Role of Cerebral Cortex in Voluntary Movements
A Review
PAUL D. CHENEY

Findings from studies using electrical stimulation of cortex, recording from single neurons in awake animals, and measuring regional cerebral blood flow in humans have revealed some specific motor functions for several cerebral cortical areas. These areas include primary motor cortex, supplementary motor area, premotor area, parietal areas 5 and 7, and prefrontal area. Execution of movement is a function of the primary motor cortex, which translates program instructions for movement from other parts of the brain into signals. These signals encode variables of movement, such as the muscles to contract and the force and timing of their contraction. Long-latency reflex responses of muscles to stretch and cutaneous stimulation are also mediated by the motor cortex; other motor areas seem to perform higher order motor functions. The supplementary motor area controls input-output coupling in motor cortex and the programming of complex sequences of rapidly occurring discrete movements, such as playing the piano. The premotor area participates in the assembly of new motor programs. The parietal areas 5 and 7 are involved in directing attention to objects of interest in visual space and issuing commands for arm movements and eye movements to these objects. The prefrontal cortex performs cognitive functions, such as short-term memory of correct motor responses in delayed response tests.

Key Words: Brain, Motor cortex, Movement, Volition.

Early cortical stimulation experiments in human beings and animals firmly established the motor function of the primary motor cortex. In more recent work, motor functions have been demonstrated for additional cortical areas. The purpose of this article is to review current concepts relating to the functional roles of five different cerebral cortical areas in motor programming and execution—primary motor cortex, supplementary motor area, premotor cortex, parietal cortex, and prefrontal cortex. Emphasis has been placed on aspects of cortical motor function that may be relevant to physical therapy in patients with cortical damage.

FUNCTION OF CORTICAL AREAS

Overview

According to a scheme proposed by Allen and Tsukahara, ideas for movements are translated into specific programs by premotor association areas of cortex (frontal and parietal areas), basal ganglia, and the lateral hemisphere of the cerebellum (Fig. 1). These programs are then executed through the motor cortex, which acts on brain-stem neurons and spinal motoneurons to bring about the intended (desired) voluntary movement. Of course, not all movements are completed as intended and midcourse adjustments are sometimes needed, for instance, when an obstacle or unexpected change in load is encountered. In addition to these external perturbations of movement, internal factors, such as muscle fatigue, can also cause a movement to deviate from its intended course. Several feedback loops exist to monitor the progress of the actual voluntary movement. One is the visual system—a highly effective source of feedback for reflex or volitional modification of movements under visual guidance. Another source of feedback is somatic receptors including cutaneous receptors, joint receptors, muscle spindles, and Golgi tendon organs. These receptors supply the CNS with continuous and prompt information about limb position, muscle tension, and external stimuli. This information reaches the intermediate division of the cerebellum, which is believed to use the information to make automatic corrections for deviations from the course of the intended movement. To do this, the cerebellum is thought to compare information from somatic receptors about the progress of the actual movement with information from the motor cortex about the intended movement. If these differ, the cerebellum issues a correction signal that acts through the motor cortex and brain-stem descending systems to return the movement to its intended trajectory. In addition, information from somatic receptors reaches the motor cortex through a more direct lemniscal pathway. Evidence now exists that this pathway participates in reflexes elicited by muscle stretch and cutaneous stimulation. These reflexes will be considered in more detail in a later section.

Figure 1 identifies four general aspects of motor function: 1) motivation, 2) ideation, 3) programming, and 4) execution. The phenomena of motivation and ideation are not unique to motor behavior but are components of a wide variety of behaviors and, therefore, will not be discussed further here. The programming and execution aspects of motor function will be the primary focus of this paper.

Motor programming refers to neural routines (communications) that convert abstract ideas or thoughts about a desired movement into the proper strength and pattern of muscle activity to bring...
about the movement. The program must specify the detailed sequence of activity in different muscles, the force each muscle should produce, and the duration of its activity.

Movement execution has two components: 1) intention or the contribution of central commands to movement and 2) feedback control or the modification of movement by signals from sensory receptors. Execution is performed by the most peripheral components of the nervous system (final common pathways), including muscle, sensory receptors, and motoneurons. Cells of descending systems that provide central “drive” to motoneurons, such as corticospinal neurons, occupy an intermediate position between programming and execution. These neurons translate program instructions into motor commands in which the force of movement is encoded by the cell’s firing rate.

I must emphasize that different types of movements require different control strategies. Although a functionally meaningful subdivision of different types of voluntary movements is difficult, the following list is suggested as representing factors that pose different control problems and that, therefore, may require different central programs. These categories, however, are not necessarily mutually exclusive. Movements may be classified according to:
1. Their speed—slow (ramp), ballistic.
2. The number of joints involved—simple (1 joint), compound (coordination of two or more joints).
3. The type of feedback guidance—somesthetic, vestibular, auditory, visual, some combination of these, or none.
4. Their complexity (e.g., the number of discrete steps in a movement sequence).
5. The mechanism by which the movement is stopped—self-terminated or externally terminated (mechanical stops).
6. Accuracy constraints—absolute, relative, or none.
7. The degree of learning—most automatic or stereotyped (locomotion, writing), least automatic (exploratory activity with the hands).

