

Lecture 21 - Lower motor systems: the spine and pattern generation

Pre-class notes for November 18, 2019

Reading: *Neuroscience* ed. 6 by Purves et al., pages 357-375, 381-382, 397-392

Behavioral output - the motor system give rise to behavior. Movement is produced by the coordinated activation of motor neurons, which causes the coordinated contraction of skeletal muscles.

Skeletal muscle (Extrafusal muscle fibers) - type of muscle under the control of the motor system and produces voluntary movement. Also known as *striated muscle* since it is made of multiple long, thin, multi nucleated fibers that have a regular pattern of red and white lines. Contractions in skeletal muscle fibers causes a shortening in the length of a fiber.

Tendon - fibrous collagen tissue that connects muscle to bone. Contains proprioceptive *Golgi tendon organs* that sense changes in muscle tension. The golgi tendon system is a feed back system that monitors and maintains muscle force.

Flexion/Extension - muscles of the body are often in opposing pairs. A *flexor* is a muscle whose contractions bend a limb or other part of the body. An *extensors* is a muscle whose contractions straighten a limb or other part of the body.

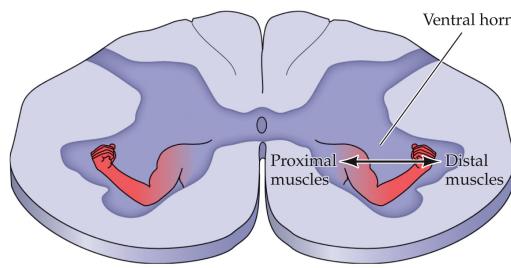
(Lower) Motor neuron - neuron who's cell body is in the gray matter of the spinal cord and send its axon out of the spinal cord to innervate individual muscle fibers.

Motor unit - the set of muscle fibers from a muscle that is innervated by a single lower motor neuron. The size of a motor unit is determined by the number of fibers.

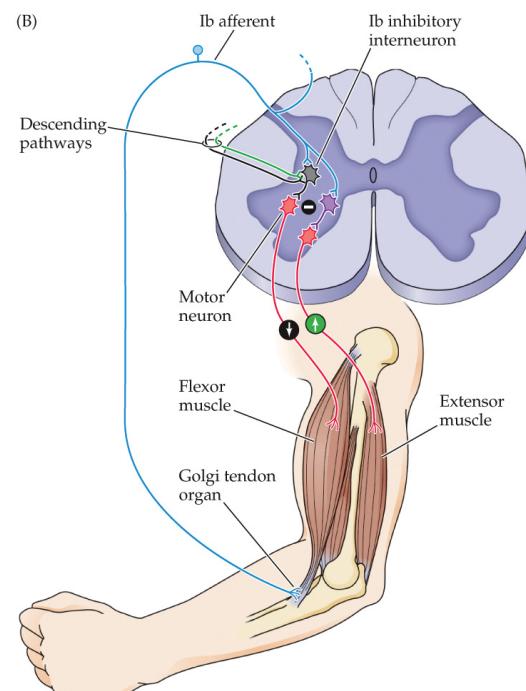
Motor pool - a cluster of motor neurons that innervate the same muscle.

Henneman's Size Principle - motor neurons that have smaller motor unit sizes, which usually have smaller axon diameters, fire before neurons with larger motor unit sizes. Enables the incremental control of the magnitude of an individual muscle's contraction in response to varying inputs received by its motor pool.

Ventral horn of the spinal cord - location in the gray matter of the spinal cord that contains the cell bodies of the lower motor neurons. Motor neurons innervating the axial musculature are located medially, whereas those Innervating the distal musculature are located more laterally.



Reverse myotatic reflex - prevents tears. The Ib ("one B") afferents from golgi tendon organs contact inhibitory interneurons that decrease the activity of a motor neurons innervating the same muscle.

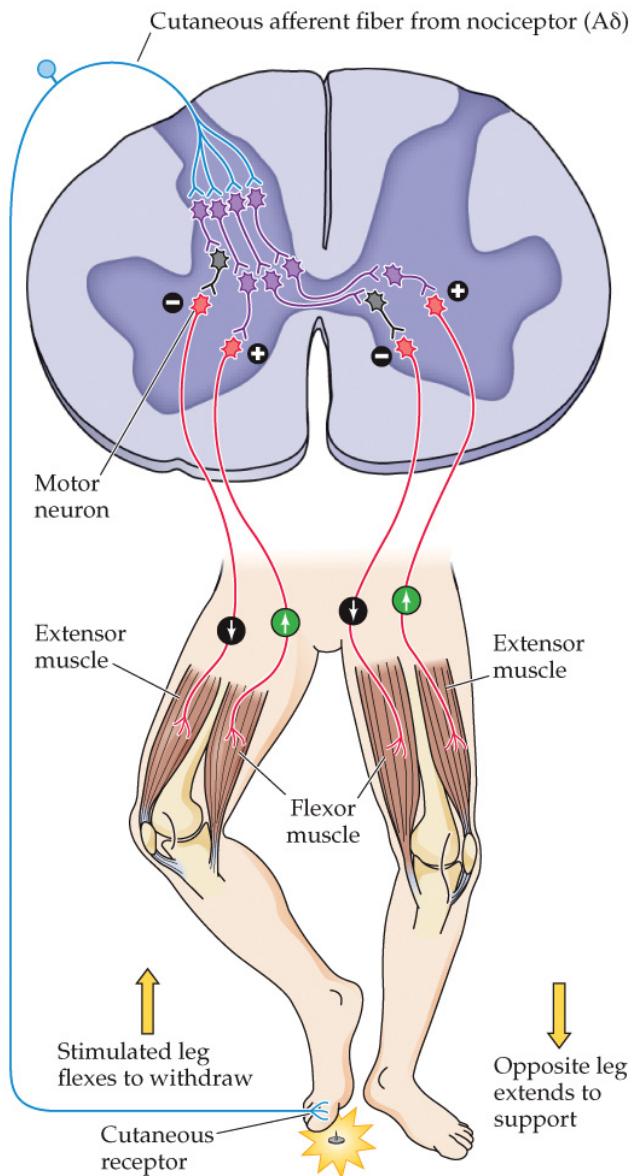


Crossed extension reflex - provides postural support during withdrawal of the affected limb from the painful stimulus. Stimulation of cutaneous receptors in the foot (by stepping on a tack, in this example) leads to activation of spinal cord local circuits that serve to withdraw (flex) the stimulated extremity and extend the other extremity to provide compensatory support.

Central Pattern Generators (CPGs) - a circuit that is capable of producing rhythmic output for coordinated contraction of different muscles without sensory feedback.

Primary Motor Cortex - provides commands to initiate voluntary movement and control complex movement. Primary motor cortex is topographically organized. The motor cortex, in coordination with other areas of the brain integrates information from multiple sensory systems and sends depending axons to the motor control regions of the brainstem, to spinal cord interneurons, and to lower motor neurons themselves.

Neurons in motor cortex are tuned to different parameters of movement, including direction, velocity, joint angle etc. There is some evidence that stimulation of specific sites in motor cortex can lead to coordinated movements across multiple joints



NEUROSCIENCE 6e, Figure 16.14
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Learning Objectives: (By the end of Lecture 21 you should be able answer the following)

1. Explain how all observable behavior is the result of the coordinated activity of muscles.
2. Apply the size principle to connect motor unit size to recruitment priority when activating a muscle.
3. Analyze reflex diagrams to predict behavioral output.
4. Explain how a central pattern generator can control rhythmic behaviors like walking.

MCB/Neuro 80 - Neurobiology of Behavior

Today's Topic:

MOTOR SYSTEMS - 1

Lecture 21

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Lecture notes, review questions, office hour times available at:

<https://canvas.harvard.edu/courses/59120>

CLIMBING MT. POTENTIAL (IN PRACTICE)



Response

Sensory/motor diseases
Upper Motor
Spinal Circuits

Neuronal processing

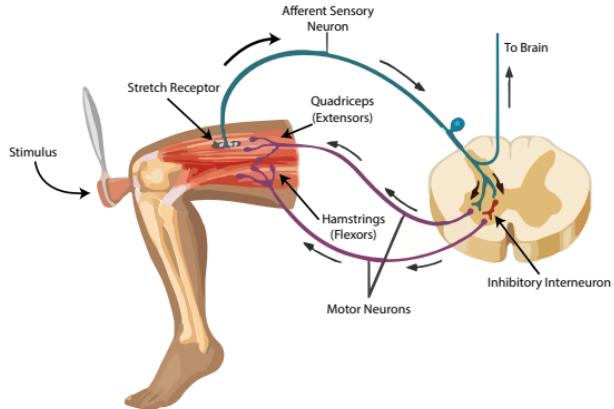
Cognition
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Stimulus (sensing information)

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Visual system:

- Sensory transduction
- Visual circuits
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Motor system gives rise to all behavior



Charles Sherrington (1857-1952), pioneering English neurophysiologist who first studied reflexes (like patellar tendon reflex)

“To move things is all that mankind can do... for such, the sole executant is muscle, whether whispering a syllable or felling a forest”

(Linacre lecture, Oxford 1924)

Motor system seems COMPLEX!

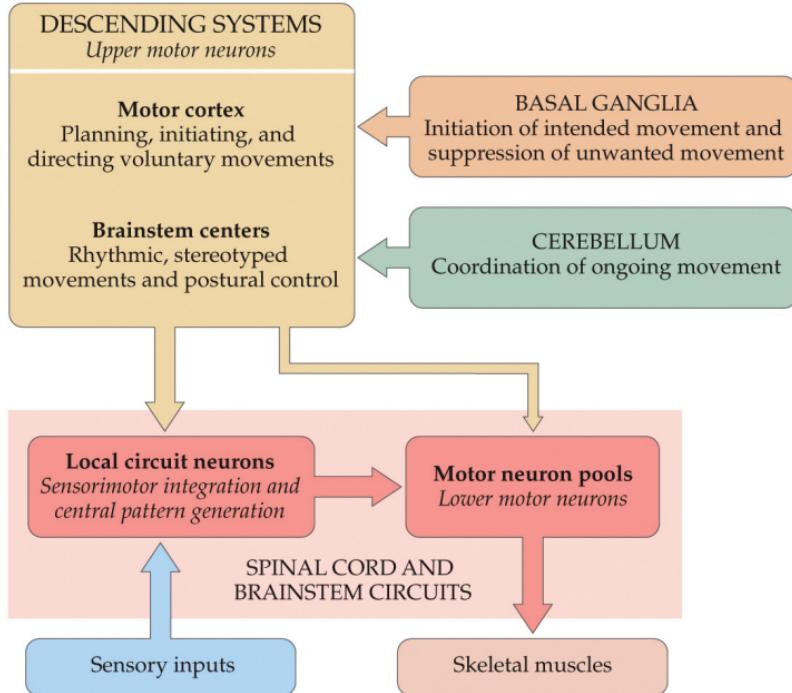
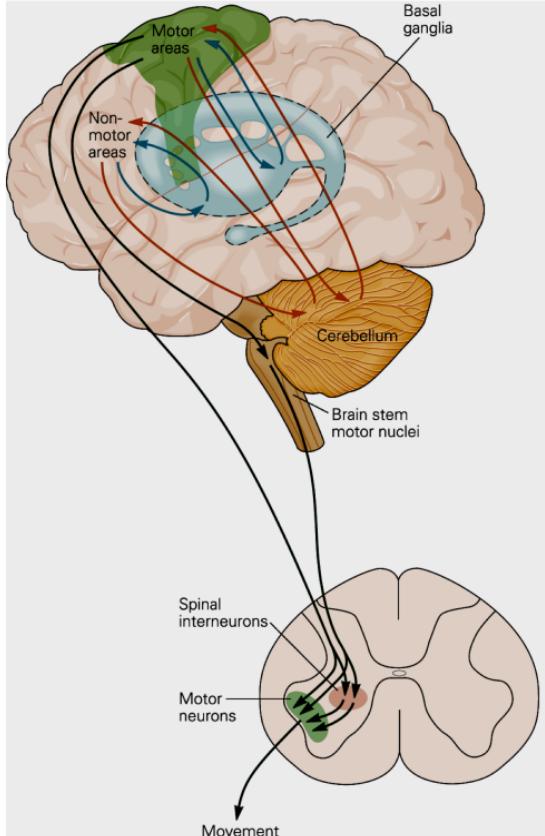
Why is the motor system so complicated?

