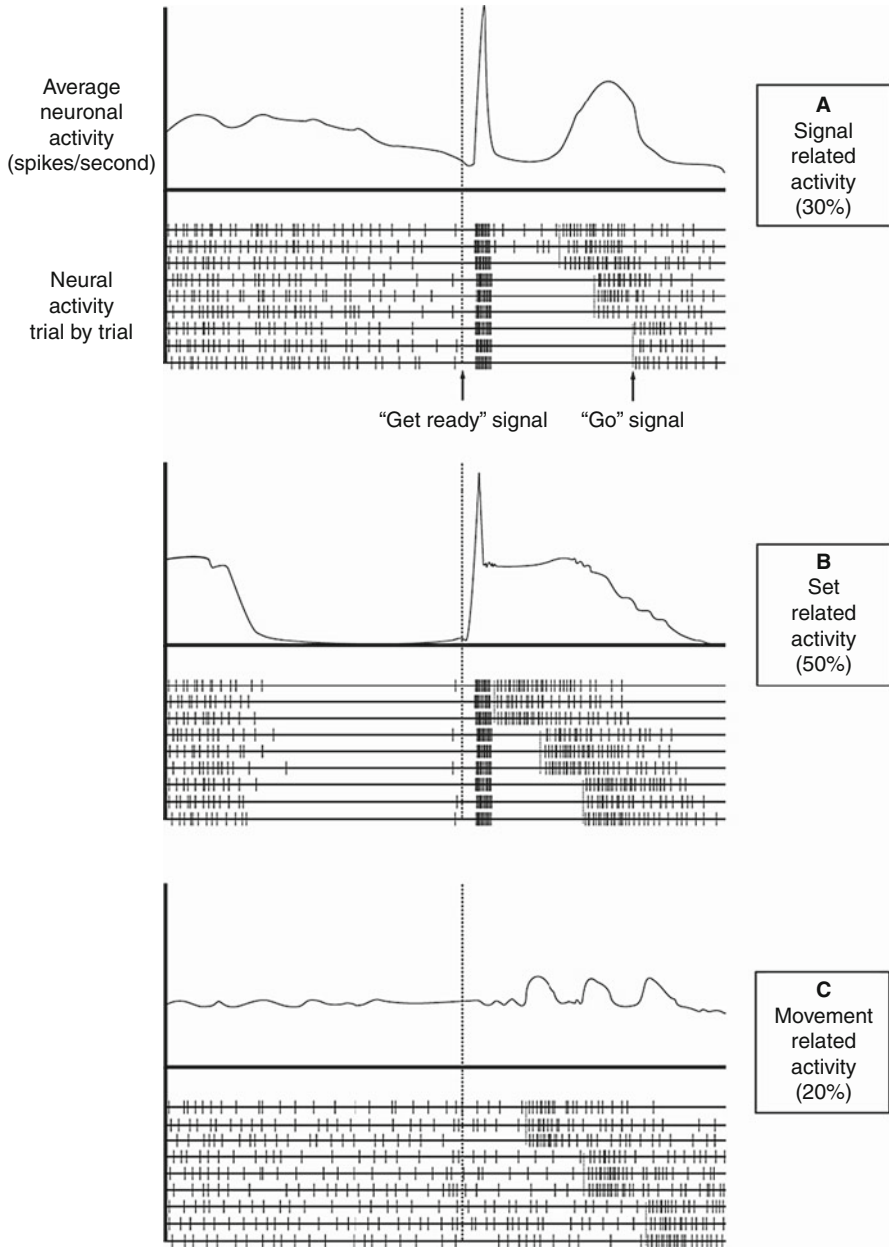
Fig. 37.7 Human brain imaging studies were able early on to show activity in the primary motor cortex during simple finger movements and in addition in the SMA during complex finger sequences. When the participant only mentally imagined the sequence, then SMA remained active, but the primary motor cortex was inactive (Adapted from Roland et al. 1980)

environment ("peripersonal space") probably rely on spatial information from the posterior parietal cortex. The inferior parietal lobe is still not fully understood, but appears to have important functions in spatial processing and in representing the salience of objects in the environment. Between the two, the intraparietal sulcus contains a cluster of distinct areas that have roles in spatial control of eye, head, and hand actions.

Lesions of the PPC result in some extraordinary deficits that highlight some of the hemispheric specialization of function found in humans. Patients with lesions of the right PPC can suffer *neglect* of the left hemisphere. They therefore fail to respond to objects, including their own limbs, on their affected left side. They may also show quite complex deficits of spatial representation, for example, failing to recall from memory the left half of any scene. The right PPC is therefore closely linked to voluntary movement. Lesions of the left PPC can produce alexia and agraphia – acquired disorders of reading and writing – in which some aspects of processing of written text are disturbed, as well as ideomotor apraxia, in which appropriate choice of actions can be impaired, for example, with patients failing to recall the normal use of an everyday tool like a hammer.

