OBJECTIVES

After studying the material of this lecture the student should be familiar with:

1. Mechanoreceptors located in hairy and glabrous skin
2. Mechanisms of tactile discrimination
3. Receptive fields and feature detection
4. Sensory receptors that mediate proprioception

INTRODUCTION

The somatosensory system receives information from mechanoreceptors (touch and position sense), thermoreceptors (temperature), and nociceptors (pain). This information is transmitted by two sensory pathways, the anterolateral system and the dorsal column system. The anterolateral system transmits information perceived as simple (light) touch, temperature and pain. The dorsal column system mediates information about the spatial and temporal aspects of touch (tactile discrimination) as well as limb position (proprioception).

I. TOUCH

Simple touch (anterolateral system) involves contact with the skin and a sensation of light pressure and a crude sense of localization of the stimulus. Simple touch is typically tested by lightly stroking the skin with a wisp of cotton. Tactile discrimination (dorsal column system) conveys a sense of spatial localization and perception of size and shape of objects. Tactile discrimination is tested by placing objects in a subject's hand and asking them to identify the size and shape of the object (stereognosis) or asking the subject to report if one or two points on the skin are being stimulated (two point discrimination) and where on the skin the stimulus is applied (point localization).

A. RECEPTOR TYPES

Tactile (touch) and Proprioceptive (joint position and movement) sensations are typically associated with mechanoreceptors. Some mechano-receptors are rapidly adapting and detect changes in the stimulus (velocity detection) while others are slowly adapting and signal both the intensity and duration of the stimulus. There are several types of cutaneous and subcutaneous mechanoreceptors. They are found in both hairy and hairless (glabrous) skin.
Figure 1. Types of mechanoreceptors found in nonhairy and hairy skin (Costanzo, 2006)

1. Meissner's Corpuscles

These encapsulated receptors are found in non hairy (Glabrous) skin and are most abundant on the fingertips, lips and other areas of the skin where tactile discrimination is very good. They have relatively small receptive fields (2-4mm). They are rapidly adapting mechanoreceptors and produce brief bursts of impulses when the skin is indented. They adapt rapidly to steady pressure and respond to changes in stimulus intensity (onset and end of the displacement). They respond best to stimulus frequencies of about 30-40 Hz and contribute to a sensation known as Flutter.

2. Pacinian Corpuscles

Pacinian corpuscles are encapsulated structures located in both Hairy and Glabrous skin and are found in both subcutaneous and intramuscular connective tissue. They adapt even more rapidly than Meissner's corpuscles and have best frequencies of about 200-300 Hz. They mediate a sensation referred to as vibration.

3. Hair Follicle Receptors

These are rapidly adapting mechanoreceptors and consist of an arrangement of nerve fibers surrounding the base of hair follicles. Deflection of hairs on the surface of the skin results in excitation of hair follicle receptors. These receptors provide information about velocity and direction of movement across the surface of the skin.
4. Merkel's Discs

Merkel's discs are found in glabrous and hairy skin. They have small punctate receptive fields (2-4mm) and signal vertical indentations of the skin. Although they are classified as slowly adapting mechanoreceptors and maintain a steady state response for the duration of the stimulus, they can give a transient response at the onset of the stimulus. Their response is proportional to stimulus intensity (e.g., displacement).

5. Ruffini Corpuscle

These receptors can be stimulated by stretching the skin, even if the stimulus is located some distance from the receptor. They are found in both glabrous and hairy skin and have relatively large receptive fields. Ruffini end organs have a resting discharge even in the absence of any stimulation. When the skin is stretched there is a rapid increase in discharge rate which slowly adapts to a new level corresponding to the stimulus intensity. These receptors are also located in joint capsules and help to signal the degree of joint rotation.

