Touching

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Touching

- Body-world interface
- Passive vs active touch
- Perceptual loops
Figure 8.3 The skin harbors a variety of morphologically distinct mechanoreceptors. This diagram represents the smooth, hairless (also called glabrous) skin of the fingertip. The major characteristics of the various receptor types are summarized in Table 8.1. (After Darian-Smith, 1984.)
Mechanoreception underneath the skin

~200 μm
Mechanoreception underneath the skin
Proprioceptive receptor types

Name:
- Muscle spindle receptors
- Golgi tendon organs
- Joint receptors

Sensitive to:
- Muscle length
- Muscle tension
- Flexion, extension
Body-world interface

Underneath the skin

<table>
<thead>
<tr>
<th>Receptor type</th>
<th>Anatomical characteristics</th>
<th>Associated axons (and diameters)</th>
<th>Axonal conduction velocities</th>
<th>Location</th>
<th>Function</th>
<th>Rate of adaptation</th>
<th>Threshold of activation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Free nerve endings</td>
<td>Minimally specialized nerve endings</td>
<td>C, Aδ</td>
<td>2–20 m/s</td>
<td>All skin</td>
<td>Pain, temperature, crude touch</td>
<td>Slow</td>
<td>High</td>
</tr>
<tr>
<td></td>
<td></td>
<td>.5 – 2 m/s</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meissner’s corpuscles</td>
<td>Encapsulated; between dermal papillae</td>
<td>Aβ 6–12 μm</td>
<td>Principally glabrous skin</td>
<td>Touch, pressure (dynamic)</td>
<td>Rapid</td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>Pacinian corpuscles</td>
<td>Encapsulated; onionlike covering</td>
<td>Aβ 6–12 μm</td>
<td>Subcutaneous tissue, interosseous</td>
<td>Deep pressure, vibration (dynamic)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>muscle of viscera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>skin, hair follicles</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ruffini’s corpuscles</td>
<td>Encapsulated; oriented along stretch lines</td>
<td>Aβ 6–12 μm</td>
<td>All skin</td>
<td>Stretching of skin</td>
<td>Slow</td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>Muscle spindles</td>
<td>Highly specialized (see Chapter 8 and Chapter 15)</td>
<td>Ia and II</td>
<td>Muscles</td>
<td>Muscle length</td>
<td>Both slow and rapid</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Golgi tendon organs</td>
<td>Highly specialized (see Chapter 15)</td>
<td>Ib</td>
<td>Tendons</td>
<td>Muscle tension</td>
<td>Slow</td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>Joint receptors</td>
<td>Minimally specialized</td>
<td>—</td>
<td>Joints</td>
<td>Joint position</td>
<td>Rapid</td>
<td>Low</td>
<td></td>
</tr>
</tbody>
</table>

Mechano-receptors (ex-afferents)

Proprio-(re)ceptors (re-afferents)

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*In the 1920s and 1930s, there was a virtual cottage industry classifying axons according to their conduction velocity. Three main categories were discerned, called*
Receptors

Evolutionary specialization

Selection process - ?
Signal transduction
The receptor potential is produced by a **mechanically sensitive channel** that opens when the membrane is deformed.

The channel is permeable to positive ions, primarily $\text{Na}^+$, $\text{K}^+$ and $\text{Ca}^{2+}$. 

![Diagram of a mechanically sensitive channel with $\text{Na}^+$ ions进出]
Mechanoreceptors are depolarized by stretch of the cell membrane and the depolarization is proportional to the stimulus amplitude.

A. The spindle organ in skeletal muscle mediates limb proprioception. These receptors signal muscle length and the speed at which the muscle is stretched. The receptor consists of a bundle of specialized (intrafusal) muscle fibers enclosed by a capsule. The sensory nerve endings respond to stretch of the muscle fibers. Stretch-sensitive ion channels in the nerve membrane are linked to the cytoskeleton by the protein spectrin. Mechanical deformation of the membrane opens these cation-selective channels. The influx of Na\(^+\) and possibly Ca\(^{2+}\) depolarizes the nerve ending, producing the receptor potential. (Adapted from Sachs 1990.)

B. Response of an isolated muscle spindle to stretch. Upper records show the depolarizing receptor potentials recorded from the sensory axon when the muscle spindle is stretched to different lengths. Lower records show the amplitude and rate of stretch. Action potentials in this nerve have been blocked with tetrodotoxin to allow analysis of the receptor potentials. The initial depolarization of the muscle spindle in response to change in muscle length (dynamic response) is proportional to both the rate and amplitude of stretch. When stretch is maintained at a fixed length, the receptor potential decays to a lower value proportional only to the amount of stretch (static response). (Adapted from Ottoson and Shepherd 1971.)

