Chapter 12: Touch

During normal foraging activity, the tentacles are constantly being used to feel the mole's surroundings, moving so rapidly that they appear as a blur of motion, touching as many as 12 objects per second. Using these supersensitive organs, identification of prey can be made in under half a second.

Art & Sensation

Vision – art
Hearing – music
Touch – massage?
Taste – French food
Smell - perfume
Skin – 1.8 square meters, weighs ~4Kg

Cutaneous System

- **Skin** - heaviest organ in the body
  - Epidermis is the outer layer of the skin, which is made up of dead skin cells
  - Dermis is below the epidermis and contains four kinds of mechanoreceptors that respond to stimuli such as pressure, stretching, and vibration.
Mechanoreceptors

**Merkel receptor** - disk-shaped receptor located near the border between the epidermis and dermis

**Meissner corpuscle** - stack of flattened disks in the dermis just below epidermis

**Ruffini cylinder** - branched fibers inside a cylindrical capsule

**Pacinian corpuscle** - onion-like capsule located deep in the skin

Attributes of Touch Receptors

1. **Type of stimulation to which the receptor responds.**

2. **Size of the receptive field.**

3. **Rate of adaptation (fast versus slow).**
Surface receptors have smaller receptive fields than deep receptors.

Mechanoreceptors

(a) Slow adapting (SA)

(b) Rapid adapting (RA)
Mechanoreceptors

- Temporal Properties (adaptation)
  - Slowly adapting fibers (SA) found in Merkel and Ruffini receptors - fire continuously as long as pressure is applied
  - Rapidly adapting fibers (RA) found in Meissner receptor and Pacinian corpuscle - fire at onset and offset of stimulation

Properties of the four mechanoreceptor types.

<table>
<thead>
<tr>
<th>Receptor Type</th>
<th>Vibration Frequency</th>
<th>Adapting Rate</th>
<th>Size of Receptive Field</th>
</tr>
</thead>
<tbody>
<tr>
<td>Merkel receptors (SA1)</td>
<td>Low</td>
<td>Slow</td>
<td>Small (SA I)</td>
</tr>
<tr>
<td>Meissner receptors (RA1)</td>
<td>Low</td>
<td>Rapid</td>
<td>Large (SA II)</td>
</tr>
<tr>
<td>Ruffini (SA2)</td>
<td>High</td>
<td>Slow</td>
<td>Large (Ruffini)</td>
</tr>
<tr>
<td>Pacinian corpuscle (RA2)</td>
<td>High</td>
<td>Rapid</td>
<td>Large (Pacinian)</td>
</tr>
</tbody>
</table>

Table 14.1: Properties of Four Types of Mechanoreceptors

<table>
<thead>
<tr>
<th>Receptor (Fiber)</th>
<th>Slow Fiber/Responses</th>
<th>Frequency Response</th>
<th>Perceptions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Merkel (SA1)</td>
<td>Continuous</td>
<td>0.3–3 Hz</td>
<td>Fine details</td>
</tr>
<tr>
<td>Meissner (RA1)</td>
<td>Continuous (slow adapting)</td>
<td>3–40 Hz</td>
<td>Hand grip control (finely)</td>
</tr>
<tr>
<td>Ruffini (SA2)</td>
<td>Continuous (slow adapting)</td>
<td>15–400 Hz</td>
<td>Tactile sensitivity at upper range</td>
</tr>
<tr>
<td>Pacinian (RA2)</td>
<td>Continuous (rapid adapting)</td>
<td>10–500 Hz</td>
<td>Texture by moving fingers</td>
</tr>
</tbody>
</table>
• **Type of stimulation and adaptation rates**

Surface receptors: Merkel receptors (SA1) and Meissner receptors (RA1) have small receptive fields and respond to slow vibration rates.

Deep receptors: RA2 fibers (Pacinian corpuscle) and Ruffini (SA2) have large receptive fields and respond to high vibration rates.