Figure 2: The receptor fields of cutaneous mechanoreceptors (From Berne & Levy, 1998).
Table 1. RECEPTOR TYPES AND SOMATOSENSORY SENSATIONS

<table>
<thead>
<tr>
<th>RECEPTOR</th>
<th>LOCATION</th>
<th>RECEPTIVE FIELD</th>
<th>TYPE</th>
<th>SENSATION</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pacinian Corpuscle</td>
<td>Hairy &amp; Glabrous Skin</td>
<td>large</td>
<td>RA</td>
<td>Vibration (200-300 Hz)</td>
</tr>
<tr>
<td>Meissner's Corpuscle</td>
<td>Glabrous Skin</td>
<td>small</td>
<td>RA</td>
<td>Touch-skin indentation, tap Flutter (30-40 Hz)</td>
</tr>
<tr>
<td>Hair Follicle Receptors</td>
<td>Hairy Skin</td>
<td>small</td>
<td>RA</td>
<td>Hair deflection (direction and velocity detection)</td>
</tr>
<tr>
<td>Ruffini endings</td>
<td>Hairy &amp; Glabrous Skin</td>
<td>large</td>
<td>SA</td>
<td>Skin displacement-stretch</td>
</tr>
<tr>
<td>Merkel's Discs</td>
<td>Hairy &amp; Glabrous Skin</td>
<td>small</td>
<td>SA</td>
<td>Skin displacement-vertical</td>
</tr>
<tr>
<td>Free Nerve Endings</td>
<td>Hairy &amp; Glabrous Skin</td>
<td>large</td>
<td>SA</td>
<td>Touch, Pressure, Temperature and Pain</td>
</tr>
</tbody>
</table>

B. TACTILE DISCRIMINATION

Tactile discrimination is mediated by fibers projecting to the cerebral cortex by way of the dorsal column system (posterior fasciculi → VPL → post central gyrus). This system provides information about the place, intensity, and temporal and spatial patterns of mechanical stimuli on the skin. It also mediates touch, pressure, flutter, vibration and kinesthesia. Tactile discrimination has several components including point localization, two-point discrimination, stereognosis and complex tactile discrimination.

1. Point localization

When a position on the surface of the skin is stimulated, mechanoreceptors beneath the surface are activated. Those directly under the stimulus receive the greatest amount of stimulation, adjacent receptors a lesser amount. There is a divergence of fibers as they project centrally to the next set of relay neurons and the stimulus activity is distributed across a population of neurons. At each relay level there are inhibitory interneurons that provide feedback inhibition to ascending neurons as well as their neighbors. This feedback causes lateral inhibition of adjacent projecting fibers and results in a sharpening of the stimulus localization. At the level of the cortex, cells in the center of the projection field receive excitatory input while surrounding cells are inhibited. There is a topographical projection of positions on the surface of the body to cells in specific locations in the cortex. The somatotopic mapping of body parts onto the cortex is...
referred to as the sensory homunculus. Each part of the body is represented in the brain in proportion to its relative importance in sensory perception. Areas of the body with large cortical representations (e.g., fingers, face, lips) typically have the greatest tactile discrimination.

2. Two point discrimination

The ability to recognize two separate points applied simultaneously to the skin from a single point is called two point discrimination. Two point discrimination varies with location on body surface. It is about 2mm on the finger tip and increases to over 40 mm on the back. The density of receptors in a given area of the skin play an important role in determining the spatial resolution of stimuli. Lateral inhibition also plays a critical role in establishing the spatial resolution of tactile stimuli perceived at the level of the cortex. In experiments where embossed letters are moved across the surface of the finger in monkeys it was observed that the firing patterns of both rapidly and slowly adapting mechanoreceptors could faithfully reproduce a neural image of the letters. Pacinian corpuscle responses were unable to do this. This neural representation of the letters was maintained in somatosensory cortex in slowly adapting neurons located in area 3b.

3. Receptive fields and feature detection

The receptive field of a neuron is defined as that area of the body that when stimulated will excite or inhibit that neuron. Receptive field size varies with body position. For example, on the fingers receptive fields are relatively small (approx 1-4mm). The receptor field size increases for the hand, wrist, and arm respectively. The receptive field of somatosensory neurons in the cortex can be simple or complex. Simple receptive fields typically have a central region of excitation with a surrounding region of inhibition.

