Mind, Brain & Behaviour 1
Behavioural Neuroscience

The auditory and somatosensory systems

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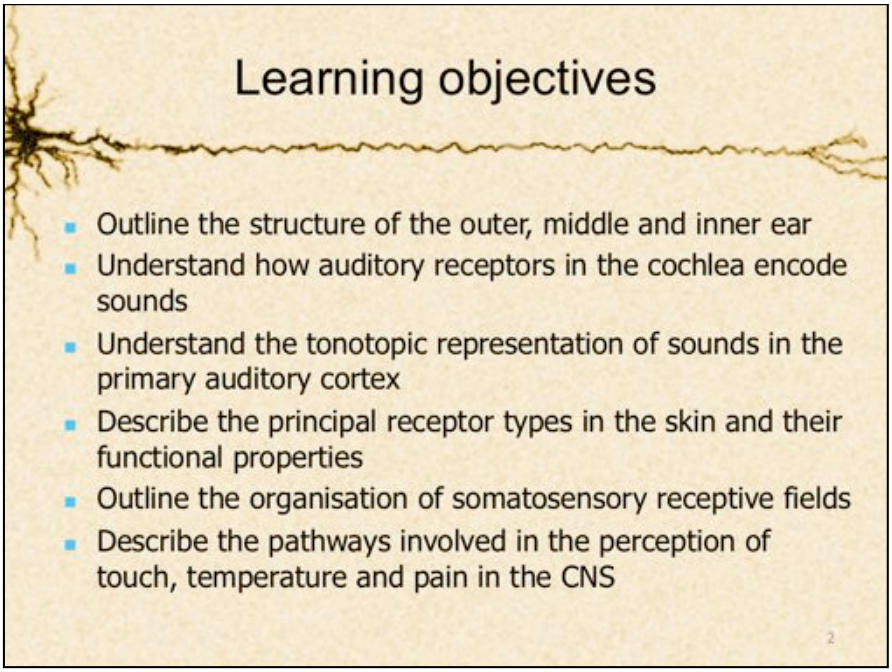
Learning objectives
Outline the structure of the outer, middle and inner ear
Understand how auditory receptors in the cochlea encode sounds
Understand the tonotopic representation of sounds in the primary auditory cortex
Describe the principal receptor types in the skin and their functional properties
Outline the organisation of somatosensory receptive fields
Describe the pathways involved in the perception of touch, temperature and pain in the CNS
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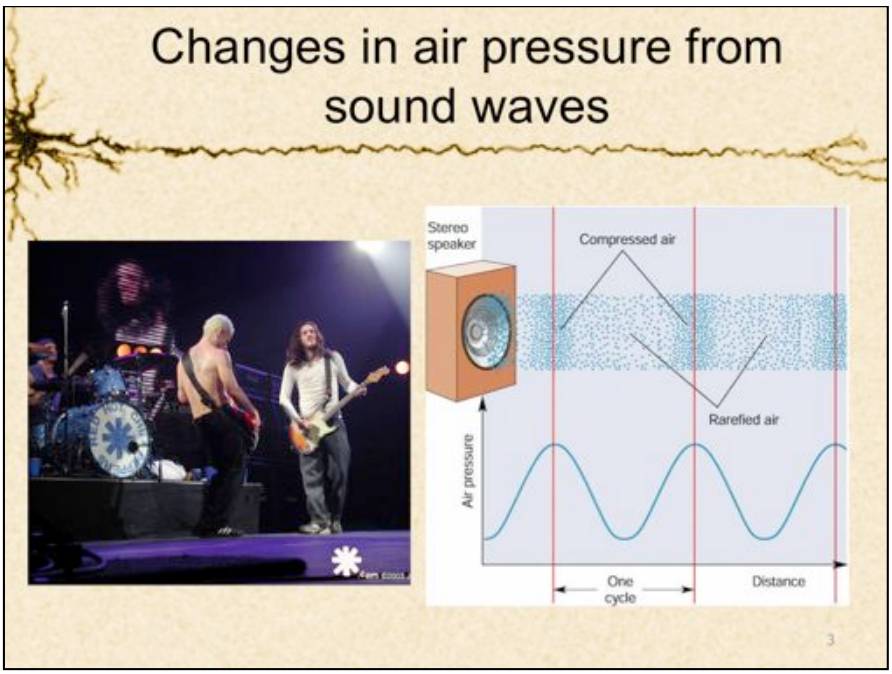
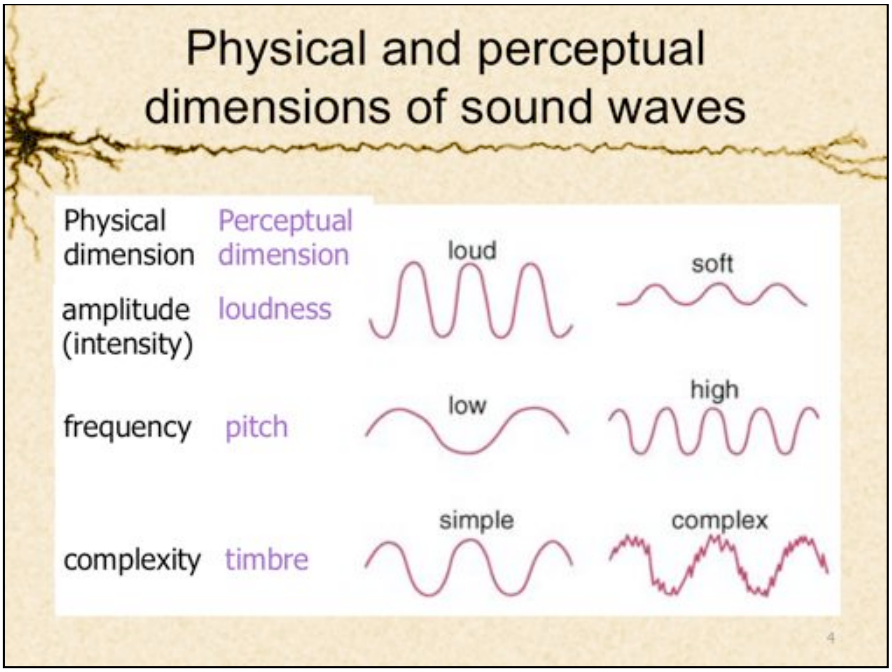