<table>
<thead>
<tr>
<th>Vibration frequency</th>
<th>Adapting Rate</th>
<th>Slow</th>
<th>Rapid</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>Merkel receptors (SA1)</td>
<td>○</td>
<td>○</td>
</tr>
<tr>
<td></td>
<td>Meissner receptors (RA1)</td>
<td>○</td>
<td>○</td>
</tr>
<tr>
<td>High</td>
<td>Ruffini (SA2)</td>
<td>○</td>
<td>○</td>
</tr>
<tr>
<td></td>
<td>Pacinian corpuscle (RA2)</td>
<td>○</td>
<td>○</td>
</tr>
</tbody>
</table>

**Table 12.2 Mechanoreceptors: Feature sensitivity and associated functions**

<table>
<thead>
<tr>
<th>Mechanoreceptor population</th>
<th>Maximum feature sensitivity</th>
<th>Primary functions</th>
</tr>
</thead>
<tbody>
<tr>
<td>SA1 (Merkel)</td>
<td>Sustained pressure, very low frequency (&lt; ~5 Hz)</td>
<td>Texture perception, Pattern/form detection “slot on a screw”</td>
</tr>
<tr>
<td></td>
<td>Spatial deformation</td>
<td></td>
</tr>
<tr>
<td>FA I (Meissner)</td>
<td>Temporal changes in skin deformation (~5–50 Hz)</td>
<td>Low-frequency vibration detection, “vibration as the coffee cup slips”</td>
</tr>
<tr>
<td>FA II (Pacinian)</td>
<td>Temporal changes in skin deformation (~50–700 Hz)</td>
<td>High-frequency vibration detection, texture perception “mosquito”</td>
</tr>
<tr>
<td>SA II (Ruffini)</td>
<td>Sustained downward pressure, lateral skin stretch, skin slip (low sensitivity to vibration across frequencies)</td>
<td>Finger position, stable grasp “stretch holding a coffee cup”</td>
</tr>
</tbody>
</table>
### Table 12.2 Mechanoreceptors: Feature sensitivity and associated functions

<table>
<thead>
<tr>
<th>Receptor Type</th>
<th>Sensitivity and Associated Functions</th>
</tr>
</thead>
</table>
| **SA I (Merkel)** | Sustained pressure, very low frequency (<~5 Hz)  
Spatial deformation  
Texture perception  
“Slot on a screw” |
| **FA I (Meissner)** | Temporal changes in skin deformation (~5–50 Hz)  
Low-frequency vibration detection  
“Vibration as the coffee cup slips” |
| **FA II (Pacinian)** | Temporal changes in skin deformation (~50–700 Hz)  
High-frequency vibration detection, texture perception  
“Mosquito” |
| **SA II (Ruffini)** | Sustained downward pressure, lateral skin stretch, skin slip  
(low sensitivity to vibration across frequencies)  
Finger position, stable grasp  
“Stretch holding a coffee cup” |

#### Sensitivity as a function of frequency

![Graph showing sensitivity as a function of frequency for SA I, FA I, and FA II receptors.](image)

- **SA I**
- **FA I**
- **FA II**
Adaptation Experiment by Hollins et al.

- Participants' skin was adapted with either:
  - 10-Hz stimulus for 6 minutes to adapt the SA1/FA1
  - 250-Hz stimulus for 6 minutes to adapt the FA2
- Results showed that only the adaptation to the 250-Hz stimulus affected the discrimination of fine textures.

Kinesthetic receptors
Thermoreceptors

Pathways from Skin to Cortex

- Nerve fibers travel in bundles (peripheral nerves) to the spinal cord
- Two major pathways in the spinal cord:
  - Fast medial lemniscal pathway consists of large fibers that carry proprioceptive and touch information
  - Slow spinothalamic pathway consists of smaller fibers that carry temperature and pain information
  - These cross over to the opposite side of the body and synapse in the thalamus, and then on to the Somatosensory cortex, or SI1

![Diagram of neural pathways](image-url)
Primary somatosensory receiving area

Map is distorted, based on body sensitivity to detail
Perceiving Details

• Measuring tactile acuity
  – Two-point threshold - minimum separation needed between two points to perceive them as two units
  – Grating acuity - placing a grooved stimulus on the skin and asking the participant to indicate the orientation of the grating