The Primary Motor Cortex Is the Area Most Directly Involved with the Final Movement

The primary motor cortex, as implied by its name, is the area of the cerebral cortex that is most closely involved in the generation of "purposive" or voluntary movements. It is the area in which stimulation can most easily evoke movements. It is also a major source of "upper motor neurons" that project from the cortex to the spinal cord, where they directly or indirectly excite motor neurons that connect to the muscles ("lower motor neurons"). It can therefore be thought of as the major output site of all the cortical motor areas. In reality, most other areas also contribute to different degrees to the descending tract (the *pyramidal tract,* see section "The Motor Cortex Contributes to the Corticospinal Pyramidal Tract").

Connections with Other Cortical Areas

The main inputs to the primary motor cortex are from the somatosensory cortex lying just behind the central sulcus, and from the premotor cortex, SMA, and the parietal cortex (Fig. 37.3). There is also a large input from the cerebellum via the thalamus (Fig. 37.4). Given the importance of vision in control of our movements, it is perhaps surprising that there is no direct visual input to the motor cortex. Instead, visual information is relayed from the parietal cortex via the premotor cortex and also via the cerebellum. Lastly, the motor cortex receives diffuse inputs from the reticular system, locus coeruleus, and the interthalamic nuclei, which modulate the level of motivation or arousal within the voluntary motor system.

The inputs from somatosensory cortex and thalamus provide detailed sensory information from proprioceptors in muscles and joints and from cutaneous receptors in the skin of the effectors it controls – especially the fingers and face.
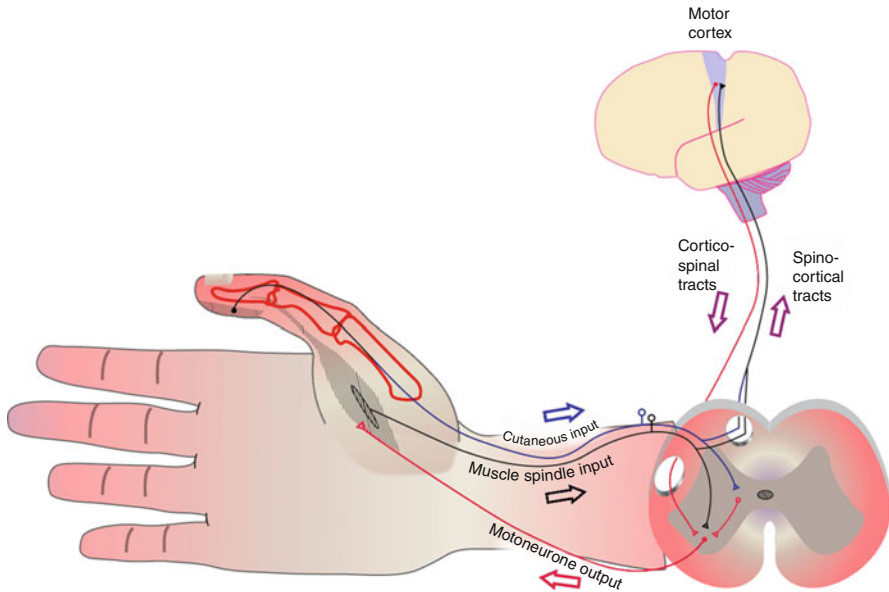
Fig. 37.8 The input-output relationship of the motor cortex. Proprioceptive and cutaneous signals project topographically to the motor cortex from which descending corticospinal fibers arise. The sensory information is processed in parallel by this long cortical loop as well as by local spinal circuits. Note that, although individual connections are drawn, in fact, each descending fiber makes many synaptic connections of which the bulk are onto spinal interneurons rather than onto motor neurons (Adapted from Asanuma 1973)

This input is topographically organized. It therefore provides the motor cortex with feedback of the consequences of the movements that it evokes (Fig. 37.8). This is particularly important in fine hand movements, for which tactile information from the fingers is vital.

The main output of the motor cortex descends through the internal capsule to the brainstem and to the pyramidal tract.

