

The Physiology of the Senses  
Lecture 7 – Touch, Pain, Taste and Smell  
<http://www.tutis.ca/Senses/>

Contents

Objectives .....	2
Touch Receptors .....	3
Labeled Lines .....	7
The Pathway to the Primary Sensory Cortex.....	9
Three Features of the Somatosensory Cortex.....	13
Taste.....	15
Smell.....	18
See problems and answers posted on .....	20
References .....	21

## Objectives

1. List the sequence of events that converts pressure on the skin into neuronal activity.
2. Evaluate unique qualities that are detected by each touch receptor type.
3. Contrast the connectivity of the Internet and the touch receptors to the cortex.
4. Describe 3 ways in which the activity from the skin is transformed in the dorsal column nuclei.
5. Specify the distinguishing feature in each of the 4 maps of the body in the somatosensory cortex.
6. Compare the processing of taste and smell.

## Touch Receptors

As in vision, we can use touch to distinguish edges, feel textures, read letters, and recognize objects as complex as faces. And, as in vision, we can do this with very few receptor types. There are five receptors sensitive to touch (Figure 7.1). In addition, there are receptors that sense pain and temperature.

Let's first consider how the Pacinian touch receptor, located deep in the skin, the dermis, converts the mechanical force of touch into neural electrical activity. This is the receptor that is activated by the vibrations from your cell phone. It is also the receptor located on the elephant's sole that allows it to hear the foot stomp of another elephant many kilometers away.

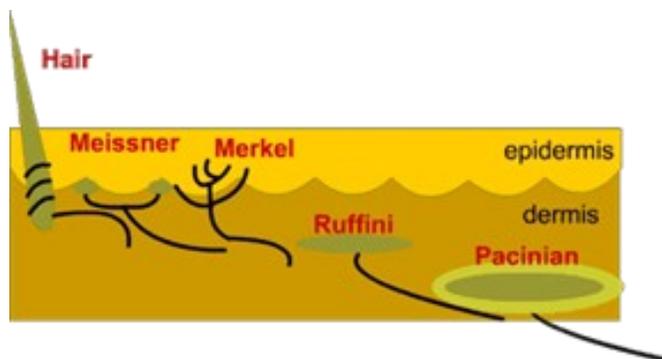


Figure 7.1 The five touch receptors are located at various depths within the skin.

### a) Transforming Mechanical Energy into Electrical Activity

Step 1: Mechanical stimulus (e.g. pressure) deforms the receptor's onion-like outer membrane (Figure 7.2) at the end of the nerve cell.

Step 2: The receptor's channels open and  $\text{Na}^+$  flows through membrane. The inside of the receptor depolarizes (voltage becomes more positive).

Step 3: If the graded potential is above a threshold level, action potentials are generated and propagated down the axon. Touch afferents have myelinated axons, an insulation which allows action potentials to hop from gap to gap in the myelin sheath. This speeds up the conduction of action potentials.

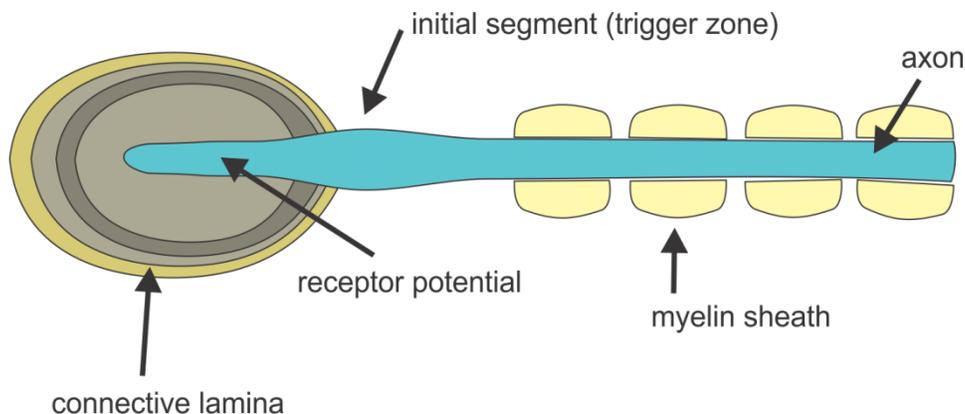
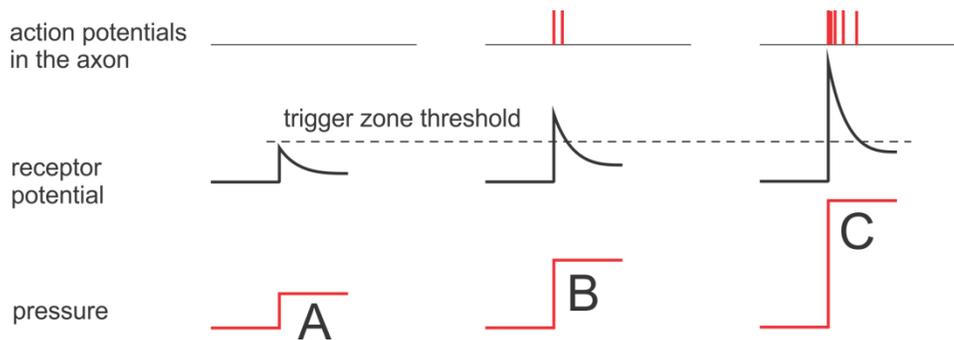


Figure 7.2 The Pacinian receptor produces action potentials which travel down the axon to the spinal cord.

*b) How is the magnitude of the stimulus encoded?*

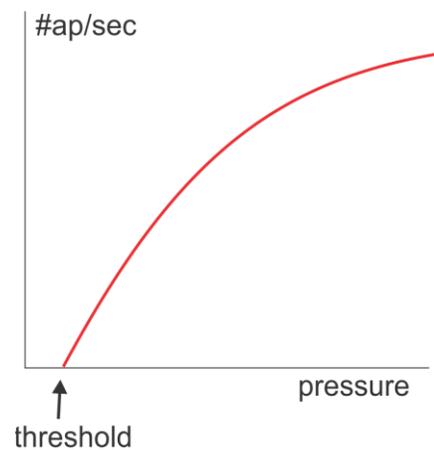


**Figure 7.3** The Relationship Between Touch Pressure and Electrical Activity **A:** The receptor potential from a small pressure does not reach threshold and no action potential is generated. **B:** A medium pressure produces a receptor potential larger than threshold which then generates two action potentials. **C:** A large pressure produces a large increase in receptor potential and a large burst of action potential.

Stimulus magnitude is encoded in part by a frequency code: the greater the pressure, the more the receptor depolarizes and, if above threshold, more action potentials/second (#ap/sec) are generated (Figure 7.3).

As plotted in Figure 7.4 the relationship between the action potential frequency and pressure is not a straight line. It tends to flatten out at high pressures.

**Figure 7.4** A plot of pressure against the frequency of action potentials is a curved function. At low pressures a larger increase in frequency is produced than at large pressures.



*c) The response to the stimulus adapts. How does this occur and why?*

**How:** The #ap/sec adapts because the receptor potential adapts. Receptor potential adapts in part because the onion-like laminae slip back to their original shape, closing the channels.

**Why:** Adaptation enhances the detection of changes in pressure. The constant pressure, such as that exerted by your clothes, is not as important.

