Mechanoreceptors

Exteroceptors: touch
  Bacteria
  Paramecium
  Round worms
  Arthropods
    fishing spiders
    cockroaches
  Mammals
    cutaneous mechanosense (touch)
    whiskers

Interoceptors:
  Mammalian osmosensors
  proprioception
    Arthropods
      joint receptors
    Vertebrates
      spindles, GTOs
Bacterial Mechanochannel – Function Unclear

Only cell membrane level forces are needed to pull apart protein subunits.

Subunits tugged apart $\rightarrow$ ionic current flows.

Patch clamp results
Paramecium motor control (cilia) via mechanosensor
Power and recovery strokes

Sequential power & recovery strokes – paramecium swims in a straight line.

Uncoordinated strokes, or stall in recovery stroke – paramecium tumbles.
Touch anterior part of paramecium:

  depolarization and local influx of calcium
tumble
takes off in a different direction

Touch posterior part of paramecium:

  efflux of potassium and hyperpolarization of cell
increase forward velocity (fewer tumbles/unit time)
C. elegans
C. elegans cuticule mechanosensors

Internal structural anchor needed for this to work! (next slide)
C. elegans.

20 – 50 micronewtons of force will cause response.
Arthropod touch sensors.

Basic plan - sensory dendrite extends to a portion of the cuticle that is deformed by touch.
Spider touch-sensitive hairs on cuticle.

X.S. (Smith 8.7)
Spider trichobothria are the most sensitive of this style of mechanosensor organ.

Hair length determines optimal frequency response.
Interesting uses of arthropod touch sensors

- Fishing spiders
- Beetle water wave communication
- Cockroach wind detectors
Fishing Spiders and Prey Detection

- Genus *Dolomedes*
- Approximately 100 species worldwide
- Large spiders that can run on the surface of water and even dive or swim under water

**Habitat**
- Littoral zones of lakes, ponds, or in pools of sluggish streams
- Found with its entire body on the water anchored to shore with only a silk thread, or resting on the surface with legs anchored on a leaf or rock near the shore
Fishing spider anchored to vegetation by silk thread
Wind vs Prey Waves

- Amplitudes of prey generated waves are in the range 2.2 ± 0.4 μm to 80.6 ± 17.9 μm.

- Very small wind-induced waves are 10X greater than the largest prey-generated waves. (Lang 1980)

- So how detect a much smaller signal in the presence of much larger noise?
Amplitudes of prey verses wind generated waves

Spiders prefer locations where wind generated waves are smaller, but this turns out to be not so critical.

**Fig. 4.** Top: Mean pp-wave amplitudes measured at locations A–E (X-axis) under similar wind conditions (6.1–12.1 km/h). The upper and lower ends of the rectangle correspond to the minimal and maximal values measured. The upper amplitude limit of prey waves (Lang 1980) is given by the horizontal broken line. Bottom: Number of spiders per meter of shoreline at locations A, B, C, D and E. The vertical lines reflect the SD of the results.
The spectral composition of prey-generated and wind-generated waves is different!

- Peak energy of wind-produced waves is 1.4 ± 0.56 Hz

- Upper frequency limit (at 60 dB bandwidth) of wave values is 8.2 ± 1.2 Hz, and no frequency components above 10 Hz found

- So wind-generated waves have only low-frequency components.
Typical power spectra of wind verses prey generated waves: Only prey-generated waves include higher frequency components!

Thus prey waves are detected on the basis of their high frequency components relative to wind generated waves. (Bleckmann and Barth 1984)

Fig. 5. Typical power spectra of wind-generated waves at locations B, C, and D. For comparison, the power spectrum of waves generated in the laboratory by a fly (*Calliphora vicina*) struggling at the water surface (measured at 5–7 cm distance) is shown. In all cases the greatest power value is placed equal to 0 dB.
Water striders use species-specific water vibrations for territorial communication.

Some insects spend most of their lives on the surfaces of ponds, lakes and rivers. The water strider, *Gerris remigis*, rapidly vibrates its legs producing surface waves to attract mates or to repel rival males, thus declaring their territorial rights. The vibratory pattern of these ripple signals is stereotyped and species-specific. The vibration-sensitive receptors in the leg joints sense not only the ripple signals of other water striders, but vibrations coming from potential prey that fall into the water.

