Cortical Control of Movement

Four parts of this lecture:
I) Anatomical Framework, II) Physiological Framework, III) Primary Motor Cortex Function and IV) Premotor Cortex Function

I. Anatomical Framework:

This section will describe the organization of motoneurons and then, the organization of inputs to motoneurons.

1. (Fig. 1) A segment of spinal cord.
   Three general areas:
   - Dorsal horn
   - Intermediate zone
   - Ventral horn.

2. (Fig. 2) Organization of motoneuron pools.
   Two main columns of motoneurons:
   - Axial muscles = ventromedial cell column
   - Limb muscles = the lateral cell column

   The lateral column has an overall somatotopic organization

3. (Fig. 3) Organization of motoneurons in the Lateral cell column.
   - Distal flexor = located dorsolaterally
   - Proximal extensor = located ventromedially

   *** Interneurons in the intermediate zone have a similar organization. ***

Organization of descending pathways which terminate in the spinal cord.

Two general patterns of descending systems from the brainstem

4. (Figs. 4&5; fig. 35-6a) Ventromedial brainstem pathway-
   a. Travels in the ventral funiculus (descends bilaterally).
   b. Terminates in the ventromedial part of the intermediate zone and somewhat in the ventromedial cell column.
   c. Originates in the descending portions of several brainstem nuclei including the reticular formation, and vestibular nuclei.

5. (Figs. 4&5; fig. 35-6b) Dorsolateral brainstem pathway-
   a. Travels in the dorsolateral funiculus (largely unilateral).
   b. Terminates most heavily in the dorsolateral portion of the intermediate zone.
   c. Originates largely from the magnocellular component of the red nucleus.
The Corticospinal System contributes to both the medial and lateral systems.

6. (Fig. 6; fig. 35-7) **Lateral Corticospinal-pathway and termination.** Part of the corticospinal system travels in the dorsolateral funiculus and terminates in the dorsal horn, in the intermediate zone (dorsolaterally) and in the dorsolateral portion of the lateral motoneuron cell column.

7. (Fig. 6; fig. 35-7) **Ventral Corticospinal-pathway and termination.** Another part of this system travels in the ventromedial funiculus and terminates medially in the intermediate zone and in the ventromedial motoneuron cell column.

Note-
I. The corticospinal and rubrospinal systems travel and terminate in the same regions of the spinal cord. The number of rubrospinal neurons appears to decline in higher primates.

II. The majority of the terminations from most descending pathways end in the intermediate zone, thus interneurons play a very important role in movement generation.

We will focus on the corticospinal system because it has: a) the most direct input to limb motoneurons and b) features common to all the other descending systems.

Two questions about the corticospinal system:

1) Which cortical areas contribute to the corticospinal system?
2) Where do the axons from these cortical areas terminate in the spinal cord?

8. (Figs. 7 & 8; fig. 40-2) **Question 1: Which cortical areas contribute to the corticospinal system?** Method: Retrograde axonal transport.

ans.: The corticospinal system originates from multiple cortical areas including the primary motor cortex (area 4), all the premotor areas [including lateral premotor cortex (lateral area 6) and the supplementary motor area (medial area 6)], primary somatic sensory cortex (areas 3a, 3b, 1 and 2) and posterior parietal cortex (areas 5 and 7).

9. (Figs. 8 & 9) **Question 2: Where do the axons from these different cortical areas terminate in the spinal cord (which laminae and near which types of neurons)?** Method: Anterograde axonal transport.

a. somatic sensory (areas 3a, 3b, 1 and 2) and posterior parietal cortical areas terminate in different portions of the dorsal horn.

b. primary motor cortex (area 4) terminates in the intermediate zone and ventral horn; projections directly to distal motoneurons arise from the most caudal part of the primary motor cortex (i.e., the part of the motor cortex in or near the central sulcus)

c. premotor cortical areas (e.g., SMA and the lateral area 6) have terminations similar to that of the primary motor cortex (still under study).
Comments and Conclusions:

1. The dorsal horn is very important in the processing of peripheral afferent information. Projections to the spinal cord are thought to be involved in **controlling the flow of somatic sensory information** from the spinal cord to more central structures.

