Cutaneous mechanoreceptors

A mechanoreceptor is a sensory receptor that responds to mechanical pressure or distortion. The cutaneous mechanoreceptors are classified by function in Tab. 1.

Tab. 1. classification of the cutaneous mechanoreceptors by function.

Mechanoreceptor	Detection	Adaptation rate	Specialization	Location	Encapsulation	Responsiveness to continuous deformation (property related to encapsulation)
Pacinian corpuscles	- rapid vibratory pressure and touch (max sensitivity at about 250 Hz)	rapid	yes	deep skin	yes	no
Meissner's corpuscles	- light touch - changes in texture - relatively slow vibrations (up to 50 Hz)	rapid	yes	superficial skin	yes	no
Merkel's discs	- touch - pressure - changes in texture. Respond from steady state to low frequencies (up to 15 Hz)	slow	yes	superficial skin	no	yes
Ruffini endings	- continuous tension	slow	yes	deep skin	no	yes
Free nerve endings	- touch - pressure - stretching and also - temperature - pain	different types have different rate	no	wide distribution	no	yes

Mechanoreceptors are primary neurons or nerve endings that respond to mechanical stimuli by firing action potentials. When a mechanoreceptor receives a stimulus, it begins to fire action potentials at an elevated frequency (the stronger the stimulus, the higher the frequency).
Cutaneous mechanoreceptors have different function (see tab. 1) and location (see tab. 1 and Fig. 1).
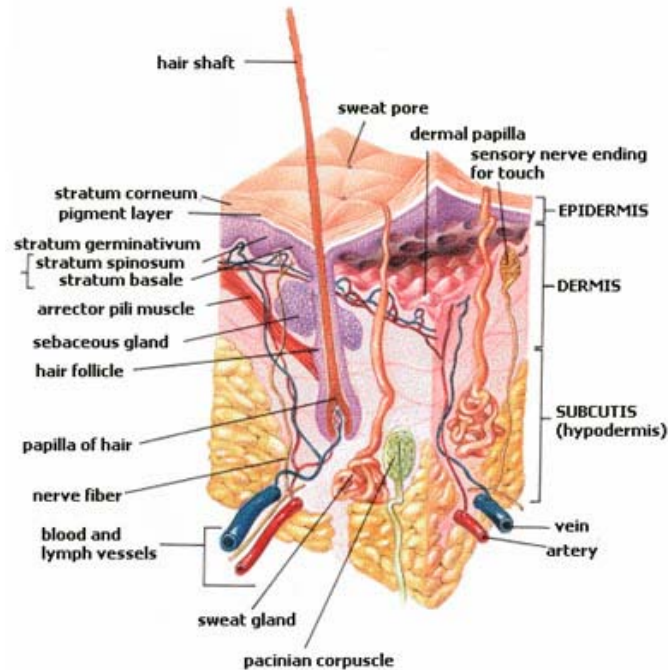

Fig. 1. Sectional view of the skin.

They can also be classified according to their rates of adaptation. In fact, the cell will soon "adapt" to a constant or static stimulus, and the pulses will subside to a normal rate. Receptors that adapt quickly (i.e. quickly return to a normal pulse rate) are referred to as "phasic". Those receptors that are slow to return to their normal firing rate are called "tonic". Phasic mechanoreceptors are useful in sensing such things as texture or vibrations, whereas tonic receptors are useful for temperature and proprioception among others.

Two types of mechanoreceptors (Pacinian and Meissner's corpuscles) are encapsulated, while all of the others are not (Fig. 2).
This has implications for the receptor sensitivity to continuous (steady-state) deformation. In fact, encapsulated receptors are covered by a capsule that consists of lamellae composed of fibrous connective tissue, separated by gelatinous material. The center of the capsule hosts a single afferent unmyelinated nerve ending. Upon deformation, the gelatinous constitutive material of the capsule re-arranges itself, by tending to a re-distribution of the deformation over the whole receptor. This makes the encapsulated receptors less sensitive to continuous (steady-state) deformation.
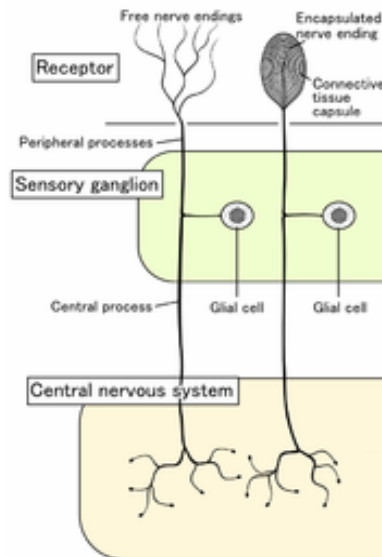
Fig. 2. Schematization of an encapsulated nerve ending as compared to a free nerve ending.