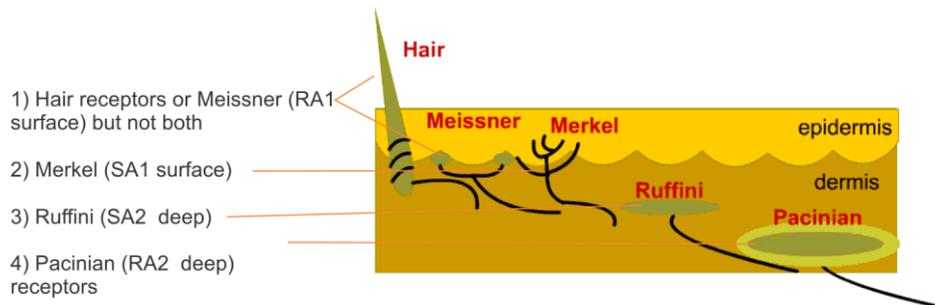
## Other Receptors for Touch

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

Because each has an receptor of a different shape each is best activated by a different quality of touch and the combination is what provides the richness of touch much like the perception of color by the eye's cones. Recall that three types of cones allow us to distinguish between 2,000,000 colors. Likewise, we need a variety of touch receptors to code a large variety of touch stimuli (possibly in the millions). Without 5 different types of touch receptors touch would be like being color blind, feeling in greys rather than vivid colors.

*a) Some receptors are rapidly adapting (RA) and others slowly adapting (SA).*



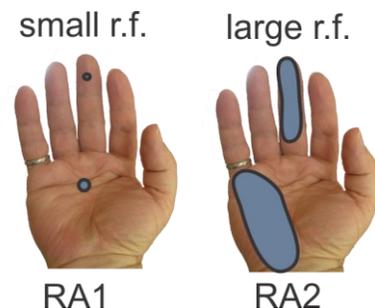
**Figure 7.5** The touch receptors are located at various depths within the skin.

RA signifies rapidly adapting and SA slowly adapting. #1 is close to the skin surface and #2 deep within the skin..

Figure 7.5 shows that the surface and deep layers of the skin contain both RA and SA receptors. We will use the number 1 for receptors at the epidermis near the skin surface and 2 for those in the deeper dermis.

*b) Which receptor has the largest receptive field size?*

Receptive field size increases with depth in the skin. Pacinian corpuscles have the largest receptive fields. Recall that it is the small receptive fields that allow for the perception of details.



**Figure 7.6** RA1 receptors close to the skin surface have smaller receptive fields (blue circles on the left) than RA2 receptors located deeper within the skin. The finger tips have smaller receptive field than do the hand's palms.

## Pain and Temperature Receptors

In addition, there are 2 types of nerve endings that are sensitive to painful stimuli.

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

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

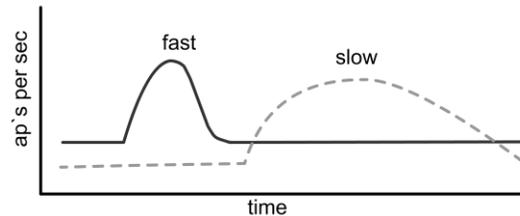
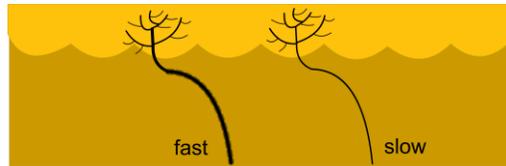


Figure 7.7 There are two types of pain afferents, slow and fast conducting.

As well there are 2 types of 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.

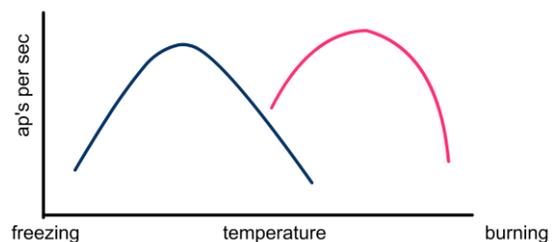
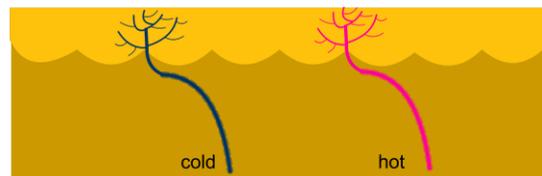


Figure 7.8 Two types of afferents sense temperature, hot and cold.

Touch afferent fibers have large diameters. Pressure on a nerve fiber first blocks the conduction of action potentials in large fibers (Figure 7.9). Your limb "falls asleep". But the sense of temperature and pain, which is mediated by small diameter fibers, is often preserved.

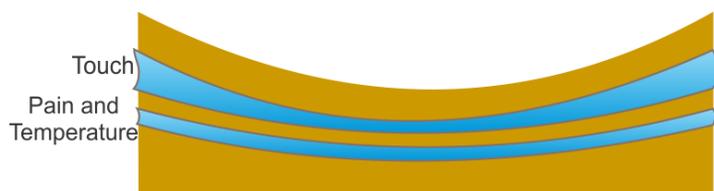
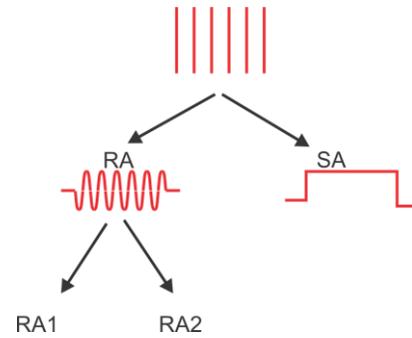


Figure 7.9 Nerve compression blocks large afferents before small afferents.

The Gate Control Theory proposed by Patrick Wall and Ronald Melzack suggests that pain sensation is dependent on the balance between input from the large nerve fibers (e.g. those of touch) and that from small nerve fibers (e.g. those of pain). If there is more large than small fiber input, there should be little or no pain. If there is more small than large fiber, then one will sense pain. By activating large fibers through rubbing, one can alleviate pain.

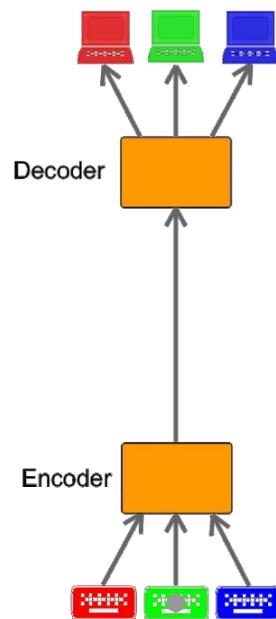
## Labeled Lines

In the brain, the same input from a different axon often signals very different sensations. How do we know what the stimulus is? Suppose that action potentials at the top of the Figure 7.10 are the response of an afferent that sends a signal to the brain. What is the stimulus? It could be an RA afferent repeatedly activated by a vibration. It could also be an SA afferent activated by a steady pressure. If it is a surface afferent, then the stimulus could be something small. If the afferent comes from deep tissue, then the stimulus could be something big. For the brain to recognize that a stimulus is a vibration that is coming from the surface of the skin, perhaps an insect, the brain must somehow label the afferent type that has been activated as an RA1 afferent.