- Behaviors require the coordinated actions of various combinations of over 650 muscles (in humans) in a changing and sometimes unpredictable environment (e.g. stand on one foot, catch a ball on a windy day or even open a door)

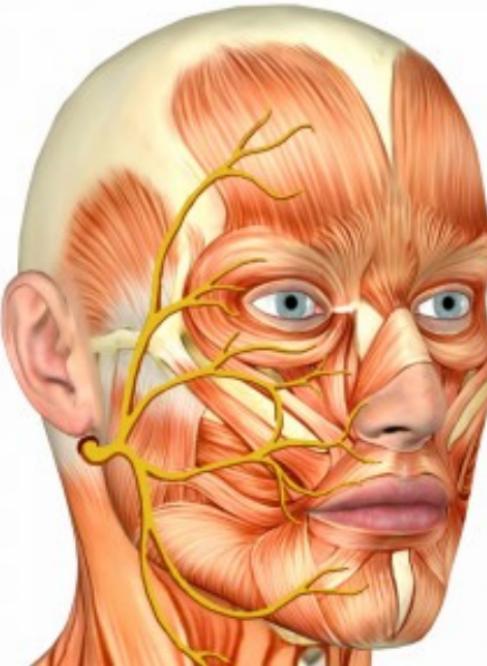
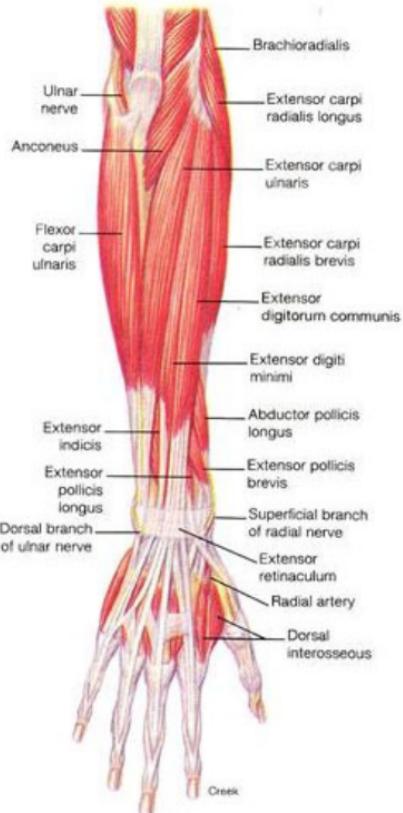
Historically it has been harder to understand than sensory systems. Why?

- Know more about the output than the initiation of movement (like a sensory system in reverse— we know more about the retina than object perception)

Overall organization



Skeletal muscles provide the output of the animal

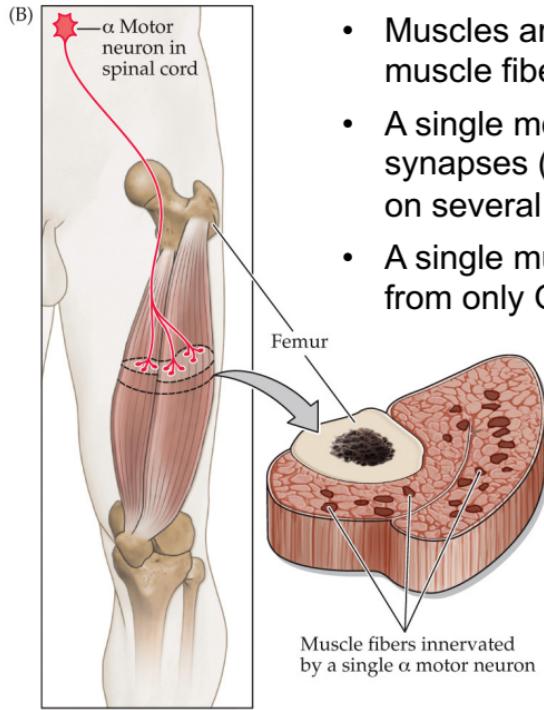


Skeletal muscles move bones around joints: **flexion** or **extension** or both (for rigidity)

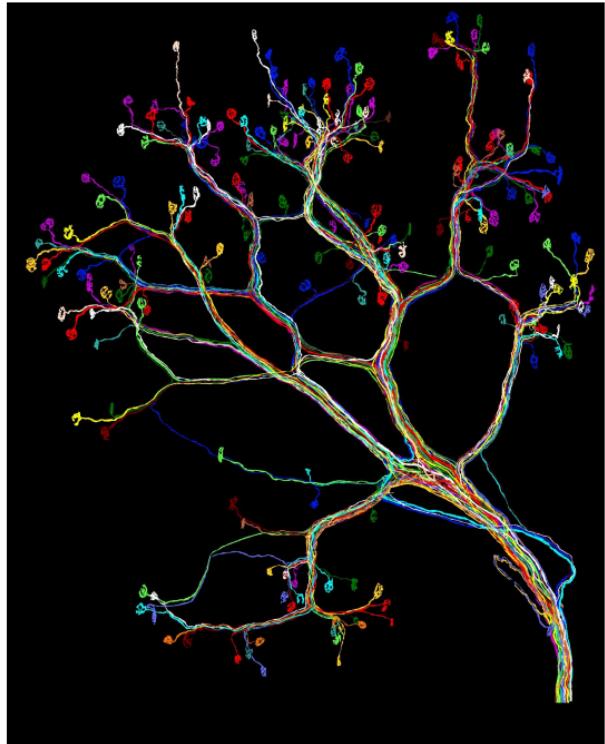
All muscles are innervated by nerves containing motor axons

Motor neurons that innervate muscle fibers are called **lower motor neurons** (or α motor neurons)

Motor Unit



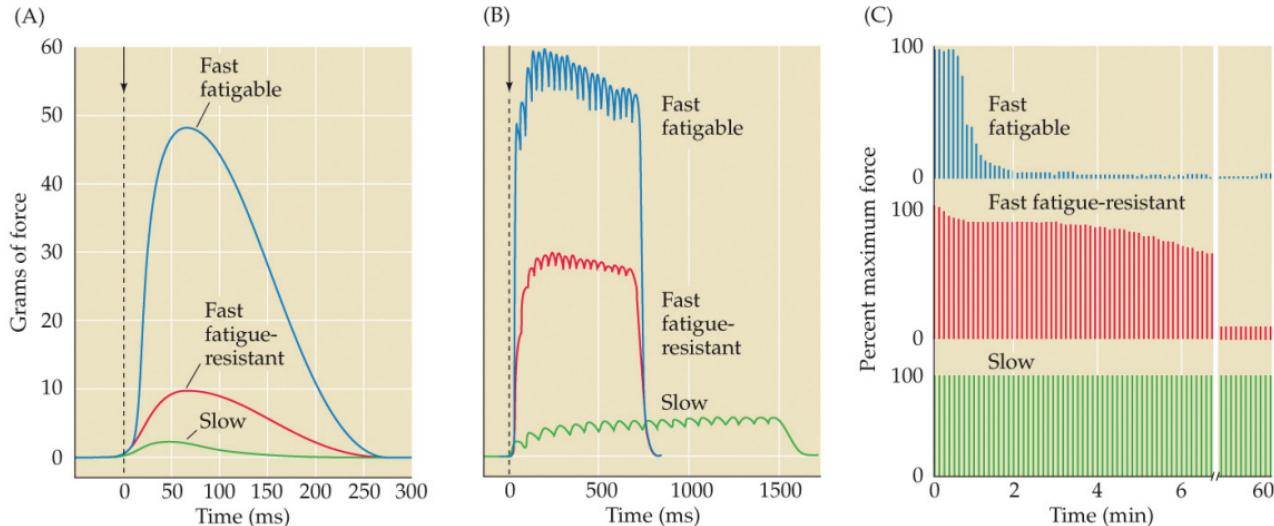
- Muscles are made of individual muscle fibers
- A single motor axon makes synapses (neuromuscular junction) on several muscle fibers
- A single muscle fiber gets inputs from only ONE motor neuron



NEUROSCIENCE 6e, Figure 16.5 (Part 2)
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From Lichtman lab: Neuromuscular junctions of one motor unit in same color

Different types of motor units

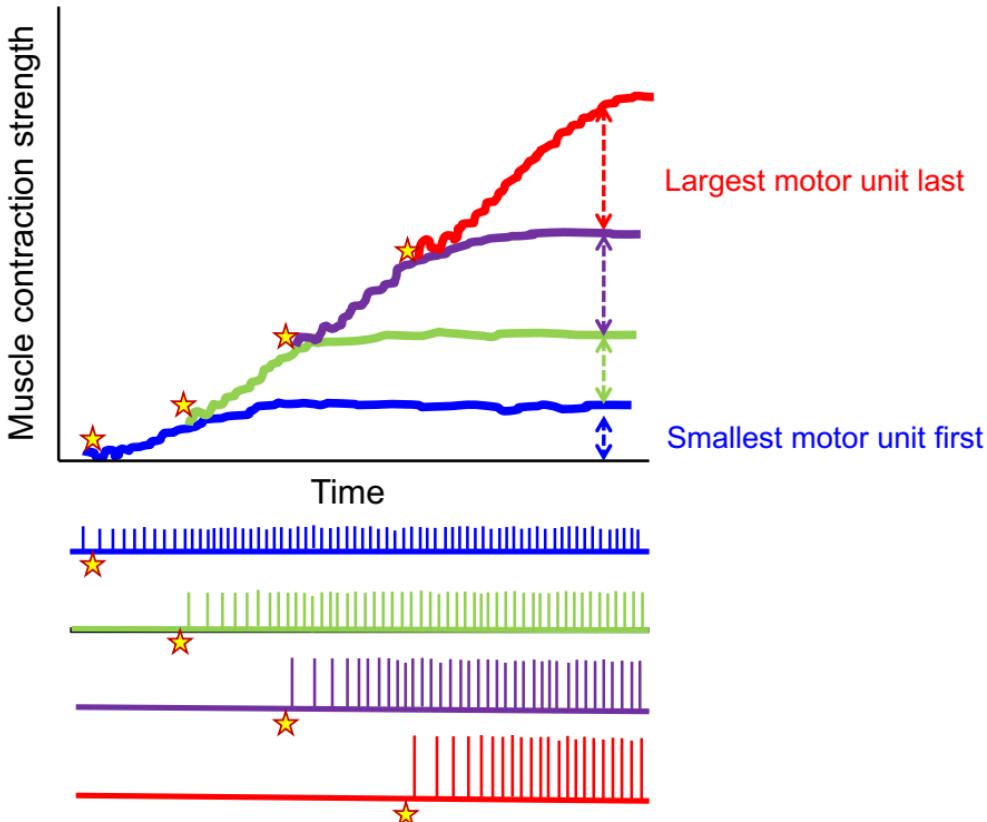


After Burke et al. (1973) *J. Physiol.* 234: 723–748.