Our sense of hearing (audition) is vital for many aspects of everyday life. It serves as an 'early warning system' when vision is not available (e.g., when our line of sight is occluded, or at night). Hearing also underlies our ability to communicate using spoken language.

We hear sounds when objects vibrate, which in turn causes air molecules to **compress** and **rarefy** (become more dispersed) leading to waves that travel away from the object at around 1,100 km/h. The frequency of the vibration is measured in cycles per second (Hertz, Hz).

Humans can perceive sounds in the range of 30 – 20,000 Hertz (Hz).



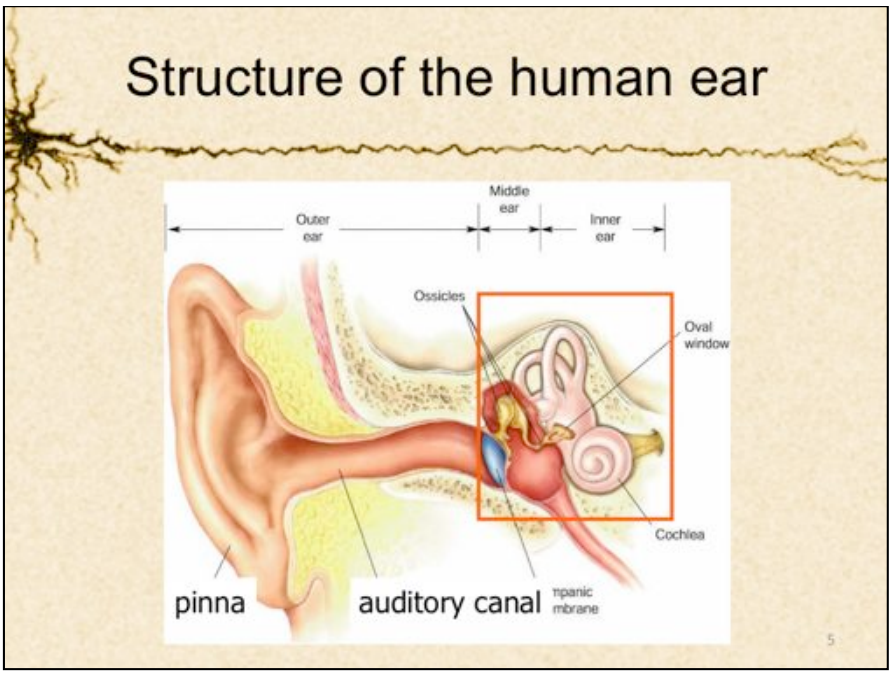
Several aspects of the travelling sound wave determine how things sound.