The Motor Cortex Contributes to the Corticospinal Pyramidal Tract

The outputs of the motor cortex arise from large *pyramidal cells* within layer 5. Their axons project either to surrounding regions of the motor cortex or to the contralateral motor cortex via the corpus callosum (*cortico-cortical fibers*) or descend via the internal capsule to the brain stem (*corticobulbar fibers*) or spinal cord (*corticospinal fibers*). The corticospinal fibers join a large tract known as the *pyramidal tract* (Fig. 37.9). Confusingly, this is named after the pyramid-shaped part of the brain stem through which it travels, rather than for the pyramidal cells from which it originates. About 80–90% of the tract crosses over the midline below the medulla, forming the lateral corticospinal tract. The remaining 10–20% travels uncrossed in the anteromedial regions of the cord. Hence, the effects of pyramidal tract lesions above the medulla are mainly contralateral.
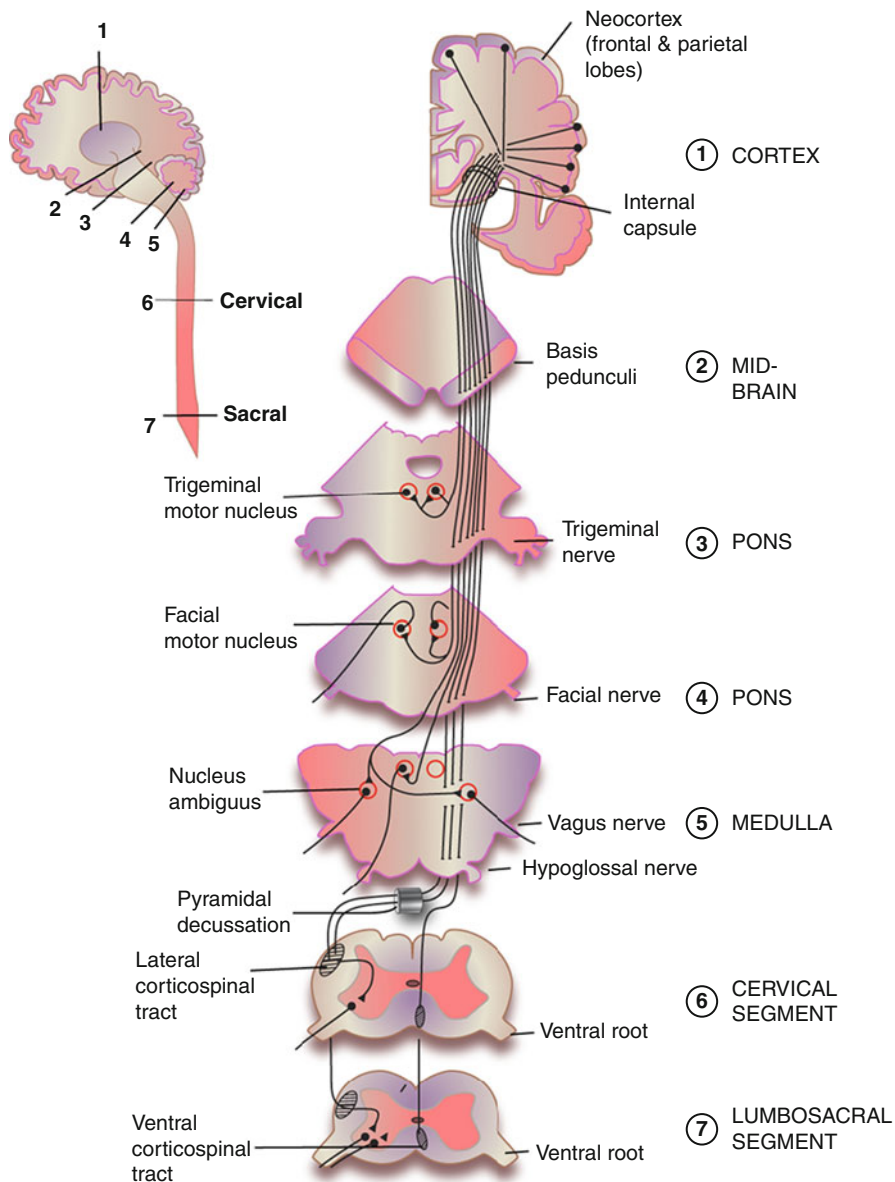
Fig. 37.9 The pyramidal tract. Descending corticofugal fibers ("upper motor neurons") and motor neurons ("lower motor neurons") are shown as if penetrating a series of sections through the brainstem and spinal cord. The six sections numbered on the *right side* are schematically shown against a cross section of the brain and spinal column on the *upper left* of the figure (Adapted from Barr and Kiernan 1988)

The contribution of the motor cortex to the pyramidal tract is in fact quite small, about 30–40%. The remainder arises from other areas of the cortex, predominantly the premotor cortex (including SMA), parietal cortex and a large projection from the somatosensory cortex. Most of the descending (*corticofugal*) fibers terminate within the brain stem without reaching the spinal cord (see Fig. 37.9); so, only about 20% of the fibers from the motor cortex travel directly to the spinal cord. Of those that do, the largest fibers arise from the giant *Betz cells* of the motor cortex and terminate onto interneurons of the spinal cord as well as onto both a and g motor neurons in the ventral horn of the gray matter of the spinal cord.