NEUROSCIENCE 6e, Figure 16.6
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- All the muscle fibers innervated by a single motor axon together make up a “motor unit”
- Motor units vary in many properties: size (how many fibers and how big the fibers are), speed (slow or fast contraction), fatigue.

Motor unit recruitment – size principle



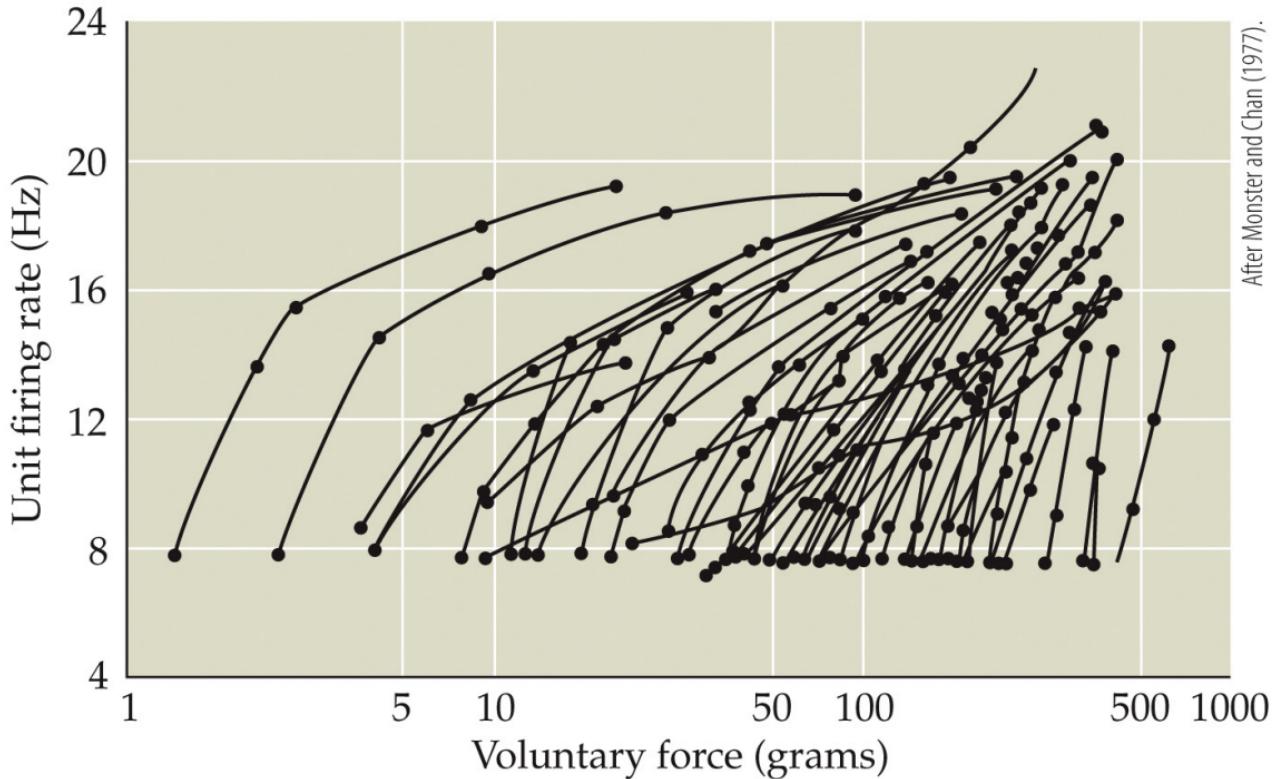
Larger motor neurons make up larger motor units (that is, they contact more muscle fibers)

Smaller motor neurons, contacting fewer muscle fibers, are more easily excited in the spinal cord – so they are recruited first

As more force is needed, the larger motor units are successively recruited

The larger units tend to fatigue more quickly

Motor unit recruitment

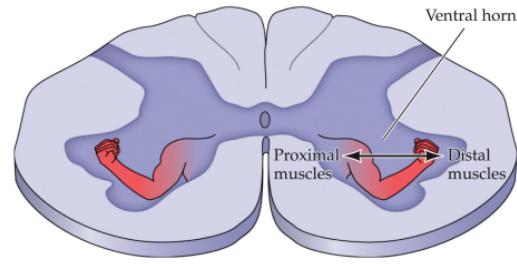
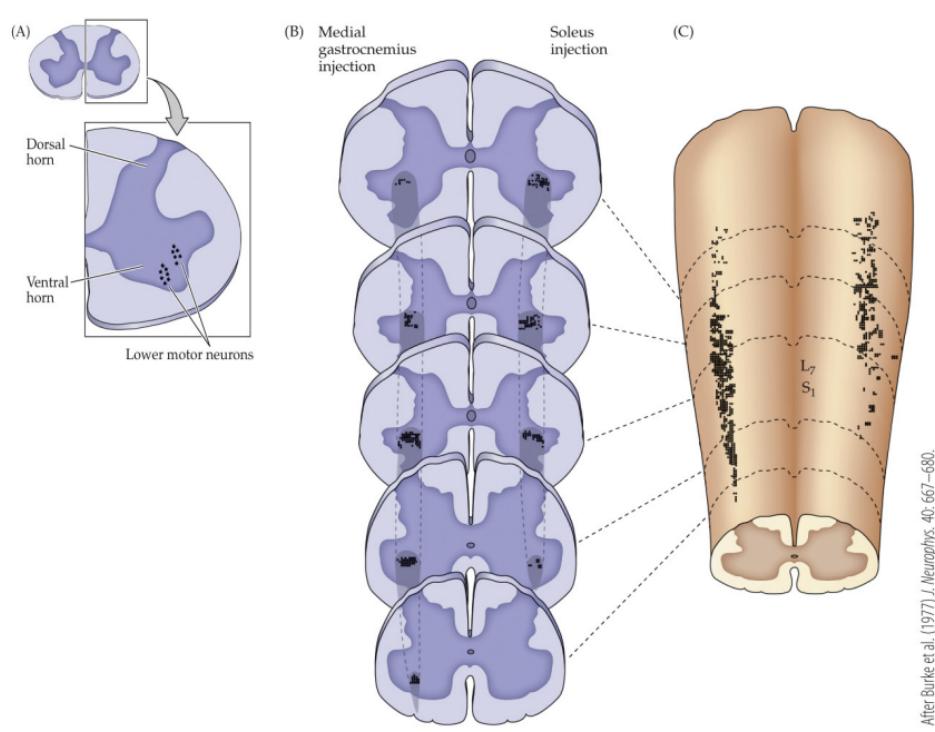


After Monster and Chan (1977).

If you plot the firing rate of many motor units as a function of the force (eg, the amount of weight you are lifting), you will get something like this.

Can you explain this plot?

Organization of motor neurons in the spinal cord



NEUROSCIENCE 6e, Figure 16.3
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Final common pathway for all motor behavior

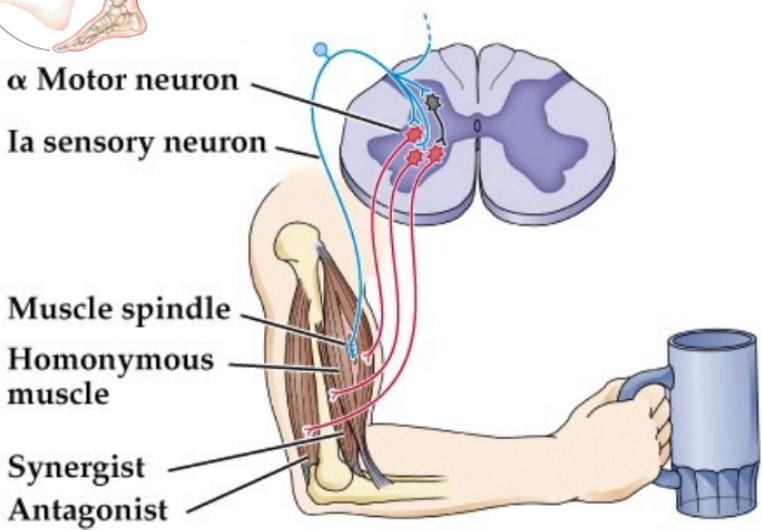
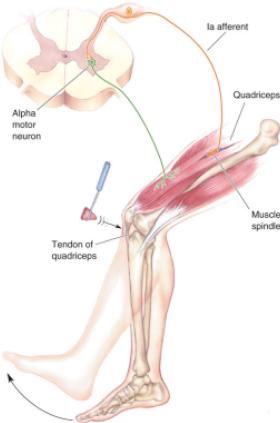
Cells mostly in ventral horn of spinal cord

They are organized in three maps:

Segmental map that relates to the rostrocaudal position of the muscle in the body

Mediolateral map that relates to the proximal (near body axis) to distal (far from body axis)

Flexor (dorsal) to extensor (ventral) map

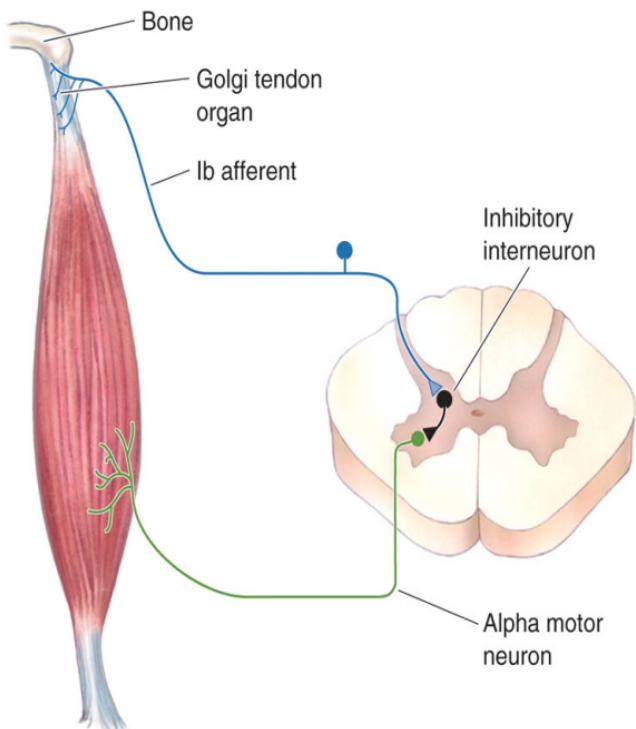


Circuits in the spinal cord

Myotatic (stretch) reflex prevents falling

- Adjusts to unexpected stretch/force on the muscle
- Stretch receptor on muscle spindle activates the Ia (“One A”) afferent
- Ia afferent synapses directly on to the flexor to relieve stretch
- Ia afferent also inhibits the antagonist muscle to allow movement

