Somatosensory modalities

• The somatosensory system codes five major sensory modalities:
  1. Discriminative touch
  2. Proprioception (body position and motion)
  3. Nociception (pain and itch)
  4. Temperature
  5. Visceral function

• Senses external objects contacting the body
• Provides self-awareness of our bodies
Dorsal root ganglion neurons mediate somatic sensation

- Detect mechanical, thermal or chemical signals
- Transduce stimulus energy into electrical signals
- Encode depolarization as a spike train
- Transmit encoded information to spinal cord or brainstem
Common properties of DRG neurons

- Sensory transduction occurs in the nerve endings, not in the DRG or trigeminal cell bodies.
- Sensory modality determined by the receptor proteins expressed in the nerve terminals, and anatomical structures enclosing these endings.
- DRGs often express receptor proteins in their somas allowing transduction mechanisms to be studied *in vitro*.
Dorsal root ganglion neurons differ in:

- Cell body *size*
- *Morphology* and sensitivity of nerve terminal
- *Sensations* mediated
- Body *region* innervated
- Axon *conduction velocity* and fiber diameter
- Spinal and brainstem *termination sites*
- Ascending *pathways* to higher brain centers
- Sensitivity to *neurotrophins* during development
DRGs develop from neural crest cells
DRGs express neurotrophin receptors

- trkA: free nerve endings (pain and temperature)
- trkB: mechanoreceptors in skin, muscle, joints
- trkC: muscle spindles and tendon organs
Fiber diameter profile for different modalities

Cutaneous nerve

Muscle nerve

<table>
<thead>
<tr>
<th>Axon diameter (µm)</th>
<th>Conduction velocity (m/s)</th>
<th>1</th>
<th>5</th>
<th>12</th>
<th>20</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>30</td>
<td>6</td>
<td>30</td>
<td>72</td>
<td>120</td>
</tr>
</tbody>
</table>
Compound action potential reflects whole nerve activity
Conduction velocity classification

<table>
<thead>
<tr>
<th>Alphabet</th>
<th>Velocity (m/s)</th>
<th>Description</th>
</tr>
</thead>
</table>
| \( A^\alpha \) | 72–120 | \( \alpha \) motor neurons to muscle  
Group I muscle sensory  
Cutaneous mechanoreceptors |
| \( A^\beta \) | 30–96 | Cutaneous mechanoreceptors  
Secondary muscle receptors |
| \( A^\gamma \) | 12–48 | \( \gamma \) motor neurons |
| \( A^\delta \) | 4–30 | Group III sensory nerves |
| B | 3–15 | Autonomic preganglionic |
| C | 0.5–2 | Unmyelinated sensory nerves  
Autonomic postganglionic |
The Sense of Touch

Jusepe de Ribera

C. 1615-16

Norton Simon Museum

Pasadena CA
The sense of touch

• Touch is the special sense by which contact with the body is perceived in the conscious mind

• Touch allows us to recognize objects held in the hand and use them as tools

• Touch enables the blind to perceive the three dimensional form of objects, and to read Braille with their fingers

• Touch guides skilled hand movements of the surgeon, the sculptor, the musician, the pitcher, and the chef

• Touch is mediated by mechanoreceptors in the skin
Properties coded by the sense of touch

- Spatial dimensions (size, shape, weight)
- Surface compliance (hard or soft)
- Surface texture (smooth or rough, regular or irregular)
- Temperature (hot, warm, cool, cold)
- Motion (active or passive, velocity, direction)
- Cognitive function (object recognition)
The sense of touch is mediated by skin indentation

LaMotte RH, Srinivasan MA. J Neurophysiol 1987
Mechanoreceptors detect tissue deformation

A Direct activation through lipid tension

B Direct activation through structural proteins

C Indirect action through membrane structural proteins

Lin S-Y, Corey DP. 
Curr Opin Neurobiol  2005
Multiple receptor types in the skin
Scanning EM of fingerprint ridges in glabrous skin
Four types of mechanoreceptors in glabrous skin

- Meissner’s corpuscles (RA1)
- Merkel cells (SA1)
- Ruffini endings (SA2)
- Pacinian corpuscles (RA2)
Touch receptors in the glabrous skin

A. Meissner corpuscles and Merkel cell receptors

B. Pacinian corpuscle

- RA1 fibre
- SA1 fibre
- Pacinian corpuscle capsule
- RA2 fibre

Papillary ridge

50 μm
SA1 fibers innervate clusters of Merkel cells
Receptor density in glabrous skin

• **Fingertip**
  - RA = 141 /cm²
  - PC = 21 /cm²
  - SA I = 70 /cm²
  - SA II = 9 /cm²

• **Palm**
  - RA = 25 /cm²
  - PC = 9 /cm²
  - SA I = 8 /cm²
  - SA II = 16 /cm²

Johansson RS, Vallbo ÅB. *J Physiol* 1979
Why have multiple touch receptors?