The role of various forms of feedback in motor control deserves further discussion. Two general models of motor control have been proposed—closed loop and open loop. Closed loop control involves the use of sensory feedback signals from somatic, visual, and vestibular receptors to guide the movement continuously and maintain the intended trajectory. Corrections initiated under closed loop control may be generated by input from somatic receptors, which act rapidly in a reflex manner to modify motor cortex output, or by the visual system, which acts more slowly and may involve voluntary effort. Although the closed loop mode of motor system function is well documented, open loop control, in which movement execution relies entirely on central preprogramming, may also apply in many situations either because sensory feedback is ignored by the CNS or because the movement sequence is too fast to permit effective feedback correction. Examples of such rapid movement sequences would be batting a ball or playing the piano. Even slower movements may be executed largely in open loop mode once they have been thoroughly learned through repetition. Preprogramming through practice and repetition may be an important process by which motor learning occurs.

WHAT AREAS OF CEREBRAL CORTEX PARTICIPATE IN VOLUNTARY MOVEMENT?

Areas of cerebral cortex involved in voluntary movement have been identified by 1) motor deficits associated with lesions, 2) neural unit activity related to

---

**Fig. 1.** Flow chart of interactions between the major brain areas involved in voluntary movement. An idea for a specific movement is translated into detailed neural programs by basal ganglia, premotor cortical areas, and the lateral division of the cerebellum. These detailed instructions for movement are then decoded and executed by motor cortex. Sensory receptors provide feedback about the actual movement to various levels of the CNS, but particularly the intermediate cerebellum, which can compare this information with information about the intended movement and initiate a correction if necessary. Premotor areas include supplementary motor area, premotor cortex, and parietal areas 5 and 7. (Adapted from Allen and Tsukahara.)

Volumes 65 / Number 5, May 1985
movement, 3) motor responses evoked by electrical stimulation, and 4) measurement of regional cerebral blood flow in human beings. Cerebral blood flow to a region is a measure of its metabolic activity, which, in turn, varies with functional (electrical) activity. 9, 10

Figure 2 is a sketch of the lateral cortical surface of a monkey brain that identifies different areas based on their distinctive histological features (cytoarchitectonics). 11, 12 Areas that appear to have a specific role in motor control are given in Table 1.

**TABLE 1**

Cortical Areas Involved in Motor Control and Their Corresponding Cytoarchitectonic Designations

<table>
<thead>
<tr>
<th>Area</th>
<th>Cytoarchitectonic Field</th>
</tr>
</thead>
<tbody>
<tr>
<td>Motor cortex</td>
<td>Field 4 (and 6Aα)</td>
</tr>
<tr>
<td>Premotor</td>
<td>6Aβ (lateral part)</td>
</tr>
<tr>
<td>Supplementary motor area</td>
<td>6Aβ (medial part)</td>
</tr>
<tr>
<td>Prefrontal</td>
<td>9, 10</td>
</tr>
<tr>
<td>Posterior parietal area</td>
<td>5, 7</td>
</tr>
</tbody>
</table>

**Major Connections of Cortical Motor Areas**

The interconnections between brain areas involved in movement can provide important clues about the functional roles of these areas. Figure 3 summarizes the major neural circuitry of the cortical motor system. 13 Within the cerebral cortex, the general pattern of information flow from sensory input to motor output seems to be from the sensory systems to the parietal and temporal association areas to the prefrontal cortex to the supplementary motor area (SMA) and premotor area and finally to the motor cortex. 11 In this organization, the temporal and parietal cortex are sites of converging input from the major sensory systems. Although this is the predominant organization that emerges from studying the interconnections of major cortical areas, other more direct routes to the motor cortex exist. For example, parietal area 5 projects directly to the motor cortex. In addition, frontal or parietal association areas can influence the motor cortex through either of two major reentrant loops—one involving the cerebellum and the other the basal ganglia.
Figure 3 represents the motor cortex as the only link between cortical areas and motoneurons. Although the motor cortex provides the brain with access to motoneurons of virtually all somatic muscles (excluding extraocular muscles), the phylogenetically older brainstem descending systems represent important and powerful additional inputs to motoneurons through which the basal ganglia, cerebellum, and cerebral cortex may act, independent of the motor cortex, to influence movement. Furthermore, the premotor area and SMA have direct corticospinal projections through which they may influence motoneurons. Nevertheless, in primates, which show a high degree of encephalization, the motor cortex is clearly a key structure from which descending command signals for intended movements emanate.