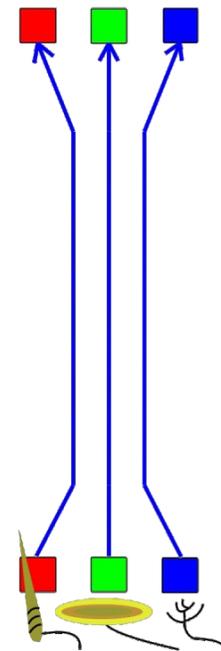
**Figure 7.10** The same firing rate can be produced by a variety of afferents.

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 first given a tag or label by an encoder. At the end of the line, a decoder separates your packet from that of others and directs it to your friend.



**Figure 7.12** Messages on the internet share a common line and are identified by a unique tag.

The sense of touch solves this problem in a different way. It gives each type of touch afferent 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!



**Figure 7.11** Touch afferents are identified by their unique private lines.

We perceive a stimulus as a vibration from the surface of the skin because of the label that is attached, by experience during childhood, to the activated fiber. A definition of a labeled line is: “a label attached to each afferent fiber as to what sub-modality it is (e.g. RA1 or RA2)”. Each afferent type is designed to be best activated by a particular type of touch. Through experience we learn to associate that afferent’s activity with that quality of touch.

We will see in session 9 that this is similar to place coding in the auditory system. We sense the tone (frequency) of a sound not by how fast a fiber is firing, but by which fiber it is. Labeled lines illustrate an important principle as to how the brain codes information for touch and for the other senses. We sense information in two ways: 1) the **intensity** of the stimulus by the firing **frequency** of a particular neuron and 2) **quality** of the stimulus by **which** neuron is active.

We saw that richness of color vision stems not from the isolated activation of one cone or another, but from the number of ways in which they can be combined. The sense of touch is the same. Touch afferents are rarely activated in isolation. Which are active and to what intensity is what makes this sense especially rich.

*Summary*

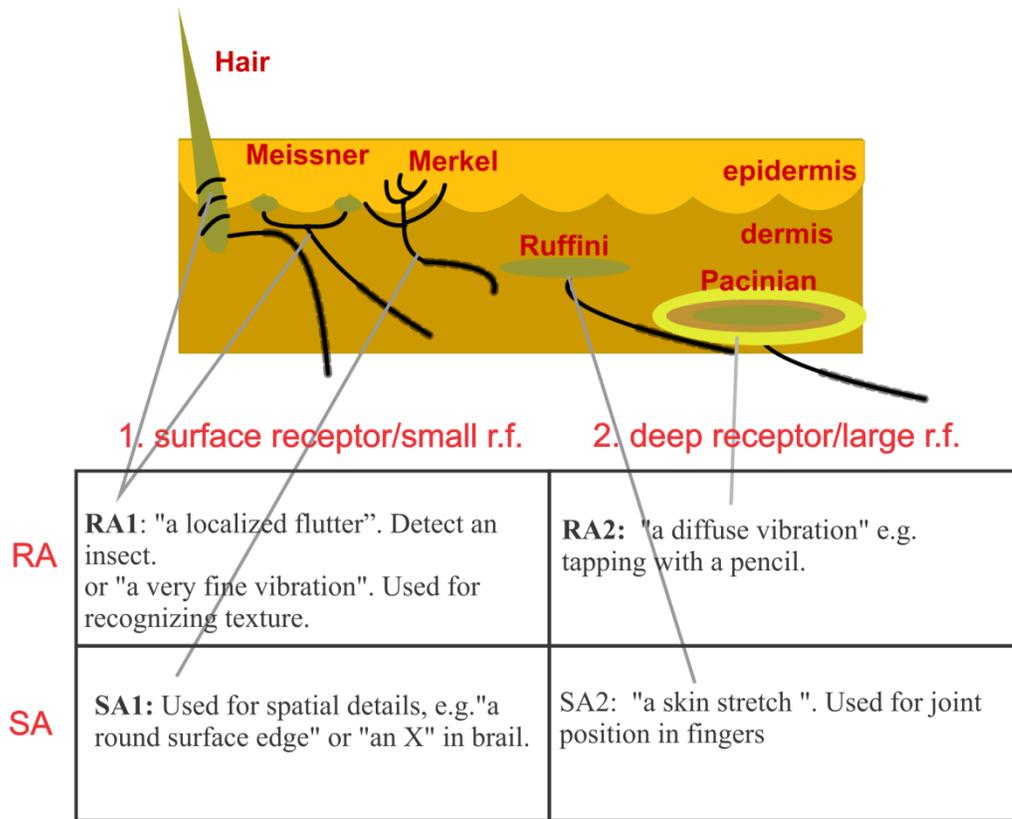


Figure 7. 13 The four touch receptor types are separated by how fast they adapt (rapidly RA or slowly SA) and their depth within the skin (1 on the surface or 2 deeper in the skin). Each elicits a unique sensation (Goodwin et al 1997).

*An 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 RA1 receptor. Rubbing produces vibrations as grains repeatedly pass over each receptor. RA1 receptors have small receptive fields and thus, the ability for 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 RA1 receptors rapidly adapt to steady pressure. If you do not have sand paper, rub your fingertips over a tabletop. Try to find a small scratch on the table. Compare this sensation to that produced by just placing your fingertips on the table. Or do the same with the cloths you are wearing.

## The Pathway to the Primary Sensory Cortex

The pathway responsible for the conscious perception of touch is the dorsal column **medial lemniscal system** (Figure 7.14). This is the path for the labeled line to the cortex, e.g., the path from an RA1 afferent, located on the arm, to the first stage in the cortex.

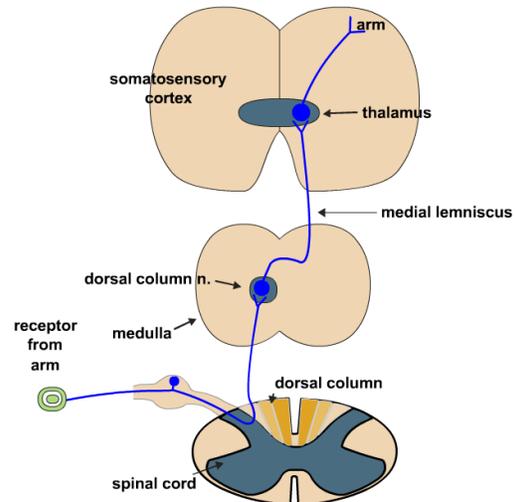
In the spinal cord, the dorsal column is the first stage in the development of a somatotopic organization. In the lower segments of the spinal cord, only afferents from the leg are found. As one moves up the spinal cord, new afferents enter laterally. Thus, in high segments of the spinal cord one finds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

**Are you confused as to why dorsal here refers to the back of the spinal cord while dorsal in the dorsal stream refers to the top of the head?**

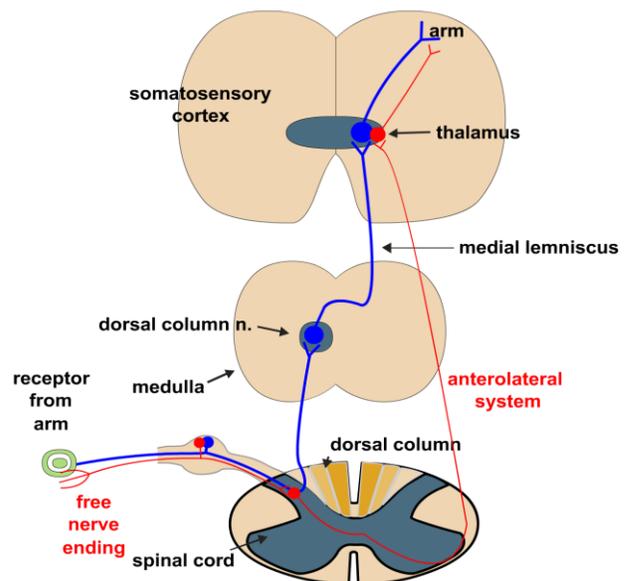
Think of a dog or cat. Here dorsal means the top of both the head and back. Unfortunately naming in anatomy started with species such as the dog and cat and used Latin names.