- Specialize for dynamic and static sensitivity
  - Motion sensors (RA1 and RA2)
  - Pressure sensors (SA1 and SA2)
- Different sensory **thresholds** extend range of intensities encoded (RA2<RA1<SA1<SA2)
- Different **receptive field** areas encode fine (RA1 and SA1) and broad (RA2 and SA2) spatial information
Phasic and tonic responses to touch

A. Modality
- Meissner’s corpuscle
- Merkel cells
- Pacinian corpuscle
- Ruffini endings

B. Location
- Receptive field

C. Intensity and time course
- Neural spike train
- Stimulus: RA1, SA1, RA2, SA2
Slow and rapid adaptation of touch receptors

Neural firing rate codes stimulus intensity

Mountcastle VB, et al. 1966
Merkel cells (SA1 fibers) signal shape and pressure

Srinivasan MA, LaMotte RH. 1991
Fingertip SA1 responses to object curvature

Goodwin AW, Wheat HE. *Ann Rev Neurosci* 2004
Merkel cells are used to read Braille dots

4.0 mm dot spacing         2.8 mm dot spacing         1.7 mm dot spacing
Ruffini endings (SA2 fibers) respond to skin stretch

Edin BB, Abbs JH. *J Neurophysiol* 1991
Hand posture and skin stretch codes object shape

Hsiao SS (2008)
Slowly-Adapting Receptor Function

• **Merkel** cell (SA1 fiber):
  – Pressure, object weight
  – Precision grip force
  – Small object shape discrimination
  – Braille reading and texture discrimination

• **Ruffini** ending (SA2 fiber):
  – Whole hand grip
  – Hand posture and skin stretch
  – Large object shape discrimination
Meissner’s corpuscles sense hand motion on surfaces.
Meissner’s corpuscles detect motion of a small dot

LaMotte RH, Whitehouse J.
J Neurophysiol 1986
RA spike trains code motion and vibration
RA1 and RA2 fibers detect low and high frequencies

RA1 40 Hz
(Meissner)

RA2 200 Hz
(Pacinian)
Tuning curves quantify vibratory threshold

RA1 fibers

Vibration thresholds are frequency dependent

1. Human perceptual thresholds

2. Neural thresholds

Rapidly-Adapting Receptor Function

• **Meissner’s corpuscle (RA1):**
  – Motion
  – Texture
  – Edges
  – Flutter (low-frequency vibration)

• **Pacinian corpuscle (RA2):**
  – Vibration (tool use)
  – Contact and release
Threshold diversity extends dynamic range
Touch receptor thresholds differ

Johansson RS et al. *Brain Res* 1980
Receptive fields determine spatial properties

- The *receptive field* of a sensory neuron defines the spatial location where it responds to stimuli of the appropriate energy.

- Spatial position of a receptor within the sense organ localizes the stimulus in space.

- Where we are touched is coded by which specific touch fibers are activated.
Nerve branch patterns define receptive fields
Receptive fields of touch receptors differ in size

A Slowly adapting mechanoreceptors
- Merkel cells (SA1)
- Ruffini endings (SA2)

B Rapidly adapting mechanoreceptors
- Meissner's corpuscles (RA1)
- Pacinian corpuscles (RA2)

C Receptive field sensitivity
Receptive and perceptive fields coincide

A = RA1 fiber:
(Tap or vibration)

B, C = SA1 fiber:
(Pressure)

Two-point thresholds are smallest on the hand
Receptive field size determines spatial resolution
Two-point thresholds correlate with receptive field size

Weinstein S. *The Skin Senses* 1968
Spatial Resolution ... and Receptive Fields

20 x 20 pixel  
60 x 60 pixel  
400 x 400 pixel
Two-point discrimination threshold

- Reflects receptive field diameters of Meissner’s corpuscle (RA1) and Merkel cell (SA1) afferents
- Receptive field diameter correlates inversely with innervation density
- Spatial acuity highest on densely innervated body regions (fingertips, lips, toes) that are used to touch external objects
**Touch receptor response properties**

<table>
<thead>
<tr>
<th>ADAPTATION</th>
<th>RECEPTIVE FIELDS</th>
<th>INNERVATION DENSITY</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fast, no static response</td>
<td>Small, sharp borders</td>
<td>Increase distally</td>
</tr>
<tr>
<td>FA-I (43%) Meissner</td>
<td>(140; 70 cm(^{-1}))</td>
<td>(40; 36 cm(^{-1}))</td>
</tr>
<tr>
<td>Slow, static response present</td>
<td>Irregular</td>
<td>(24; 9 cm(^{-1}))</td>
</tr>
<tr>
<td>SA-I (25%) Merkel</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mechanical transients &amp; vibration (~40 - 400 Hz)</td>
<td>Directional strain in deep dermal and subdermal tissues</td>
<td>(22; 12 cm(^{-1}))</td>
</tr>
<tr>
<td>FA-II (13%) Pacini &amp; Pacini-like</td>
<td></td>
<td>(10; 16 cm(^{-1}))</td>
</tr>
<tr>
<td>SA-II (19%) Ruffini</td>
<td></td>
<td>(10; 18 cm(^{-1}))</td>
</tr>
</tbody>
</table>

Johansson RS, Flanagan JR. *Nature Rev Neurosci* 2009