Touching

Ehud Ahissar
Touching

- Body-world interface
- Mechanisms of sensory processing (across senses)
- Motor-sensory coupling
- Passive vs active touch
- Neuronal coding
- Morphological coding
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
### The Major Classes of Somatic Sensory Receptors

<table>
<thead>
<tr>
<th>Receptor type</th>
<th>Anatomical characteristics</th>
<th>Associated axons(^a) (and diameters)</th>
<th>Axonal conduction velocities</th>
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<th>Function</th>
<th>Rate of adaptation</th>
<th>Threshold of activation</th>
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<tbody>
<tr>
<td>Free nerve endings</td>
<td>Minimally specialized nerve endings</td>
<td>A(\delta)</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>Meissner’s corpuscles</td>
<td>Encapsulated; between dermal papillae</td>
<td>A(\beta) 6–12 (\mu)m</td>
<td>.5 – 2 m/s</td>
<td>Principally glabrous skin</td>
<td>Touch, pressure (dynamic)</td>
<td>Rapid</td>
<td>Low</td>
</tr>
<tr>
<td>Pacinian corpuscles</td>
<td>Encapsulated; onionlike covering</td>
<td>A(\beta) 6–12 (\mu)m</td>
<td>30 – 70 m/s</td>
<td>Subcutaneous tissue, interosseous membranes, fascia</td>
<td>Deep pressure, vibration (dynamic)</td>
<td>Rapid</td>
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</tr>
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<td>Merkel’s disks</td>
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<td></td>
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</tr>
<tr>
<td>Muscle spindles</td>
<td>Highly specialized (see Figure 8.5 and Chapter 15)</td>
<td>Ia and II</td>
<td>80 – 120 m/s</td>
<td>Muscles</td>
<td>Muscle length</td>
<td>Both slow and rapid</td>
<td>Low</td>
</tr>
<tr>
<td>Golgi tendon organs</td>
<td>Highly specialized (see Chapter 15)</td>
<td>Ib</td>
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<tr>
<td>Joint receptors</td>
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<td></td>
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<td>Joint position</td>
<td>Rapid</td>
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\(^a\)In the 1920s and 1930s, there was a virtual cottage industry classifying axons according to their conduction velocity. Three main categories were discerned, called
Muscle spindle

Golgi tendon
Proprioceptive receptor types

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

Sensitive to:
- muscle length change
- muscle tension
- Joint angle
Body-world interface

Underneath the skin

**TABLE 8.1**
The Major Classes of Somatic Sensory Receptors

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**Mechano-receptors (ex-afferents)**

**Proprio-(re)ceptors (re-afferents)**

Why does the brain need 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*
Evolutionary specialization

Selection process - ?

Morphological processing
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 $\text{Ca}^{2+}$.
Figure 21-2 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.
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

Meissner’s corpuscle  Merkel cells  Pacinian corpuscle  Ruffini endings

RA  SA  PC

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 (by JND)
• Break ?
Signal conduction
Sensory signal conduction

Pseudo-unipolar neurons
Sensory signal conduction
Table 8.1: The Major Classes of Somatic Sensory Receptors

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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...
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

Accurate spatial organization

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

Relative size reflects innervation density ontogenetically

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Normal whisker map

Hebbian forms of plasticity

All whiskers intact

All but D1 removed

All but D1 and D2 removed

Non-Hebbian forms of plasticity

Enriched environment

Over-stimulation of D1

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Daniel E. Feldman, and Michael Brecht Science 2005;310:810-815
Motor signal conduction

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

The cortico-bulbar tract
Face, head, neck
Motor signal conduction

The cortico-spinal tract (not reversal of the afferent pathway)
Motor signal conduction

The cortico-spinal tract

Cortico-centric view
Vs
Evolution-based view

1st synapse
Sensory signal conduction

The vibrissal system
Sensory signal conduction

The vibrissal system

whisker

Meisner
Merkel
Ruffini
Lanceolate
free endings
More on this in the Active-Sensing lecture
Common mechanisms of sensory processing
Rich muscular system
Receptor types

whisker

Meisner
Merkel
Ruffini
Lanceolate
free endings

eye

finger

rad
cone

R G B

RAI  SAI  RAIi  SAIi

RA  SA  PC  Ruffini endings
Receptors mix in clusters

eye

whisker

finger

Merkel cells
Idiosyncratic clustering

Human cone mosaic

Subject JW, temporal
Subject JW, nasal
Subject AN, nasal

one degree eccentricity

Do they see the same world?

http://www.cns.nyu.edu/~david/courses/perception/lecturenotes/retina/retina.html
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

why?
Email me your speculations…
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
- Bipolar cells
- Ganglion cells
- Brainstem cells

Whisker
- Receptors
- Ganglion cells

Drive for clustering?
Efficient coding

(by coding changes only)

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**
- K
- P
- M
- W
- X
- Y

**Frequency (Hz)**
- 0.5
- 2
- 8
- 32

**Whisker**

**Finger**
- SA
- RA
- PC

**Frequency (Hz)**
- 1
- 10
- 100
- 1000
Figure 22-6B 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.)
• Break ?
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 => Probing the world
- Probing the world => 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

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

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

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

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#### 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

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**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: Sensory organs consist of receptor arrays:

- **Somatosensory**: ~200 µm
  - Finger pad

- **Audition**: 10 µm
  - Cochlea

- **Vision**: 10 µm
  - Retina

What receptors tell the brain...
Sensory encoding:

Sensory organs consist of receptor arrays:

- **somatosensation**
  - *Finger pad*
  - $\sim 200 \mu m$

- **audition**
  - *cochlea*
  - 10 $\mu m$

- **vision**
  - *retina*
  - 10 $\mu m$

**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.*

<table>
<thead>
<tr>
<th>events</th>
<th>neurons</th>
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<tr>
<td>A</td>
<td>a</td>
</tr>
<tr>
<td>B</td>
<td>b</td>
</tr>
<tr>
<td>C</td>
<td>c</td>
</tr>
<tr>
<td>D</td>
<td>d</td>
</tr>
<tr>
<td>E</td>
<td>e</td>
</tr>
<tr>
<td>F</td>
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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?

$$(X) \iff x$$  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

Thus

Sensors must move in order to sense stationary objects
How sensor motion constrains sensory coding?
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) \(\xrightarrow{=}\) x \hspace{1cm} \text{Neuron x fires if and only if X is pressed}

Is this assumption valid?

2. The “problem” of sensor motion
Sensory organs consist of receptor arrays:

- **Somatosensation**: Finger pad (~50 µm)
- **Audition**: Cochlea (10 µm)
- **Vision**: Retina (10 µm)

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

**Movements** => **Temporal coding** ("when are receptors activated")
Evolutionary specialization

Selection process - ?

Morphological processing
Morphological phase plane

$G_\kappa - \theta_a$ phase plane

$B_\kappa - \theta_p$ phase plane

Morphological processing

Motor-sensory phase plane
Morphological phase plane

Gκ - θα phase plane

Sensory

Global curvature (Gκp, m⁻¹)

Angle absorption (θa, deg)

Motor

Base curvature (Bκp, m⁻¹)

Angle protraction (θp, deg)

Organism-environment attractors

More on this in the Active-Sensing lecture
Touching

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Touching

The End