The signal from touch afferents on one side of the body crosses over to the other side of the brain and makes a synapse in a part of the thalamus called the ventral posterior nucleus. From there the signal goes to the arm area of the **primary somatosensory cortex (area S1)**.

The pathway for transmission of pain and temperature information to the primary sensory cortex is the **anterolateral system** (Figure 7.15). This first makes a synapse on entering into the spinal cord, then crosses to the opposite side, ascends along the anterior lateral nerve of the spinal cord, synapses in the thalamus, and ends in the same region of the cortex as the sense of touch.



**Figure 7.14** Touch Perception is transmitted along the dorsal column medial lemniscal pathway with synapses in the contralateral thalamus and somatosensory cortex. Three slices are shown from the cortex (top), the medulla (middle) and spinal cord (bottom).

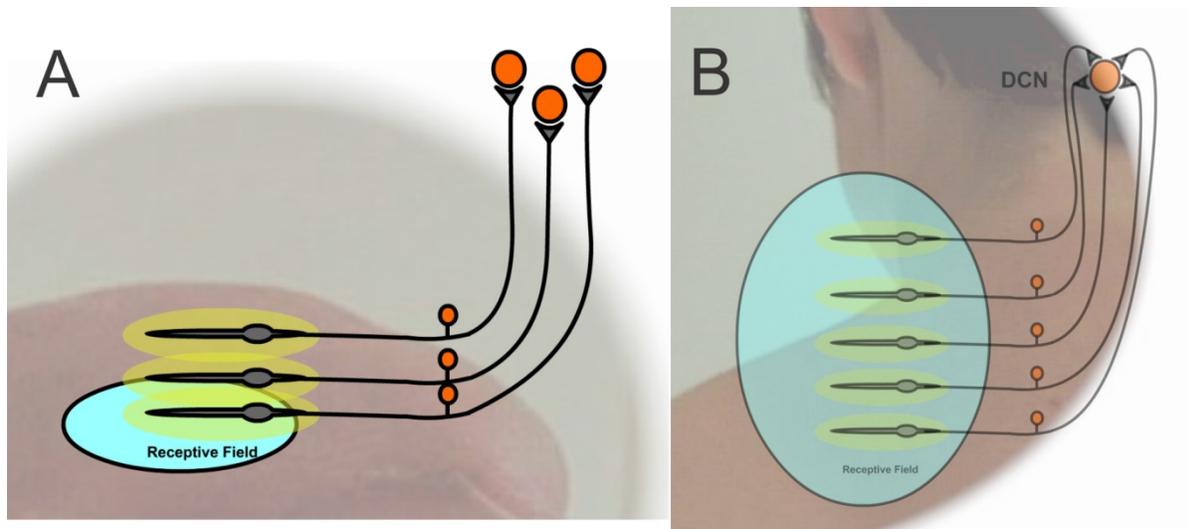


**Figure 7.15** Pain and temperature perception is transmitted along the anterolateral pathway with synapses in the spinal cord, the contralateral thalamus, and the contralateral somatosensory cortex.

## The Three Functions 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 need for a relay nucleus because axon potentials do not need to be boosted by a synapse. A synapse on its own simply adds an unnecessary delay. Neurons form synapses in a nucleus in order to transform or change the incoming signal. There are three distinct transformations that take place in the DCN.

### Function 1 of the DCN: Convergence



**Figure 7.16** Convergence in the Dorsal Column Nucleus (DCN) **A:** Afferents from the fingertip show little convergence and have a large DCN representation, **B:** Afferents from the back have a large convergence and a small DCN representation.

The skin on your fingertip has 1) a **high** afferent density, and 2) **few afferents** converge onto a single DCN neuron (Figure 7.16A shows only one afferent but a few more are possible). The consequence is small receptive fields and a high tactile discrimination (like the fovea). This is why you use your finger tip to read Braille (100 times more resolution than your back).

The skin on your back has 1) a **low** afferent density (Figure 7.16B) and 2) **many** afferents converge onto a single DCN neuron. Because of these **two factors** only a **few DCN neurons** are required to represent a given area of skin on the back. The consequence is a large receptive field and a low tactile discrimination (like the peripheral retina).

Because of these differences in convergence, the representation of the body in the DCN begins to become distorted; some parts becoming large, others small.

**Experiment:** Take a paper clip and bend it into a loop (like a U). Start with the tips of the U far apart. With your eyes closed, touch your skin with the clip tips. Open your eyes to check whether two tips are touching or just one. Move the tips closer together and try again. The distance at which the tips first feel like one is your two-point discrimination. Compare this for different parts of body, e.g., fingertips, arm, back, lips, tongue.

### Function 2 of the DCN: Inhibitory Surround

As with retinal ganglion cells, a stimulus in the center of a cell's receptive field will activate the DCN neuron while a stimulus in the surround, through inhibitory feedback, will inhibit the same DCN neuron (Figure 7.17).

Receptive fields, with an inhibitory surround, first occurs in the DCN, not the skin. In contrast to the skin, the retina, being part of the brain, can be organized into a complex neural network while the skin cannot.

The function of inhibitory surround is the same as in vision: it accentuates the activity near the edge of an object.

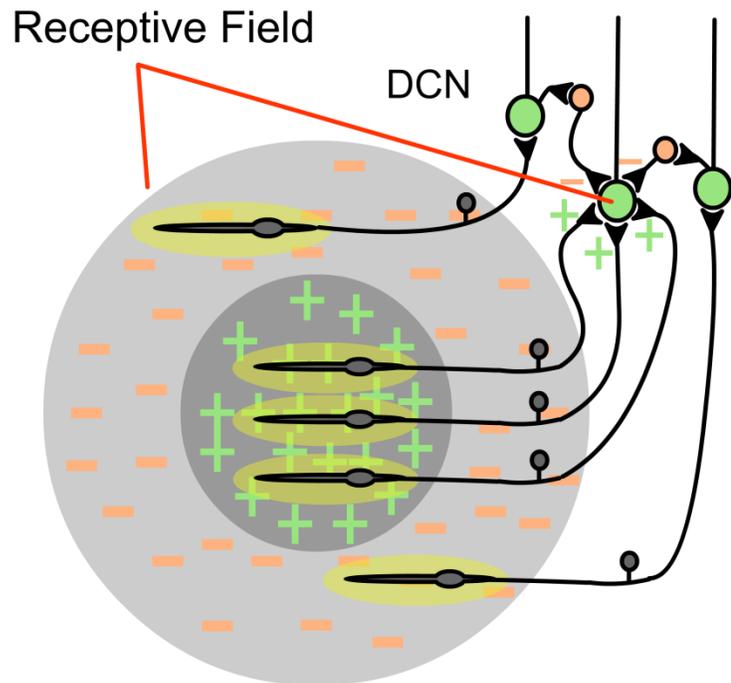


Figure 7.17 The Receptive Field of a Neuron in the DCN

DCN neurons receiving input from the surround inhibit DCN neurons receiving an excitatory input from the center.