RIPPLE SIGNALS FROM THREE WATER STRIDER SPECIES
The vibrations of the insect were detected by a nearby floating transducer. The output of the transducer was fed into a recording galvanometer. (From Wilcox, unpublished.)
Cockroach escape behavior (predator detection) triggered by wind gust of predator

The roach’s own walking movements and random wind gusts create larger amplitude air movements, but the acceleration of air is never as great as that from a toad strike.
Very fine, long hairs provide exceptional sensitivity

**FIGURE 16.** Scanning electron micrograph of the cerci of a newly hatched cockroach *Periplaneta americana*. Only two wind-receptive hairs like those found in the adult are present on each cercus (arrows). Calibration bar = 200 mm. (From Dagan and Volman, 1982.)
Air-detector hairs organized to provide directional information

**FIGURE 8.** Organization of wind-receptive hairs on the cerci. A. Top: Underside of four of the 19 segments from an adult cecum. Each circle shows the position of a wind-receptive hair. Columns a, d, f, h, etc. run along most of the cecum length. Double-headed arrows show the two directions of maximal mechanical pliancy of each hair. Bottom: A single segment from each cecum. The single-headed arrows show the optimal wind direction for each hair. All hairs of a given column have the same optimal wind direction. B. A single wind-receptive hair, drawn to scale. At the hair mark, three-fourths of the actual length of the hair has been omitted. (A from “The Escape System of the Cockroach” by J. Camhi. Copyright 1989 by Scientific American, Inc. All rights reserved.)

**FIGURE 10.** Directional response of a single wind-receptor cell. Constant wind puffs were delivered to the cockroach from different angles within the horizontal plane. The mean number of action potentials evoked from each angle is plotted. Representative recordings for each angle tested are also shown. This cell responded best to wind from the cockroach's left rear quadrant. Wind from the opposite quadrant (right front) evoked no action potentials. Though not shown here, the latter direction also inhibited any spontaneously occurring action potentials in the cell. (After Westin, 1979.)
Mammalian touch
Cutaneous mechanoreceptors in mammalian skin

Figure 5.13
Touch receptors in the glabrous skin of a primate finger pad
Glabrous (hairless) skin of primate contains four types of touch receptors: Meissner corpuscles, Merkel disks, Ruffini endings, and Pacinian corpuscles. (After Darian-Smith, 1984a.)
A diversity of receptor types for a more complete picture of surface texture:

- **Merkel cells**: touch, pressure, slow adaptation. 10-20 Merkel cells synapse onto one afferent. Respond to sudden displacement of skin as in stroking.

- **Ruffini corpuscles**: touch, pressure. Slow adaptation. Respond to steady displacement.

- **Hair follicle receptors**: hair displacement, rapid adaptation

- **Meissner corpuscles**: touch, vibration, rapid adaptation (velocity detection) (= Krause’s end bulbs in non-primate mammals)

- **Paccinian corpuscles**: touch, vibration, very fast adaptation (acceleration detection)
Adaptation rates determine sensitivity to different kinds of stimuli.

**FIGURE 25.3** Response of slowly adapting (SA) and rapidly adapting (RA) peripheral afferents to a sustained indentation of the skin surface. SA afferents (A) respond with an early peak in activity and a lowered but sustained discharge that persists as long as the indentation continues (C). In contrast, RA afferents (B) respond to the onset and termination of the stimulus and not to the continued indentation.
Accessory structure provides slip, so Paccinian corpuscle is effectively an acceleration detector.

**FIGURE 17.7 Adaptation in a Pacinian Corpuscle.**
(A) A pressure step applied to the body of the corpuscle (lower trace) produces a rapidly adapting receptor potential (upper trace), as a result of a transient wave of deformation that travels through the capsule to the nerve terminal. A similar response occurs on removal of the pulse. (B) After removal of the capsule layers, pressure applied to the nerve terminal produces a receptor potential that lasts for the duration of the pulse. (After Loewenstein and Mendelson, 1965.)
<table>
<thead>
<tr>
<th><strong>Superficial</strong></th>
<th><strong>Deep</strong></th>
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<tr>
<td>Merkel important for form and texture determination. High density of Merkel at fingertips (50/mm$^2$… but dropping to 10/mm$^2$ by age 50!)</td>
<td>Paccinian corp. can respond up to 1000Hz, but best response is between 200 and 400 Hz. Extraordinary sensitivity of 10 nm to 200 Hz vibration!!!!</td>
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<tr>
<td></td>
<td>Meissner corp. a slower vibration detector: 10 – 200 Hz. Meissner responsible for sensation of objects moving across the skin, and adjustment of grip force if an object starts to slip across skin.</td>
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Uneven distribution of cutaneous mechano-receptors on hand surface.

FIGURE 25.5  Map of receptive fields on the human hand displayed by the various receptor types. Receptive fields vary in overall size from punctate zones displayed by RA and SAI afferent to broad regions of the palm or entire fingers with Pacinians. SAlI afferents respond to stimuli that produce skin stretch and are often selective for the direction of stretch.
The combination of receptor types leads to some remarkable abilities...