In man, the corticospinal fibers project preferentially to motor neurons supplying distal muscles, particularly of the hand. The bulk of direct and indirect excitatory connections are onto flexor motor neurons. Note that the flexors are by and large the muscles used for careful, skilled movement (e.g., in closing the fingers). As well as exciting these motor neurons, by its projections onto inhibitory 1a interneurons, the motor cortex can also produce disynaptic inhibition of other motor neurons. As one might guess, the bulk of this inhibitory control is to extensor muscles. Thus the cortex can both evoke contraction the flexors and the necessary relaxation of the opposing extensors. Extensor muscles tend to be those required in the return movement or to oppose gravity ("anti-gravity" muscles). The large pyramidal cells in the primary motor cortex are active just prior to movement and are often inactive at other times. They may be important in setting up the coactivation of a and g motor neurons needed to regulate muscle spindle responses during voluntary muscle shortening.

The remainder of the direct corticofugal fibers are much smaller, with correspondingly lower conduction velocities. They tend to be active continuously, with modulated activity during movement. They probably contribute mainly to setting the background level of spinal activity and also to modulate spinal reflexes.

Cortical projections that terminate within the brain stem (*corticobulbar fibers*) reach most subcortical structures: the basal ganglia, the pontine nuclei and inferior olive (and hence, the cerebellum), and the red nucleus, reticular formation and cranial motor nuclei (Fig. 37.9). In fact, the corticospinal fibers often give off collateral branches that also reach these same sites. Many of these subcortical areas also project to the spinal cord, so that spinal motor neurons frequently receive parallel direct ("pyramidal") and indirect ("extra-pyramidal") input from the motor cortex. These extrapyramidal systems will be considered in the following chapter.

The Motor Cortex Is Topographically Arranged

Electrical stimulation techniques have gradually moved toward a finer and finer mapping of the cortex with smaller and smaller electric shocks (see "Clinical Box 1"). The map in motor cortex has now been plotted out in some detail, and the topography is maintained down to the level of individual digits of the hand (Fig. 37.10). The area of the cortical map devoted to each parts of the body is unequal, however, and varies from species to species. The rule seems to be that the
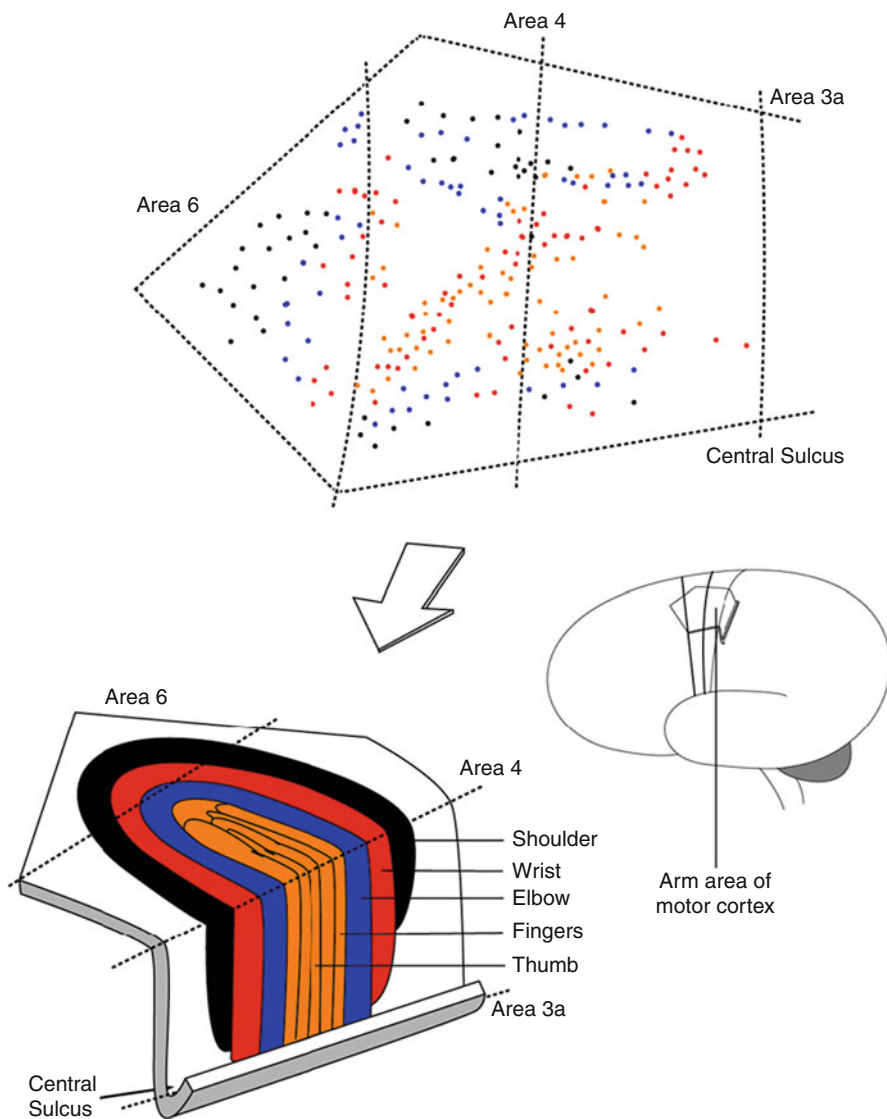
Fig. 37.10 The topographical organization of the motor cortex. By mapping the projection of small cortical zones to the muscles (*upper diagram*), a map of the contralateral limb can be drawn on the motor cortex (*lower diagram*). The representation of the limb is "telescoped" inward, forming concentric bands, from shoulder to elbow to wrist, etc. This probably allows the motor cortex to first stabilize proximal joints before finely adjusting more distal joints. Compare these maps to the very simplified homunculus shown in Fig. 37.1 (Adapted from Murphy et al. 1978)

