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Almost all research regarding motor functions of the brain and spinal cord have been done using animals. (i) In the spinal animal the cord is transected, usually in the neck so that most of the cord is intact. After a few hours or days (higher animals) the cord returns to normal function. (ii) In the decerebrate animal the brainstem is transected in the middle to lower part of the mesencephalon. This blocks the normal inhibitory drive and allows the spinal cord to have increased reflexes. However, removing the brain inhibitory and excitatory input to the spinal cord gives us only a partial picture of normal motor control.

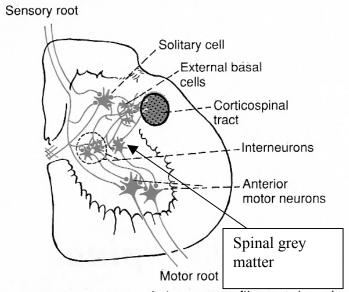


Figure 54–1. Connections of the sensory fibers and corticospinal fibers with the interneurons and anterior motor neurons of the spinal cord.

from Guyton and Hall (1996)

Spinal Cord Grey Matter

In the above figure, which shows the cross section of half the spinal cord, sensory nerve fibers enter in the dorsal region (sensory root) and synapse with various neuron bodies in the spinal grey matter and also ascend or descend the cord to other segmental levels and the brain. The spinal grey matter is the integrative area for cord reflexes and motor function. The white matter of the cord contains the nerve trunks (tracts) of ascending and descending nerve fibers, which look white because of the myelin sheaths around each fiber, e.g. Corticospinal tract. Each segment of the cord has several million neurons composed of the following types:

Anterior Motor Neurons

These are the largest type (50 to 100% larger) and their axons exit the spinal cord at the ventral (frontal) part of the spinal cord at the motor root. There are two types: *a Motor Neuron*

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Their axons are A α nerve fibers with avg 14 μ m diameter with each one innervating a few to hundreds of muscle fibers to form a motor unit (MU).

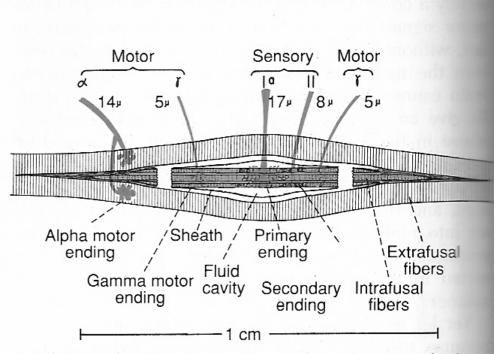
y Motor Neurons

About half as many as α motor neurons with axons being Ay fibers with average diameter 5 um innervating small specialized intrafusal muscle fibers of the muscle spindles. Interneurons

These are everywhere in the spinal grey matter and are 30 times as numerous as motor neurons. They are small, highly excitable, and spontaneously active with firing rates up to 1500/sec. They are both excitatory and inhibitory and have numerous connections with each other as well as with motor neurons and spinal neurons. They form the neuron pools, convergent, divergent and reverberant spinal circuits. Most sensory input and descending inputs terminate on interneurons.

Renshaw Cells

Located in the ventral horn of the spinal cord near the motor neurons. The axons of these motor neurons send back branches to the inhibitory Renshaw cells almost immediately after leaving the spinal cord. The Renshaw cells send inhibitory signals to adjacent motor neurons to focus activity to a particular MU (recurrent inhibition).