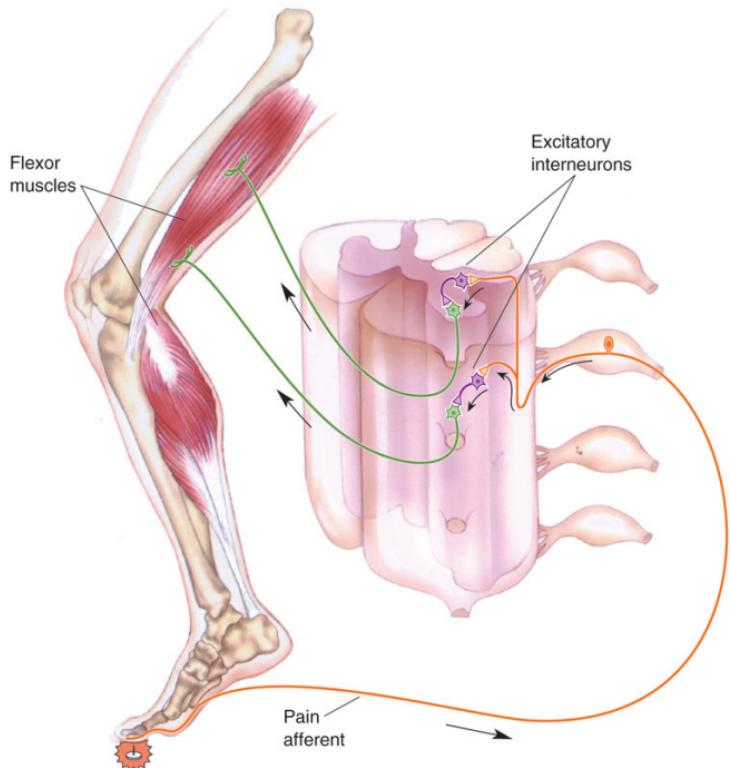
Circuits in the spinal cord



Reverse myotatic reflex prevents muscle tears

- Opposite of the stretch reflex – negative feedback system
- Sensory apparatus in the golgi tendon organ at the junction of a muscle and tendon.
- Innervated by Ib (“One B”) sensory afferents (slightly thinner than Ia)
- Ib axons make synaptic contacts with GABAergic inhibitory local neurons which synapse on the α motor neurons

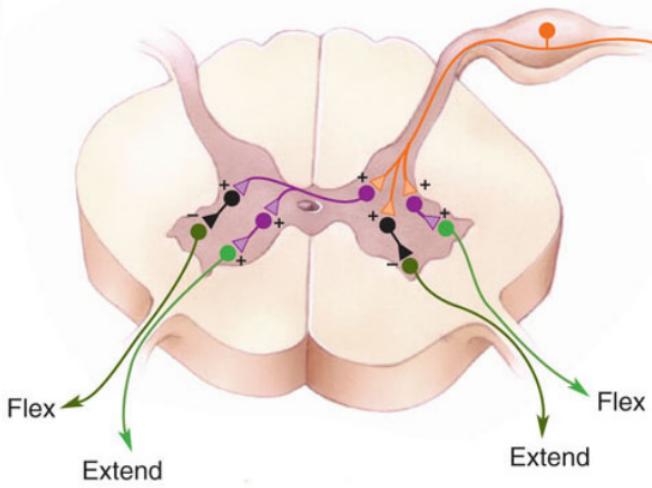
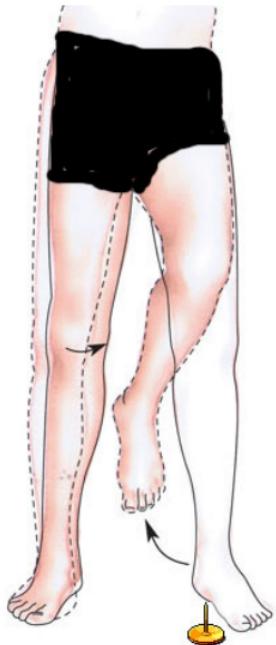
Circuits in the spinal cord



Flexor reflex helps withdraw quickly from noxious stimuli

- Triggered by a noxious stimuli activating an A δ afferent
- Can activate multiple muscle groups to remove the limb from the source of pain.

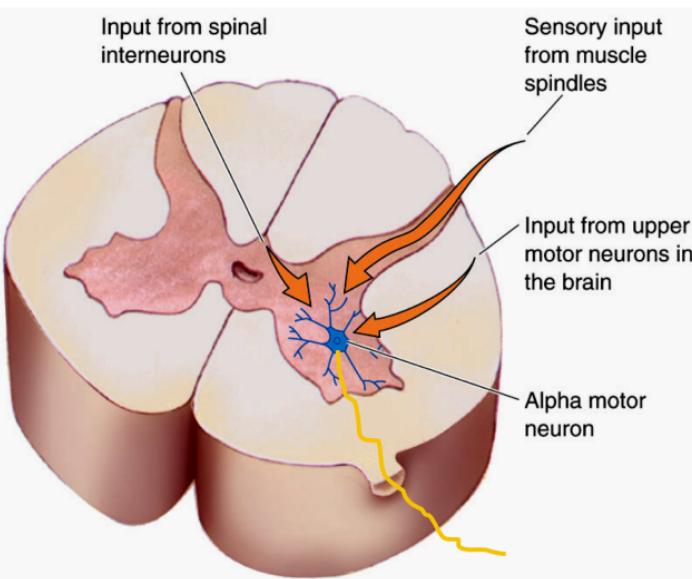
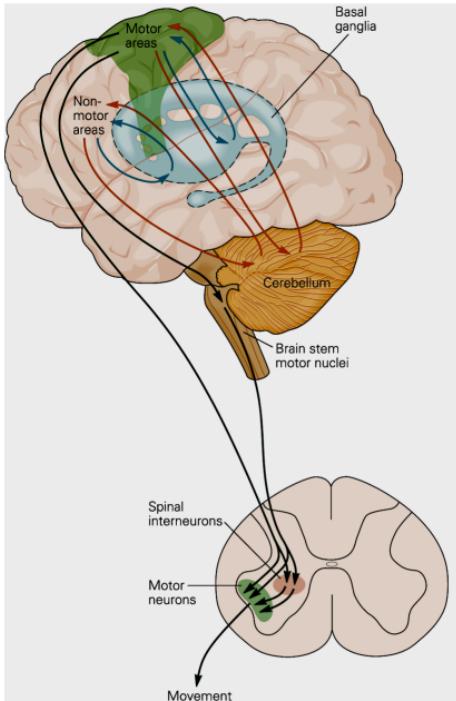
Circuits in the spinal cord



Crossed-extensor without falling over

- In addition to removing limb from painful stimuli, reflex can also activate contralateral extensors

Inputs to motor neurons



Three sources:

- Dorsal Root Ganglion cells (sensory)
- Upper motor neurons
- Spinal interneurons (excitatory and inhibitory)

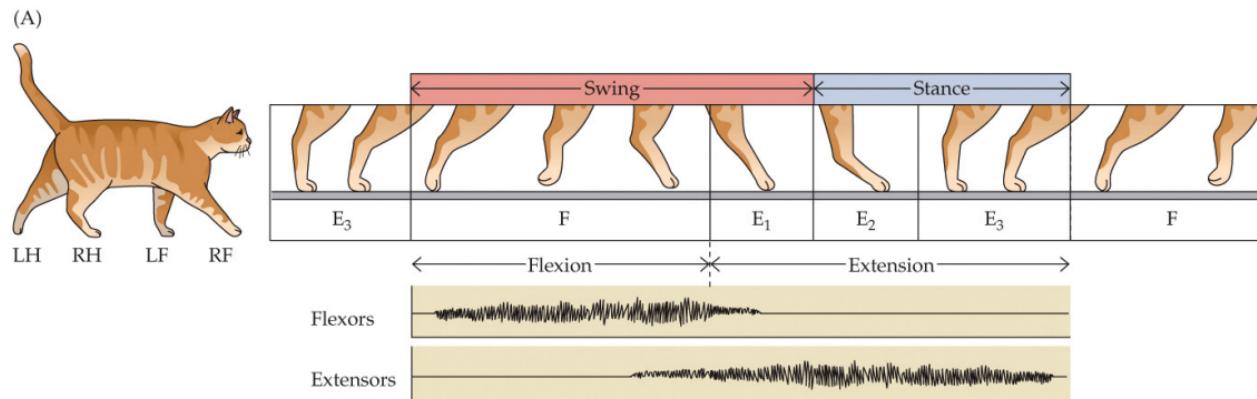
A few circuits (intrinsic reflexes) underlie lots of behaviors

Central Pattern Generators

The crossed-extensor reflex in which one side extends the other side flexes seems to provide a building block for locomotion.

Subconscious (reflexive) alternation of arms and leg swinging

What is needed is some way to get rhythmic activity. Where might that be coming from?



After Pearson (1976) *Sci. Amer.* 235: 72–86.

NEUROSCIENCE 6e, Figure 16.15 (Part 1)
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Central Pattern Generators

(C)

Extensors

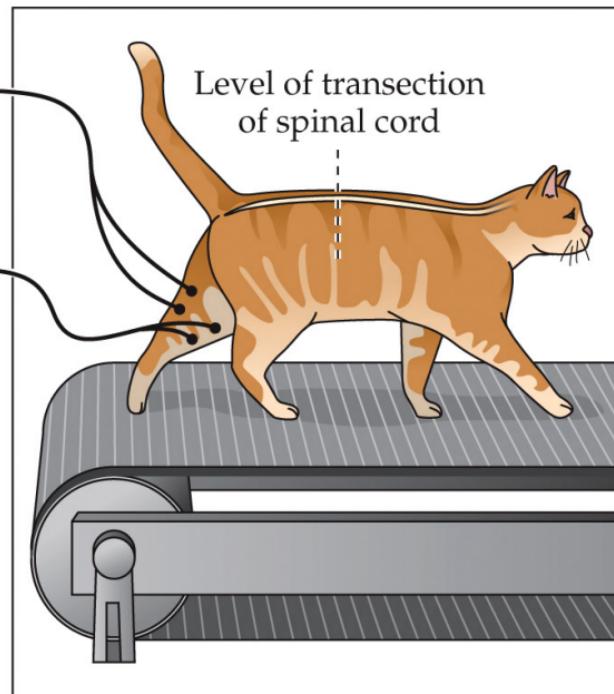


Flexors



Stance

Swing



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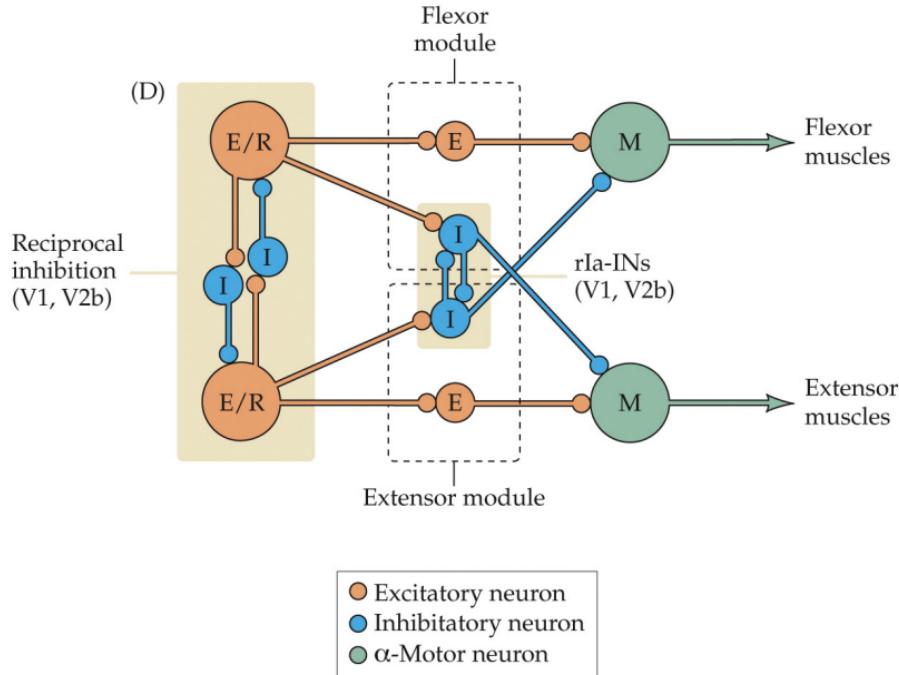
Central Pattern Generators

Two modules – flexor and extensor

At the top of the hierarchy (left most), excitatory neurons (**E/R**) are reciprocally coupled through mutual inhibition (through interneurons **I**)

In the middle layer, there are excitatory neurons (**E**) that convey excitation to the appropriate motor neurons (**M**).