Figure 3 also shows that the motor cortex receives convergent input signals from a multitude of sources. Central input is received from several cortical areas including premotor, SMA, parietal area 5, and from two, major, central reentrant loops. Motor cortex is also influenced by two, major, sensory feedback loops. One of these (dorsal column pathway) provides relatively direct feedback for use in reflex compensation; the other (spinocerebellar pathway) goes first through the cerebellum, which, in turn, can alter activity in the motor cortex or brain-stem descending systems. One of the roles of the motor cortex is to transform these diverse input signals, including sensory signals, into appropriate output commands coding which muscles should contract and at what force.

**MOTOR CORTEX FUNCTIONS**

The motor cortex has been the most extensively studied of all motor cortical areas, and some of its properties are relatively well understood. In general terms, these functions involve the execution of intended movements and mediation of specific reflex responses. Specific functions may be summarized as follows:

1. Decodes central program instructions from other cortical and noncortical areas and translates them into specific output command signals that specify a) the muscles to contract and relax (target muscles), b) the force of contraction, and c) the timing of contraction.

2. Informs other brain areas (cerebellum and basal ganglia) of the "intended" movement through corollary discharge.


**Program Decoding and Command Signals**

How is the voluntary contraction of a muscle specified by the motor cortex? Work on both human beings and monkeys has shown that motor cortex cells influencing different muscles are arranged in an orderly fashion across the precentral gyrus. For example, in Figure 4, the image of a monkey's body is superimposed on the surface of motor cortex to show the relative location of cells involved in movements of different body parts. Two points relating to this motor map should be emphasized. First, the projection is largely contralateral, that is, most motor cortex cells influence muscle activity on the body side opposite to the location of the cell. Second, movements involving distal muscles are represented by a much larger amount of cortical tissue than those involving proximal muscles despite the fact that distal muscles have a smaller mass. This disparity suggests a preferential role of motor cortex in distal movements.

Such somatotopic maps indicate a general spatial separation of cells controlling movements at different joints, but can individual muscles be selected through the output circuitry of motor cortex? Recent evidence demonstrates that although some individual cortical cells activate motoneurons of only a single muscle, the majority of cortical cells have more widely branching axons and activate not one but a group of synergist muscles. Nevertheless, the motor cortex clearly provides the brain with access to virtually all the body musculature and, in many cases, appears to have adequate specificity for selective activation of single muscles. Of course, other components of the motor program must channel activity to the appropriate motor cortex cells.
The patterns of functional influence exerted by the motor cortex on different muscle groups can be examined at two levels: first, the total or net effect of motor cortex output on different motoneuron pools and second, the actions of single motor cortex cells on different motoneuron pools. The net output effects of motor cortex on forelimb and hindlimb muscle groups have been determined by Preston et al. who used a monosynaptic reflex conditioning procedure to test the effect of electrical stimulation of motor cortex on motoneuron pools. Motor cortex stimulation can either increase or decrease the magnitude of the summed discharge volley of a motoneuron pool evoked by monosynaptic spindle Ia input. Increases represent net excitatory actions of motor cortex on the recorded motoneurons; decreases represent net inhibitory actions. The findings from experiments in primates are summarized in Figure 5. The dominant pattern of motor cortex action is different for different muscle groups. For the hindlimb, muscles whose contraction opposes the action of gravity during static posture (all extensors of the hindlimb) are predominantly inhibited by the motor cortex while the flexors are predominantly facilitated. This pattern is meaningful for understanding voluntary movement because the initiation of a voluntary movement, which is thought to be mediated by motor cortex, generally requires inhibition of tonic antigravity postural mechanisms. For example, to initiate walking from a standing posture, one leg must flex at the hip, knee, and ankle while the extensors of the opposite leg stiffen to support the shift in load. The effects on the forelimb in the monkey are more complex and may reflect a transition from quadrupedal to bipedal locomotion.

These findings can also be extrapolated to human beings and may help explain some of the abnormal postures observed in cases of cerebral damage. Such patients typically exhibit extensor rigidity in the leg and tonic flexion of the elbow. If the motor cortex has a tonic action in the absence of movement, with net effects resembling those in Figure 5, then removing the motor cortex input to motoneurons would release leg extensors and elbow flexors from inhibition and would produce the typical pattern of decorticate posturing.

A second, more refined, level from which the motor cortex actions on muscle activity can be viewed is that of the single cortical cell. Recently developed techniques have enabled determination of the types of effects single cells have on agonist and antagonist muscles acting at a joint. Three major types of cortical cells have been identified based on the organization of their synaptic inputs to forearm motoneurons (Fig. 6). Cortical cells of one type facilitate muscles that they coactivate during voluntary movement (agonist muscles) but have no effect on the antagonists. Others only suppress the antagonists and have no effect on agonists. Still other cortical cells have a reciprocal pattern of organization in which they simultaneously facilitate agonists and suppress antagonists.
facilitate agonists and inhibit antagonists.

How is the force and timing of muscle contraction encoded? Force appears to be encoded in the frequency of discharge of corticomotoneuronal cells. The relationship in Figure 7 shows that the maintained discharge of motor cortex cells specifies the force of target muscle contraction during steady holding against a load. In addition, the firing of many cells appears to encode the dynamic features of movement such as the rate of force change.

