The Motor System: Lecture 4
Sensory system of muscles

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Slide 1. Recall that muscles are composed of two types of muscle fibers: extrafusal and intrafusal. Extrafusal fibers are much larger than the intrafusal fibers. Extrafusal fibers are responsible for the main force generating function of the muscles. .Intrafusal fibers are part of the sensory system of the muscle. Alpha motor neurons innervate the extrafusal fibers. Gamma motor neurons innervate the intrafusal fibers. The intrafusal fibers have a fluid filled region where afferent neurons wrap their axons about. This region of the intrafusal fiber is called a spindle. Stretching the spindle causes the afferent neuron to produce action potentials. This is the primary mechanism with which the CNS senses length changes in the muscle.

Extrafusal muscle fibers have varying contraction and fatigue properties

Slide 2. The exact content of the myosin molecule determines the functional characteristics of the extrafusal muscle fiber. In adults, we see three varieties of the myosin molecule. These isoforms are designated as type I, IIa, and IIx. Type I fibers are known as slow fibers, while type II are fast fibers. The fibers are called slow and fast because of their rate of force production in response to a single action potential. When they are electrically stimulated, Type I fibers contract at about a tenth the speed of type IIx fibers (type IIa are somewhere in between).

Slide 3. Recall that a motor unit is made up of a single motor neuron and a collection of muscle fibers. There are 3 basic types of motor units: we categorize them based on their twitch contraction time and fatigability.

1) Fast fatiguing (FF). These motor units have a small contraction time and produce a high twitch tension, but tend to fade fast. FF motor units are composed of muscle fibers with relatively large diameter and are supplied by fast conducting, large diameter axons from large motor neurons.

2) Fast, fatigue resistant (FR). These motor units have an intermediate contraction time and can maintain force longer.

3) Slow non-fatiguing (S). These motor units have a long contraction time and show little or no loss of force with repeated stimulation. S type motor units are composed of muscle fibers with small diameter, and are supplied by slow conducting, small diameter axons from small motor neurons.

Different muscles have different proportions of motor units: for example, the diaphragm muscle is composed almost entirely of S type motor units, while gastrocnemius, which is sometimes used for jumping, has a larger proportion of FR and FF units.

Extrafusal muscle fibers change based on their history of activation

Slide 5. A muscle fiber cannot split to form a new fiber. So a muscle can become bulkier only if the individual fibers become thicker. This happens by addition of new myofibrils. The process starts when there is additional stress at the tendons, for example, when one lifts weights. This triggers signaling proteins to activate genes that cause muscle fibers to make more contractile proteins (chiefly myosin). But activity (or lack of) can also change a muscle fiber's type.

A leg muscle like quadriceps in the thigh in a typical person is made up of about equal number of type I and type II fibers. If a person suffers a spinal cord injury and is paralyzed in the lower limbs, the lack of use results in loss of tissue, as is expected, but also a surprising change in the muscle types. The paralyzed individual experiences a sharp decrease of the relative amount of slow myosin, whereas the amount of fast myosin increases. Ten years after paralysis, an individual may have little or no slow type muscles in their quadriceps. The neural input from the spinal cord may be essential for expression of the slow type myosin isoform. Without it, the myosin's default state is the fast type. This might account for the different ratio of slow to fast fibers in marathon runners and sprinter.

There is change in muscle simply due to aging. By age 50, 10% of muscle mass is lost. At 80, loss is at 50%. Motor neurons also die, particularly large motor neurons that supply the type II fibers. In an elderly individual, proportion of fibers tends to be more of the slow type.

Grading of muscle force is accomplished in two ways

1. **Slide 6.** During voluntary contraction, as force requirements increase, new motor neurons are recruited.
2. As force requirements increase, the frequency of activation of already recruited motor neurons increases.

Slide 7. <u>Spike-triggered averaging</u> allows one to measure the twitch tension produced by a single motor unit. In this experiment, an electrode is inserted into the thumb flexor muscle and the electrical signals are amplified. A force transducer is inserted between the thumb and the index finger. Every time the amplifier signals an action potential, it triggers an "event". A 200ms force record aligned to the trigger is selected for all events. The average of this force record is the twitch tension produced by the average action potential.

Slide 8. Motor units that are recruited early tend to have slow contraction time and produce small peak force. Motor units that are recruited later tend to have faster contraction time and larger peak force. The motor neurons that are recruited early will control slow (type I) muscle fibers. The motor neurons that are recruited late will innervate fast (type II) muscle fibers.