Muscle Spindles

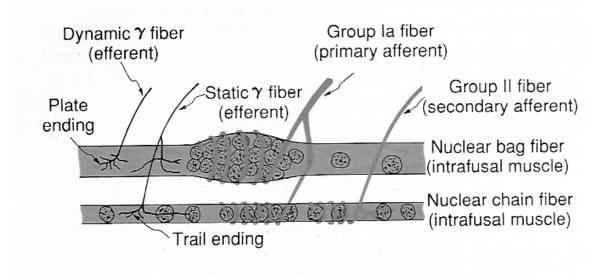
Figure 54–2. Muscle spindle, showing its relation to the large extrafusal skeletal muscle fibers. Note also both the motor and the sensory innervation of the muscle spindle and the extrafusal large muscle fibers.

from Guyton and Hall (1996)

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These are physiological transducers, located in the belly of the muscle that send information via pulse trains to the spinal cord and brain about the length of each muscle and the velocity of shortening (or lengthening). They are about 3 - 10 mm long and composed of 3 - 12 intrafusal muscle fibers attached to the surrounding larger force producing extrafusal muscle fibers as shown in the above figure. The middle section of each intrafusal fiber has no actin or myosin filaments, so does not contract and these are the sensory transducers. The end portions contract in response to A γ input from the γ motor neurons in the spinal grey matter, as shown in the figures above and below. The middle section of the intrafusal fibers can be lengthened to give a stretch reflex either in when the parallel extrafusal fibers lengthen or when the intrafusal fibers themselves are contracted. There are two types of intrafusal fibers as shown below, (i) nuclear bag (1 - 1)3) in each spindle which are innervated by Ia afferent fibers (primary afferent) and (ii) nuclear chain (3 - 9) which are 50% smaller and are innervated by both Ia and II (secondary) afferent fibers. In the primary endings (also called annulospiral endings) the Ia afferent fiber encircles the sensory portion of both types of intrafusal fibers. The Ia fiber is 17 μ m in diameter and signals are conducted at 70 – 120 m/sec. The secondary endings are innervated by smaller II fibers 8 µm in diameter, which conduct signals at slower velocities

Centre Section of Intrafusal Fibers



from Guyton and Hall (1996)

Static Response

When the receptor portion is stretched slowly, primary and secondary afferent fibers increase their firing rates proportionally with the increase maintained up to several minutes. This static response is mainly due to the nuclear chain fibers.

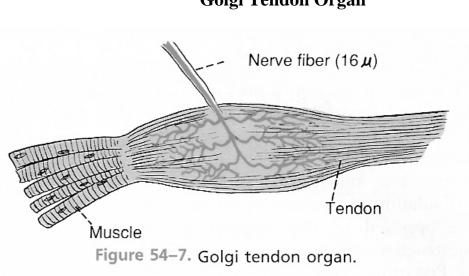
Dynamic Response

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When the length L of the spindle increases suddenly the primary endings are stimulated especially powerfully (much more than static). Even if ΔL is in the μm range the increase in firing rate is very large but the rate returns to the static level as soon as the stretch velocity drops to 0, that is the dynamic response is a function of stretch velocity not length. Similarly if L decreases suddenly the firing rate decreases dramatically and returns to the static rate when the stretch velocity goes to 0. It is assumed that the nuclear bag endings are responsible for the dynamic response since they only have primary endings.

Control of Response through y Efferents

 γ fibers form 31% of all efferent fibers to the muscle. When activated they keep the sensor portion of the intrafusal fibers from being stretched or shortened. γ – dynamic input mainly excites the nuclear bag fibers, which enhances the dynamic response, i.e. increases the gain of the nuclear bag sensor. Similarly γ static input to the nuclear chain fibers increases the gain of the static response. Spindle afferents have continuous firing at rest (with some γ drive) and these rates are driven up or down with lengthening and shortening respectively.



Golgi Tendon Organ

from Guyton and Hall (1996)

These are sensors located in the tendon in series with groups of muscle fibers. They are inervated by type IB fibers, $16 \,\mu\text{m}$ in diameter, which transmit signals quickly to inhibitory interneurons in the spinal grey matter or up to the brain or other segmental levels. Although the Golgi tendon organs can provide both static and dynamic responses (muscle or tendon tension plus rate of change of tension) their primary function is to provide negative feedback to the force generation system to avoid damage to muscle fibers or tendons. They could also monitor tension produced by groups of muscle fibers and modulate those that produce too much.