2. Area 4 is the major cortical region with direct access to motoneurons and is the major cortical input to the intermediate zone. (Note: premotor areas)

**Anatomical Evidence that the Corticospinal System is important for Manual Dexterity**

10. (Fig. 10; fig. 35-8) **The density of corticospinal projections directly to motoneurons in different animals correlates with manual dexterity.** Compare the pattern of terminations in the ventral horn of the opossum, cat, rhesus monkey, and chimp. In general, there is an increase in the density and extent of direct connections from cerebral cortex to motoneurons as you ascend the phylogenetic scale. There is a clear correlation between the ability of an animal to make relatively independent finger movements and the density of corticospinal terminations around motoneurons in the ventral horn.

11. (Fig. 11) **Development of corticospinal connections.** Direct connections from cortex to motoneurons are the last to develop. This anatomical feature correlates with the late development of relatively independent movements of the fingers. In macaques, independent finger movements and direct projections to motoneurons both first appear at about the same time (9 months).

II. Physiological Framework:

1. (Fig. 12; fig. 40-2) **Topography of human and macaque left hemisphere.** Multiple cortical areas are involved in the control of movement. Note the location of the primary motor cortex, supplementary motor area (SMA), and lateral premotor area. Movements can be evoked in some of these areas when they are stimulated with small amounts of electrical current. Using this method it has been possible to define 'motor maps' of the body in the primary motor cortex and the SMA.

2. (Fig. 13) **Sample of results from a single mapping experiment in the primary motor cortex and SMA of a monkey.** C = the central sulcus; i = the arcuate sulcus; d = midline of the hemisphere (where the medial wall begins); e = the beginning of the dorsal bank of the cingulate sulcus.
Note:

a. stimulation caudally in the motor cortex (i.e., near the central sulcus) evokes contractions of distal musculature

b. stimulation more rostrally in the primary motor cortex evokes contractions of more proximal body musculature.

c. stimulation medially along the central sulcus evokes foot movements

d. stimulation laterally along the central sulcus evokes face and tongue movements

e. stimulation between the leg and face regions evokes arm movements

f. a second region where movements can be evoked lies rostrally on the medial wall of the hemisphere. This represents the location of the SMA.

g. the map of the body in the SMA has a rostro-caudal orientation with head rostral, leg caudal and arm intermediate.

3. (Fig. 14) One way that the results of mapping studies have been summarized is to place distorted figures of the body in each cortical area. These diagrams show the body part that is on average represented at each site.

4. (Fig. 15; fig. 40-1b) **Body map in the primary motor cortex of humans.** The map is grossly distorted. More space is allotted to the representation of distal musculature (and the tongue and lips) than to the representation of proximal musculature.

Comments on mapping studies:

I) Those body parts with the largest cortical representation have the lowest electrical threshold for evoking movements.

II) Those body parts with the largest cortical representation are capable of the most refined movements.

Maps have some important clinical implications:

I) Those body parts with the largest representation suffer the most following lesions of the motor cortex.

II) Those body parts with the largest representation (and lowest threshold for electrical stimulation) are the ones first involved in an epileptic seizure.
Final note on physiological framework-

4. **The primary motor cortex receives somatosensory input**

Some neurons in the primary motor cortex (area 4) become active when somatic sensory afferents are stimulated. For example, in the hand area of the primary motor cortex, some neurons can be activated by gently touching the palm of the hand (i.e., a cutaneous stimulus) and other neurons will be activated by moving finger joints or stretching finger muscles (i.e., a 'deep' or kinesthetic stimulus). The neurons which are activated by cutaneous input appear to be clustered in the caudal part of the primary motor cortex, whereas those activated by kinesthetic input are located slightly more rostrally. The somatic sensory input to the primary motor cortex may be important for adjusting movement (based on muscle or joint feedback) or for directing movement (based on cutaneous afferent input).