Slide 9. We noted earlier that the distribution of muscle fibers in a leg muscle depends on its history of use. Extensive use of a limb can skew distribution of fibers in a muscle toward the slow type. During voluntary contraction of a muscle that has a large proportion of slow fibers, a large proportion of motor units will be recruited. In this experiment, the authors tested this idea by recording the activity from the first interosseuss (FDI) muscle of the dominant and non-dominant hands of a few healthy volunteers as they produced a voluntary contraction. In each volunteer, they randomly sampled from the motor units of this muscle and plotted the percentage of motor units that came on when the muscle was producing small vs. large amounts of force. They found that in the dominant hand, a larger proportion of motor units were recruited to produce a small amount of force than in the non-dominant hand. This is consistent with the idea that because the dominant hand is used more, it tends to have a larger proportion of slow fibers, and therefore a larger proportion of motor units that are recruited early during a voluntary contraction

Muscle receptors measure length and force of the muscle

Slide 10. Based on the diameter of the afferent fiber, muscle receptors are divided into groups I and II. Group I has the larger fiber diameter. Groups Ia and II wrap themselves around interfusal muscle fibers. They are sensitive to length changes. Group Ib afferents innervate the junction between extrafusal muscle fibers and the tendon. They are sensitive to force changes in the muscle.

Muscle spindles afferents measure length, Golgi tendon afferents measure force

Slide 11. Spindle is a term used to describe a group of fine intrafusal muscle fibers that are tapered at the end and have a fluid-filled capsule at the center. Within the capsule the muscular elements are entwined with afferent fibers (from the group Ia and II afferents). Intrafusal fibers are innervated by gamma motor neurons. Spindle afferents respond to changes in muscle length.

The tendon area is innervated by a different kind of afferents, called the Ib afferents. These afferents are also called the Golgi tendon afferents. They respond to changes in muscle force.

The gamma motor neuron system controls spindle sensitivity. When the extrafusal muscle fibers shorten due to activation from a motor neuron, the intrafusal fibers can go slack. This would lead to a sudden loss of firing in the spindle afferents, resulting in a loss of information regarding muscle length.

To prevent this, the CNS activates the gamma motor neurons during contraction to maintain the tension in the intrafusal fibers.

Our sense of limb position is mainly via muscle spindles

Slide 12. Because muscle spindles are sensitive to muscle length, it is reasonable that the brain would rely on their discharge to estimate where our limbs are, that is, proprioception. To investigate this, a subject was seated with her elbows on a table and had eyes closed. The subject was instructed to try to match the angle of the right elbow with the left arm. To investigate how the subject is estimating the position of the right elbow, a mechanical vibrator (100 Hz) was positioned immediately over the tendons at a point just above the right elbow. This vibration strongly stimulates the spindle afferents. During the stimulation, the subject moved her left arm (the tracking arm) to a more extended position. As the stimulation stopped, the tracking arm was quickly flexed back to its original position. This suggests that the brain perceived the stimulation as an extension of the biceps on the right arm, and therefore extended the left elbow to match its perceived position.

Spindle afferents excite motor neurons of the same muscle

Slide 13. Ia fibers, coming from the spindles, terminate in the part of the spinal cord where the motor neurons are (ventral horn). They have monosynaptic excitatory connections on alpha motor neurons of the same muscle A single Ia afferent sends afferents to nearly all of the MNs in the same muscle. They make excitatory synaptic input to inhibitory interneurons acting on alpha motor neurons of antagonist muscles.

Golgi tendon afferents inhibit motor neurons of the same muscle

Slide 14. Group Ib fibers, coming from the Golgi tendon organs, terminate in the regions of the spinal cord where interneurons are located. These internneurons inhibit the alpha motor neurons that go to the same muscle.

The stretch reflex can be tested by suddenly extending a muscle

Slide 16. The sudden stretching of a muscle, for example through tapping of the tendon with a hammer, results in lengthening of the muscle spindle afferents. This produces action potentials in the afferents. The afferent neuron makes synapses on the motor neurons of the stretched muscle, exciting these motor neurons and contracting the muscle.

Stretch reflex has both a short latency and a long-latency component

Slide 17. When the limb is suddenly perturbed, the spinal reflexes respond. This response cannot be voluntarily controlled. However, a later response is also observed which can be voluntarily controlled. This long-latency response is believed to have a cortical origin.