area is proportional not to the number of muscles controlled at each body site, but the number and accuracy of different movements that each site can contribute to. Hence, in man, the map has greatly exaggerated hands, face, and mouth (Fig. 37.1) and rather small areas devoted to the feet or back. The maps in the motor cortex of an elephant or a mouse would be very different.

Clinical Box 1: Stimulation of Motor Cortex in Man

Electrical stimulation of the cortex evokes movement or, in non-motor areas, can evoke vocalization, memories, or visual images. Because the technique needs only local anesthesia of the patient, it can be used in neurosurgery to locate the foci of epileptic seizures prior to their removal.

Much of our basic understanding of the motor system has been gained by observations of the effects of electrical stimulation. In early experiments, the surface of the cortex was stimulated with alternating current through a spherical electrode. Much more precise stimulation can be provided by fine microelectrodes placed within the cortex, however, and much smaller current levels are needed to evoke movement. The importance of reducing the current is to limit *current spread*. If unchecked, this can confuse the effects of stimulation by activating neighboring areas of the cortex.

Less precise electrical stimulation can be given transcranially, through the scalp. This of course has the advantage that the brain need not be exposed and can, therefore, be used clinically. The technique involves passing a very brief high voltage between two electrodes placed on the skull. Unfortunately, most of the current passes through the bone and scalp tissues, which is quite painful, but a fraction passes through and stimulates the cortex beneath the electrodes.

More recently, this technique has been surpassed by the technique of transcranial magnetic brain stimulation (TMS). In this, a coil is placed on the scalp, and a very strong stimulating current pulse through the coil generates a brief, powerful magnetic field that can pass through the skull and induce electrical currents within the underlying brain tissue. It is much less painful than transcranial electrical stimulation and is now widely used as a probe to understand the function of the normal brain, as well as for clinical purposes. For example, when coupled with electromyographic recordings from the muscles, the conduction velocity in central pathways can be determined to help the clinician localize lesions within the central motor system. Alternatively, TMS can be used to briefly disrupt the neural processing with the motor cortex, and the effects of such "virtual lesions" can help expose the normal function of the targeted area of the cortex.

Cortical Organization. Within very small areas of the cortex, the topography of the map breaks down, and small patches or "hot-spots" about 1 mm across can be found that separately evoke twitches of the same muscles

(Fig. 37.11). The motor cortex, like other areas, seems to be functionally and histologically organized into *columns* about 100 μm across, and recurrent branches of pyramidal cell axons frequently innervate adjacent columns. Hence, the patches are probably made up of several adjacent columns. Detailed tracing of the paths of descending corticospinal fibers has revealed that individual cortical neurons innervate motor neurons within groups of muscles, usually related muscles acting about a single joint. There is, then, both convergence and divergence in the direct projections from cortex to muscle motor neuron pools in the spinal cord.

The current suggestion is that these patches or columns of cells with similar projection fields bring together neurons involved in related computations. Their separation into discrete areas reflects excitatory connections *within* columns and inhibitory interactions *between* nearby columns. It may also reflect an efficient way to map multidimensional information about movements onto the two-dimensional surface of the cortex. Thus, the total amount of neuronal wiring needed within the cortex may be reduced by clustering like-minded cells together.

What Is Encoded in the Motor Cortex?

Recording the activity of single cells in the motor cortex of alert and active experimental animals has now taught us a lot about their operation, although a definitive answer to this question still cannot be given. In general, the cells fire in proportion to the forces that need to be generated by the muscles to which they project and are active about 100 ms before the onset of muscle activity (Fig. 37.12). Many cells are found to encode the dynamic or static components of force or a mixture of the two. However, these relationships are not rigid, and individual cells can radically alter their activity during different movements that use the same muscle.