### Function 3 of the DCN: Cortical Gating

Experiments show that a tactile tickling stimulus is much more potent when administered by someone else than when self-administered. Why can't you tickle yourself? When you try tickling yourself or making any movement, a copy of the command (Blakemore et al 2000) (corollary discharge) inhibits the touch signals ascending through the DCN. The purpose of this inhibition is to block the touch afferent signals that arise when the skin is stretched or compressed by the movement itself. The corollary discharge signals the afferent signal expected from the movement. If the expected match the actual, little signal is sent on to the cortex. It is the unexpected that generates the strong signal.

*In summary, three transformations are performed in the DCN.*

- 1) Differential convergence leads to a distorted somatotopic representation of the body. Many neurons represent important tactile body parts, such as the fingertips and the lips.
- 2) Lateral inhibition accentuates the changes in touch stimuli.
- 3) Corollary discharge selectively gates input based on motor output.

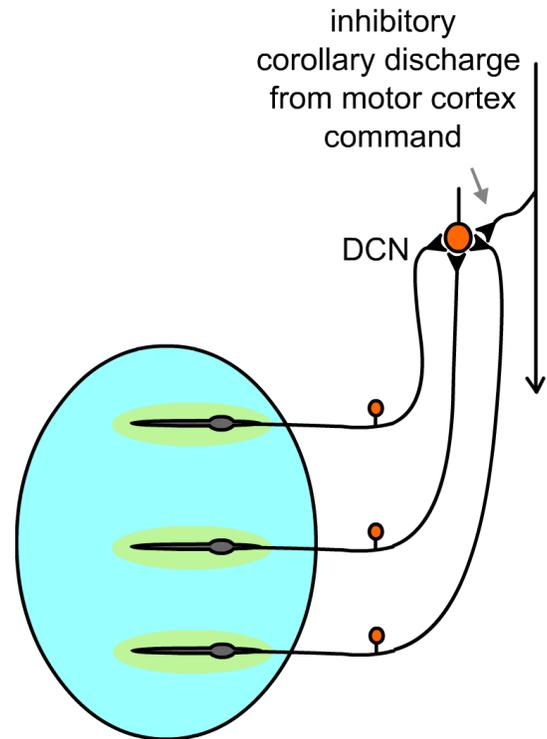


Figure 7. 18 Corollary discharge can inhibit DCN neurons.

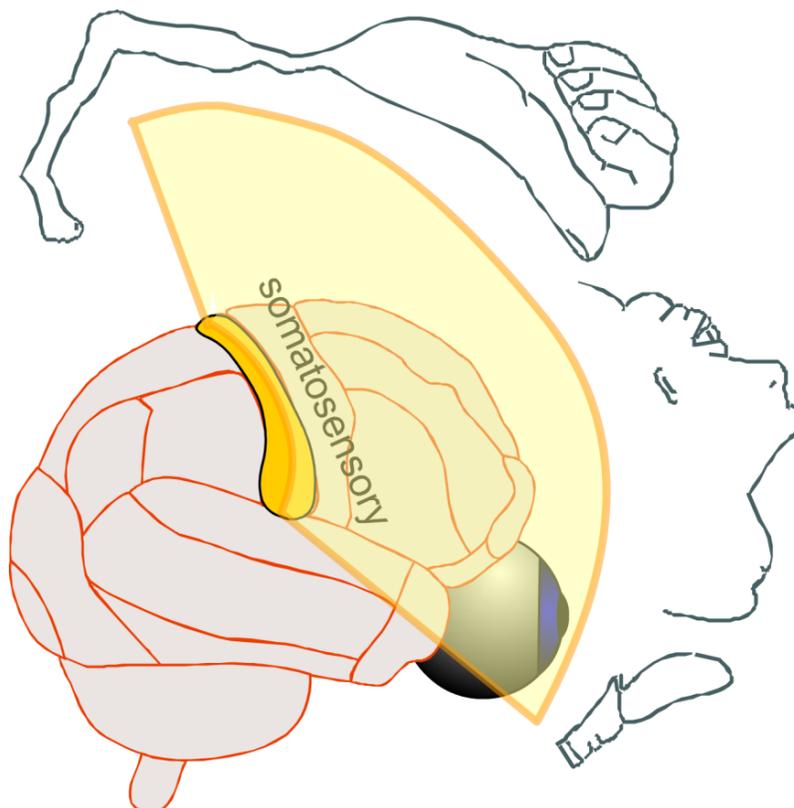
## Three Features of the Somatosensory Cortex

### *Feature 1: Somatotopic Organization*

Our conscious perception of touch begins in the primary somatosensory cortex (S1). This is somatotopically organized with the body surface laid down sequentially in the brain on the ridge behind the central sulcus, 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.

### Phantom Limbs

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 received input, it was gradually taken over by the face area. As it did so, the face area surrounded the arm area, temporarily leaving an island representing the arm in the face area. This demonstrates that the somatotopic organization of this area retains a great deal of plasticity even in adulthood.



**Figure 7. 19** The somatosensory cortex represents a distorted map of the skin surface with areas of high sensitivity (the fingers and lips) being represented by a large number of neurons.

### Feature 2: Multiple Maps

In the somatosensory cortex, a map of the body is repeated 4 times in 4 parallel strips: areas 3a, 3b, 1, and 2 (Figure 7.20). Area 3b receives input from the touch afferents. Area 3a receives inputs from afferents in the muscles and joints which signal proprioception (the sense of position and movement, the subject of the next lecture). Together areas 3a and 3b can be considered the **primary somatosensory cortex (S1)**, the equivalent of V1. Areas 1 and 2 are higher order areas. Note that the hand's skin surface representation is mirrored in 3b (Kaas 1983) and in the higher order areas 1 and 2, as is that of the rest of the body. This is similar to the mirroring of the retinotopic representation in V1, V2, and V3. Area 3a does not show a clear mirroring of 3b because its receptors are in the deep muscles, tendons, and joints, not the skin surface.