There are three perceptual dimensions of sound, and each if these corresponds with a particular physical dimension:

Loudness is determined by the degree to which air molecules are pushed together and pulled apart; more vigorous vibrations of an object cause larger amplitude sound waves, which in turn leads to more intense sounds.

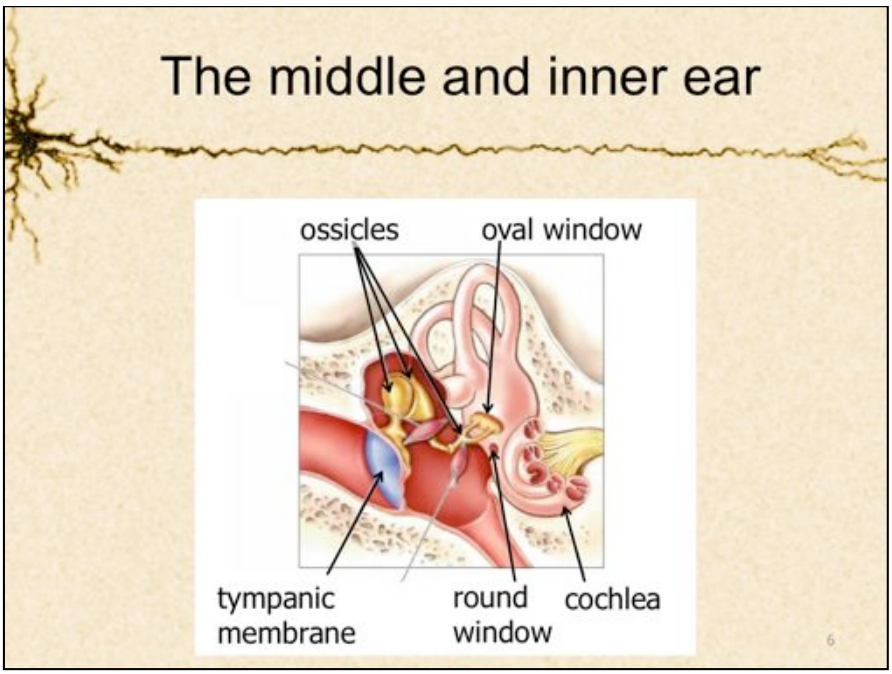
Pitch is determined by the frequency of sound waves produced by a vibrating object; the more sound waves per second the higher pitched the sound.

Timbre (sound 'quality') is determined by the complexity of the sound waves; the more little peaks and troughs in the waveform the more complex the sound. A completely smooth sinusoidal waveform is a pure tone.