The short-loop: mono-synaptic activation of motorneurons by the Ia afferents. When you stretch a muscle, spindles afferent neurons increase their activity, resulting in excitatory input onto the motorneurons, and activation of the muscle that was elongated.

Slide 18. The long-loop: In humans, particularly for the muscles of the arm, wrist and fingers, there is a second pathway through which a stretch can result in a compensating activity in the motorneurons. This pathway begins with the Ia afferents, goes up the spinal cord through the dorsal column-medial lemniscal pathway, reaches the thalamus, then the somatosensory and motor cortex, and then comes back down to the spinal cord through the cortico-spinal tract. The latency of this loop is about 70 ms. However, unlike the short-loop, its activity is programmable by the brain: voluntarily we can change the response to a stretch (if the stretch is expected, we can ignore it, or respond vigorously).

There are long delays associated with transfer of information from the spinal cord to the cortex and back

Slide 19. In this slide, we have the results of an experiment where the ankle of a healthy volunteer was suddenly stretched. The experimenter is recording with a small surface electrode from the scalp, about the region of the cortex where somatosensory cortex lies. In response to the stretch, an "evoked" potential at the scalp is recorded. This potential reflects the activity of neurons in the somatosensory cortex. Notice that the delay from the stretch to the onset of the evoked potential is about 45ms. Next, the experimenter stimulates the scalp around the region of the motor cortex. This activates neurons in the motor cortex, activates the corticospinal tract, and then activates the motorneurons in the spinal cord. The result is muscle contraction, which is picked up with EMG electrodes. The delay from activation of the motor cortex to the activation of muscles is about 30ms. Therefore, the fastest possible loop time from the spinal cord to the cortex and back is about 95ms. Now on the bottom row of this figure, you see the EMG on the ankle muscle when it is suddenly stretched. Notice that there are three peaks. Only the last peak can be due to activity in the spinal-cortex-spinal loop (long loop). The first two peaks are due to pathways within the spinal cord or brainstem.

A stroke in the brainstem can disrupt the long-latency stretch reflex on the ipsilateral arm

Slide 20. The thumb flexor in a patient with a lesion in the right brain-stem (due to stroke) is suddenly stretched. In this patient, the stroke has resulted in a complete loss of proprioception (sense of limb position) from the right arm and hand. In response to the stretch at time 0, we see the EMG record from the left (middle trace) and right (bottom trace) hand. The EMG response at 25 msec is due to the short loop stretch reflex. The response at 40-55 msec is due to the long-loop stretch reflex. Note that in the right hand, the short-loop EMG response is present, but the long-loop response is missing.

Parkinson's disease can reduce the ability to voluntarily control the long-loop reflexes

Slide 21. Normally, we can voluntarily suppress the long-latency component of the stretch reflex. In Parkinson's disease, some patients lose this ability. Regardless of instructions, they produce a large response. Here, the wrist of a normal and Parkinsonian patient is suddenly extended. We see the position of the wrist, and the EMG of a wrist flexor muscle. In the active condition, the subjects are told to move against the stretch as soon as possible. In the passive condition, they are told to do nothing. Whereas the normal individual can suppress the long-latency reflexes in the passive condition, the Parkinsonian patient cannot.

Movements can take place even without sensory afferents

The major role for our reflexes is to respond when there is an unexpected perturbation. They tend to change the activations of motor neurons so to stabilize the limb. However, to what extent are these reflexes important for generation of voluntary movements where there are no perturbations? To answer this question, we can look at patients who have a neurodegenerative disease the specifically destroys the spindle and Golgi tendon organ afferents.

Large fiber sensory neuropathy: In large fiber sensory neuropathy, the large afferent fibers degenerate (Ia and Ib fibers). Patients can't sense the position of their limb, nor can they detect its motion. They need to see their limb in order to be able to make accurate movements. They feel pain and temperature on the limbs because these afferent fibers are not affected

Slide 22. Here we have the records for a rapid thumb flexion in a normal individual and in a patient with large fiber sensory neuropathy affecting his arm and hand. We see the 3-phase EMG pattern in the normal subject, as well as in the patient. Therefore, the origin of the EMG pattern is likely through direct descending commands to the alpha-motor neurons and not through a feedback loop.

Slide 23. However, the brain still needs sensory information from the hand in order to generate the appropriate pattern of muscle activity. We need to know where the hand is before we can accurately move it. In the case of the neuropathy patient, he needs to see where the hand is. Now if we were to cover the hand after the flexion of the thumb has been made, the finger drifts.