The topographical nature of the motor cortex implies that its neurons might encode for the activation of individual muscles of the body. An opposing view is that it encodes not for muscles but complete movements (which involve several muscles acting about one or more joints). Brief electrical stimulation evokes twitches of single muscles. More prolonged stimulation evokes apparently purposeful movements covering several joints, for example, like a grasping action that might then bring the hand to the mouth. This view is supported by finding that individual cells within the motor cortex can be active during movements which involve very different sets of muscles. In practice, however, these two viewpoints are not clearly distinct. The motor system already has a "muscle-map" in the spinal cord, at the level of the pools of motor neurons that project to individual muscle, so there seems no reason to simply duplicate it within the cortex. And yet, in controlling movements, which normally involve several joints, it makes good sense that the cortex has a topographical "muscle" map so that interactions between neighboring muscles and joints can be controlled by neighboring cortical patches.
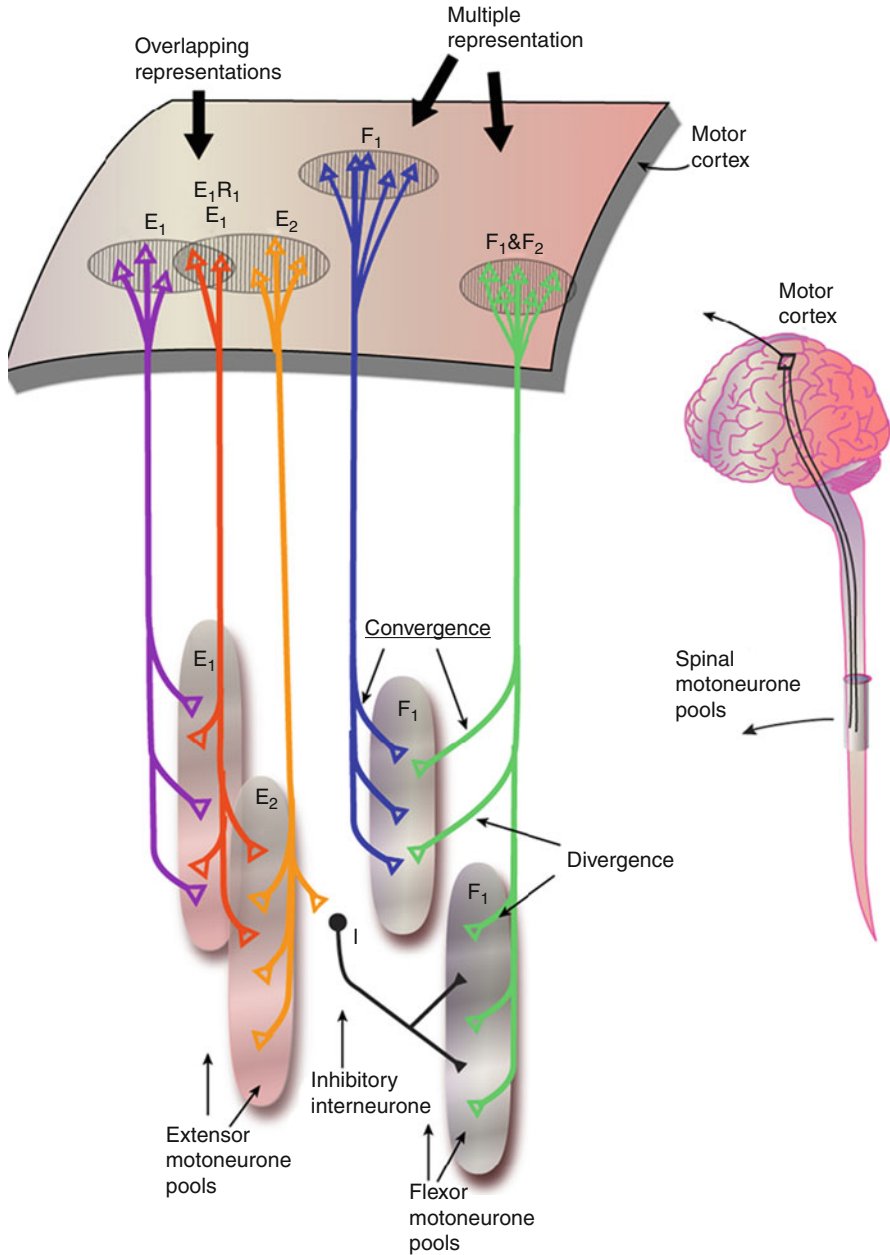
Fig. 37.11 The columnar organization of pyramidal neurons. Clusters of cells from each column project to each motor neuronal pool in the spinal cord. A single cluster can project to more than one muscle (*divergence*), and any one muscle pool can receive from more than one cluster (*convergence*). So microstimulation of motor cortex (Fig. 37.10) shows a scattered and uneven representation of individual muscles or joints