### III. Analysis of Function: Primary Motor Cortex

- **Stimulate**- Does the primary motor cortex control *movements* or *individual muscles*?

  **Is the motor cortex the piano or the piano player?**

  What is represented at a site in the motor cortex- single muscles or movements? When you stimulate the cortex do you evoke contractions of single muscles or groups of muscles?

  There are multiple answers to these questions because the organization of the cortex can be viewed from several perspectives.

  a. Recent studies indicate that some single output neurons in the motor cortex branch extensively and make direct connections with motoneurons innervating several related muscles. Thus, an output neuron from the primary motor cortex may be involved in generating a pattern of muscle activity.

  b. **Groups** of output neurons innervating a particular muscle are clustered together (although the branching patterns of the neurons in the cluster may differ). Thus, single muscles may be represented in small regions of the motor cortex.

  c. The same muscle can be activated from widespread regions of cortex. This multiple representation may reflect the multiple uses of a muscle. For example, the elbow representation at one site may be responsible for activating elbow muscles when they function as prime movers. At another site, the elbow representation may be responsible for activating elbow muscles when they function to fixate the joint.

**Conceptual and technical concerns:** First, can you really study the function of an area of cortex by stimulating it? Electrical stimulation is a very artificial method for activating cortex. Second, the extent of current spread and the actual elements activated by most types of stimulation are unclear (e.g., single cells or small groups of cells).
2. **Lesion**- What functions (or movements) are lost when you remove the motor cortex:

Immediately after a lesion of the primary motor cortex:

1) there is a severe poverty of movement;
2) there is a great reduction in the tone in limb muscles;
3) movement is slow

Several weeks later:

1) considerable recovery of motor function occurs;
2) reaction times may be slightly prolonged;
3) finger movements like grasping in which all of the fingers move in concert, recover;
4) **however, the ability to make independent movements of the fingers does not recover**, i.e., the ability to fractionate movements is lost forever.

**Conclusion:** A motor cortex lesion produces a long lasting deficit in independent finger movements. The primary motor cortex is especially concerned with generating patterns of muscle activity, and particularly those patterns which involve turning on some muscles while inhibiting others.

**Conceptual concern**- Can you really learn the function of a part of the brain by removing it? **What do you learn about the function of a spare tire by removing it?**

Real example-

Remove area 4, you will lose the crude placing reaction in the contralateral forelimb. Months or years later, remove the opposite area 4, crude placing returns.

Conclusion: The interpretation of lesion experiments is not always as straightforward as one might wish.

3. **Neuron Recording in Awake Animals**-

When you record in the motor cortex:

1) **TIMING:** Some neurons in the motor cortex become active before movement begins, others become active during movement. Thus, neurons in the motor cortex may be involved in both the initiation of movements and the ongoing control of movements.

2) **RELATION TO DIFFERENT TYPES OF MOVEMENT:** Some neurons in the motor cortex change their activity during all different types of movement (e.g., locomotion, scratching, chewing, reaching). Thus, they are involved in the control of all different types of movement and not just the most voluntary.

3) **SPECIAL RELATION TO DYNAMIC CHANGES:** Some neurons in the motor cortex seem particularly active during changes in movement (e.g., changes in force or direction).

4) **FRACTIONATION OF MOVEMENT:** Some neurons show enhanced activity when fractionated movements are performed. For example, a neuron with direct connections to a
finger motoneuron may show a small change in activity during a “power grip” (when all the fingers are moved together), but may show a large change in activity during a “precision grip” (when the thumb and second finger are used in isolation).