C. Patch clamp records of a single stretch-sensitive channel recorded from skeletal myocytes. Pressure is applied to the receptor cell membrane by suction. At rest (top record) the stretch-sensitive channel opens sporadically for short time intervals, producing a transient depolarizing current. As the pressure on the membrane is increased (lower records), the channel opens more often and remains in the open state for longer time intervals (indicated by the bar above the channel openings). Each channel opening increases the membrane conductance to cations. The increase in the probability of opening and open time produces longer and larger depolarizations. (Adapted from Sachs 1990.)
Receptive Fields (RFs):
Spatial and temporal
Receptive Fields (RFs): Spatial and temporal

RF size?
Receptive Fields (RFs): Spatial and temporal

Response dynamics?
Receptive Fields (RFs): Spatial and temporal

- **RAI**: Meissner’s corpuscle
- **SAI**: Merkel cells
- **RAII**: Pacinian corpuscle
- **SAII**: Ruffini endings

**Receptors**

**RA**

**SA**

**PC**

**Receptive field**

**RAI**

**SAI**

**RAII**

**SAII**

**Neural spike train**

**Stimulus**
Cutaneous Mechanoreceptor Channels

Rapidly Adapting (RA1)
These are associated with Meissner’s corpuscles.

Rapidly Adapting (RA2)
These are also called PC because they are associated with Pacinian corpuscles.

Slowly Adapting (SA1)
Associated with Merkels cells

Slowly Adapting (SA2)
Associated with Ruffini’s endings
Figure 22-4 The distribution of receptor types in the human hand varies. The number of sensory nerve fibers innervating an area is indicated by the stippling density, with the highest density of receptors shown by the heaviest stippling. (RA = 5 rapidly adapting, SA = 5 slowly adapting.) Meissner’s corpuscles (RA) and Merkel disk receptors (SA I) are the most numerous receptors; they are distributed preferentially on the distal half of the fingertip. Pacinian corpuscles (PC) and Ruffini endings (SA II) are much less common; they are distributed more uniformly on the hand, showing little differentiation of the distal and proximal regions. The fingertips are the most densely innervated region of skin in the human body, receiving approximately 300 mechanoreceptive nerve fibers per square centimeter. The number of mechanoreceptive fibers is reduced to 120/cm² in the proximal phalanges, and to 50/cm² in the palm. (Adapted from Vallbo and Johansson 1978.)
Neurometric – psychometric matching

Spatial resolution
Signal conduction
Sensory signal conduction

Pseudo-unipolar neurons
Sensory signal conduction
Sensory signal conduction

1st synapse

1st synapse
Sensory signal conduction

2nd synapse

3rd synapse
Figure 8.7  Diagram of the somatic sensory portions of the thalamus and their cortical targets in the postcentral gyrus. The ventral posterior nuclear complex comprises the VPM, which relays somatic sensory information carried by the trigeminal system from the face, and the VPL, which relays somatic sensory information from the rest of the body. Inset above shows organization of the primary somatosensory cortex in the postcentral gyrus, shown here in a section cutting across the gyrus from anterior to posterior: (After Brodal, 1992, and Jones et al., 1982.)
The Homunculi

A  Sensory homunculus

B  Motor homunculus
The Homunculi

Relative size reflects innervation density

phylogenetically

Figure 20-5 Different species rely on different parts of the body for adaptive somatosensory information. These drawings show the relative importance of body regions in the somatic sensibilities of four species, based on studies of evoked potentials in the thalamus and cortex.
The Homunculi

Relative size reflects innervation density

ontogenetically
Motor signal conduction

The cortico-spinal tract
30% - M1
30% - premotor
30% - somatosensory, parietal

The cortico-bulbar tract
Motor signal conduction

The cortico-spinal tract
Motor signal conduction

The cortico-spinal tract

1\textsuperscript{st} synapse
The Homunculi
Accurate spatial organization

Figure 23-9 The representation of whiskers in the somatosensory cortex of the rat. (Adapted from Bennett-Clarke et al. 1997).
Sensory signal conduction

The vibrissal system
Sensory signal conduction

The vibrissal system

whisker

Meisner
Merkel
Ruffini
Lanceolate
free endings
Common mechanisms of sensory processing
Rich muscular system
Receptor types

whisker

eye

Meisner
Merkel
Ruffini
Lanceolate
free endings

guine fowl

finger

SAI
SAII
RAI
RAII

R G B

Figure 1

ra
sa
pc

Ruffini endings
Receptors mix in clusters

Merkel cells

eye @ 1°

whisker

finger
Receptor convergence / divergence

Human eye: 5M cones (+ 120M rods) --> 1M fibers

Human skin: 2,500 receptors/cm² --> 300 fibers / cm²

Rat whisker: 2,000 receptors --> 300 fibers
  ~ 10 -> 1 convergence

Human ear: 3,000 hair cells --> 30,000 fibers
  ~ 1 -> 10 divergence
Processing stations

eye
- Receptors
- Bipolar cells
- Ganglion cells
- Thalamus
- Cortex

finger
- Receptors
- Ganglion cells
- Brainstem cells
- Thalamus
- Cortex

whisker
- Receptors
- Ganglion cells
- Brainstem cells
- Thalamus
- Cortex
Spatial processing (by Lateral inhibition)