The duration of muscle activity is determined by the duration of the motor cortex cell activity that the motor program specifies. The activity of motor cortex cells, however, begins slightly in advance (60 msec) of muscle activity, as would be expected for neurons that initiate muscle activity.

In conclusion, the muscles to be contracted in a movement are specified by the set of motor cortex cells selected for activation by the central motor program and the distribution of synaptic connections between these cells and motoneurons. Furthermore, the motor cortex cells encode in their activity the detailed characteristics of movement, including static force, rate of change of force, and the timing of muscle activity.

**Corollary Discharge to Cerebellum**

Corollary discharge to the cerebellum is an aspect of motor cortex function about which few details are known. The basic theory, however, is that the cerebellum must have information about the "intended" movement to compare with the "actual" movement and to issue appropriate "error correction" commands. Therefore, a command for movement from the motor cortex destined for motoneurons is transmitted simultaneously to the cerebellum (Fig. 3). This "corollary discharge," as it is called, is used by the intermediate division of the cerebellum to compare the intended movement with the actual movement and to make appropriate corrections if an error is detected.

**Long-Latency Muscle Responses to Stretch**

The reflex responses of muscle to stretch have been a subject of great interest in studies of motor control. The existence of a spinal reflex mechanism originating with muscle spindle afferents, which, in turn, excite motoneurons directly, is well-established. The spinal stretch reflex is a negative feedback mechanism in which muscle stretch elicits a reflex contraction that opposes further lengthening of the muscle. Recent data demonstrate the existence of a transcortical stretch reflex pathway by which the motor cortex contributes to a longer latency of stretch reflex responses of muscle (M2 in Fig. 8). Both the spinal and transcortical pathways are illustrated in Figure 8, which also shows the relative timing of muscle responses evoked by activity in each pathway. The longer latency of the cortically mediated reflex compared with the spinal reflex is due to the additional conduction distance between spinal cord and motor cortex.

Transmission through the transcortical reflex pathway is not obligatory but rather depends on the subject's intended movement. For example, the long-latency reflex is enhanced in a subject instructed to resist an impending perturbation and is diminished or absent if the instruction is to assist or ignore the perturbation. The underlying instruction-related changes in the excitability of CNS pathways made in preparation for a voluntary movement are referred to as "motor set."

The long-latency stretch reflex pathway may also be of clinical significance because it is potentiated in Parkinson's disease and may contribute to the rigidity associated with this disorder. Lee et al reported that in Parkinson's disease, the long-latency component of the stretch reflex (M2) is almost as large under passive conditions as when subjects are instructed to oppose actively the perturbation. This suggests that feedback from muscle afferents to sensorimotor cortex is improperly regulated in Parkinson's disease so that the efficiency of transmission is always maximum.

**Cortical Mediation of the Grasp Reflex**

Lesions of SMA result in exaggerated reflex grasping that can be elicited by lightly stroking the glabrous skin of the hand. This reflex is cortically mediated because it is abolished by lesions of either the sensory or motor cortex. Moreover, the specific mechanism underlying the grasp reflex can now be understood in terms of the input-output coupling of motor cortex cells. Recordings from single motor cortex cells have revealed a basic principle of input-output coupling. Cells whose electrical stimulation produces movement in a particular direction are also activated by stimulation of the skin facing that direction. For example, motor cortex cells mediating finger flexion are generally activated by cutaneous stimulation of the glabrous surface of the palm and fingers. This circuitry, thus, forms a positive feedback loop for reinforcement of grasping because contact between an object and the glabrous surface of the hand will activate those specific motor cortex cells that facilitate finger flexors. This, in turn, will strengthen the grip force, further enhance cutaneous input from the glabrous skin, and further increase the activity of flexor motor cortex cells.

**SUPPLEMENTARY MOTOR AREA FUNCTIONS**

Current evidence suggests that the SMA is involved in two functions: 1) control of input-output coupling in motor cortex and 2) assembly of motor programs, specifically, the elaboration of motor subroutines for rapid sequences of movements, such as those involved in playing the piano, writing, and speaking.

**Control of Input-Output Coupling in Motor Cortex**

Evidence that the SMA is involved in controlling input-output coupling in
motor cortex derives from observations in human beings and monkeys that lesions of the SMA consistently produce a hypersensitive grasp reflex so that light tactile stimulation of the glabrous skin on the palm of the hand or fingers produces an exaggerated, powerful reflex grasp. The transcortical circuit for this reflex was described in the previous section. Subjects are often unable to release their grip on objects placed in the palm of the hand. This control of the SMA over input-output coupling in motor cortex may also extend to proprioceptive transcortical reflexes (Fig. 8) because recent evidence has demonstrated that stimulation of the SMA in monkeys produces prolonged suppression of motor cortex cell responses to muscle stretch. This finding also suggests a possible explanation for the spasticity that accompanies lesions of the SMA.