5) MOVEMENT DIRECTION: (figs. 40-8,9) In general, neurons in the primary motor cortex are 'broadly tuned' for movement direction during reaching movements. In other words, a single neuron may be most active for movements in one direction (i.e., its preferred direction), but it will also be active for movements in other directions. This implies that, for any one direction of movement, a population of neurons will be active in the primary motor cortex. It has been suggested that movement direction could be coded by summing the activity of this population of neurons (for further details see text, pgs. 614-616).

CONCLUSIONS: Some neurons in the primary motor cortex appear to be narrowly tuned to specific pieces of behavior (e.g., enhanced response during a precision grip). Other neurons seem to be more broadly tuned (e.g., population activity during reaching movements). Thus, a variety of parameters which control movement execution may be coded by the activity of neurons in the primary motor cortex.

IV. Function of Premotor Areas: (SMA and lateral premotor area)

Two organizational schemes for viewing the cortical control of movement

1. Classical Model. Primary Motor Cortex as a Nodal point (Fig. 16)

The motor cortex has classically been viewed as the upper motoneuron- the final common pathway for the central control of movement. According to this view, premotor areas (and basal ganglia, cerebellum and inputs from other cortical areas) gain access to motor output through their connections with the primary motor cortex.

- somatic sensory cortex = provides knowledge of the consequences of action
- posterior parietal lobe = indicates the location of objects in space, may provide some indication of their behavioral relevance
- lateral premotor areas = guide limb movements in extrapersonal space
- medial premotor area = guide limb movements based on internal control

* The cerebellum and basal ganglia gain access to the motor cortex through their connections with the ventrolateral nucleus of the thalamus, the major thalamic input to the motor cortex.

Important points of model:

- because the primary motor cortex is the final common pathway for the central control and generation of movement-
- a) lesions ought to abolish the ability to evoke movements by stimulating premotor areas
- b) lesions of primary motor cortex ought to abolish central control of movement

Old (and, in some instances, incorrect) evidence: (** = incorrect)

a. All of the premotor areas have direct connections with the primary motor cortex, but only the primary motor cortex projects to the spinal cord. (**
b. Stimulation of the SMA evokes movements of proximal and distal body parts, but usually at higher currents than required for the primary motor cortex.

c. The movements evoked from the SMA are generally more complex than in the motor cortex.

d. After a lesion of the primary motor cortex, distal movements can no longer be evoked by SMA stimulation. (***)

e. Changes in cerebral blood flow in the SMA do not occur during simple movements, but do occur during the performance or mental rehearsal of complex movement sequences (Fig. 17). Thus, the SMA can function as a supramotor area (i.e., one level above the primary motor cortex in a hierarchical scheme). (***)

2. More Current Model. Multiple Parallel pathways (Fig. 18)

Each of the cortical motor areas is a nodal point. It is now clear that there are at least 6 premotor areas in the frontal lobe. These include: a) 2 lateral premotor areas (both in area 6 on the lateral surface of the hemisphere) and b) 4 medial premotor areas (the SMA and 3 others located in and around the cingulate sulcus). In addition to their projections to the primary motor cortex, each of these premotor areas has substantial direct projections to the spinal cord.

Important points of this model:

- Each cortical area has an independent access to the spinal cord and thus, the potential to influence the control of movement independently from the primary motor cortex.
- Each cortical area can act as a nodal point for a distinct set of cortical and subcortical inputs.

Evidence:

a. Neuron activity in the SMA and other premotor areas is related to the performance of simple movements. In some cases this activity begins before movement onset.

b. Neuron activity in the SMA changes during training. SMA activity also is affected by a lesion to the primary motor cortex.

1. Record neuron activity in primary motor cortex and SMA early during the training of a monkey to perform a simple movement. Neurons in both the primary motor cortex and SMA discharge prior to movement onset.

2. Overtrain the animal on the task. Only neurons in the primary motor cortex discharge prior to movement onset. After overtraining, few SMA neurons even change their activity during the task.

3. Remove the primary motor cortex and allow the animal to recover. When the animal can again perform the simple movement, neurons in the SMA are now active prior to movement onset.

c. Recent studies with more sensitive techniques find changes (albeit small) in the cerebral blood flow of the SMA during the performance of even simple movements.