Receptive field properties can also be complex. They can have a directional component to their response as well as sensitivity to the velocity of movement across the surface of the skin. Some directionally sensitive cells have inhibitory components when objects are moving in the opposite direction. Complex cortical receptive fields can include edge detection and width of the stimulus. A population of cortical neurons with different receptive field properties would permit the sensation of relatively complex shapes, sizes and textures of tactile stimuli.
4. Stereognosis - patterns and shapes

The ability to recognize the size, shape, and texture of objects by palpation is known as stereognosis. Stereognosis involves multiple sensory receptors as well as integration of information from motor systems. This ability requires a higher level of cortical processing and the convergence on input from a variety of mechanoreceptors as well as muscle and joint receptors. Although interruption of inputs from receptors and thalamic relay neurons may severely impair stereognosis, the actual physiologic mechanism resides in the somatosensory cortex.

5. Columnar organization

The somatosensory cortex is organized in columns. These sections of cortex extend from the surface to the white matter to form functional units. Within each column, cells have similar receptive fields representing a specific region of the body and receive input from the same receptor type (e.g., rapidly adapting or slowly adapting but not both).

II. PROPRIOCEPTION (position and movement)

Limb proprioception includes the sense of position as well as movement of the limbs. There are two types of limb proprioception: limb position (limb position sense) and limb movement (kinesthesia). These sensations are important for maintaining balance and controlling limb movements.
A. RECEPTORS

Joint capsules contain Ruffini like endings and signal both joint movement and position. In addition muscle ligaments contain Golgi tendon organs as well as a few Pacinian Corpuscles. Stretch receptors (muscle spindles) also signal changes in muscle length and contribute to the sense of limb position.

<table>
<thead>
<tr>
<th>Receptor Type</th>
<th>Sensory Fiber</th>
<th>Sensation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Joint capsule (Ruffini endings)</td>
<td>Aβ / II</td>
<td>limb position</td>
</tr>
<tr>
<td>Golgi tendon organ</td>
<td>Aα / Ib</td>
<td>limb position</td>
</tr>
<tr>
<td>Muscle spindles</td>
<td>Aα / Ia (primary)</td>
<td>limb movement (dynamic)</td>
</tr>
<tr>
<td></td>
<td>Aβ / II (secondary)</td>
<td>limb position (static)</td>
</tr>
</tbody>
</table>

B. POSITION SENSE

The sensation of joint position relies on input from different receptors: muscle receptors, joint receptors, and cutaneous receptors. If the input from joint and cutaneous receptors is selectively blocked leaving muscle receptors intact, there is a deterioration in the ability to judge limb position. Likewise, if the muscles sensors are disengaged leaving joint and skin receptors intact, limb position acuity is impaired. Thus, a combination of different receptor inputs contributes to the sense of limb position.

1. Response properties

The response of joint receptors has two components. The initial transient signals the rate of joint movement and the steady state response signals the limb position. Some receptors are position sensitive and others are velocity sensitive.

The output from a single receptor covers a limited range of joint angles and the set of receptors from a given joint covers the entire range of limb movement.

Some cortical neurons receive input from multiple joints. Information about the angle and position of each joint helps to determine the position of the body in three dimensional space.

C. SENSATION OF JOINT MOVEMENT- KINESTHESIA

At higher levels of the nervous system (e.g. ventrobasal complex), cells respond to a wider range of joint angles. Some cells increase their activity when the joint is flexed,
others increase when the joint is extended. These cells signal both the direction and the rate at which the joint is being rotated.

III. LOSS OF SOMATOSENSORY SENSATIONS

A complete loss of proprioceptive and tactile sensations requires a bilateral lesion of the spinal cord interrupting both the anterolateral (anterior spinothalamic tract) and dorsal column systems.

Injuries limited to the dorsal columns can be evaluated by looking for the following clinical signs:

a. Loss of two-point discrimination
b. Loss of vibration sense
c. Inability to recognize limb position without visual information
d. Inability to recognize letters or numbers drawn on the skin (agraphesthesia)
e. Loss of ability to recognize objects by palpation and handling (astereognosis)
f. Inability to maintain posture (balance) when feet are close together and eyes closed (Positive Romberg sign)

Lesions of the dorsal columns do not result in a loss of pain and temperature sensations (anterolateral systems). Lesions of the dorsal columns without injury to the anterolateral system results in a loss of tactile discrimination and the ability to detect movement on the skin, but a crude sense of touch is maintained.
ADDITIONAL REFERENCES