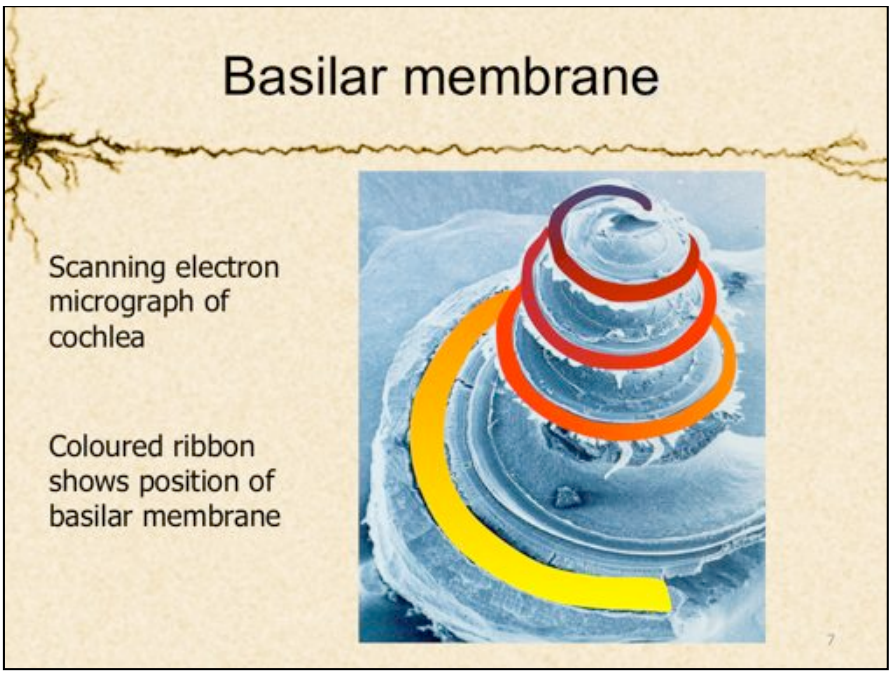
The human ear consists of three basic parts:

Outer ear: consists of the outer fleshy **pinna**, the **auditory canal**, and the **tympanic membrane** (eardrum). The tympanic membrane vibrates with the soundwaves that enter the auditory canal, and this signal is transmitted on to the middle ear.

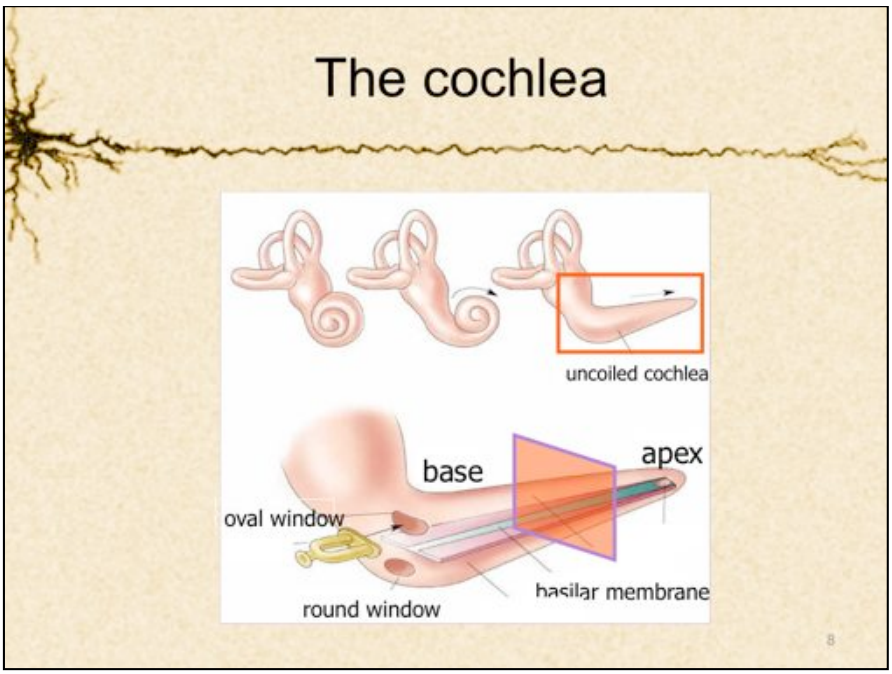


Middle ear: consists of three tiny bones called **ossicles**. The **malleus** (hammer) is connected to the tympanic membrane. It transmits vibrations via the **incus** (anvil) to the **stapes** (stirrup), which is connected to a structure called the cochlea (snail), which is part of the inner ear.