Thus, it is now clear that the premotor areas are involved not only in the programming of movement sequences, but also in the execution of simple movements.

Major Unanswered Question: Why do we have all these cortical motor areas?

Which movements are dependent on the primary motor cortex?
Which movements are dependent on the premotor areas?
What specific aspects of movement are controlled by each cortical motor area?
Do the roles of the various motor areas change with training? Which cortical areas are involved in skill acquisition and which are involved in skill retention?

Figure 1

Figure 2
Figure 5

Dorsolateral Pathways
Distal > Proximal
Flexors > Extensors
(e.g., Rubrospinal)

Ventromedial Pathways
Proximal > Distal
Extensors > Flexors
(e.g., Reticulospinal
Vestibulospinal
Tectospinal)

Bilateral

Figure 6

Lateral Corticospinal
(Contralateral, with only a small ipsilateral component)

Ventral Corticospinal
(Ipsilateral, with some crossing in the cord)
Figure 7

The cortical regions responsible for the central motor program lie near the motor cortex [Brodmann’s area 4]. A. Human cortex. B. Macaque monkey cortex. The somatotopic organization in the motor and premotor cortices is indicated.

Figure 8

Retrograde transport of tracer by corticospinal neurons

Anterograde transport of tracer by corticospinal neurons
Figure 9

Retrograde transport of tracer by corticospinal neurons

"6" "4" "3a" "3b" "1" "2" "5"

Figure 10

Retrograde transport of tracer by corticospinal neurons

Anterograde transport of tracer by corticospinal neurons
Figure 11

Figure 12

Distribution of corticospinal fibers from left hemisphere to low cervical spinal gray matter in opossum, cat, rhesus monkey, and chimpanzee.
Figure 13

Distribution of corticospinal fibers in low cervical intermediate zone and motoneuronal cell groups in cat, adult monkey, and 4-day-old monkey as observed in silver-impregnated anterograde fiber degeneration studies. [Adapted from Kuypers (372), copyright 1962 by the American Association for the Advancement of Science.]

Figure 14

The cortical regions responsible for the central motor program lie near the motor cortex (Brodman's area 4). A. Human cortex. B. Macaque monkey cortex. The somatotopic organization in the motor and premotor cortices is indicated.
Composite figurine charts of precentral and supplementary motor areas of monkey brain derived from several experiments in which left cortex was mapped by systemic punctuate electrical stimulation. C, central sulcus; area between C and C' folds down to depth of sulcus. d, Medial edge of hemisphere; area between e and e' is supplementary motor area located on medial surface of hemisphere. Except for responses from points in ipsilateral motor face area (at extreme left); muscle responses are on right side of body. Strongest and earliest movements indicated in solid, intermediate in cross-hatching, and weakest in stippling. Symbols with crosses on ankles indicate eversion of foot; symbols with open centers on hip and ankle signify adduction and inversion; curved lines with arrows designate rotation. e, Sulus cinguli; i, inferior precentral sulcus. [From Woolsey et al. (163).]

Diagram of monkey cortex showing locations of precentral motor (MII; Ms I and II on figure) and postcentral tactile (SI; Sm I and II on figure) areas. [From Woolsey (175a).]
Figure 17

Body representation in the human motor cortex. (Adapted from Penfield and Rasmussen.

Figure 18

Branching vs Focused

Area 4

Motoneurons

Muscle

Common Target

Area 4

Motoneurons

Muscle

Figure 19

Motor Cortex

Sensory Inputs

Premotor Areas

Posterior Parietal

Basal Ganglia

Cerebellum
Changes in cerebral blood flow (increase indicated by stippling) during finger tasks indicate different roles by the different cortical areas. A. Activity during simple extension against a spring. B. Activity during a complex of finger movements. C. Activity during mental rehearsal. (Adapted from Roland et al., 1980.)