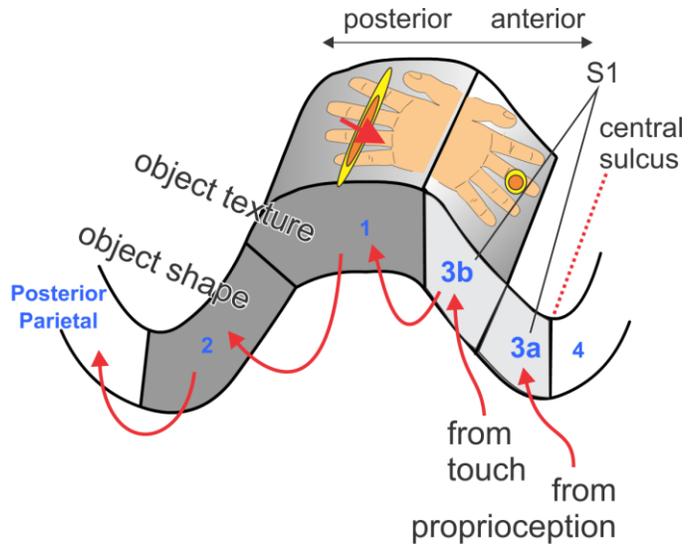


Figure 7.20 The body's skin is mapped four times, in area 3a, 3b, 1 and 2. Area 3a receives proprioceptive information and area 3b that from touch (S1). Area 1 specializes in texture and area 2 in shape (higher order).

**Higher order areas** extract more complex features. Area 1 receives input from RA1 afferents. This area is important in recognizing texture. Area 2 receives input from SA2 afferents which are used to estimate finger position. Finger position is important in recognizing the size and shape of objects.

As one moves from area 3b to the higher order area 1, the cells' receptive field characteristics become more complex. Area 3b cells have small simple circular surround receptive fields. Area 1 cells have larger receptive fields that can encompass more than one finger and are orientation and movement direction selective.

Somatosensory information is then sent to **secondary somatosensory cortex (S2)** in the posterior parietal cortex where **stereognosis** takes place: the 3D identification of an object through touch. Stereognosis occurs when you reach in a bag of unknown objects and are able to identify them.

### Feature 3: Columns

If one looks more closely at area 3b, one finds that each column receives input from one afferent type (Figure 7.21). This separation of afferent types into columns is what produces labeled lines. A light vibration will excite the cells of one

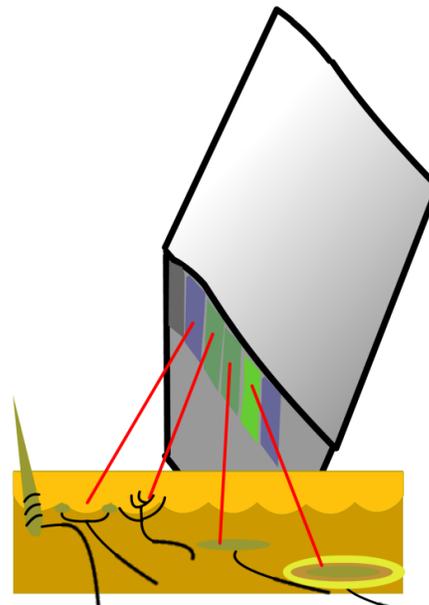


Figure 7.21 All neurons in a column in area 3b receive input from a single afferent type (e.g. RA1). Adjacent columns have neurons which receive input from different afferent types.

column type and not others. Activation of this column, and not another, is associated with a light vibration.

## Taste

### *The Five Basic Tastes*

Taste and smell, our chemical senses, are important in distinguishing between foods that are nutritious versus those that are harmful, as well as those providing pleasure.

The tongue, because of its large representation in S1, is as sensitive to touch, temperature, and pain as is the thumb. Pass your tongue over your teeth. Notice how you can feel the exact shape of each tooth. It senses coffee that is too hot and pain when you bite it inadvertently. 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 Figure 7.22, different areas show preferences. The middle of the tongue has relatively few taste cells. As we sip wine or juice, the sweetness receptors at the front of the tongue are first activated, then the sour receptors in the middle, and finally the bitter receptors at the back. Thus, the tongue sends a spatial temporal pattern to the brain that allows it to differentiate between a variety of wines or juices.

Sourness ( $H^+$ ) and saltiness ( $Na^+$ ) act on receptor 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 cell, as in the retina's receptors. The newly discovered umami receptors are activated by monosodium glutamate and other proteins and give bacon a savory taste.

For bitterness, sweet, and umami tastes, each receptor site is rather specific for the shape a particular taste molecule, like a lock that can only be opened by a specific key. However, there may be several molecules that have similarly shaped endings that fit the key. For example, there is one specific key for glucose but other sweet molecules have similar endings or keys. The goal of the artificial sweetener industry is to make molecules whose shapes look like a sugar but has no nutritional value.

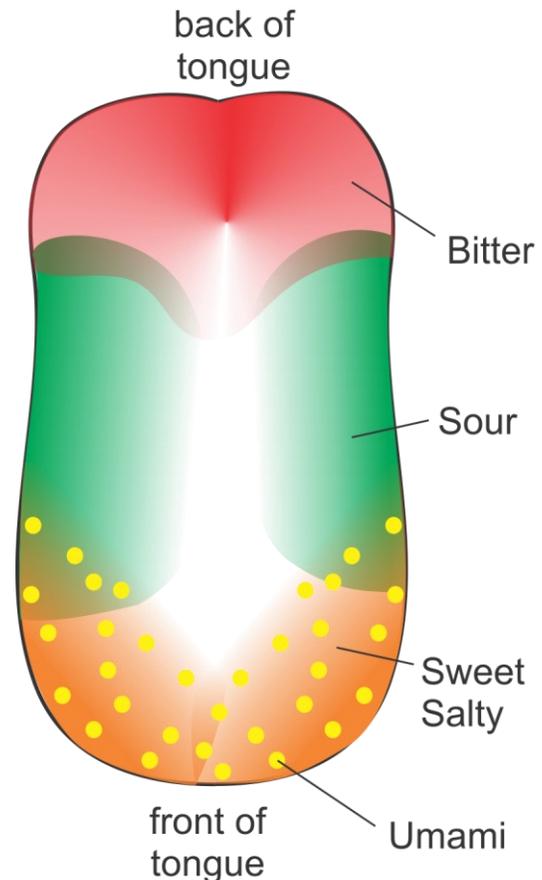
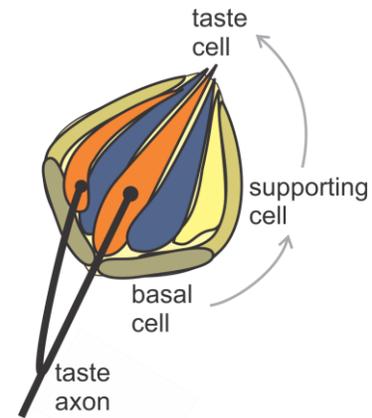


Figure 7.22 The Areas of the Tongue that have the Greatest Sensitivity to Different Flavours

## 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 become taste cells.

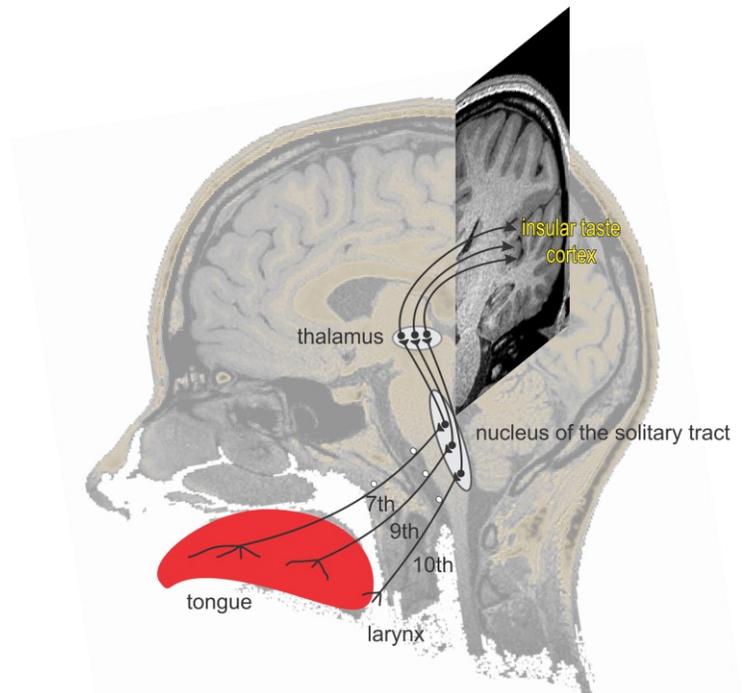
Taste cells need innervation to survive. Substances required to maintain healthy taste cells are transported along the taste axon from the spinal cord. If these axons are damaged the taste cells degenerate.



