Chapter 9

Touch, Pain, Taste and Smell
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The steps involved in transforming pressure into action potentials

Let us begin with a touch receptor called the Pacinian corpuscle.

Step 1: Pressure deforms the onion-like membrane.

Step 2: Channels open and Na+ and K+ flow through the membrane (Na+ in and K+ out). The receptor depolarizes.

Step 3: If the graded potential, summed at the initial segment, is above threshold, action potentials are generated and propagated down the axon.

How is the magnitude of the stimulus encoded?

Stimulus magnitude is encoded in part by a frequency code. The greater the pressure, the more the receptor depolarizes. When the receptor potential is above threshold, the number of action potentials/second (firing rate) increases with receptor potential.

The relationship between the firing rate and pressure is nonlinear. It tends to saturate at high pressures. The change in the firing rate for a 1gm change in weight is greater at low pressures than high pressures.

How and why does the stimulus adapt?

How: The firing rate adapts because the receptor potential adapts in part because the onion-like laminae slip back, closing the channels.

Why: Adaptation enhances the detection of changes in pressure. Constant pressure, such as that exerted by your clothes, is not as readily detected.
Other receptors responsible for touch and pressure sensations?

In any one part of your skin you will find 4 receptors:
1. Hair receptors (back of hand) or Meissner (palm of hand)
2. Merkel
3. Ruffini
4. Pacinian

There are rapidly adapting (RA) and slowly adapting (SA) receptors. The surface layer contains both RA and SA receptors, as does the deep layer.

Receptive field size increases with depth in skin. Pacinian receptors are deep in the skin and have the largest receptive fields (r.f.).
Besides touch, are there other receptors in the skin?

There are 2 types of free nerve endings that are sensitive to **painful** stimuli.

A fast-conducting myelinated fiber that signals an early, localized, intense pain. This also mediates the sensation of itching.

A slow-conducting unmyelinated fiber that signals a later, poorly-localized, long-lasting, dull pain.

There are also 2 types of free nerve endings that are sensitive to **temperature** stimuli.

1. a fast-conducting myelinated fiber that fires most for hot, but not burning, stimuli.
2. a fast-conducting myelinated fiber that fires most for cold, but not freezing, stimuli.

Burning or freezing stimuli activate pain receptors.

Touch afferent fibers have large diameters. Pressure first blocks the conduction of action potentials in large fibers. Your limb "falls asleep". But the sense of temperature and pain, which is mediated by small diameter fibers, is often preserved.
Experiment on texture detection

Take two sheets of sandpaper of slightly different grades. By rubbing your fingertips over the surface you can easily distinguish which is rougher. The rubbing is necessary to activate the RA Meissner receptor. Rubbing produces vibrations as grains repeatedly pass over each receptor. These surface receptors also have small receptive fields and thus, fine spatial discrimination.

Now place your fingertips steadily on each sheet. Note that it is hard to say which is rougher. This is because the Meissner receptors rapidly adapt to steady pressure.

If you do not have sandpaper, rub your fingertips over a tabletop or your shirt. Compare this sensation to that produced by just placing your fingertips on the surface.

Likewise, the other receptor types each have a specialized function.
How does the brain determine what the stimulus is?

The pattern of action potentials coming from an afferent is not sufficient to fully sense the quality of a touch stimulus. For example, suppose that this is the response of an afferent that sends a signal to the brain. What is the stimulus?

It could be a RA afferent activated by a continuing vibration.

It could also be a SA afferent activated by a steady pressure.

If it is an RA afferent, which comes from the skin surface, then it could be something small.

If the afferent comes from deep tissue then it could be something big.

For the brain to know that a stimulus is a vibration that is coming from the surface of the skin, the brain must know (i.e. label) which afferent type has been activated (e.g. a RA surface afferent).

A similar problem occurs on the internet. When you use the internet, your message, as well as those of many others, travels down a shared common line. To separate your message from that of others, each packet of information is given a tag or label. At the end of the line, a decoder separates your packet from that of others.

The sense of touch solves this same problem in a different way. It gives each type of touch sensor its own private line. This is called its labeled line. Because of this, there is no reason for encoding and decoding each packet of information. But you do need lots of lines in your spinal cord.

Each afferent input to the CNS is given a labeled line (e.g. RA-surface). We perceive a stimulus as a vibration from the surface of the skin because of the label that is attached, by experience, to the activated fibre.

This is similar to place coding in the auditory system. We perceive the frequency of a sound not by the frequency with which a fibre is firing but by which fiber it is, i.e. from where on the basilar membrane it originates.
The pathway for transmission to the primary sensory cortex

The dorsal column medial lemniscal system

This is the path for the labeled line to the cortex i.e. the path from a RA afferent, deep in the skin (Pacinian) of the arm, to the first stage in the cortex. The dorsal column nuclei are also called the cuneate and gracile nuclei.

