The Physiology of the Senses Lecture 8 - Muscle Sense <u>www.tutis.ca/Senses/</u>

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Objectives

1. List the qualities that best suit the different proprioception receptor types and specify how each is best suited for that quality.

2. Specify how one's sensitivity to position and velocity can be selectively altered.

3. Demonstrate how the function of the spinal reflexes is met by the choice of appropriate afferent and circuit design.

4. Explain the role of corollary discharge in sensing absolute position.

Introduction

Close your eyes and touch your nose with your finger. Your ability to do so depends on 1) proprioception, the sense of limb position and 2) kinesthesia, the sense of limb movement.

Receptors which signal the position and movement of your limbs.

i) joint afferents are located in the joints and are most sensitive to positions at extreme joint angles.

ii) muscle spindles are located in the muscle and are very important for sensing position and movement (velocity)

iii) golgi tendon organ are located in the muscle tendon and detect tension.

iv) tactile receptors in the overlying skin that were covered in the previous session. Recall that the slowly adapting Ruffini afferents are important for sensing the position of your fingers.

What else might affect one's sense of position?

When you command your hand to move, you can also estimate its position by the internal sense of effort. This signal is derived from corollary discharge.

Note 1: All receptors contribute to proprioception.

Different receptor types are better at providing different information (e.g. spindles signal position and velocity; Golgi tendon organs signal force).

While all receptors can provide some information on position, the CNS relies more heavily on particular receptors in different body parts (e.g. tactile afferents are important for position sense in the hand and less important in the shoulder).

Note 2: If one receptor is lost.

If one receptor is lost, other receptors can provide the missing information. Examples:

1) Patients with artificial joints lack joint receptors, but their position sense is almost normal.

2) Position sense in the hand is reasonable after the skin is anaesthetized because of position signal from muscle spindle.

3) If one has no afferent input at all, one has a sense of position from the motor commands one sends out (corollary discharge). For example one can still drive a car that one is used to, even one with standard transmission. If a command to move the arm to the left is sent out, one assumes that the arm will move to the left.



The anatomy of muscle spindles & Golgi tendon organs.

Muscle spindles are located in parallel with the regular muscle fibers.

Here they undergo the same length changes as the rest of the muscle.

Golgi tendon organs (1b) are located in the tendon of the muscle, in series with the muscle fibers.

Here they sense the force the muscle exerts.



Within spindles there are two types of fibers: nuclear bag and nuclear chain.

Large, primary afferents, #1a, originate from both bag and chain fibers. Smaller, secondary afferents, #2, originate only from chain fibers.

The numbers 1a, 1b, 2, etc. refer to the size of the fiber. 1a is the largest and thus the most rapidly conducting. 1b, from the Golgi tendon organ, is slower and #2 is the slowest.

Afferents from nuclear bag fibers signal velocity. They, like the Pacinian corpuscles, adapt quickly when stretched. Bag fibers give a phasic response during stretch and adapt quickly to a constant position.

Both afferents from a nuclear chain fiber fire in proportion to the fiber's length.



Comparing passive muscle stretch to active muscle contraction.

Passive stretch (someone else stretches your muscle):

la afferents come from both bag and chain fibers and are therefore sensitive to velocity, the rate of change in length (phasic response) and to position (tonic response). They are also very sensitive to vibration.

#2 afferents come from chain fibers and are therefore sensitive to position.

1b afferents' activity changes little, primarily because the force acting on the tendon during passive stretch is small.

Active contraction against a load (you contract your muscle):

Contraction causes the tendon to stretch and the spindles to shorten. Spindles become silent. Golgi tendon organ (1b) afferents are very sensitive to active contraction because the tendon is stretched.

Note: Comparing the change in activity during passive and active contraction is a good technique for identifying the fiber type.

Gamma drive controls the sensitivity of muscle spindle.

During passive stretch



Gamma drive from the spinal cord causes contraction of the ends of bag and chain fibers. This stretches the central region where the afferents are located, increasing their sensitivity.

Gamma static drive contracts chain fibers. Chain fibers provide the position signal. Stretching the afferent causes an increased sensitivity to position. Both 1a and #2 fibers originate from chain fibers. Thus in both, position sensitivity is increased.

Gamma dynamic drive activates bag fibers. Bag fibers provide the velocity signal. Stretching the afferent causes an increased sensitivity to velocity. Only 1a afferents originate from bag fibers. Thus only the velocity sensitivity of 1a afferents is increased.

During active contraction

When there is activation of alpha motoneurons but not gamma motoneurons, the muscle shortens and silences the spindle.

When there is activation of alpha and gamma motoneurons, the fiber ends in the spindles contract and maintain the spindle sensitivity.

This is called alpha gamma co-activation.

Three spinal reflexes.

For each we will consider:

- a) What is the spinal circuit?
- b) What is the stimulus and the muscle response?
- c) What is the function?