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Control of Skeletal Movement

The following figure shows the motor axis of the central nervous system. Control of γ motor neurons can be initiated in the cerebral cortex primary motor area and facilitated by the bulboreticular region and cerebellum as shown, especially when related to antigravity contractions. This results in stabilizing joint positions through activation of γ motor neurons in both agonist and antagonist muscles. Upper motor neurons can also send signals directly to the α motor neurons to initiate movements. Other areas of the midbrain such as the thalamus are also involved in controlling movements and modulating sensory inputs from muscle spindles, etc.

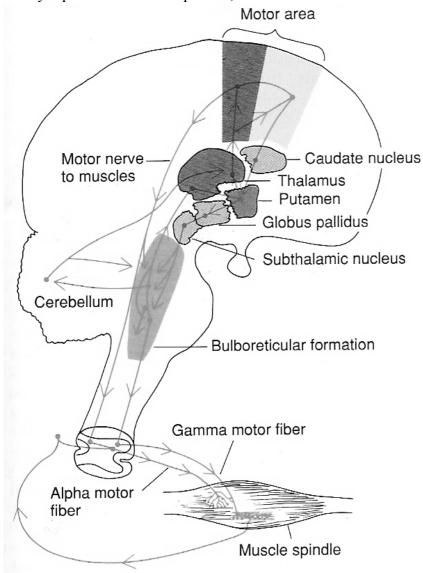


Figure 45-3. Motor axis of the nervous system.

from Guyton and Hall (1996)

The motor area of the cerebral cortex is shown in the following figure with the primary motor cortex highly differentiated to different anatomical areas just as for the sensory cortex. The supplementary and pre-motor areas plan more complex movements requiring activation of many different muscles. The numbers in the figures are the identified Brodmann areas.

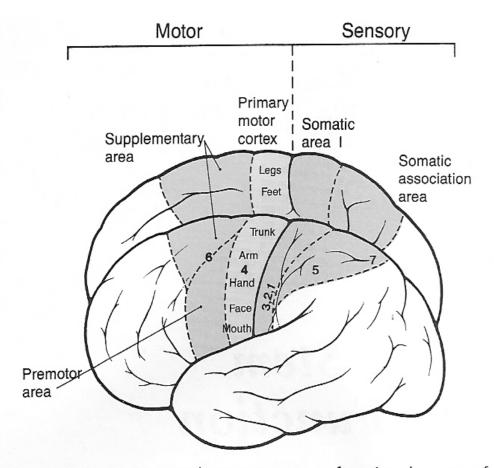


Figure 55–1. Motor and somatosensory functional areas of the cerebral cortex.

from Guyton and Hall (1996)

The figure below shows in very graphical form the primary motor cortex areas relating to muscles at each anatomical location. What is extremely noteworthy is the large section of the primary cortex devoted to control of the hand, especially the thumb and fingers and the face and mouth, especially the muscles required for vocalization. This is not surprising since in humans we require a great number of degrees of freedom in controlling these muscles. Think of all the complex hand movements we can make and the incredible vocalization skills required for the range of normal speech, not to mention the production of music and different accents and intonations. The lower body and limbs

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requires a much smaller area of the cortex since many movements can be controlled by the interneuron pools in the spinal cord at each segmental level.

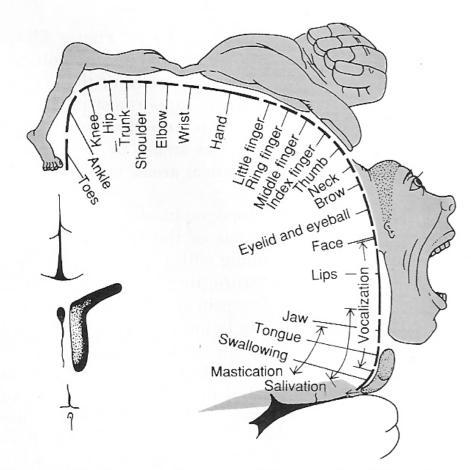


Figure 55–2. Degree of representation of the different muscles of the body in the motor cortex. (From Penfield and Rasmussen: The Cerebral Cortex of Man: A Clinical Study of Localization of Function. New York, Macmillan Co., 1968.)