Recent experiments in which regional cerebral blood flow (RCBF) was measured in human beings during performance of different motor tasks have been particularly revealing as to the functional roles of the SMA and other frontal and parietal areas in voluntary movement. Regional cerebral blood flow is proportional to oxygen consumption and provides an indirect measure of total neuronal activity in an area. Roland et al injected 133Xe into the carotid arteries of awake human subjects and monitored its washout from different areas of the cerebrum with 254 gamma detectors surrounding one side of the head. The RCBF for 254 separate regions of each cerebral hemisphere were calculated from these measurements with a computer and displayed in color-coded form on a video monitor. The functional areas for which RCBF measurements were made are labeled on the Reference Brain in Figure 10. F. The subjects were instructed to perform five different motor tests. These tests are fully described below, and the major findings are summarized in Figure 10.

Motor sequence test. Subjects were instructed to perform with eyes closed a sequence of opposing movements with the thumb and fingers. Within a 10-second time period, the subject had to touch briefly with the thumb the following fingers in succession: the index finger twice, the middle finger once, the ring finger three times, and the little finger twice. The sequence was then repeated in the reverse order. This task, therefore, consists of a rapid series of discrete, low force, finger flexion-extension movements. Subjects were thoroughly trained before measurements were made.

Repetitive finger flexion test. Subjects compressed a spring held between the thumb and index finger once every second. This test required more forceful contractions than the motor sequence test but was routine in that no complex movement sequence was involved.

Internal programming of movement sequence test. Subjects were asked to simulate mentally the motor sequence test but were instructed not to make any actual movements (Fig. 10.A). Electromyograms confirmed that no muscle activity occurred.

Maze test. Subjects were asked to move the index finger in a specific pattern through a grid divided into 49 separate, 26- x 36-mm squares. Partitions separated adjacent squares. For example, in response to the verbal instruction, “move two forward, three left,” the subject was expected to move the index finger two squares forward then three squares left at a rate of one step every second without skipping any squares. This test, like the motor sequence test, required memory of a movement sequence but differed from the motor sequence test and all other tests in that the movement sequence changed with each new verbal instruction and required reassembly of the motor program. This test also differed from the motor se-
sequence test in that execution involved use not only of finger muscles but also of proximal arm muscles, and targets were objects in immediate extrapersonal space, that is, space surrounding but not part of the body.

**Spiral test.** With ears plugged and eyes closed, subjects drew in space with the index finger (guided by compound arm movements) a spiral of increasing and then decreasing size. Subjects were told to move about 120°/sec, make the longest spiral about 75 cm in diameter and the smallest about 2 cm; the number of turns was not crucial. This test, like the motor sequence test and the maze test, involved a complex sequence of activity in the muscles. This test differed from the motor sequence test in that 1) it required movement toward a target object in extrapersonal space, 2) it involved primarily use of proximal limb muscles, and 3) its movements were continuous with smooth transitions in activity from one set of muscles to another. Because the subjects’ eyes were closed when the test was performed, target coordinates had to be stored during training, recalled during performance, and transformed into appropriate commands for muscle activity just as in the maze test. This test differed from the maze test in that 1) movements were continuous rather than discrete steps and 2) the required movement sequence remained unchanged during the test.

Figure 10.A shows the cortical areas that were activated during the motor sequence test. Recall that the complex sequence of movements in this test had to be completed within 10 seconds and left inadequate time to think about each move. The movement sequence and motor commands necessary to achieve the movements had to be preprogrammed through experience during which the subjects practiced the test. All numbers in Figure 10 show the percentage increase in the blood flow to an activated cortical area over the control blood flow to the same area when the subject was sitting quietly at rest. The increases indicated by cross-hatching were significant at the .0005 level, those indicated by hatching at the .005 level, and the outlined areas at the .05 level. The medial surface of the hemisphere is represented above each lateral view. Associated with the motor sequence test (Fig. 10.A) were large increases in RCBF to the hand area of primary motor cor-

Fig. 10. Numbers represent increases in regional cerebral blood flow in human beings during performance of various motor tests described in the text. A. Motor sequence test. B. Repetitive finger flexion test. C. Internal programming of movement sequence test. D. Maze test. E. Spiral test. F. Reference figure for identification of different cortical regions. Increases are averages of several subjects and are expressed as percentages above control. Control measurements were obtained with subjects sitting at rest with ears plugged and eyes closed; subjects were instructed not to move or tense muscles and to “think of nothing.” Experimental tests were performed with eyes closed. Results shown are for the left hemisphere (tests A–D) and right hemisphere (test E). Movements were all performed with the hand and arm contralateral to the hemisphere shown. Both the lateral and medial (upper drawings) cortex are represented. (Adapted from Roland et al. 27, 30)
tex on the contralateral side (ipsilateral motor cortex showed no change) and in SMA, bilaterally. The increase in contralateral primary motor cortex presumably reflects increased neuronal activity associated with the issuing of commands for activity in specific finger muscles. The finger representation of primary sensory cortex on the contralateral side also showed increased blood flow possibly as a result of increased sensory input from the moving digits.