Interneurons in the middle get input from the E/R neurons, to inhibit the opposing motor neurons. Interneurons also reciprocally inhibit each other



After Kiehn (2016) *Nat. Rev. Neurosci.* 17: 224-238.

NEUROSCIENCE 6e, Figure 16.15 (Part 4)
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Voluntary control of movement

Conscious processes are not necessary for the moment to moment control of movement

Movements appear “effortless” as long as there is a steady stream of sensory information (vision, somatic sensation, vestibular) - take walking for example (you slow down with eyes closed).

Successively higher levels of the motor hierarchy specify increasingly more complex aspects of a motor task

Reflexive (“lowest”) then rhythmic then voluntary (“highest”) - but even more complicated: learned movements become reflexive with practice!

Learning Objectives

Explain how all observable behavior is the result of the coordinated activity of muscles.

Apply the size principle to connect motor unit size to recruitment priority when activating a muscle.

Analyze reflex diagrams to predict behavioral output.

Explain how a central pattern generator can control rhythmic behaviors like walking.

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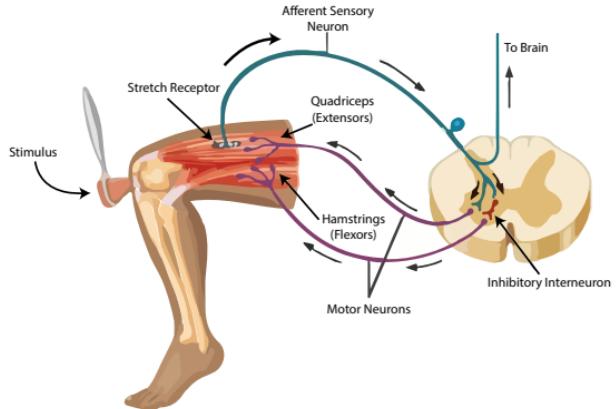
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Visual system:

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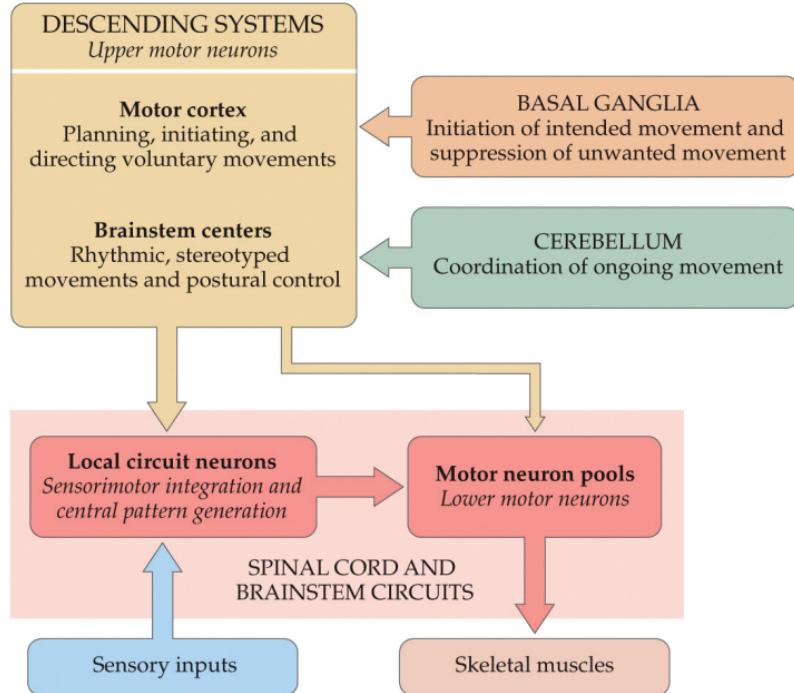
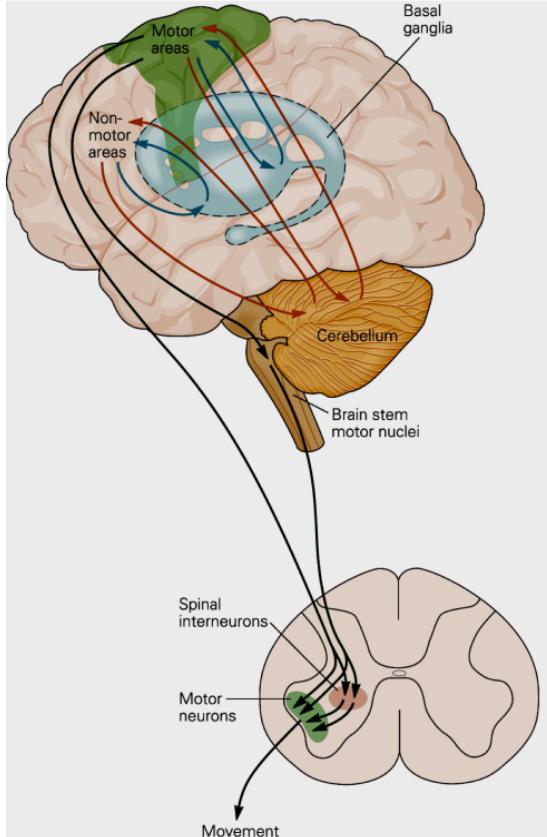
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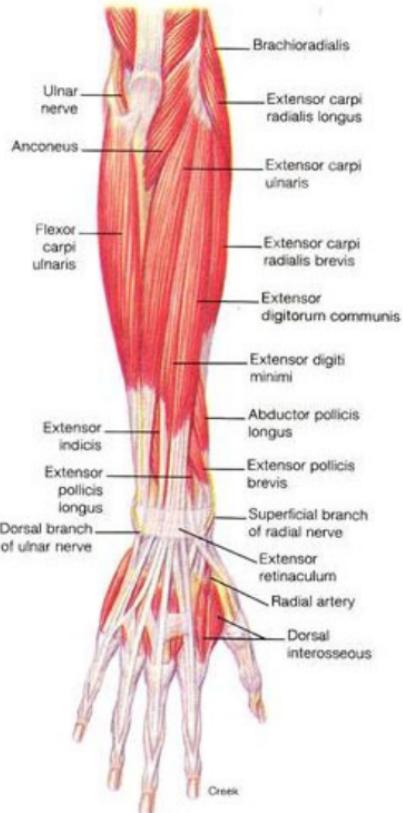
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Overall organization



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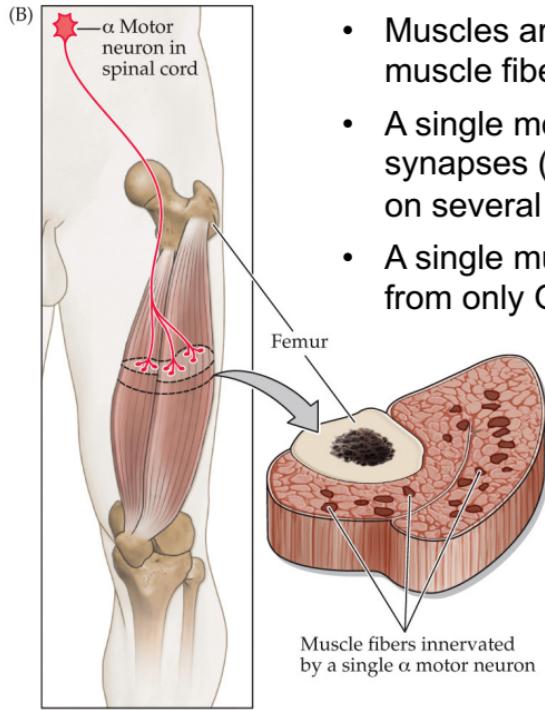


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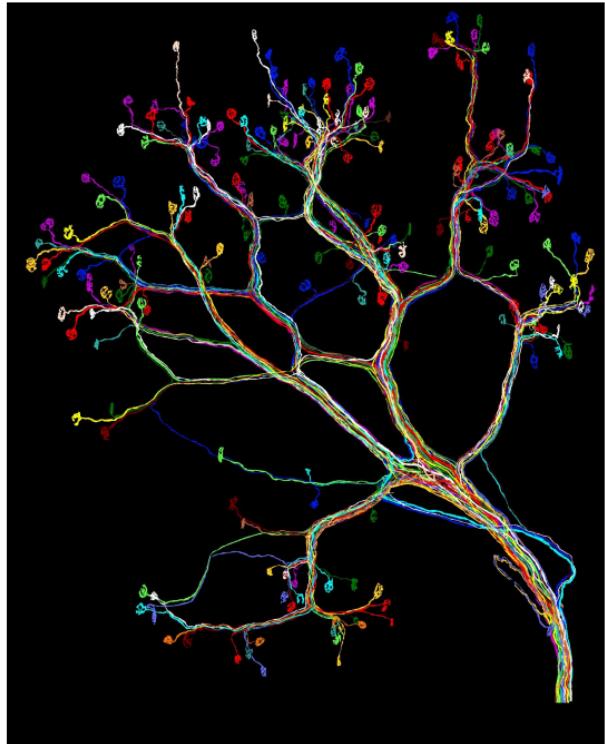
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Motor Unit