from Guyton and Hall (1996)

The signals from the brain descend to the spinal cordcsegments via the pyramidal tract as shown in the following figure. The descending fibers cross over at the medulla to control the opposite side of the body. Figure 55-6 from Guyton shows a spinal segment in which can be seen the various inputs to the anterior motor neurons. These inputs can be from the sensory transducers such as the muscle spindles from the same muscle as well as descending signals from the brain and other segments via the various spinal tracts (bundles of axons in the spinal white matter). These very many inputs can be both excitatory and inhibitory.

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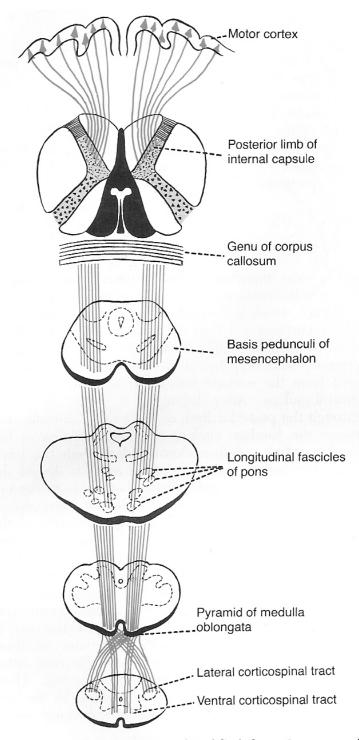
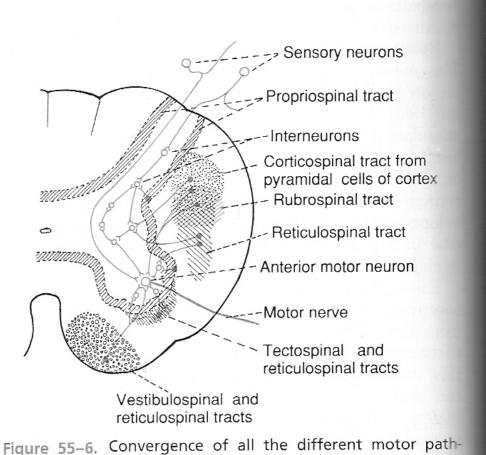


Figure 55–4. Pyramidal tract. (Modified from Ranson and Clark: Anatomy of the Nervous System. Philadelphia, W. B. Saunders Co., 1959.)

from Guyton and Hall (1996)

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ways on the anterior motor neurons.

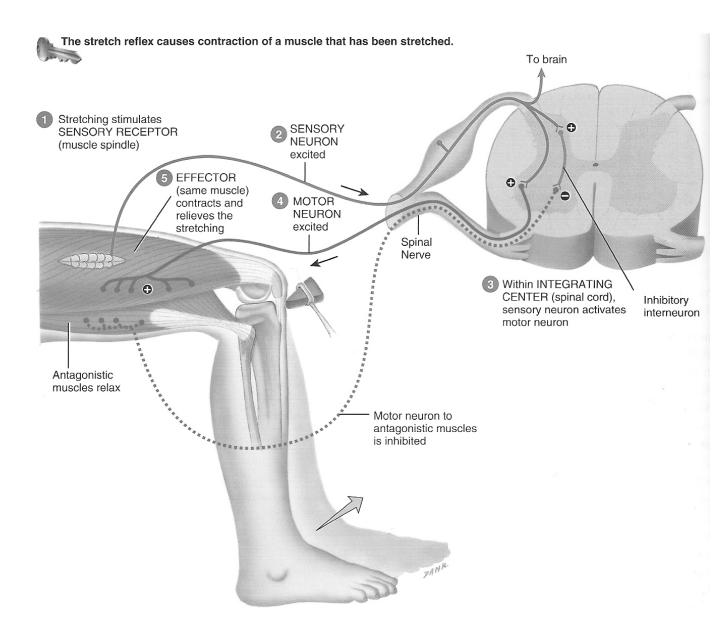
from Guyton and Hall (1996)