High spatial and temporal resolution allow some people to read Braille at 100 characters per minute!

FIGURE 25.2  Results of psychophysical experiment illustrating that the threshold for tactile acuity on the finger pad is about 1 mm. In the experiments, subjects were required to correctly identify the presence of gaps that varied in width, the orientation of gratings that varied in spacing, or the letter embossed onto an otherwise smooth surface. An increase in stimulus dimension (width of the gap, spacing between gratings, or height of the letter) produced an increase in psychophysical performance in all three tasks.
The barrel cortex of an animal with whiskers.

One hair is one vibrissa, many vibrissae make up the set of whiskers. One vibrissa activates neurons in one barrel.
The vibrissae are position mapped onto the cortex.
Mechanical (&electrical) signal concepts relative to how vibrissae work…

- Mechanically resonant systems
  - Driving energy, damping
  - examples
- Types of filters
  - Frequency, time
  - Low-pass, high-pass, bandpass
  - Resonance (electrical or mechanical or chemical) can be used to make filters
Response of a mechanically resonant system to different driving frequencies. Each curve is a different damping factor.

Below the resonance point the system is "stiffness dominated".

Above the resonance point the system is "mass dominated".
Celebrated resonance phenomena

- Tacoma Narrows Bridge (lasted 4 months after dedication in 1940)
- Bay of Fundi (Nova Scotia) – water transit time is similar to tide cycle (12 hours)
- Early 1900’s SF-size buildings had $F_n$ close to earthquake shock intervals
Back to vibrissae and whisking...

- Quiescent animal: best response is “low-pass” (< 1 Hz), broad point spread in cortex.
- Whisking animal: best response 4-12 Hz (rats peak at 8 Hz), narrow point spread in cortex.
- Due to:
  - dynamic filtering using feedback loops (in the ventral posterior medial nucleus of the thalamus).
  - 2-5 Hz phasic spike rate (fast adaptation) – quiescent activation
  - Total spike rate over a whisking episode greater for higher frequencies of stimulation (integration time constant changes)
  - Time-locked action potentials (phase locking) or fidelity of spike timing better during whisking.
Active whisking generates mechanical resonance which sharpens the perception of the mechanical disturbance.

Whiskers of different lengths have different resonance points.

As whiskers travel across surface, each whisker “ping”s at its resonant frequency.

The amplitude of the driven oscillation for a given whisker is a function of surface texture.
Different whisker lengths lead to resonant peaks for different very high rates of vibration (100’s of Hz).
Aquatic mammals have more vibrissae than terrestrial mammals, and more innervation per vibrissa
- Norway rat: 100-150 axons/vibrissa
- Australian water rat: 500 axons/vibrissa
- Sea Lions: 1500 axons/vibrissa
- Manatees: ? axons/vib, but 600 vibrissae just on prehensile lips

Marine mammals that dive in cold waters allow their skin surface to cool to conserve thermal energy (peripheral vasoconstriction) with the notable exception of the whisker regions that are maintained at full body temperature. This allows maximum performance when searching for food.

Whiskers are also found on marine mammals
Guido Dehnhardt: train seals to track a toy submarine! The seal wears a blindfold and ear muffs, so can only use whiskers for detection. In 256/326 attempts the seal found the sub. The size of the wake trackable is on the order of $10^{-6}$ m.
Whiskers of marine mammals also can discriminate surface textures.

Marine mammals can also use their whiskers to detect water flow patterns.

next....
Hydrodynamic flow field around three different fish, measured using scanning particle image velocimetry.

Fish swim from left to right across the panel (2 trials per fish). The top most raster of each panel is the pass of the fish, and subsequent rasters are increasing time following the pass of the fish.

Note that at 60 s after the fish swims there is still a hydrodynamic signature that is distinct for each species.
Interoceptors
Mammalian Hypothalamic Osmosensors

Paraventricular & supraoptic nuclei cells most sensitive to volume change.
Magnocellular cell cation channels sensitive to lipid bilayer stretch (stretch inactivated).

Stretch occurs because of volume change.
Interoceptors: Kinesthesia/Proprioception – mechanosense related to body/joint position and movement. (Smith Chapter 7).

Arthropods

spiders
insects

Vertebrates
Slit sensilla of spiders

Joint position detectors relative to the spiders movement, but also can act as exteroceptors.
Neck Sense Organs in Insects

- Detect head posture.
  - The head is positioned using visual input from the eyes.
  - If the head is twisted from the body, these hair sensilla will be bent and the body will be adjusted.