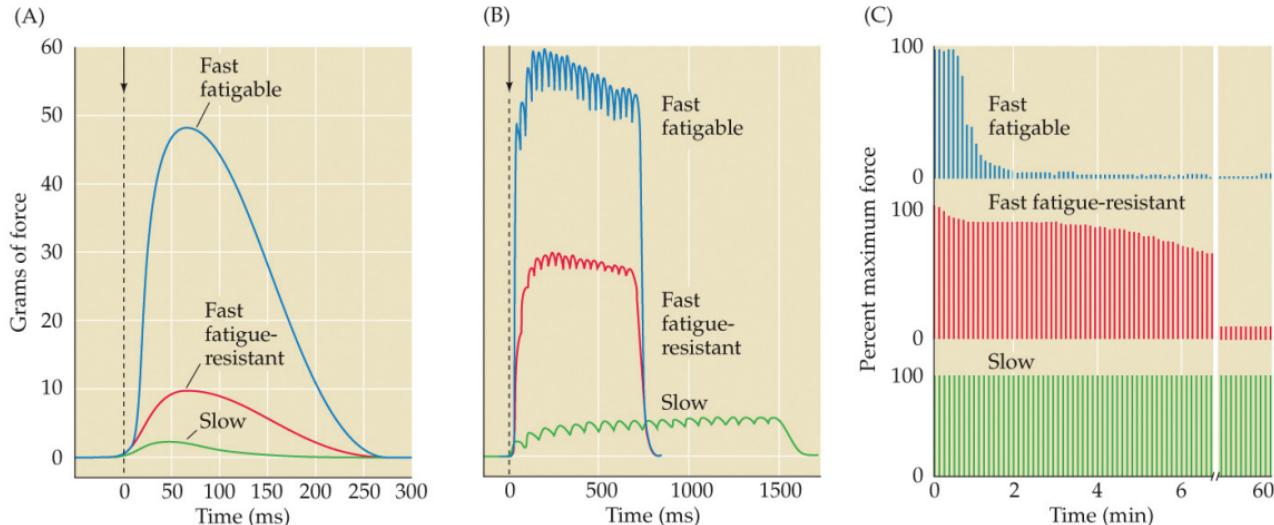
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From Lichtman lab: Neuromuscular junctions of one motor unit in same color

Different types of motor units

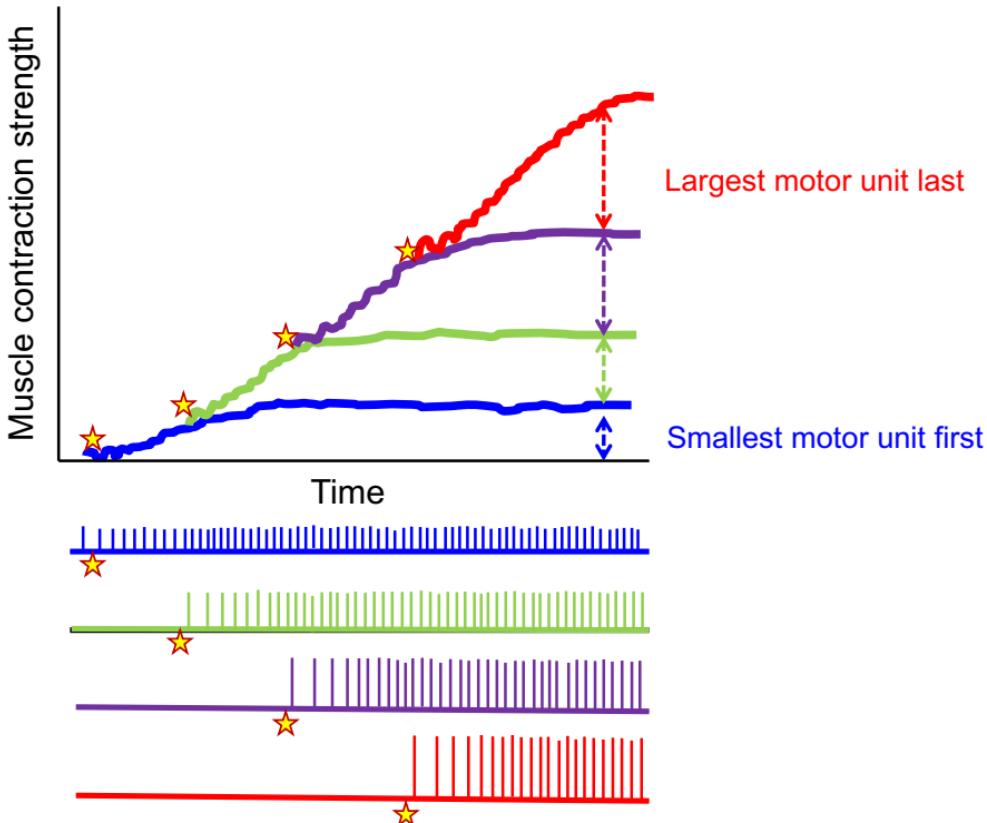


After Burke et al. (1973) *J. Physiol.* 234: 723–748.

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Motor unit recruitment – size principle



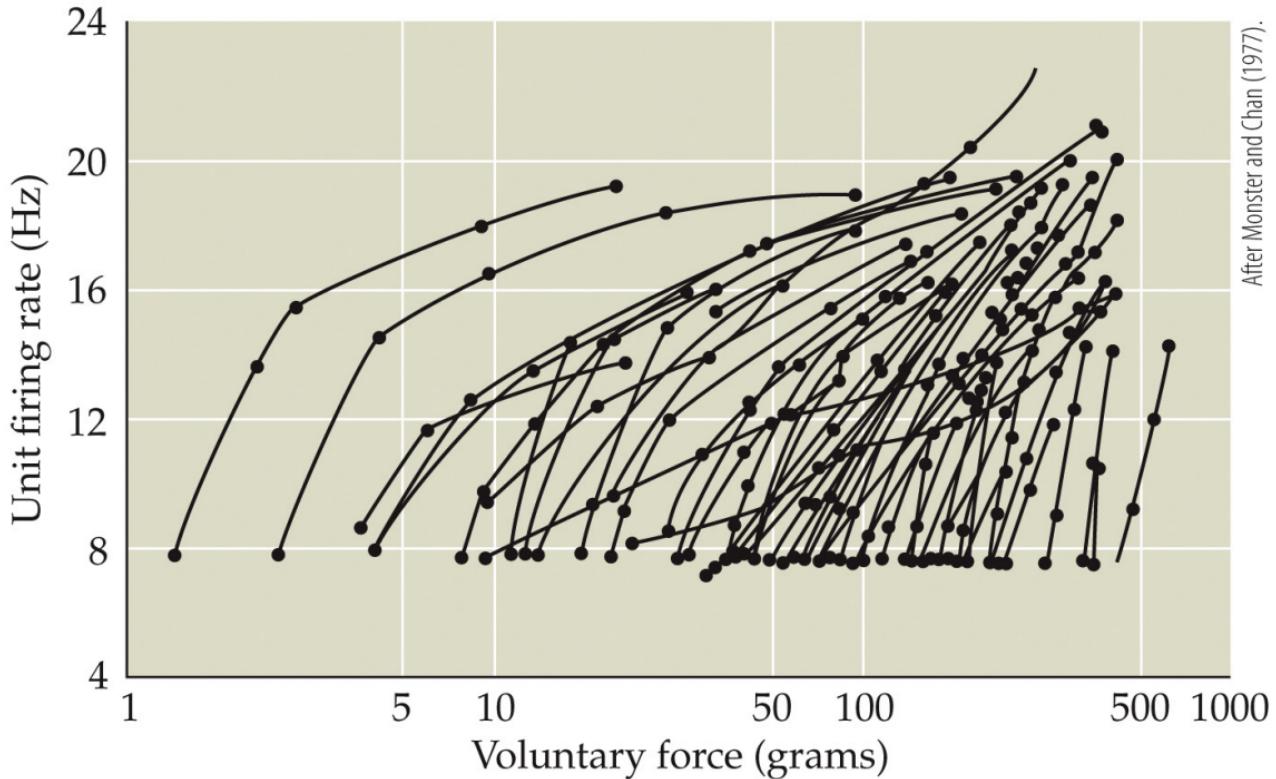
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Motor unit recruitment

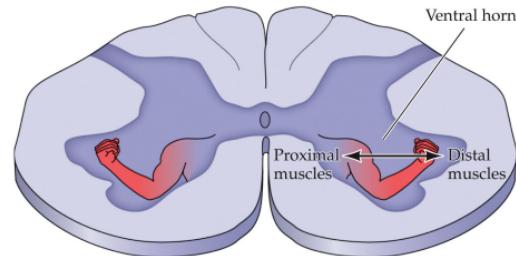
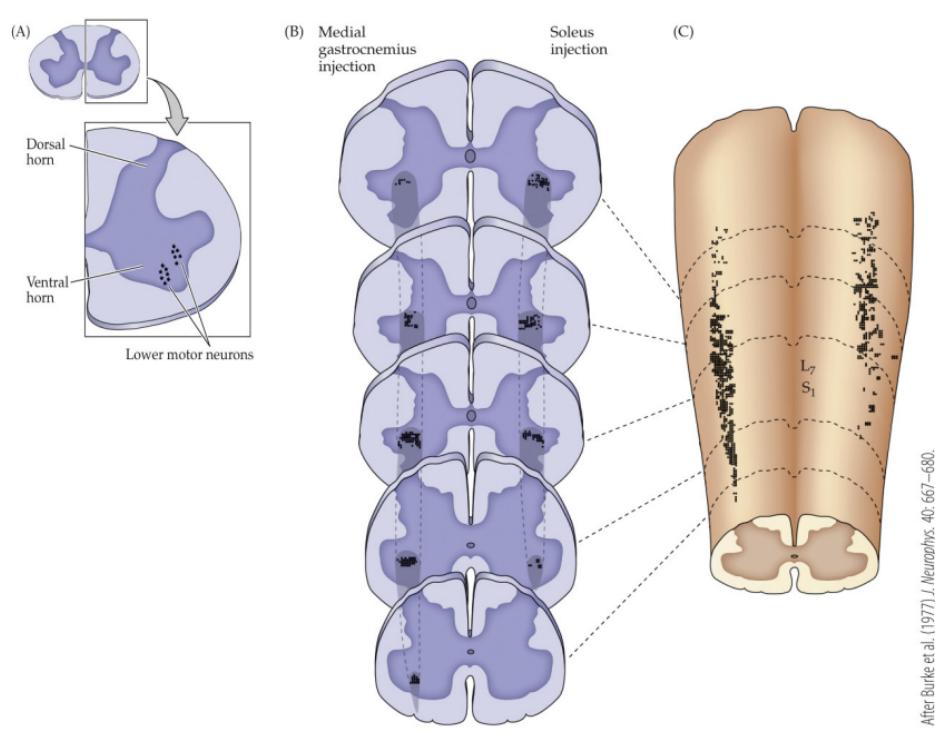


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Final common pathway for all motor behavior