The monosynaptic stretch reflex is activated by spindle (1a) afferents.

When the muscle lengthens, the spindle is stretched and 1a activity increases. This increases alpha motoneuron activity. The muscle contracts and its length decreases.

This reflex regulates length. It tries to maintain a constant length.

Because this reflex is monosynaptic and is carried by large fibers, it has the shortest latency of all spinal reflexes.





The reflex mediated by the Golgi tendon organ

When too much force is generated by the muscle, the Golgi tendon organ is activated. Via an inhibitory interneuron, this reduces the activity of motoneurons. This decreases muscle contraction and muscle force.

This reflex regulates force i.e. it maintains a constant force. It is used, for example, when attempting to maintain a constant grip on a paper cup.



Reflexes mediated by Pain and Cutaneous receptors

This reflex produces two responses:

1. Contraction of flexors on the same side, which results in a withdrawal from the painful stimulus.

2. Contraction of extensors on the opposite side, which allows one to maintain posture and balance.



Tremor

Why not keep gamma activity high (and thus spindle sensitivity) all the time?

Because too much of a good thing is bad. It can cause tremor. Do you remember a fine tremor when trying hard to preform something precise (e.g. threading a needle)?

Normally the 1a reflex stops the return movement exactly in the correct position. How does that occur, via the agonist or via the antagonist?

Normally, when a limb position changes, the 1a reflex is activated. Stretch of the agonist causes a reflex activation of the agonist. This initiates a return movement.

The return movement stretches the antagonist spindle, causing reflex activation of the antagonist muscle. If this is the right size, it will correctly stop the return movement.



If spindle sensitivity is too high, the stretch reflex in the agonist will be too large, causing a very fast return movement that overshoots the target.

This fast return movement and high sensitivity will produce a large reflex response in the antagonist. This will reverse the movement rather than stop it (something like trying to stop your car with the reverse gear rather than the brakes).

This process will be repeated, causing tremor



The cortical response to the stretch reflex

Muscle stretch activates two responses, i) the spinal monosynaptic stretch reflex and ii) the cortical long loop response.

Long loop responses, through Motor cortex, are under voluntary control. The responses are set or context dependent and are controlled by the cerebellum. This is what adds learnt motor skills to our responses.

A good example of a state learnt motor skill is catching a ball. The catch is pre-set to the expected characteristics of the ball.



An experiment involving muscle vibration

This demonstrates that muscle spindle afferents contribute to a conscious sensation of muscle length.

Vibrate the tendon of the biceps muscle. The vibration of the tendon vibrates the whole muscle and activates the 1a spindle afferents. Now ask the subject, whose eyes are closed, to indicate the felt limb position with the other arm. The perceived position, as indicated by the other limb (light color), is longer (more extended) than the actual position of the vibrated limb. This is because the vibration activates 1a afferents. This additional activity is interpreted as a longer muscle length.



Revised 31/10/2012

How is absolute muscle length sensed?

If you pull a subject's arm while it is actively contracted, the subject can correctly signal the position of that arm with the other arm even with his eyes closed. The contracted arm has a lot of alpha gamma co-activation, the other has little. Presumably, in the contracted arm, the spindles will be more active than the other.

Yet one can sense correctly when both are at the same length. One is able to do so because of corollary discharge (an internal sense of effort). As first proposed by Helmholtz, motor commands go both to muscles and to the areas of the CNS that sense position. The corollary discharge modifies how the afferent signal is interpreted.

A) In a relaxed muscle, low alpha is accompanied by low gamma activity (because of alpha gamma co-activation)

The low gamma produces a low spindle activity

B) If one maintains the same position while actively contracting the muscle, high alpha is accompanied by high gamma activity. High gamma produces a high spindle activity.

In perceiving length, the brain compares the command to the arm (corollary discharge) to the afferent spindle feedback.

The sensed position in both is the same because during active contraction, a high spindle signal is canceled by a high corollary discharge.



Coordinate Transformations

Suppose you are sitting at your desk and want to push a lemon to the left. What muscles do you contract? If your arm is in position A, you need to contract one set of muscles. If you are in position B, you need to contract another set.

To choose which, the CNS needs to sense how the forearm is rotated. The CNS also needs to sense the elbow angle and the shoulder angle to compute where the hand is relative to the rest of your body.



An integrated sense of egocentric position, e.g. where the wrist is relative to you, is computed as proprioceptive information passed from primary sensory cortex to higher order areas and then to association areas within the dorsal stream.

You also need to know whether the lemon is to the left or right. This information of where the lemon is usually comes up the dorsal stream from the eye.

Comparing where the lemon is relative to your retina and where your wrist is relative to you allows the CNS to generate the appropriate movement.



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See problems and answers posted on

http://www.tutis.ca/Senses/L8Muscle/L8Muscl eProb.swf