Fig. 6. Prosternal organs during head roll. Ventral aspect of the prosternal organs after a mechanically imposed head roll to the left (HR = -45°). The left contact sclerite (right side of the picture) is depressed over the left prosternal organ, bending more mechanosensory hairs than in the neutral position of the head. In contrast, the right contact sclerite is lifted off the right prosternal organ and the previously bent hairs return to their resting position. KS contact sclerite, CS cervical sclerite
Insect Campaniform Sensillum

Movement of the cuticle distorts the dome and mechanically activates the dendrites in the dendritic sheath (DS).
A scolopodium, the sensory apparatus associated with insect chordotonal organs
Vertebrate proprioception
Amount of stretch detected by spindle → feedback to maintain position.
(C) Descending facilitation and inhibition

α Motor neuron

Muscle

Load

Disturbance (addition of liquid to glass)

Force required to hold glass

Length change in muscle fiber

Increase spindle afferent discharge

Spindle receptor

NEUROSCIENCE, Fourth Edition, Figure 16.10 (Part 3)
(A) α Motor neuron activation without γ

Stimulate α motor neuron

Stimulate extrafusal muscle fibers

Intrafusal muscle fibers

Spindle afferent

Record

Contraction unloads spindle

Afferent activity

Muscle force

Contraction

Would lead to jerky compensation

(B) α Motor neuron activation with γ

Stimulate α motor neuron

Stimulate γ motor neuron

Spindle afferent

Record

Ia response “filled in”

Afferent activity

Muscle force

Contraction

γ activated to keep up with muscle shortening

Constant update/control with no lag (non-jerky)
Feedback for force
STRETCH BUT NO LOAD $\rightarrow$ ↑ spindle, ↓ GTOs
MUSCLE ACTIVELY CONTRACTED

1. Muscle spindles
   - Stimulate \( \alpha \) motor neuron
   - Stimulate \( \alpha \) motor neuron
   - Record spindle afferent
   - Shorten muscle
   - Muscle length
   - Afferent activity

2. Golgi tendon organs
   - Stimulate \( \alpha \) motor neuron
   - Stimulate \( \alpha \) motor neuron
   - Record Golgi tendon organ afferent
   - Shorten muscle
   - Muscle length
   - Afferent activity

Active unloading of spindle (negative stretch) \( \downarrow \) resp.

Incr force = incr. loading \( \uparrow \) ATO response
α MNs are held back from applying too much force by GTO feedback.

Descending control: push hard.
Local control: maybe not the max possible.
Fast reflex to maintain posture (only needed in bipeds) with rapid withdrawal of foot. [Note - antagonist inhibits still in place].

Extend & shift weight/balance to good foot.

TACK (cowie)
Crayfish Stretch Receptors

- **Fig. 4.** Digging behaviour of *Bathynomus doederleini*. Video frames show (A) the start of digging of a burrow, (B) advancing towards the bottom, using the thoracic legs and beating swimmerets, (C) reversing direction by rolling up to leave the burrow and (D) creeping out of the burrow. This animal was 11 cm long.
• **Fig. 5.** (A) Lateral view of the spatial organisation of thoracic and abdominal stretch receptors. Segmental stretch receptors are located on the dorsal side and extend axons that run towards the central nervous system (CNS) via nerve 3 (N3). Note that, as in crayfish, the axons of the abdominal stretch receptors project to the eighth thoracic ganglion. (B) The CNS and central projection of the axon of TSR-2. The CNS is depicted dorsally, and the CNS posterior to TG3 is not drawn, and the oesophageal connectives are interrupted. Ascending and descending central projections of the axon of TSR-2 are shown (*camera lucida* drawing). This was revealed by electrophoretically applying Lucifer Yellow to the centrifugal cut end of N3. (C) Ventral view of the organisation of thoracic stretch receptors. Thoracic stretch receptors are located dorsally and bilaterally. Dendritic branches from the receptor cell of TSR-1 innervate the extensor muscle, while those of TSR-2 entwine with the receptor muscle-like strand, which is exaggerated in size. TSR-3 to TSR-7 have two receptor cells and a single receptor muscle. AS, abdominal segment; ASR, abdominal stretch receptor; TS, thoracic segment; TSR, thoracic stretch receptor; ROS, rostrum; Deutero, deuterocerebrum; Mx, maxillary nerve; Proto, protocerebrum; Trito, tritocerebrum; TG, thoracic ganglion.
Johnston’s Organ

- This sensory organ is located in the pedicle of the antenna (2nd antennal segment).
- Primary function is to sense movement of the flagellum.
- It can be used to detect gravity and flight speed.
- It can also detect courtship air vibrations made by conspecifics.
References

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Hinrichsen RD, Schultz JE
Some references

• Australian Museum on-line 2002
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