**Figure 7.23** The taste bud contains about 100 taste cells. These are replaced from basal cells, which turn into supporting cells, and finally into taste cells over a two week period.

## The 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 thalamus and **hypothalamus**. The hypothalamus, a part of the limbic system, regulates hunger. From the thalamus the signal goes to several areas of the cortex including the **insular taste cortex**, which has a rough somatotopic representation of different tastes (Figure 7.24). The taste signal is projected to the cortex using a labeled line system similar to that of touch.



**Figure 7.24** Taste afferents synapse onto neurons in the nucleus of the solitary tract. These in turn project to the thalamus and to the insular taste cortex.

## *Inborn Hunger*

We have an inborn ability to compensate for diet deficiencies by selecting foods that will compensate for these deficiencies. We have a craving for salts because they are essential for maintaining our electrolyte balance. Activation of umami and sweet afferents produce a pleasurable sensation which promotes eating proteins and sugars. Sweet, salty, and fatty substances used to be rarities. Unfortunately, they are plentiful now and these inborn hungers have to be voluntarily tempered.

At the beginning of this century there were frequent cases of lead poisoning in young children. In most cases, these were children who suffered from a calcium dietary deficiency. These children would often attempt to compensate for calcium deficiencies by eating the plaster from the walls. The walls were, unfortunately, painted with lead based paints.

## *Genetic Taste Deficiencies*

Taste deficiencies can be genetic (as are forms of color blindness). Genes code the development of particular receptor sites. Some individuals cannot detect different forms of bitterness because of the absence of a particular receptor on the tongue. For example, some individuals cannot detect a form of bitterness found in cabbage.

## *Learned Taste Aversion*

Animals have an innate aversion to bitter or sour substances, as do many infants. This is because such tastes signify food that had spoiled or is poisoned. These taste aversions can also be learned. If a rat is given a particular food combined with a tasteless poison that results in nausea, the rat will be conditioned to avoid that particular food. If you go to a restaurant and develop food poisoning, you may also develop an aversion to what you had ordered. The aversion to that food can last a lifetime. This is not the same as classical conditioning because you would not become averse to the music that was playing at the restaurant or the people you were with.

## Smell

Smell is the oldest of all the senses. The combination of smell and taste gives food its **flavour**. Sadly, our sense of smell becomes less acute with age and this can lead to a loss of appetite and sometimes weight loss.

Most odors (smells), such as a perfume, are composed of a complex mixture of odorants. Each odorant is a molecule with a distinctive shape. These molecules 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. These cells project directly through the skull to **mitral cells** of the olfactory bulb, a part of the cortex. After a sudden head impact, these olfactory afferents can be sheared off, interrupting the sense of smell. But this is restored because the olfactory cells regrow in about a month.

Olfactory cell axons are **unmyelinated** because the distance to the olfactory bulb is short and because speed is not important. It takes some time for an odor molecule to diffuse across the mucus film and attach to a particular receptor site. When we sniff, different odor molecules diffuse across the mucus film at different rates. Because of this, the response at any particular time provides little information as to the odor. One needs to remember the **temporal pattern** of the whole sniff (Haddad et al 2013). For this reason, memory is an important element in recognizing odors. Conversely, odors often elicit strong memories.

Smell is the only sense that activates the cerebral cortex without first passing through the thalamus. The mitral cells in the olfactory bulb project to the pyriform cortex (Figure 7.25), the primary olfactory cortex, which codes the perception of the smell produced by a particular mixture of odorants (e.g. a particular perfume). The pyriform cortex then sends information to the amygdala and hippocampus and through the thalamus to the orbital frontal cortex. The amygdala is activated by the pleasant or unpleasant aspects of odors and the hippocampus facilitates the storage of odor memories. The orbital frontal cortex combines our sensations to odors with those of taste, texture (somatosensory), spiciness (pain) and vision. The combination of two or more of these modalities 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.

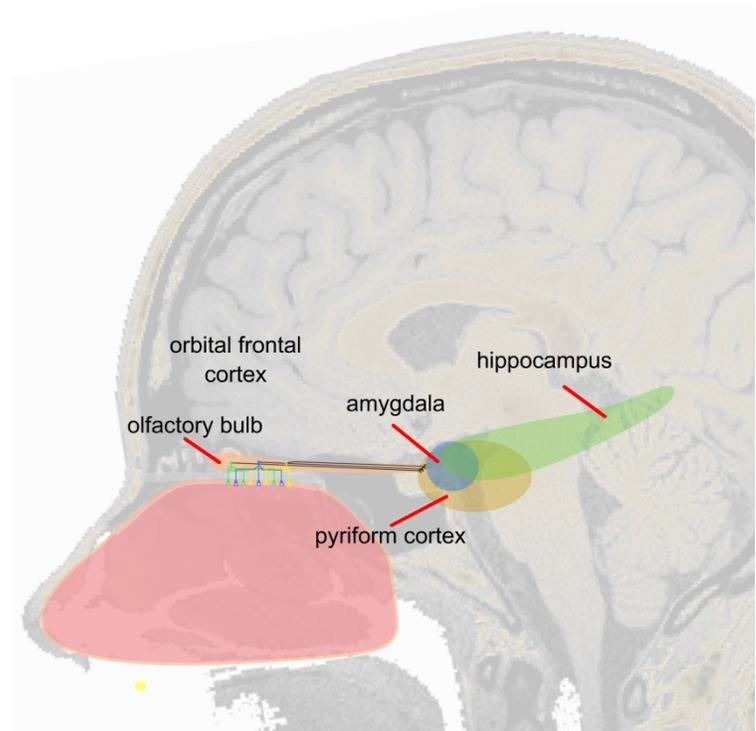


Figure 7. 25      The Areas Involved in the Sense of Smell

### Are there basic smell qualities?

No. The sense of smell does not have a small number of basic receptor types (as there are 5 types of basic tastes, 3 types of cones for color, or 5 types of touch receptors). Instead humans have over **300 receptor types**, and other species, such as dogs, have many more.

In Figure 7.26 we see three (in green, blue, or yellow) of the over 300 subtypes of olfactory cell receptors. These are randomly distributed in the nasal cavity.