In the spinal cord, the dorsal column is the first stage in the development of a somatotopic organization. In the lower segments, only afferents from the leg are found. As one moves up the spinal cord new afferents enter laterally. Thus, in high segments of the spinal cord one finds that leg afferents are medial, arm afferents lateral, and trunk afferents in the middle.

The anterolateral system

The pathway for transmission of pain and temperature information to the primary sensory cortex is the anterolateral system.

The anterolateral system first makes a synapse in the spinal cord and then crosses at the same segment. It ends in the same region of cortex as touch.
Dermatomes

The territory innervated by each spinal nerve is called a dermatome. The territory innervated by each spinal nerve overlaps producing a blur at the edges of the dermatomes.

The overlap is greater for touch than for pain and temperature. Thus, testing for pain sensation provides a more precise assessment of segmental nerve injury than testing for touch.

The function of the dorsal column nuclei (DCN)

Are the DCN predominantly relay nuclei or do they transform incoming information? Contrary to popular anatomical terminology, there is no such thing as a relay nucleus. Neurons form synapses in a nucleus in order to transform or change the incoming signal.

There are two transformations that take place in the DCN.

1) Convergence

The skin on your back has a low afferent density. Also, many afferents converge onto a single DCN neuron. Thus only a few DCN neurons are required to represent a given area of skin from your back. The consequence is large receptive fields and a low tactile acuity (like the peripheral retina). To preserve the labeled lines, all converging afferents are of the same type.
The skin on your fingertip has a high afferent density. Only a few afferents converge on a single DCN neuron. Thus, many DCN neurons are required to represent a given area of skin. The consequence is small receptive fields and a high tactile acuity (like fovea). This is why you use your fingertip to read Braille. The finger has 100 times more resolution than the skin on your back.

2) Inhibitory surround

As with retinal ganglion cells, a stimulus in the center will activate a DCN neuron while a stimulus in the surround, through feedback, will inhibit the same DCN neuron. The function is the same as in vision: it **accentuates the edge** of an object. In this manner it also enhances two-point discrimination.
The organization of somato sensory cortex

1) Somatotopic organization.

Somato sensory cortex is somatotopically organized; i.e. the body surface laid down sequentially on the Postcentral Gyrus.

This body map is distorted with the lips, tongue and fingertips having a large representation. This distortion reflects that of the DCN. The skin of the back has a small representation because of the high convergence (and large receptive fields) in DCN neurons.

The map is plastic even in adulthood. A particular area of the cortex will expand if a particular body part is used often. The finger hand (left) of a violinist has a larger representation than the bow hand (right).

If a particular body part is amputated, its representation will shrink. Patient X had an arm amputated up to the shoulder. About a year later the patient complained of a phantom sensation of his hand coming from his cheek. The face area is adjacent to the arm area in somatosensory cortex. Because the arm area no longer receives input, it is gradually taken over by the face area. As it does so, it sometimes surrounds the arm area, temporarily leaving an island.

2) Multiple maps

Somato sensory cortex is subdivided into 4 parallel strips: areas 3a, 3b, 1, and 2. The homunculus is repeated 4 times.

**Area 3b** is the destination of touch afferents.

**Area 3a** receives input from the muscle afferents, which signal our sense of limb position and movement. From 3b information is sent to areas 1 and 2. Each extracts different features.

**Area 1** receives input from RA afferents from the skin surface. This area is important in recognizing texture.

**Area 2** receives input from SA afferents deep in skin and is used to estimate joint position. Joint position is important in recognizing the size and shape of objects.

As one moves to more posterior regions, the cells’ receptive field

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characteristics become more complex. Area 3b cells have small, simple, circular surround receptive fields. Area 1 cells have larger receptive fields that are orientation and direction selective. Somatosensory information is then sent to the parietal association cortex where stereognosis takes place: the 3D identification of an object through touch.

3) Columns

If one looks at area 3b in more detail, one finds modality specific columns. Each column receives input from one afferent type.

This separation of afferent types into columns is what produces labeled lines. A light vibration will excite the cells of one column type but not others. Over time, activation of this column and not another is associated with a light vibration.
Taste

**The 5 basic tastes**

The tongue is as sensitive to touch, temperature, and pain as is the thumb. In addition, the tongue performs a chemical analysis of substances dissolved in the saliva. It senses 5 basic tastes: **bitter, sour, salty, sweet and, the recently discovered, umami.**

Each taste can be sensed everywhere on the tongue but, as seen in the figure, different areas show preferences. The middle of the tongue has relatively few taste receptors cells.