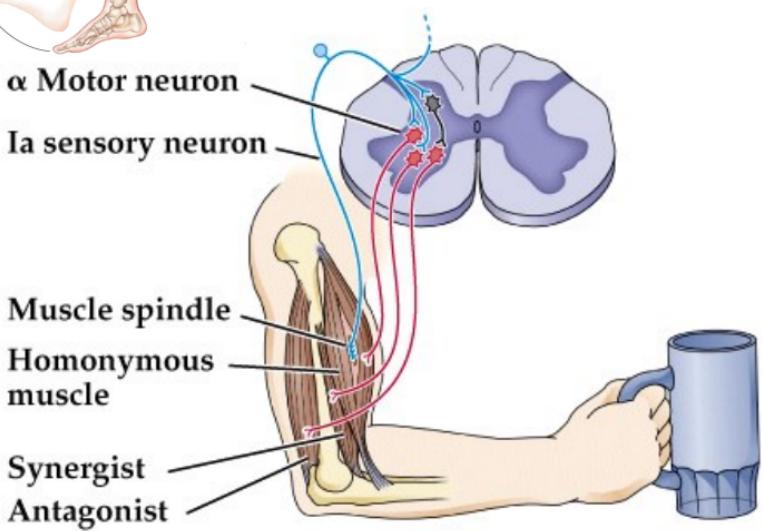
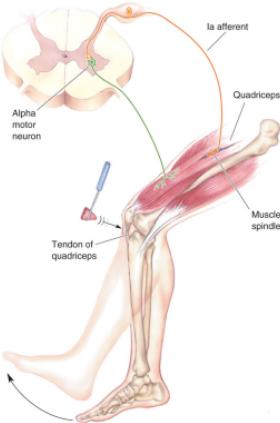
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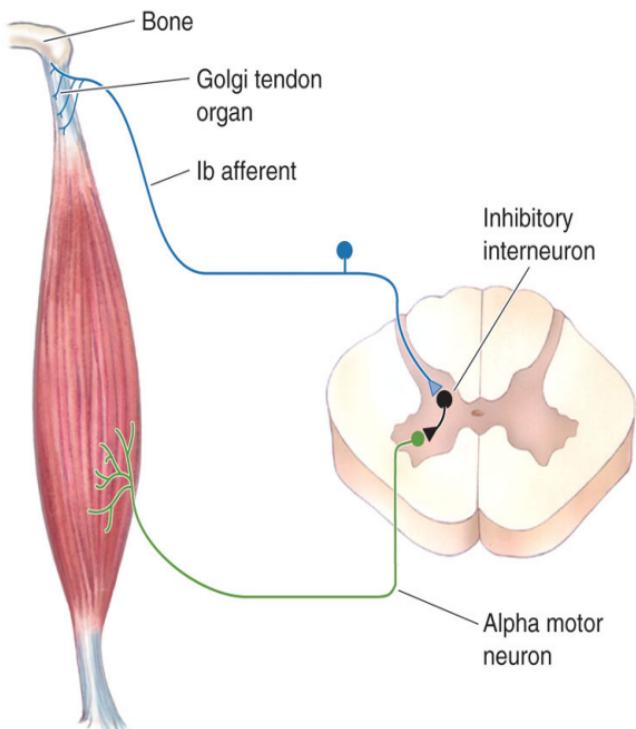


Circuits in the spinal cord

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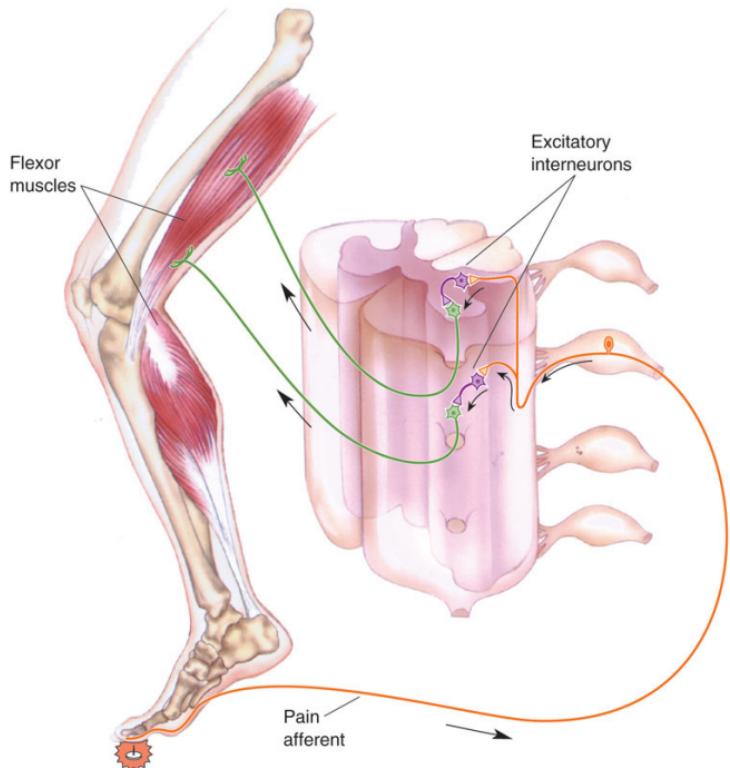
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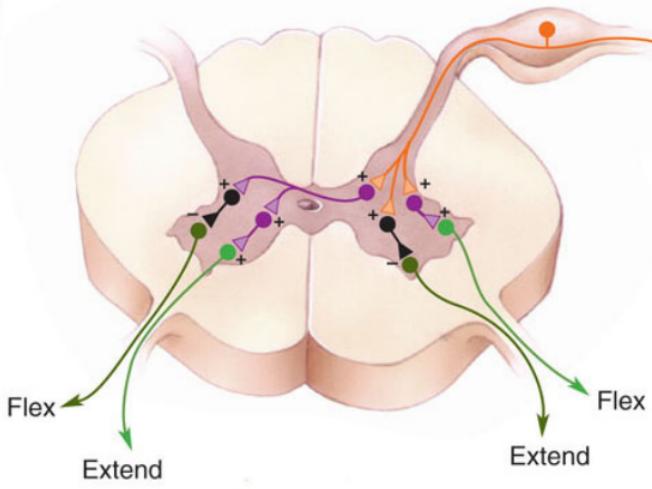
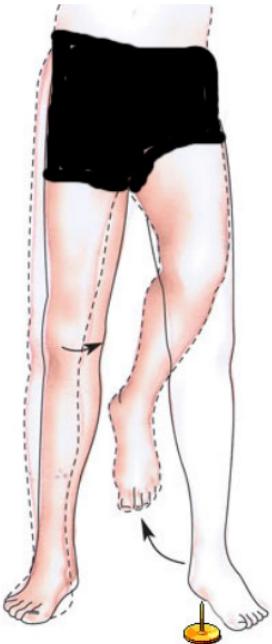
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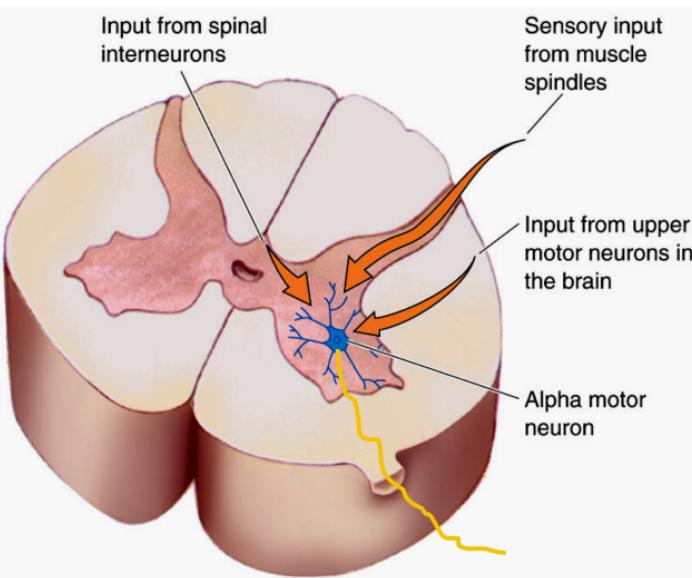
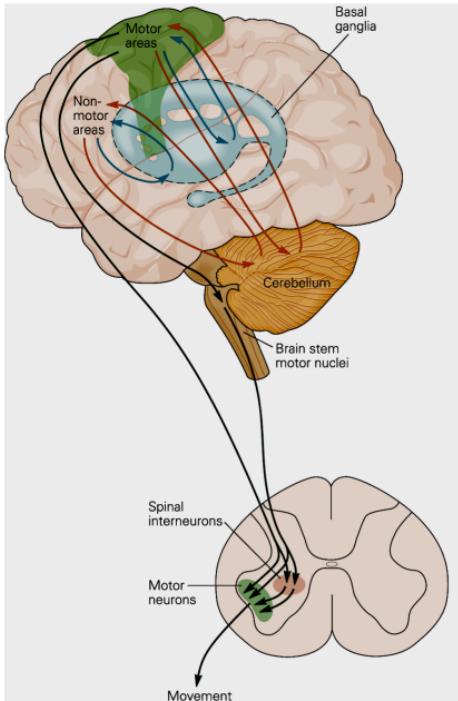
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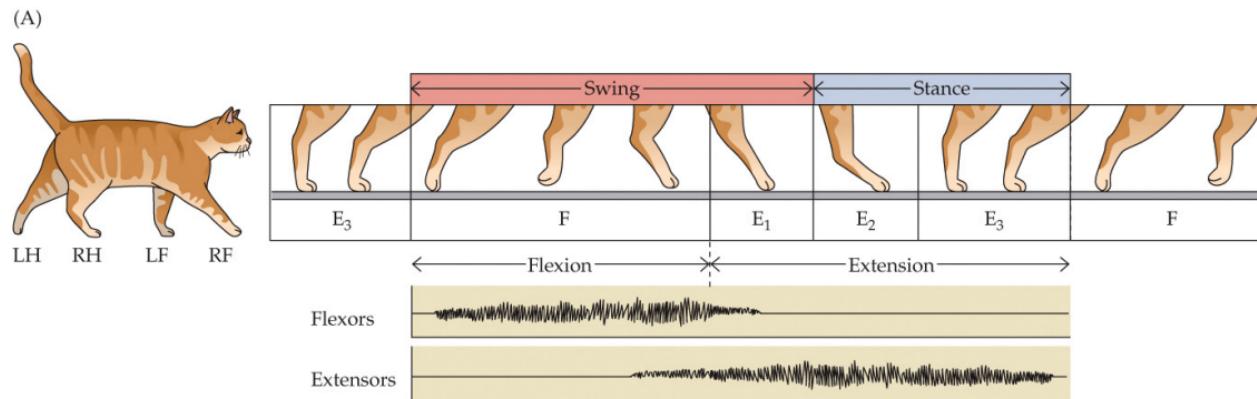
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After Pearson (1976) *Sci. Amer.* 235: 72–86.