The bilateral increase in RCBF in the SMA is most interesting. The increased neuronal activity appears to be associated with some aspect of motor programming because no increase in RCBF was observed during repetitive, forceful finger flexion-extension movements that did not involve a specific planned sequence (Fig. 10.B). In contrast, primary motor and sensory cortices did exhibit increases during the simple flexion test in Figure 10.B comparable to those during the motor sequence test. A role for the SMA in the planning of movement sequences is further supported by the experiment in which the motor task was internalized and the subjects performed the movement sequence mentally but were not allowed to execute any movements actually (Fig. 10.C). In the internal programming test, the SMA but not the primary motor cortex showed increased blood flow bilaterally, which suggests the SMA participates in the assembly of programs for ballistic movement sequences that occur in rapid succession. Blood flow measurements were not made during the learning phase of this experiment. During this learning phase, however, information about the types of movements to be executed, the body parts to be moved, and the sequence and timing of movements must have been stored in memory. Internal program execution of the motor sequence test (Fig. 10.C) involved recalling this information and generating a set of time-ordered commands. The formation of a motor subroutine specifying these aspects of planned movement sequences, therefore, seems to be a major contribution of the SMA. Even though the motor test only involved muscles on one side, the participation of the SMA in both hemispheres confirms recent experiments in monkeys showing that the activity of single cells in the SMA is related to both ipsilateral and contralateral movements.31

<table>
<thead>
<tr>
<th>Neuron Type</th>
<th>% of Sampled Units*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area 5</td>
<td></td>
</tr>
<tr>
<td>Joint rotation (passive)</td>
<td>64</td>
</tr>
<tr>
<td>Muscle (deep) receptors (passive)</td>
<td>14</td>
</tr>
<tr>
<td>Cutaneous (passive)</td>
<td>9</td>
</tr>
<tr>
<td>Arm projection and hand manipulation</td>
<td>11</td>
</tr>
<tr>
<td>Other</td>
<td>2</td>
</tr>
<tr>
<td>Area 7</td>
<td></td>
</tr>
<tr>
<td>Visual fixation</td>
<td>27</td>
</tr>
<tr>
<td>Visual tracking</td>
<td>7</td>
</tr>
<tr>
<td>Saccade</td>
<td>17</td>
</tr>
<tr>
<td>Arm projection and hand manipulation</td>
<td>15</td>
</tr>
<tr>
<td>Visual only</td>
<td>18</td>
</tr>
<tr>
<td>Other and unidentified</td>
<td>16</td>
</tr>
</tbody>
</table>

*Percentages compiled from work of Lynch et al,36 Motter and Mountcastle,37 and Mountcastle et al.27

Human speech is another type of skilled movement that involves fast sequences of muscular contractions, and RCBF to the SMA also increases during speech.32 Presumably, movements such as writing, typing, and playing musical instruments also rely heavily on the SMA.

Activation of the SMA was not limited to tests involving rapid sequences of discrete finger movements, but also occurred in the maze and spiral tests that involved arm movements into extrapersonal space. These findings suggest that the SMA also has a role in controlling complex arm movement sequences. Further support for this hypothesis derives from recent lesion experiments in monkeys showing that unilateral destruction of the SMA coupled with corpus callosum lesions severely impairs visually guided movements of the contralateral hand.33

TABLE 2
Classes of Neurons in Parietal Areas 5 and 7 of the Monkey

<table>
<thead>
<tr>
<th>Neuron Type</th>
<th>% of Sampled Units*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area 5</td>
<td></td>
</tr>
<tr>
<td>Joint rotation (passive)</td>
<td>64</td>
</tr>
<tr>
<td>Muscle (deep) receptors (passive)</td>
<td>14</td>
</tr>
<tr>
<td>Cutaneous (passive)</td>
<td>9</td>
</tr>
<tr>
<td>Arm projection and hand manipulation</td>
<td>11</td>
</tr>
<tr>
<td>Other</td>
<td>2</td>
</tr>
<tr>
<td>Area 7</td>
<td></td>
</tr>
<tr>
<td>Visual fixation</td>
<td>27</td>
</tr>
<tr>
<td>Visual tracking</td>
<td>7</td>
</tr>
<tr>
<td>Saccade</td>
<td>17</td>
</tr>
<tr>
<td>Arm projection and hand manipulation</td>
<td>15</td>
</tr>
<tr>
<td>Visual only</td>
<td>18</td>
</tr>
<tr>
<td>Other and unidentified</td>
<td>16</td>
</tr>
</tbody>
</table>

*Percentages compiled from work of Lynch et al,36 Motter and Mountcastle,37 and Mountcastle et al.27

Human speech is another type of skilled movement that involves fast sequences of muscular contractions, and RCBF to the SMA also increases during speech.32 Presumably, movements such as writing, typing, and playing musical instruments also rely heavily on the SMA.