The following sections provide a brief overview on the cutaneous mechanoreceptors.

The Pacinian corpuscle

The Pacinian corpuscle (or lamellar corpuscle) is a pressure receptor located relatively deep under the skin (about 2 mm), and also in various internal organs.
In the skin it detects rapid vibratory pressure and touch, with optimal sensitivity at 250 Hz.

Under the microscope, it resembles an onion (see Fig. 3). It is a capsule 0.5-1 mm long and 0.3-0.7 mm thick and consists of several concentric layers. The center of the capsule includes the core, where the unmyelinated terminal part of the afferent neuron is located.
In particular, the capsule consists of lamellae composed of fibrous connective tissue and fibroblasts, separated by gelatinous material. The lamellae are very thin, flat, modified Schwann cells. In the center of the corpuscle is the inner bulb, a fluid-filled cavity with a single afferent unmyelinated nerve ending.
The first node of Ranvier is also located inside the core. Several mitochondria exist in the corpuscle, indicative of high energy production.
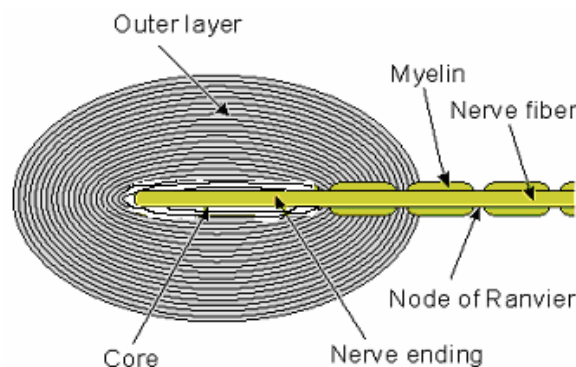

Fig. 3. The Pacinian corpuscle consists of a myelinated sensory neuron whose terminal portion is unmyelinated. The unmyelinated nerve ending and the first node lie within a connective tissue capsule, as shown.

Deforming the corpuscle creates a generator potential in the sensory neuron arising within it. This is a graded response: the greater the deformation, the greater the generator potential. If the generator potential reaches threshold, a volley of action potentials (nerve impulses) are triggered at the first node of Ranvier of the sensory neuron.

Once threshold is reached, the magnitude of the stimulus is encoded in the frequency of impulses generated in the neuron. So the more massive or rapid the deformation of a single corpuscle, the higher the frequency of nerve impulses generated in its neuron.

The *generator voltage* has properties similar to those of the excitatory postsynaptic voltage. The generator voltage is a graded response whereby a weak stimulus generates a low generator voltage whereas a strong stimulus generates a large generator voltage.

The ionic flow mechanism underlying the generator (receptor) voltage is the same as that for the excitatory postsynaptic voltage. Thus deformation of the Pacinian corpuscle increases both the sodium and potassium conductances such that their ratio (P_{Na}/P_K) increases and depolarization of the membrane potential results. As a result, the following behavior is observed:

1. Small *(electrotonic)* currents flow from the depolarized unmyelinated region of the axon to the nodes of Ranvier.
2. On the unmyelinated membrane, local graded generator voltages are produced independently at separate sites.
3. The aforementioned separate receptor voltages are summed in the first node of Ranvier.
4. The summed receptor voltages, which exceed threshold at the first node of Ranvier, generate an action impulse. This is evidence of *spatial summation*, and is similar to the same phenomenon observed in the excitatory postsynaptic potential.