NEUROSCIENCE 6e, Figure 16.15 (Part 1)
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Central Pattern Generators

(C)

Extensors

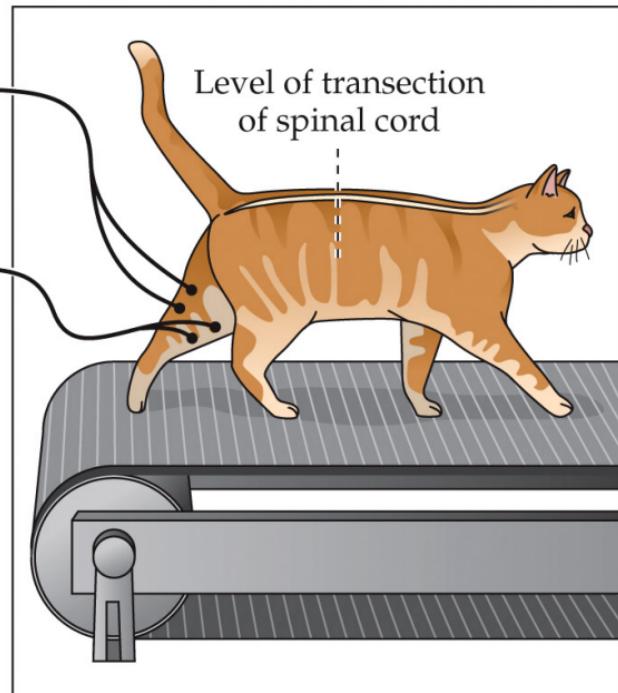


Flexors



Stance

Swing



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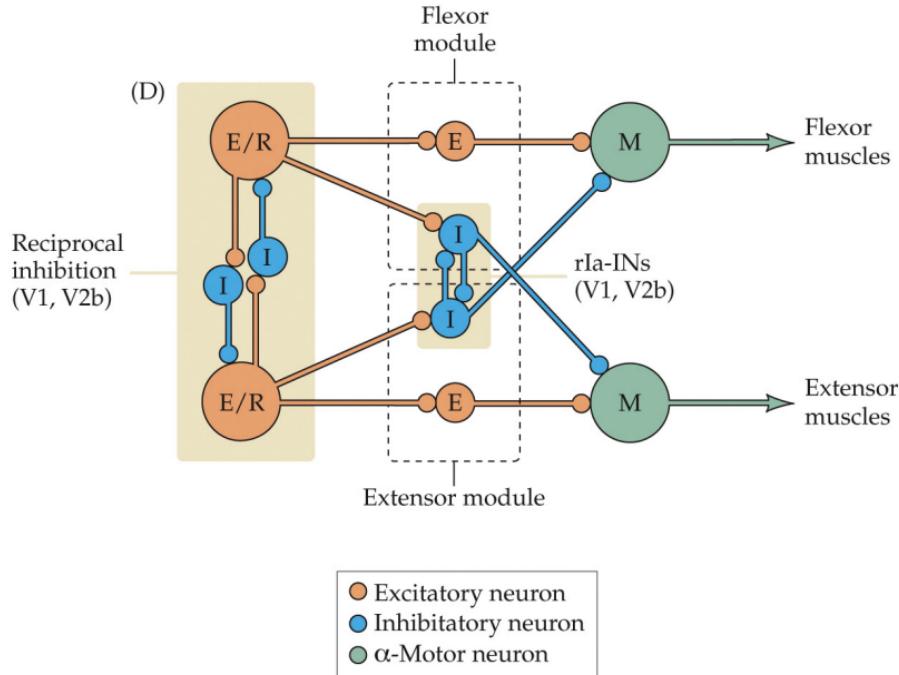
Central Pattern Generators

Two modules – flexor and extensor

At the top of the hierarchy (left most), excitatory neurons (**E/R**) are reciprocally coupled through mutual inhibition (through interneurons **I**)

In the middle layer, there are excitatory neurons (**E**) that convey excitation to the appropriate motor neurons (**M**).

Interneurons in the middle get input from the E/R neurons, to inhibit the opposing motor neurons. Interneurons also reciprocally inhibit each other



After Kiehn (2016) *Nat. Rev. Neurosci.* 17: 224-238.

NEUROSCIENCE 6e, Figure 16.15 (Part 4)
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Voluntary control of movement

Conscious processes are not necessary for the moment to moment control of movement

Movements appear “effortless” as long as there is a steady stream of sensory information (vision, somatic sensation, vestibular) - take walking for example (you slow down with eyes closed).

Successively higher levels of the motor hierarchy specify increasingly more complex aspects of a motor task

Reflexive (“lowest”) then rhythmic then voluntary (“highest”) - but even more complicated: learned movements become reflexive with practice!

Learning Objectives

Explain how all observable behavior is the result of the coordinated activity of muscles.

Apply the size principle to connect motor unit size to recruitment priority when activating a muscle.

Analyze reflex diagrams to predict behavioral output.

Explain how a central pattern generator can control rhythmic behaviors like walking.

Lecture 21 - Lower motor systems: the spine and pattern generation

Pre-class notes for November 18, 2019

Reading: *Neuroscience* ed. 6 by Purves et al., pages 357-375, 381-382, 397-392

Behavioral output - the motor system give rise to behavior. Movement is produced by the coordinated activation of motor neurons, which causes the coordinated contraction of skeletal muscles.

Skeletal muscle (Extrafusal muscle fibers) - type of muscle under the control of the motor system and produces voluntary movement. Also known as *striated muscle* since it is made of multiple long, thin, multi nucleated fibers that have a regular pattern of red and white lines. Contractions in skeletal muscle fibers causes a shortening in the length of a fiber.

Tendon - fibrous collagen tissue that connects muscle to bone. Contains proprioceptive *Golgi tendon organs* that sense changes in muscle tension. The golgi tendon system is a feed back system that monitors and maintains muscle force.

Flexion/Extension - muscles of the body are often in opposing pairs. A *flexor* is a muscle whose contractions bend a limb or other part of the body. An *extensors* is a muscle whose contractions straighten a limb or other part of the body.

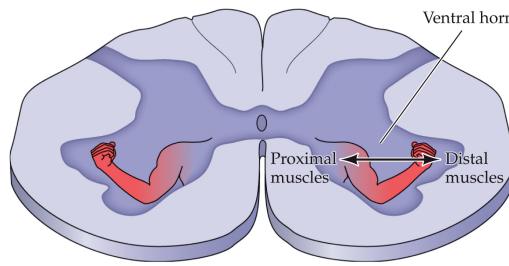
(Lower) Motor neuron - neuron who's cell body is in the gray matter of the spinal cord and send its axon out of the spinal cord to innervate individual muscle fibers.

Motor unit - the set of muscle fibers from a muscle that is innervated by a single lower motor neuron. The size of a motor unit is determined by the number of fibers.

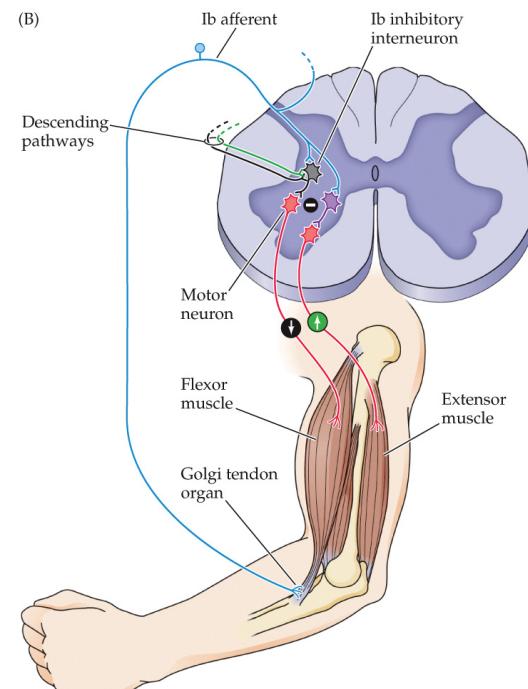
Motor pool - a cluster of motor neurons that innervate the same muscle.

Henneman's Size Principle - motor neurons that have smaller motor unit sizes, which usually have smaller axon diameters, fire before neurons with larger motor unit sizes. Enables the incremental control of the magnitude of an individual muscle's contraction in response to varying inputs received by its motor pool.

Ventral horn of the spinal cord - location in the gray matter of the spinal cord that contains the cell bodies of the lower motor neurons. Motor neurons innervating the axial musculature are located medially, whereas those Innervating the distal musculature are located more laterally.



Reverse myotatic reflex - prevents tears. The Ib ("one B") afferents from golgi tendon organs contact inhibitory interneurons that decrease the activity of a motor neurons innervating the same muscle.

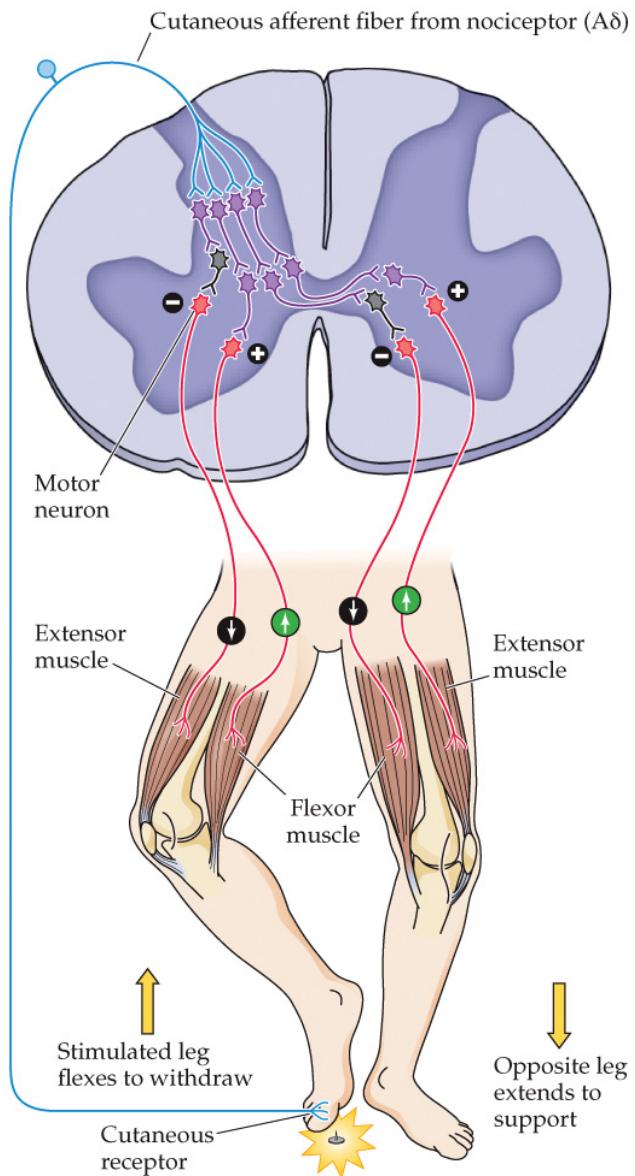


Crossed extension reflex - provides postural support during withdrawal of the affected limb from the painful stimulus. Stimulation of cutaneous receptors in the foot (by stepping on a tack, in this example) leads to activation of spinal cord local circuits that serve to withdraw (flex) the stimulated extremity and extend the other extremity to provide compensatory support.

Central Pattern Generators (CPGs) - a circuit that is capable of producing rhythmic output for coordinated contraction of different muscles without sensory feedback.

Primary Motor Cortex - provides commands to initiate voluntary movement and control complex movement. Primary motor cortex is topographically organized. The motor cortex, in coordination with other areas of the brain integrates information from multiple sensory systems and sends depending axons to the motor control regions of the brainstem, to spinal cord interneurons, and to lower motor neurons themselves.

Neurons in motor cortex are tuned to different parameters of movement, including direction, velocity, joint angle etc. There is some evidence that stimulation of specific sites in motor cortex can lead to coordinated movements across multiple joints



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Learning Objectives: (By the end of Lecture 21 you should be able answer the following)

1. Explain how all observable behavior is the result of the coordinated activity of muscles.
2. Apply the size principle to connect motor unit size to recruitment priority when activating a muscle.
3. Analyze reflex diagrams to predict behavioral output.
4. Explain how a central pattern generator can control rhythmic behaviors like walking.