- **Eye**
  - Receptors
  - Bipolar cells
  - Ganglion cells

- **Finger**
  - Receptors
  - Ganglion cells
  - Brainstem cells

- **Whisker**
  - Receptors

**Drive for clustering?**
Efficient coding

(by only coding changes)

Changes in time:
  • Intrinsic in individual neurons
  • Starting at the receptor level

Changes in space:
  • Circuits of neurons
  • Starting after lateral inhibition
Temporal filtering (by intrinsic factors)

eye

whisker

finger

Frequency (Hz)
The threshold for detecting vibration corresponds to the tuning threshold of the mechanoreceptor. The sensitivity threshold for Meissner's corpuscles is lowest for frequencies of 20-50 Hz. Pacinian corpuscles sense higher frequencies. (Adapted from Mountcastle et al. 1972.)
Passive and active touch

Passive touch
- Perceptual processing follows sensory events

Active touch
- Perceptual processing surrounds sensory events:
  - The brain probes the world
  - Compares sensory data with internal expectations
  - Updates internal expectations

Active touch is done in a loop:
- Change of expectations $\Rightarrow$ probing the world
- probing the world $\Rightarrow$ Change of expectations
Passive and active touch

Passive touch
- low thresholds
- poor accuracy

Active touch
- higher thresholds
- high accuracy
Passive and active touch

Passive touch
- low thresholds
- poor accuracy

Active touch
- higher thresholds
- high accuracy

Detection

Exploration
Object localization
Object identification
Passive and active touch

<table>
<thead>
<tr>
<th>Passive touch</th>
<th>Active touch</th>
</tr>
</thead>
<tbody>
<tr>
<td>low thresholds</td>
<td>higher thresholds</td>
</tr>
<tr>
<td>poor accuracy</td>
<td>high accuracy</td>
</tr>
</tbody>
</table>

Potential underlying mechanism: “Gating”

- Arousal, preparatory, or motor commands “gate out” sensory signals
- Example: Thalamic gating (Sherman & Guillery, JNP. 1996)

Thalamic neurons have 2 modes:
- in drowsiness: hyperpolarized, bursting, low threshold
- in alertness: depolarized, single spikes, high threshold
Passive and active touch

**Passive touch**
- low thresholds
- poor accuracy

**Active touch**
- higher thresholds
- high accuracy

Underlying mechanisms:
- Additional information
  - expectations
  - accumulation of sensory data over time
  - more coding dimensions
  - increased resolution due to scanning
- close-loop operation
Passive and active touch

Passive touch
- low thresholds
- poor accuracy

Active touch
- higher thresholds
- high accuracy

Underlying active mechanisms:
- Additional information
  - expectations
  - accumulation of sensory data over time
  - more coding dimensions
  - increased resolution due to scanning
- close-loop operation
Sensory encoding:

What receptors tell the brain

Sensory organs consist of receptor arrays:

**somatosensation**

- Finger pad

**audition**

- Cochlea

**vision**

- Retina
Sensory encoding: Sensory organs consist of **receptor arrays**:

- **somatosensation**
  - *Finger pad* (~200 μm)
- **audition**
  - *cochlea* (10 μm)
- **vision**
  - *retina* (10 μm)

Spatial organization => Spatial coding (“**which** receptors are activated”)
Spatial coding metaphors

one could think of:

the eye as a camera the skin as a carbon paper

light is

Imprinted on the retina via photo-receptors
How neurons encode external events in space?
The “labeled-line code”.

a binary code, reporting yes/no about the occurrence of a given event.

Every neuron has a “label”
**Reading out** the labeled line code

**Reading algorithm:** a location X is pressed if and only if neuron x fires

On what condition will this algorithm be valid?

(X) \( \rightarrow \) Neuron x fires if and only if X is pressed

Is this assumption valid?

1. The problem of background activity
2. The “problem” of sensor movements

receptors are sensitive to changes

Thus

If both objects and sensors are passive (stationary), nothing will be sensed
Active Sensing is a strategy that induces changes in sensed signals.

In mammals, active sensing is typically implemented by sensor movements:
Drives for sensor movements

1. The world is not flashing

2. sensory sheets are not uniform
Fovea => macro movements of the sensory organ

receptor sensitivity => micro movements of the sensory organ
Sensor motion is required for

- Foveation
- Sensing stationary environment

- Without sensor motion sensation is limited to moving or flashing objects
How sensor motion constrains sensory coding?
Eye movements during fixation

backward!
Eye movements during fixation
Sensory organs consist of receptor arrays:

- **somatosensation**: Finger pad (~200 µm)
- **audition**: Cochlea (10 µm)
- **vision**: Retina (10 µm)

**Sensory encoding**: What receptors tell the brain

- **Spatial organization** => **Spatial coding**
  ("which receptors are activated")

- **Movements** => **Temporal coding**
  ("when are receptors activated")
Body-world interface

Underneath the skin

Selection process - ?

whisker
Touching

The End