Sourness (H+) and saltiness (Na+) act on receptors cell ion channels directly.

Bitterness, sweet and umami tastes are amplified by specific **G protein-coupled receptors**, which activate second messenger cascades to depolarize the receptors cell, as in the retina receptors.

Umami receptors are activated by monosodium glutamate and other proteins and give bacon a savory taste.
**The taste bud**

On the tongue one finds **taste buds**, a cluster of about 100 taste cells.

Each taste cell is most sensitive to one of the 5 tastes.

Because the tongue is exposed to hazards such as heat, infections and toxins, these taste cells are constantly being replaced. Over a 2-week life span, basal cells become supporting cells, which in turn become taste cells.

Taste cells need innervation to survive. If the afferent fibers are damaged, taste cell degenerate. Axonal transport along fibers provides some important trophic factor.

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**Taste pathway**

Taste afferents project via cranial nerves 7, 9 and, 10 to the **nucleus of the solitary tract**. From there the signal projects to the ventral posterior medial nucleus of the thalamus and then to several areas of the cortex including the **hypothalamus** which regulates hunger and the **insulae taste cortex** which has a rough topographic representation of different tastes.
Smell

This is the oldest of all the senses. The combination of smell and taste give food their **flavour**. Our sense of smell becomes less sensitive with age and this can lead to a loss of appetite and sometimes weight loss.

Odorants (smells) enter the roof of the nasal cavity, dissolve in the moist mucosal protective layer and are recognized by receptors on the dendrites of olfactory cells. When olfactory cells are damaged due to a virus or toxic substance they are replaced within a period of 1 month from basal cells. Olfactory cells project directly to mitral cells of the olfactory bulb, a part of the cortex.

Olfactory cell axons are **unmyelinated** because the distance to the olfactory bulb is short and speed is not important. It takes time for an odor molecule to diffuse across the mucus film and attach to a particular receptor site.

The mitral cells in turn project to the **pyriform cortex**, which codes mixtures of odorants present in a particular smell (e.g. a particular perfume). The pyriform cortex then sends information to the **amygdala** and **hippocampus** and through the **medial dorsal thalamus** to the **orbital frontal cortex**.

The orbital frontal cortex combines our sensations to odors with those of taste, texture (somatosensory), spiciness (pain) and vision, which results in the perception of flavour. Cells here receive a multimodal input and can respond, for example, to the smell, sight, or taste of a banana. Patients with lesions of the orbitofrontal cortex are unable to discriminate odors.

The amygdala is activated by the **pleasant or unpleasant** aspects of odors, the hippocampus facilitates the storage of **odor memories**, and the orbital frontal cortex combines the sense of taste with smell, producing the multimodal **perception of taste**.
Are there basic smell qualities?

The distinctive difference between the sense of smell and the other senses is the following. The sense of smell does not have a small number of basic smells as there are 5 types of basic tastes, 3 types of cones, or 5 types of touch receptors. Instead humans have over 300 receptive types for smell, and other species such as dogs have many more.

On the right we see three (green, blue, or yellow) of the many subtypes of olfactory cells. These are randomly distributed in the nasal cavity.

Each odor is detected, to different extents by a many receptors. To identify a particular odor, the cortex examines the pattern of receptors that are activated.

In smell a large gene family programs the creation of hundreds of different subtypes of receptors. This is similar to the immune system where receptor molecules can recognize millions of antigens. The amplification of receptor sensitivity involves a molecular cascade mechanism similar to that found in retinal receptors.

Genetic defects such as those that produce various forms of color blindness can also result in the absence of particular subtypes of olfactory cells. These can produce anosmia for specific odors.
Practice problems

1. In the dorsal column medial lemniscal system, afferents from a pressure receptor in the finger
   a) must first make a synaptic connection in the spinal cord.
   b) are over represented in the dorsal column nuclei compared that from the elbow.
   c) exhibit inhibitory surround receptive fields.
   d) show a large convergence in the dorsal column nuclei compared that from the elbow.
   e) terminate, via three synaptic connections, in the ipsilateral cortex.

2. A Pacinian corpuscle afferent
   a) has a small receptive field.
   b) responds well to steady pressure.
   c) is located deep in the dermis.
   d) produces a greater change in action potentials for a 100 to 101 gm. change in pressure than for a 1 to 2 gm. change.
   e) does not show adaptation in the receptor potential.
Answers
1. b)
2. c)

see also http://www.tutis.ca/NeuroMD/L8Ves/VesProb.swf