Fig. 4 shows a simulation of the temporal evolution of the membrane potential of a Pacinian corpuscle stimulated by a sinusoidal pressure. The simulation results from a simplified model of the mechanoreceptor, assuming that the temporal evolution of the sodium channels conductance is a periodic signal.
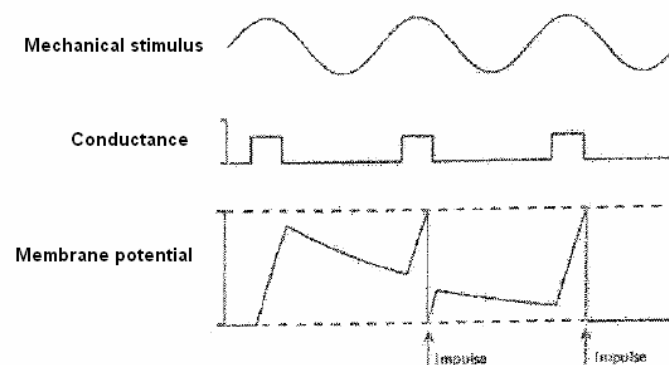

Fig. 4. Simulation of the temporal evolution of the membrane potential of a Pacinian corpuscle stimulated by a sinusoidal pressure. The simulation results from a very simplified model of the mechanoreceptor.

Werner R. Loewenstein (1959) stimulated the Pacinian corpuscle with a piezoelectric crystal and measured the generator voltage (from the unmyelinated terminal axon) and the action potential (from the nodes of Ranvier) with an external electrode. He peeled off the layers of the corpuscle, and even after the last layer was removed, the corpuscle generated signals similar to those observed with the capsule intact (see recordings shown in Fig. 5).
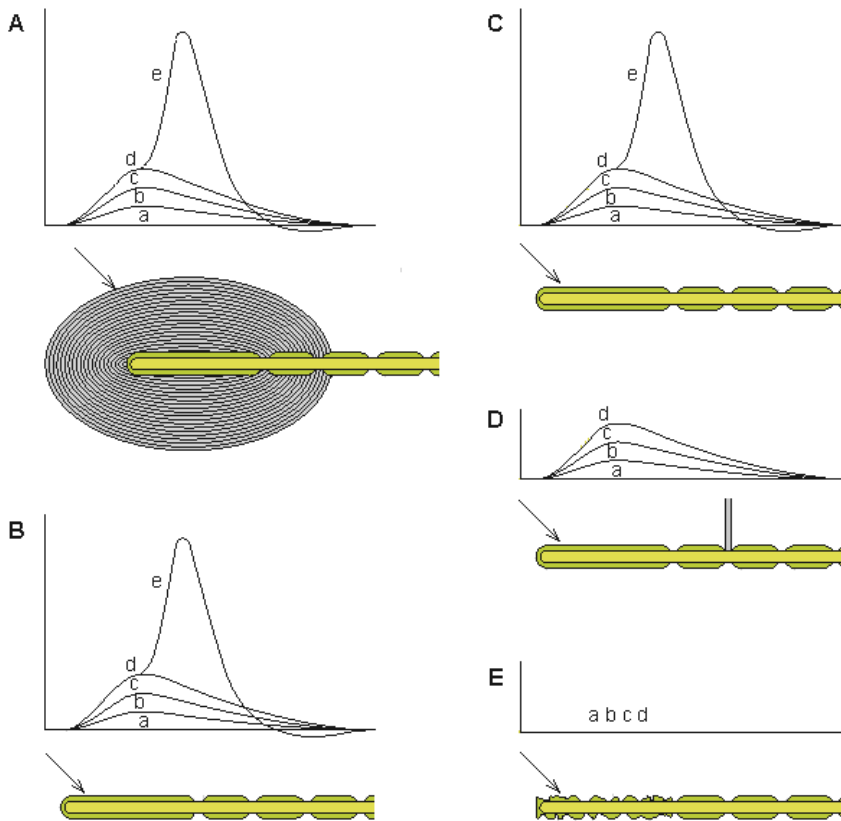
Fig. 5. Loewenstein's experiments with the Pacinian corpuscle.
 (A) The normal response of the generator voltage for increasing applied force (a)-(e).
 (B) The layers of the corpuscle have been removed, leaving the nerve terminal intact. The response to application of mechanical force is unchanged from A.
 (C) Partial destruction of the core sheath does not change the response from A or B.
 (D) Blocking the first node of Ranvier eliminates the initiation of the activation process but does not interfere with the formation of the generator voltage.
 (E) Degeneration of the nerve ending prevents the creation of the generator voltage.

Even partial destruction of the corpuscle did not prevent it from producing a generator voltage. But when Loewenstein destroyed the nerve ending itself, a generator voltage could no longer be elicited. This observation formed the basis for supposing that the transducer itself was located in the nerve ending. The generator voltage does not propagate on the nerve fiber (in fact, the nerve ending is electrically inexcitable) but, rather, triggers the activation process in the first node of Ranvier by electrotonic (passive) conduction. If the first node is blocked, no activation is initiated in the nerve fiber.