Tactile acuity thresholds are determined by Merkel receptors (SA1)
Receptor Mechanisms for Tactile Acuity

- There is a high density of Merkel receptor/SA1 fibers in the fingertips
- Merkel receptors are densely packed on the fingertips - similar to cones in the fovea
- Both two-point thresholds and grating acuity studies show these results

Cortical Mechanisms for Tactile Acuity

- Body areas with high acuity have larger areas of cortical tissue devoted to them
- This parallels the “magnification factor” seen in the visual cortex for the cones in the fovea
The ‘Somatosensory Homunculus’

Subjects with better (lower) acuity thresholds have larger representations of the fingers in S1

\[ r = -0.47, p < .05 \]

(Duncan and Boynton, 2007)
In addition to the expected responses in somatosensory cortex, experienced Braille readers show large fMRI responses in the occipital cortex while reading Braille compared to control subjects.

Three-finger Braille readers have distorted map for the finger representations in SA1 compared to 1-finger Braille readers and sighted control subjects.

Plasticity in neural functioning leads to multiple homunculi and changes in how cortical cells are allocated to body parts.

Phantom Limb Disorder

The persistent sensation of an appendage, after removal by amputation or simple denervation.

Ramachandran and colleagues has shown that touching the face of a phantom limb patient leads to sensations in the missing hand and arm.

This lead to the hypothesis that the brain is ‘filling in’ for the missing stimulation in the hand and arm representation in the somatosensory cortex.
Phantom Limb Disorder

Touching the chin stimulated the finger representation best, indicating that maybe Penfield got the face representation upside down.

Sure enough, an fMRI experiment in 1999 showed that Ramachandran was right and the somatosensory homunculus shown in textbooks (and Penfield) is wrong.

Phantom Limb Disorder

Phantom limb disorder can be painful and uncomfortable.

Ramachandran used a ‘mirror box’ to simulate the presence of the amputated hand which alleviated the symptoms in most of his patients.
The tongue may be used to as a substitute for sight. For more, see the ScienceNews article *The Seeing Tongue.*

Neurons further upstream become more specialized

Monkey’s thalamus shows cells that respond to center-surround receptive fields
Somatosensory cortex shows cells that respond maximally to orientations and direction of movement.

The Physiology of Tactile Object Perception

- The firing pattern of groups of mechanoreceptors signals shape, such as the curvature of an object.
Perceiving Objects

- Humans use active rather than passive touch to interact with the environment
- Haptic perception is the active exploration of 3-D objects with the hand
  - It uses three distinct systems:
    - Sensory system
    - Motor system
    - Cognitive system

Perceiving Objects

- Psychophysical research shows that people can identify objects haptically in 1 to 2 sec
- Klatzky et al. have shown that people use exploratory procedures (EPs)
  - Lateral motion
  - Pressure
  - Enclosure
  - Contour following
The Physiology of Tactile Object Perception

- Monkey’s somatosensory cortex also shows neurons that respond best to:
  - Grasping specific objects
  - Paying attention to the task
- Neurons may respond to stimulation of the receptors, but attending to the task increases the response

The champion of somatosensory perception: the *Star Nosed Mole*
The “where” of touch
– depends on what you are doing/experiencing
Frank sat in front of two cameras placed beside each other. Frank wore virtual-reality goggles connected to the cameras for a stereo view. The experimenter stood at Frank’s side and used a plastic rod to stroke his physical chest (unseen by the cameras). Being very careful to use exactly the same timing, the experimenter used a second rod to simultaneously “stroke” Frank’s “phantom chest,” an area in front of and just below the cameras (see figure). Frank could see the back of his body sitting in the chair and the experimenter’s hand moving down toward a point below the two cameras. When subjects were asked what they experienced, they reported viewing their own body from behind, with their heads located at the site of the cameras (like the phantom’s head in Figure 12.21). In addition they reported feeling the tap on the phantom’s chest just below the cameras.

Interactions between touch and vision
Virtual reality