Fig. 37.12 Corticospinal cells encode both dynamic and static levels of force. The cells can be classified into groups by the relationship between their activity and the force recorded in the muscles. Most neurons show a mixed response, with a phasic burst related to the rate of change of force levels (indicated in the *bottom* trace of dF/dt) and a maintained response as the force is maintained (Adapted from Vicario et al. 1983)
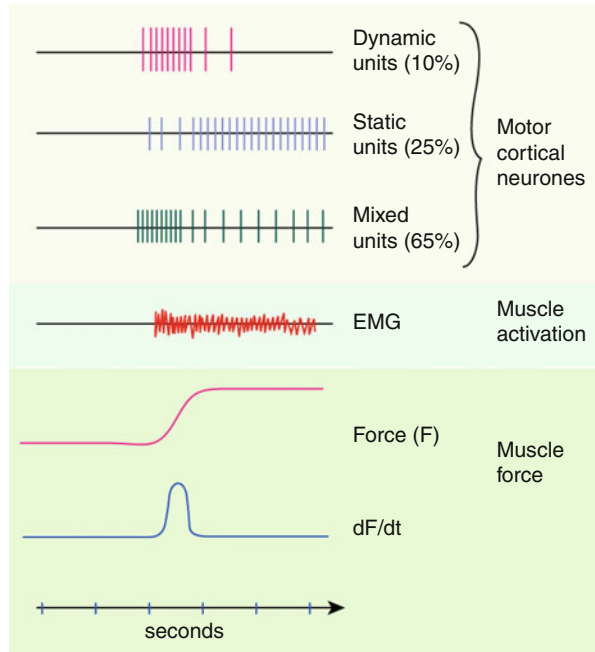
Interestingly, recent experiments have shown that the maps are not static, and change shape if the levels of activity in any one area of the map alter, for example, following electrical stimulation, or even through repeated use of individual fingers, as in the acquisition of skilful playing of a musical instrument.

Other experiments have shown that the activity levels across a population of neurons can reliably signal the *direction of movement* of a monkey's arm when reaching for a target (Fig. 37.13). This again lends support to the notion that the motor cortex represents movements and not just the levels of muscle activation. However, as with the finding that the cells relate to force, the finding that cells relate to movement direction does not give them a sufficiently demanding task in the process of generating coordinated movements. Movement direction and muscle force are only two of many variables controlled during movements, and so, the question of what is encoded in the motor cortex is still not fully answered.

Motor Areas of the Cortex Are Prone to Stroke

Cerebral vascular accidents or arterial thromboembolisms are caused by blockage of a cerebral artery, often by a blood clot, and lead to irreversible lesions of the area served by the artery ("stroke"). *Stroke* can affect the SMA, PMC, and the primary motor cortex, but the most common site of strokes is actually in the internal capsule. Damage here therefore affects the outflow of all three areas as well as fibers from the basal ganglia. These and other accidents can lead to paralysis of muscles
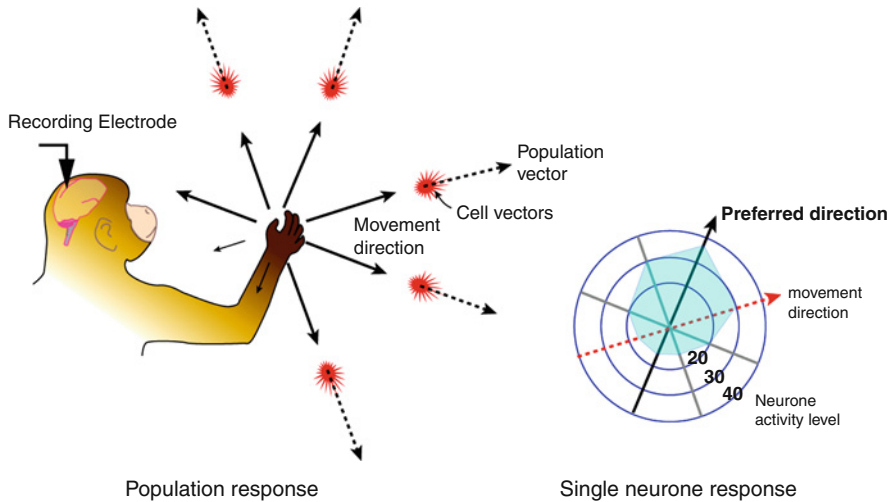
Fig. 37.13 Populations of motor cortical neurons encode the direction of movement of the whole arm. Individual neurons show a "preferred direction" and fire most strongly as a monkey reaches out in one direction to one of eight radial targets. For each movement made, each individual cell's response can be plotted as a *line* (a vector) in its preferred direction, whose length is proportional to the cell's activity when the arm moves in the preferred direction (*right*). Combining the responses of several hundred cells gives a starburst of cell vectors, one for each movement direction (*left*, with the starburst stretched in the direction the animal is currently moving). The average of all of these vectors (the "population vector") turns out to lie very close to the direction of the movement. It suggests that the whole population of neurons can combine their activity to control the multi-joint limb movement, although whether this means the motor cortex represents actions as movements through three-dimensional space, or represents the muscle activity needed to cause such movement is still debated (Adapted from Georgopoulos et al. 1983)

on the contralateral side of the body and can also affect facial muscles and speech. During this paralysis, the patients feel as though they can still issue motor commands to the affected limb, implying that their "will" to move is not impaired. It is the execution of the movements that is lacking.