Each odor is composed of several odorant molecules (Figure 7.27). Because each end of the molecule can fit a different receptor, each odorant molecule can unlock, and thus **activate, several** receptors. A molecular cascade amplifies the taste receptor's sensitivity, like retina receptors. To identify a particular odor, the cortex examines the pattern of afferents that are activated, the **odor's combinatorial code**. In Figure 7.26 the three colors signify **three of the 300 receptor types** that map smells. By comparing patterns, the number of odors that can be distinguished become enormous. This is like a combination lock in which 3 tumblers each of 10 values can produce a thousand combination possibilities. On average humans can discriminate between trillions of odors (Bushdid et al 2014). But this varies greatly between subjects, ranging from a **million trillion to only 70 million**. This is far more than the number of colors that can be distinguished. 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.

Each mitral cell receives input from many olfactory cells all of whom express the same receptor subtype (green, blue, or yellow in Figure 7.26). Each odor activates a particular combination of receptors and mitral cells. Similar odors stimulate adjacent mitral cells. Unlike other modalities, the nasal cavity is not mapped somatotopically onto the olfactory bulb. Rather the olfactory bulb is arranged in a topographical map of smells.

When olfactory cells are damaged, due to a virus, or a toxic substance, they are replaced within about a month from basal cells. These then regrow to the same mitral cell in the same region of the olfactory bulb that was previously most sensitive to that particular odor. Thus the same map of odors in the olfactory bulb is maintained, as is their memory.

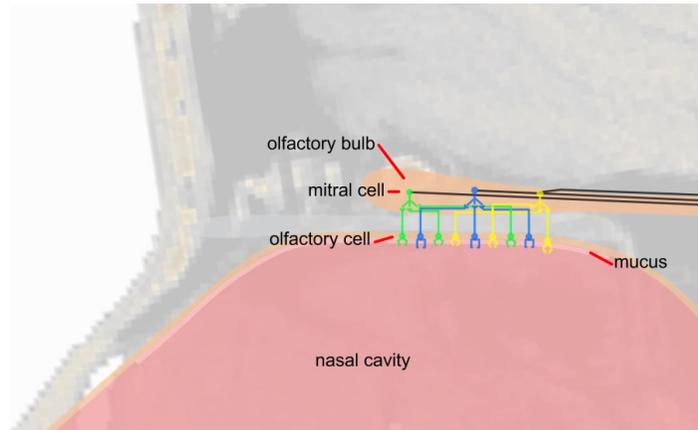


Figure 7.26 Three of the more than 300 receptor types, randomly distributed along the nasal cavity, connect to mitral cells, grouped by type.

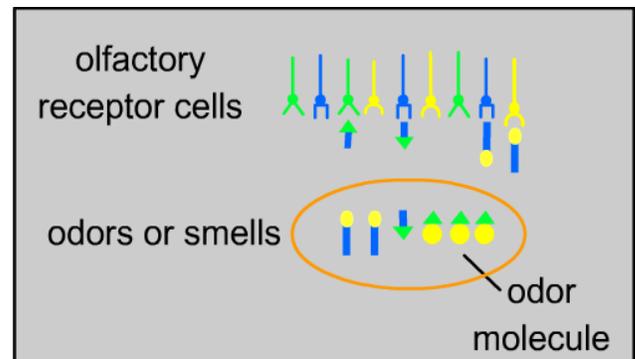


Figure 7.27 Odor molecules fit specific receptor sites in receptor cells. Some molecules can fit more than one site.

## Summary of Taste and Smell

Both olfactory cells, and taste cells in the taste bud, are constantly replaced.

Both taste and smell project to the newer cerebral cortex, the neocortex for perception, and to the older cortex in the limbic system for automatic responses of hunger, pleasure, etc.

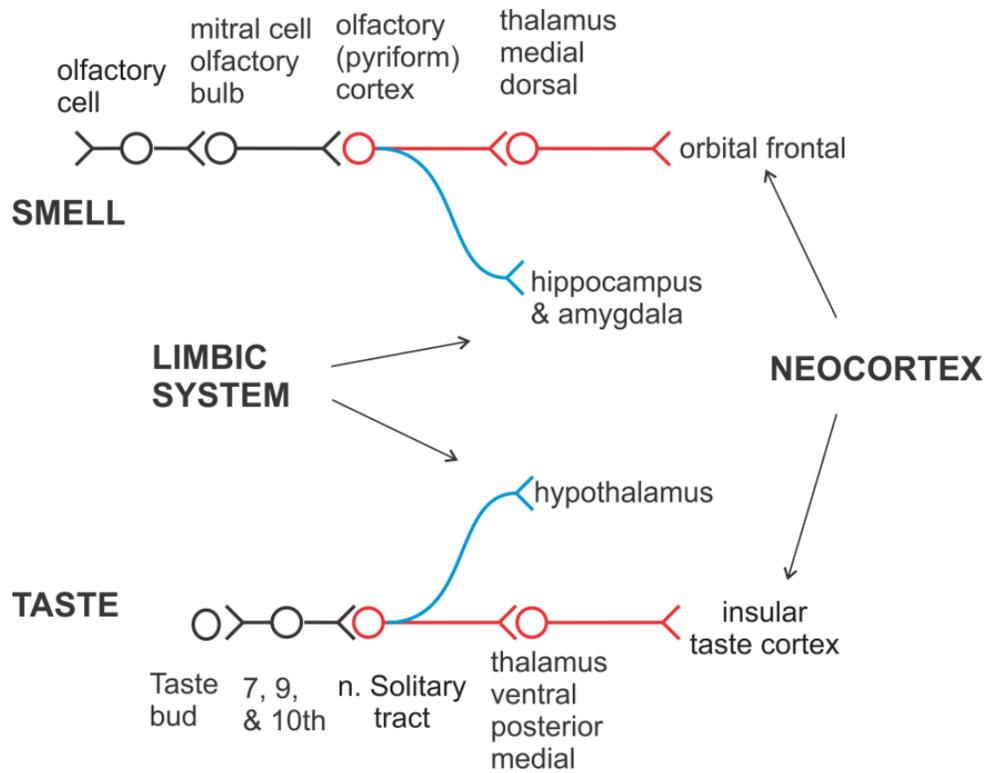


Figure 7. 28 A Comparison of the Pathways for Taste and Smell

See problems and answers posted on

<http://www.tutis.ca/Senses/L7Touch/L7TouchProb.swf>

## References

- Blakemore SJ, Wolpert D, Frith C. 2000. Why can't you tickle yourself? *Neuroreport* 11: R11-6
- Bushdid C, Magnasco MO, Vosshall LB, Keller A. 2014. Humans Can Discriminate More than 1 Trillion Olfactory Stimuli. *Science (New York, N.Y)* 343: 1370-72
- Goodwin AW, Macefield VG, Bisley JW. 1997. Encoding of object curvature by tactile afferents from human fingers. *Journal of neurophysiology* 78: 2881-8
- Haddad R, Lanjuin A, Madisen L, Zeng HK, Murthy VN, Uchida N. 2013. Olfactory cortical neurons read out a relative time code in the olfactory bulb. *Nature neuroscience* 16: 949-U227
- Kaas JH. 1983. What, if anything, is SI? Organization of first somatosensory area of cortex. *Physiological Reviews* 63: 206-31