Activation of the SMA was not limited to tests involving rapid sequences of discrete finger movements, but also occurred in the maze and spiral tests that involved arm movements into extrapersonal space. These findings suggest that the SMA also has a role in controlling complex arm movement sequences. Further support for this hypothesis derives from recent lesion experiments in monkeys showing that unilateral destruction of the SMA coupled with corpus callosum lesions severely impairs visually guided movements of the contralateral hand.33

PARIETAL CORTEX FUNCTIONS

Two parietal areas have been implicated in motor control—area 5 and area 7 (Fig. 3). Area 5 is believed to be preferentially involved in guidance of exploratory limb movements by tactile stimuli, whereas area 7 is more involved in visual feedback guidance of eye and limb movements.34,35

Area 5 receives its principal input from the primary somatic sensory cortex and projects most heavily to the SMA and premotor cortex (Fig. 3). Area 5 also sends some axons directly to the spinal cord. Mountcastle et al,35 Lynch et al,36 and Motter and Mountcastle37 have extensively investigated the properties of parietal neurons (Tab. 2). Most neurons in area 5 are driven by simple passive joint rotation (64%). A particularly interesting class of cells comprising 11 percent of the sample (arm projection and hand manipulation neurons, Tab. 2), however, discharged at high rates only when the monkey reached for or manipulated an object of interest (eg, food for a hungry animal) in immediate extrapersonal space. These neurons did not respond to visual, auditory, or somatosensory stimuli and were unrelated to similar movements in which no target object of motivational interest was present. Therefore, these neurons do not directly encode simple movement char-
acteristics such as force, nor do they respond to sensory stimuli; rather, they seem to generate commands for the manual exploration of targets of interest in extrapersonal space.

What are the functions of area 7? Electrical stimulation and unit recording experiments have shown that area 7 can be subdivided into three separate regions—the first concerned with visual guidance of arm movements, the second with visual guidance of eye movements, and the third with facial expressions. Area 7 differs from area 5 in its projections and afferent inputs. Area 7 receives input from visual, somatic (through area 5), auditory, and limbic structures and projects heavily to the prefrontal cortex and to frontal eye fields—an area known to be involved in control of eye movements.

The functional properties of cells in area 7 are summarized in Table 2. As expected, area 7 contains some neurons related to arm movements and others related to eye movements. An important property of a large fraction of area 7 neurons is that their discharge is contingent on the presence of objects of motivational interest in immediate extrapersonal space. They seem to be involved in directing attention to these objects as targets for visually guided arm-reaching movements or eye movements. Some neurons related to eye movement are driven only by visual input, others respond to both the visual and motor aspects of the task, and still others are related only to the motor response. Neurons related only to the motor aspect of the task may perform a command function bringing the eyes to focus on objects of interest in visual space (foveation). These “command” neurons can be subdivided into three categories—visual fixation, visual tracking, and saccadic (quick)—depending on the type of eye movement with which they are related. Visual fixation neurons discharge only during foveation of stationary objects that are both of interest and obtainable. For example, a visual stimulus signaling the availability of food activates these cells in a monkey providing the food is within reach and the monkey is hungry. The visual stimulus alone does not activate the cell unless the stimulus has motivational significance to the monkey. Activation of such cells, however, is visually dependent because blocking the view of the object interrupts the cell’s discharge. Visual tracking neurons discharge during eye tracking (smooth pursuit) of slowly moving, obtainable objects of interest in the visual field. The discharge of individual neurons is maximal for pursuit movements in a particular direction. Saccade neurons begin discharging just before, and throughout, saccadic eye movements toward objects of interest appearing abruptly in the peripheral visual field. The activity of these cells, however, is unrelated to spontaneous saccades, such as those occurring in the dark, or saccades toward visual stimuli of no motivational interest. These properties suggest that parietal area 7 issues commands for arm movements (like area 5) and eye movements toward objects of motivational interest in immediate extrapersonal space. This is an important part of the more general process of selective attention to specific environmental stimuli.

The deficits resulting from lesions of parietal cortex in monkeys and human beings generally reflect the properties of parietal neurons as discussed earlier. The major deficits with unilateral lesions can be summarized as follows:

1. Neglect of the contralateral arm including a reduction in spontaneous and purposive movements and neglect of objects in the contralateral visual field. These deficits are most common in human beings with lesions of the right (nondominant) hemisphere.

2. Difficulty in manipulating objects with the contralateral hand (apraxia).

3. Astereognosis—failure to recognize objects placed in the contralateral hand.

4. Errors in accuracy of arm movements. This is particularly severe in the dark where proprioceptive cues must be used to guide the limb to its target. Errors in movements made under visual guidance, however, are also easily detected.

5. Difficulty grasping an object with the contralateral hand once it is contacted (primarily with lesions of area 5).

6. Difficulty performing discrete hand and finger movements requiring visual or proprioceptive cues. Bilateral lesions produce deficits that are bilateral and more severe.