The effects of small cortical lesions lessen as surviving areas of the cortex take over the missing functions. Larger cortical lesions lead to permanent impairment. In man, the primary motor cortex seems to be essential for delicate, skillful movements; the only permanent sign of lesions of M1 is often the loss of fine movements of the fingers, face, and control of speech.

The primary motor cortex is not essential for all production of movement, however. More fundamental movements, such as those involved in reflex responses or in locomotion, are organized at lower levels (the brain stem and spinal cord). Furthermore, the premotor areas (PMC and SMA) also have direct and indirect connections to the spinal cord and can, therefore, initiate some movements without involving the primary motor cortex.

Clinical Box 2: Corticospinal Tract Lesions

Lesions of the motor areas of the cortex or of the corticospinal tract give rise to symptoms know as *upper motor neuron lesion* signs. These are distinct and opposite from the symptom lesions of motor neurons within the spinal column, *lower motor neuron lesions*.

The clinical signs of upper motor neuron lesions are as follows:

– Paralysis or weakness with a characteristic distribution in the muscles of the contralateral limbs (*hemiparesis*). If the lesion is below the pyramidal decussation (Fig. 37.9), the weakness is ipsilateral.

– No wasting of the muscles, because the motor neurons are intact. There are also no rapid twitches of the muscles (*fasciculations*), again because of the intact spinal circuitry.

– Increase in muscle tone (*spasticity*) and exaggerated tendon reflexes. A severe lesion causes flaccid paralysis and areflexia. However, after several days, this is followed by an increase in tone and reflex activity, because of the loss of inhibitory input from the corticospinal fibers onto interneurons of the spinal tract. The limbs also show *clasp-knife* reflexes, in which initial resistance to a disturbing force applied to the limb suddenly reduces as the force increases. This reflex, which is mediated by the Golgi tendon organs, is exaggerated after corticospinal lesions because it is released from descending inhibition.

– Changes in superficial reflexes. The normal *plantar* response, in which stimulation of the skin on the sole of the foot causes a flexion especially of the big toe, is replaced by an extensor reflex. This is known as a *positive Babinski sign* and is one of a family of *withdrawal* reflexes.

– Loss of *fractionation of activity* that normally allows fine differential control over the fingers. This is particularly caused by lesions affecting the primary motor cortex.

Motor Areas of the Cortex Cooperate to Generate Voluntary Movement

Brain imaging experiments has shown that widespread areas of the motor cortices (M1, PMC, SMA, and PPC) are active simultaneously in most of our normal behavior. Many hundreds or thousands of cells will in parallel formulate a motor plan that can coordinate the muscles across one or more joints. This process combines complex visual, proprioceptive, and tactile information from the all sensorimotor areas of the cortex as well as inputs from non-motor areas specifying the cognitive goal of the intended movement. It also involves considerable communication between the various separate motor cortical areas. Thus no one cortical area can be thought of as responsible for the initiation of a voluntary movement. Interestingly, recent experiments suggest that the intention to move is generated by the posterior parietal cortex, as stimulation of this area during brain surgery leads to the desire or intention to move the contralateral hand, arm, or foot, or to intended facial gestures or speech. The final plan for a voluntary action arising from

the motor cortex may well specify the *relative force levels* required by groups of muscles. It may also specify the *fractionation of activity* within these muscle groups. This plan then leaves the spinal circuits to ensure that the muscles faithfully execute the intended action. Continual sensory feedback to the cortex allows for updating and correction of the plan as the movement unfolds.

Outlook

To progress further in understanding the motor cortex, we now need to understand what whole networks of cells distributed across several cortical areas simultaneously contribute to individual movements. The way forward will probably come through advances in techniques to image the human brain in parallel with the necessary and important experimental work with laboratory animals. At present, noninvasive brain imaging is still an indirect measure of the average activity of many thousands of neurons, while invasive animal recording experiments can tell us about the detailed activity of only a few tens or hundreds of cells. Key questions to be addressed are the function of the motor areas in the learning and retention of skillful behaviors and how these functions might relate to the processes needed to ensure successful rehabilitation after cortical damage. There is also great interest in trying to understand the rules that the motor system uses to efficiently and smoothly control voluntary actions, often in the face of sudden perturbations from external events. Finally, like the sensory areas, the motor system seems to be organized into a number of discrete cortical areas. The number of subregions within these areas, and the distinctive differences between these areas, is steadily growing. A fuller understanding over the coming years may lead to some areas we currently think of as single regions being given separate zones and separate functions.

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