Spinal Reflex

The simplest muscle control loop is the muscle stretch reflex or myotatic reflex. The basic circuitry is shown in the figure below. In this figure the patellar tendon is struck with a hammer causing the attached muscle (rectus femoris) to stretch. This causes the muscle spindles to send increased signals to the spinal cord via Ia afferent fibers which enter the cord at the ventral horn. These Ia fibers branch send signals to the brain as well as exitatory inputs directly to the associated α motor neurons. If the inputs are of sufficient strength (i.e enough muscle spindles have been activated or have sufficiently high firing rates), the α motor neurons fire caused the extrafusal muscle fibers to contract, thus shortening the muscle again. This is a single synapse reflex arc requires no input from higher centres. The figure has added an additional Ia input to an inhibitory interneuron which provides inhibition of the anatagonist muscle (hamstring), thus making the shortening easier. This is an extremely simple view of reflex control, since many

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descending signals also control α motor neurons as shown in the above figure. Studying the spinal reflex in man therefore requires some effort at controlling these other inputs during delivery of the stimulus.



from Tortora and Grabowski (2003)

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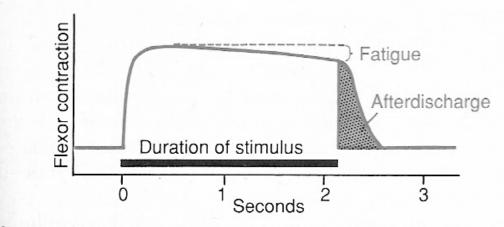


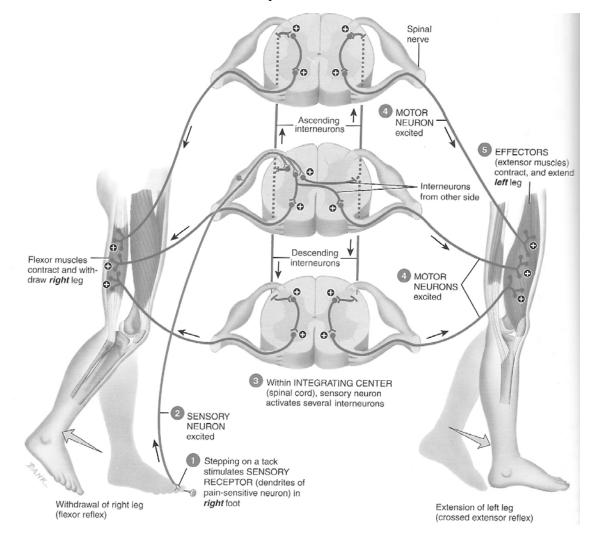
Figure 54–9. Myogram of the flexor reflex, showing rapid onset of the reflex, an interval of fatigue, and, finally, afterdischarge after the stimulus is over.

from Guyton and Hall (1996)

When the stimulus is first applied the muscle resonds very quickly followed by gradual fatigue and then some afterdischarge when the stimulus has been removed.

In the following figure a more complex reflex control system is shown with the response to a pain stimulus (stepping on a tack). This causes the knee flexor to be activated to lift or withdraw the foot, the excited motor neurons existing at different levels of the spinal cord. At the same α motor neurons for the knee extensors on the other side are also excited so that body weight can now be supported by the other limb only. These transverse (one side of body to other side) control pathways are made up of inhibitory and excitatory interneurons and all this control is effected without any involvement of the motor cortex or higher centres in the brain. In short voluntary and involuntary muscle control is a very complex system with many movements already preprpogrammed either in the motor cortex or at the spinal level.

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from Tortora and Grabowski (2003)