Cerebral blood flow measurements in human beings also suggest a role for parietal cortex in the guidance of arm-reaching movements into extrapersonal space. Only during the maze (Fig. 10.D) and spiral (Fig. 10.E) tests, which were both performed with eyes closed and presumably were guided by proprioceptive information, did the parietal cortex “light up.” Both these tests required a motor program that would draw upon task-related information generated during earlier experience to assemble program instructions for accurate limb movement trajectories into extrapersonal space. In these tests, the eyes were closed so no object of motivational interest could be directly viewed. In the maze test, however, hand contact was made with the test board. Because the test board possessed motivational interest for the subjects, its manipulation may have activated hand manipulation neurons in both areas 5 and 7.

**PREFRONTAL CORTEX FUNCTIONS**

The prefrontal cortex influences movement only indirectly (Fig. 3) through projections to basal ganglia, cerebellum, and secondary cortical motor areas. It receives afferents from limbic structures (cingulate gyrus and amygdala), hypothalamus, thalamus, and brain stem. These inputs presumably convey to the prefrontal cortex information about the animal’s motivations and internal state. In addition, the prefrontal cortex receives visual, auditory, and somesthetic information indirectly through temporal and parietal association areas.

Destruction of the entire prefrontal cortex bilaterally produces a loss of motivation, a generalized dulling of emotional behavior, and aimless hyperactivity. More restricted lesions limited to the dorsolateral prefrontal cortex, however, produce clear cognitive deficits in behavioral tests. These deficits consist primarily of disorders in attention to and short-term memory for task-related cues. A clear correlate of the short-term memory function of the prefrontal cortex has been identified in the discharge of single prefrontal neurons during performance of a delayed response task. In one such task, food is placed underneath one of two identical objects in view of the monkey (cue phase). View of the object is then blocked for a period of about 18 seconds after which the monkey must select the object containing food. A variety of firing patterns...
Fig. 11. Unit discharge patterns in prefrontal cortex during delayed-response task. Heavy lines (A, B, C, D, I, O) illustrate different types of firing patterns observed in prefrontal neurons during task performance. Upward deflections indicate increases in firing rate. Arrows indicate movements of an opaque screen located between the monkey and test objects. During the cue phase, food is placed under one of the objects. The screen is lowered for about 18 seconds, then raised, and the monkey must choose the object containing food. (From Fuster.)

have been observed in single units during this task (Fig. 11). The discharge of some units increased either transiently (Fig. 11.A) or throughout cue presentation (Fig. 11.B). These cells may be involved in attention to the cue object. Other cells (Figs. 11.C, D) showed a sustained increase in activity during the delay period (up to one minute) and may constitute a short-term memory apparatus. Over half of the cells in the prefrontal cortex showed increased activity during the delay period; a small number (8%) showed decreased activity (Fig. 11.I). Neurons of untrained animals did not show delay-related activity. Delay activation could easily be attenuated by distractions and was highly related to the proficiency of performance. Additional tests, however, have revealed that although activity during the delay period is related to short-term memory in some neurons, in other neurons, the activity is related to motor set for an impending response.

In summary, findings from both lesion and unit recording experiments strongly suggest a role for the prefrontal cortex in short-term memory of cue features or location in delayed response tasks. Additional roles of the prefrontal cortex may include the processes of selective attention and motor set in preparation for an impending movement.

SUMMARY

Several cerebral cortical areas have been shown to have a role in motor control by the methods of electrical stimulation, single unit recording in animals trained to make specific motor responses, creating lesions of specific cortical areas, and measuring RCBF in humans. The areas are the primary motor cortex, SMA, premotor cortex, parietal areas 5 and 7, and prefrontal cortex. Neurons of the primary motor cortex encode the detailed characteristics of movement such as the desired force of muscle contraction and its timing. These signals are then transmitted directly to motoneurons. Motor cortex, therefore, executes program instructions for movement by transforming input signals into signals that encode movement characteristics. The primary motor cortex also participates in reflex responses of muscle to stretch and cutaneous stimulation (grasp reflex). The SMA is involved in the programming of complex sequences of discrete movements occurring in rapid succession, such as piano playing. The SMA also appears to exert control over the efficiency of input-output coupling in transcortical reflexes evoked by muscle stretch and tactile stimulation. Parietal area 5 is strongly influenced by somatic and kinesthetic input from the limbs and appears to issue motor commands for tactile exploration of extrapersonal space with the hand. Parietal area 7 is more strongly influenced by visual input than somatic input. Its function seems to be one of selective attention to objects of motivational interest in extrapersonal space by issuing eye movement commands for foveation of such objects and for arm movements to them. The prefrontal cortex may perform multiple functions, but one of these appears to be the cognitive function of short-term memory in delayed response situations.

A large variety of different types of movements can be identified based on factors such as speed or degree of training. Different types of movements place different demands on the neural control system. Hence, the degree of involvement of different cortical areas in movement will vary widely depending on the specific requirements of the movement performed.

Acknowledgment. I thank Linda Carr for typing this paper.