

Motor Cortex

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The motor cortex comprises the primary motor cortex and the premotor areas of the frontal lobe. Primary motor cortex is abbreviated as M1 or MI, and, in primates, is often known as area 4 or the precentral cortex. The motor cortical areas play an important role in the selection and control of movement.

1. Cortical field definition

M1 has been identified in several mammals, but most information comes from monkeys, cats, raccoons, rats, and humans. In each, five characteristics serve to define M1: (1) electrical stimulation there evokes movements with relatively low levels of electrical current, usually less than needed in other cortical fields; (2) it lacks a clearly identifiable internal granular layer, layer 4, and therefore is part of the agranular frontal cortex; (3) it receives a major input from the ventrolateral thalamus, which relays information from the cerebellum and basal ganglia; (4) it lies rostral and medial to the somatosensory cortex; and (5) it sends direct projections to the spinal cord (Figure 1).

Frontal cortical fields projecting to M1 are termed premotor, and, in primates, these areas also project to the spinal cord. Premotor cortex has been divided into two major parts: lateral and medial. The medial

premotor areas include the supplementary motor area (SMA), and several cingulate motor areas (Figure 1). The lateral premotor areas include the dorsal premotor cortex (PMd) and the ventral premotor cortex (PMv). In addition to M1 and the premotor areas, some experts would include additional fields in the “motor cortex,” including the frontal and supplementary eye fields, the somatosensory areas, and parts of the posterior parietal cortex. However, the term motor cortex usually refers to areas in the frontal lobe that appear to play a relatively direct role in the selection and control of skeletal movements, a definition that excludes the eye fields and parietal cortex.

Cytoarchitectonics, myeloarchitectonics, the distribution of neurotransmitter receptors, and other architectonic methods have been used in an attempt to identify the various motor areas. Although cortical architectonics resembles art more than science, it can serve to identify the most obvious structural boundaries in the cortex. Unfortunately, those between the motor areas are rarely obvious. In general, however, Brodmann's area 4 corresponds to M1 and area 6 contains most of the lateral premotor areas as well as some medial ones. Additional medial premotor areas lie within area 24, in and near the cingulate sulcus (Figure 1).

2. Input–output organization

Inputs to M1 arise from several central sources and, indirectly, from peripheral mechanoreceptors. Both cutaneous receptors and proprioceptors provide input to M1, and neurons influenced by cutaneous inputs are concentrated in its caudal part. The main sources of input to M1 arise from the deep cerebellar nuclei, particularly the dentate and interpositus nuclei (via the thalamus), the internal segment of the globus pallidus (also via the thalamus), the somatosensory cortex, part of the posterior parietal cortex (area 5d), and the premotor areas. Projections to the premotor areas vary, but in general they receive pallidal and cerebellar inputs, via the thalamus, as well as proprioceptive and visual inputs from many subdivisions of the parietal cortex.

The outputs of the motor cortex include its well known projections to the spinal cord (Figure 1). En route, corticospinal fibers pass through the internal capsule, cerebral peduncle, and pyramidal tract. All these projections originate from cell bodies located in layer 5 of the cortex. The corticospinal system originates from many cortical fields, with the sources roughly evenly divided between M1, the parietal cortex (including somatosensory areas) and the premotor areas. At least in certain primates, some of these fibers terminate in excitatory synapses on spinal motor neurons, and individual corticospinal axons from M1 contribute inputs to several motor pools. However, most of the corticospinal fibers terminate in regions of spinal gray matter containing interneurons. For instance, in the cervical spinal cord of monkeys, 75% of the corticospinal terminations lie outside the ventral horn, the part of the spinal cord that contains the motor neurons. These interneuronal projections influence muscle activity indirectly, through polysynaptic pathways having both excitatory and inhibitory influences on motor neurons.

Among the supraspinal targets of motor cortex are a number of structures important in motor control, including the cerebellum (via the pons and other pathways), the basal ganglia, the motor cortex of the opposite hemisphere, the superior colliculus, and the red nucleus. Several motor fields, most prominently the lateral premotor areas, send a major corticofugal projection via the pyramidal tract to the medullary reticular formation, the site of many reticulospinal neurons.

M1 is characterized by a coarse topographic representation of the skeletomotor system: the hindlimb representation is located medially within M1 (toward the top of Figure 1), whereas the forelimb and face are represented progressively more laterally. A roughly comparable topography exists in the SMA, but the somatotopic organization there and in the lateral premotor areas is not as well defined as that found in M1. The same general topography can be seen for M1's somatosensory inputs as for its motor outputs, an organizational principle termed input–output coupling. If M1 neurons receive input from somatosensory receptors near a joint, electrical stimulation near those cells usually evokes movements around that joint and many of those neurons modulate their activity with movements around the same joint. The principle of input–output coupling supports the classic concept of a transcortical reflex circuit in which M1 underlies long-latency components of the stretch reflex. Despite the recognition of input–output coupling and the

general topography described above, the fine detail of motor cortex somatotopy remains poorly understood. The distal and proximal parts of the limbs in monkeys are mainly represented separately, but the detailed schemes of topographic representation that have been proposed remain controversial. For instance, cells that fire in relation to a proximal joint are often found near cells that are active with finger or hand movements. One alternative to the well known homunculus map is a nested-zone arrangement with the fingers represented centrally, and the wrist, elbow, and shoulder represented progressively further from the center. Neither that scheme nor the homunculus has received convincing experimental support, although both remain popular.