Meissner's corpuscles

Meissner's corpuscles (or tactile corpuscles) are responsible for sensitivity to light touch. They have highest sensitivity (lowest threshold) when sensing vibrations lower than 50 Hertz. They are rapidly adaptive receptors.
Meissner's corpuscles are encapsulated unmyelinated nerve endings, which consist of flattened supportive cells arranged as horizontal lamellae surrounded by a connective tissue capsule (see Fig. 1, top part, where the Meissner's corpuscle is indicated as 'sensory nerve ending for touch'). The corpuscle is between 30-140 μm in length and 40-60 μm in diameter.

Any physical deformation in the corpuscle will cause an action potential in the nerve. Since they are rapidly adapting (or phasic), the generated action potentials quickly decrease and eventually cease. For instance, this is the reason why one stops "feeling" one's clothes.

If the stimulus is removed, the corpuscle regains its shape and while doing so (i.e.: while physically reforming) causes another volley of action potentials to be generated.

Merkel's discs

Merkel's discs (or Merkel's nerve endings) are sensitive to touch. The information they provide are those regarding pressure and texture.

They are classified as slowly adapting mechanoreceptors.

In mammals, Merkel nerve endings have a wide distribution. Merkel nerve endings are found in the basal layer of glabrous and hairy skin, in hair follicles, and in oral and anal mucosa. In humans, Merkel cells (along with Meissner's corpuscles) occur in the superficial skin layers, and are found clustered beneath the ridges of the fingertips that make up fingerprints. In hairy skin, Merkel nerve endings are clustered into specialized epithelial structures called "touch domes" or "hair disks". Merkel receptors are also located in the mammary glands. Wherever they are found, the epithelium is arranged to optimize the transfer of pressure to the ending.

Their somewhat rigid structure, and the fact that they are not encapsulated, causes them to have a sustained response (in the form of action potentials or spikes) to mechanical deflection of the tissue. They are the most sensitive of the four main types of mechanoreceptors to vibrations at low frequencies, up to 15 Hz.

Because of their sustained response to pressure, Merkel nerve endings are classified as slowly adapting. This is in contrast to Pacinian and Meissner's corpuscles, rapidly adapting receptors which respond only to the onset and offset of mechanical deflection, and to higher frequency vibrations.

In mammals, electrical recordings from single afferent nerve fibres have shown that the responses of Merkel nerve endings are characterized by a vigorous response to the onset of a mechanical ramp stimulus (dynamic), and then continued firing during the plateau phase (static). Firing during the static phase can continue for more than 30 minutes.

They fire fastest when small points indent the skin and fire at a low rate on slow curves or flat surfaces. Convexities reduce their rate of firing further still.

Merkel nerve endings are extremely sensitive to tissue displacement, and may respond to displacements of less than 1 μm.

Several studies indicate that they mediate high resolution tactile discrimination, and are responsible for the ability of our finger tips to feel fine detailed surface patterns (e.g. for reading Braille).

Ruffini endings

Ruffini endings (or Bulbous corpuscle or Ruffini corpuscle) is a slowly adapting mechanoreceptor thought to exist only in the glabrous dermis and subcutaneous tissue of humans.

This spindle-shaped receptor is sensitive to skin stretch, and contributes to the kinesthetic sense of and control of finger position and movement. In fact, Ruffini endings are located in the deep layers of the skin, and register mechanical deformation within joints, more specifically angle change, with a specificity of up to 2 degrees, as well as continuous pressure states.

Ruffini endings are believed to be useful also for monitoring slippage of objects along the surface of the skin, allowing modulation of grip on an object.

They also act as a thermoreceptors that respond for a long time, so in case of deep burn there will be no pain as these receptors will be burned off.

Free nerve endings

Free nerve endings are unencapsulated and have no complex sensory structures, unlike those found in Meissner's or Pacinian corpuscles.
They are the most common type of nerve ending, and are most frequently found in the skin.
They mostly resemble the fine roots of a plant. They penetrate the epidermis and end in the stratum granulosum. They infiltrate the middle layers of skin and surround hair follicles.
Free nerve endings can detect temperature, mechanical stimuli (touch, pressure, stretch) or pain (nociception). Thus, different free nerve endings work as thermoreceptors, cutaneous mechanoreceptors and nociceptors. In other words, they express polymodality.