3. Role in the cerebral control of movement

Motor cortex function has been studied by examining the effects of motor cortex and pyramidal tract damage. In experimental animals, severe motor disabilities follow such lesions in the short term, but the long-term effects are less pronounced than often assumed. Careful testing is required to discern long-term motor deficits and, although much emphasis has been placed on species differences, comparable deficits follow pyramidal-tract transections in macaque monkeys, marsupial phalangers, rats, and hamsters. It has been concluded that M1 is necessary for *motor fractionation*, the independent control of muscle groups that usually work in concert. According to this hypothesis, motor fractionation adds an important degree of flexibility to the motor-control system. Although in some primates this fractionation is typified by independent movements of the fingers, the ability to make precise, complex movement is by no means confined to distal body parts. Results from lesion studies thus provide a general indication of motor cortical function, but have not established a specific role for the motor cortex in behavior.

Neurophysiological studies have yielded additional insight into the functions of M1 and the premotor areas. For single-joint movements, the discharge-rate modulation of some M1 neurons reflects the isometric force produced by the limb or jaw (and its first derivative), as well as the speed of movement. Many motor cortical cells change their activity 80 ms or so before the earliest detectable changes in muscle activity,

which supports the idea that these neurons play a role in generating movements. However, the lesion data cited above indicate that M1 is not necessary for voluntary movement, and its specific role may be reflected in the observation that many M1 neurons reach their maximum discharge rates with small, slow movements. M1's special role in precise movement is further supported by the finding of activity modulation during a precision grip but not during a power grip. It has been reported that M1 neuronal activity reflects changes in force exerted by the limb, rather than simply the sum of such force changes and static, postural forces. These observations, along with the effects of brain damage noted above, support the hypothesis that M1 confers upon the motor system enhanced flexibility and precision.

Much recent attention has been devoted to the representation of limb-movement direction among M1 neuronal populations during arm movements in two- and three-dimensional space. M1 neurons have their greatest neuronal modulation for movements in one direction, with systematically less modulation as the direction of movement diverges from that preferred direction. The cells are thus coarsely "tuned" for movement direction, but change activity for most, if not all, directions of movement. On the assumption that these cells all change their activity together for each movement, it is possible to compute a single vector representing a population activity of these cells. This computation is termed the population vector, and it has been shown to closely match the direction of limb movement during reaching. In addition, by addition of a time-series of these population vectors, it is possible to recover the limb's trajectory during reaching and a variety of drawing movements (Figure 2, animation). In general, the population vector precedes the limb trajectory by 50–120 ms. Recent research has focused on the possibility of using simultaneously monitored M1 cells to guide the control of robotic arms, a field of neural prosthetics that promises to give paralyzed patients enhanced control over their environment.

As for the premotor areas, behavioral and physiological studies suggest that the lateral ones function in higher order aspects of motor control such as the selection of action based on arbitrary stimulus–response associations (PMd) and the sensorially guided manipulation of objects (PMv), whereas the medial premotor areas, including the SMA, play a role in the selection of action based on internal (i.e., non-exteroceptive) information and in controlling movement sequences.

Although few doubt the existence of multiple motor areas, at least in primate brains, or that they play an important role in the selection and control of voluntary movements, the classical view that these areas work as discrete entities is under challenge, as is the idea that they function solely in activating muscles during skeletal movements. First, as noted above, the anatomical boundaries between motor areas are not easily distinguished. Second, many of the physiological properties of cells in different areas are similar. Third, large populations of cells in all the motor areas are active simultaneously for a given limb movement. Fourth, the activity of cells in these areas, including M1, reflects aspects of behavior in addition to movement or muscle activation, such as where a particular movement or target occurs in a sequence. Fifth, in tasks that resemble daily life activities, neurons in motor areas encode multiple movement parameters, and the combination of these parameters shifts from area to area without apparent discontinuity. New analyses to describe the composition of these activity patterns as they evolve within and between tasks, along with new technology to monitor many units simultaneously, promise to improve our understanding of the motor cortex and its contribution to behavior.

4. See also

Cerebellum; Cerebral cortex; Motor control; Sensory Motor Integration (animation)

5. Further reading

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Figure Legends

Figure 1. Motor areas in the frontal lobe of a macaque monkey. The left hemisphere is shown at the bottom and the medial surface of the hemisphere is shown “reflected” at the top. Rostral is to the left.

Abbreviations: ArS, arcuate sulcus; CC, corpus callosum; CgG, cingulate gyrus; CMA, cingulate motor areas, d, r and v for dorsal, rostral and ventral, respectively; CS, central sulcus; PMd, dorsal premotor cortex; PMv, ventral premotor cortex; PS, principal sulcus; CgS, cingulate sulcus; IPS, intraparietal sulcus.

The arrow shows the continuity between the medial motor cortex and the lateral motor areas. Shaded regions indicate the zones that send corticospinal projections to cervical segments of the spinal cord. Fine dotted lines approximate the borders between areas, and dashed lines indicate either the fundus or the lip of the sulcus they are nearest. For the central and arcuate sulci, the dashed line represents the fundus of the sulcus; for the cingulate and superior precentral sulci (just above the label PMd), the dashed lines indicate the lip of the sulcus. (With permission, from R. P. Dum and P. L. Strick, Motor areas in the frontal lobe of the primate. *Physiology and Behavior*, Elsevier, Amsterdam, in press.)

Figure 2. Animation of the population vector and hand trajectory.

Using population vectors to represent arm trajectory. The blue arrow at the tip of the finger represents velocity and shows the direction (arrow angle) and speed (arrow length) of hand movement. Each of the

200 yellow lines emanating from the skull represents an M1 cell's preferred direction (line angle) and instantaneous discharge rate (line length), in three-dimensional space as a rhesus monkey drew ellipses. The large yellow arrow coming from the skull shows the population vector. It shows the direction (arrow angle) and speed (arrow length) of the population vector as it changes during the movement. Note that the angle and length of the population vector matches and anticipates the movement velocity. Movement velocity is well represented in the motor cortex and can be extracted simply, using a population vector algorithm.