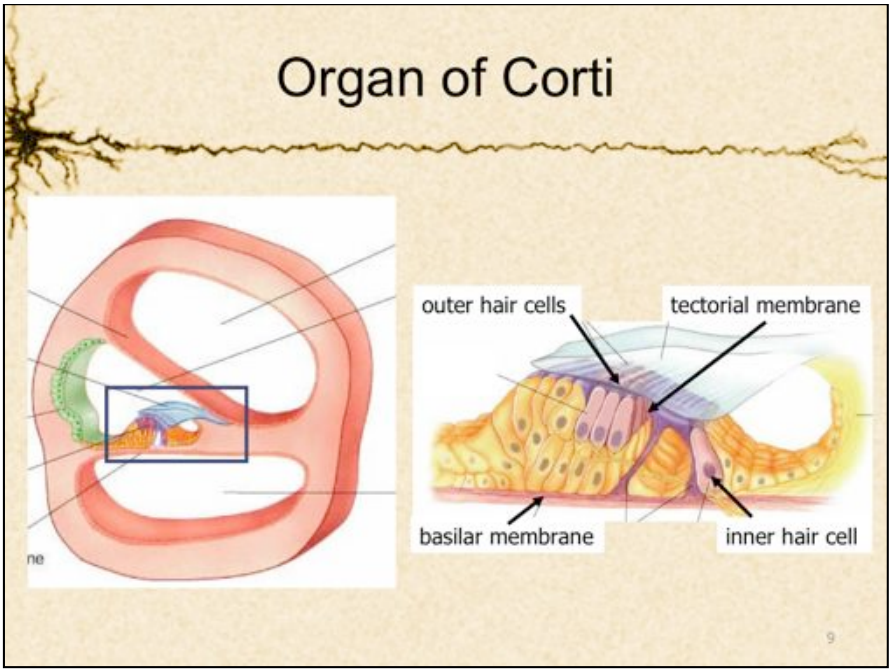
Inner ear: consists of the **cochlea**, which contains the receptors for analysing sounds. The cochlea is a bony structure, but it has two small membranes that form windows on its fluid-filled interior. The stapes is connected to the **oval window**. Sound waves that cause the stapes to move in and out move the fluid over receptors inside the cochlea. Because the cochlea is a closed structure, another membrane is needed to allow the fluid to move: this membrane is called the **round window**.



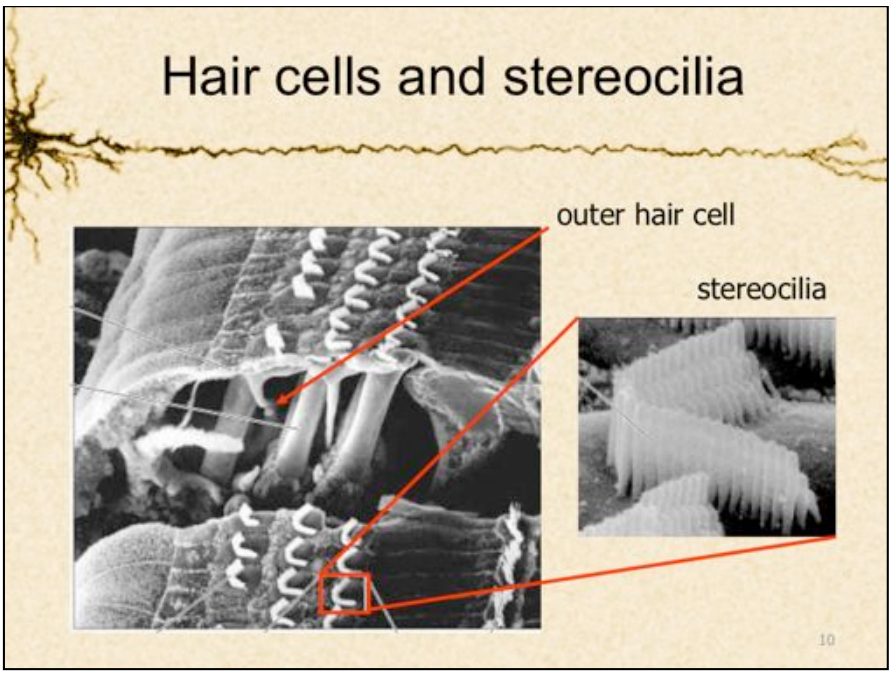
The cochlea derives its name from its snail-like shape. This scanning electron micrograph shows a cochlea whose bony roof has been cut away. The coloured ribbon has been added to illustrate the position and shape of the sheet of tissue that contains the auditory receptors – this sheet of tissue is called the **basilar membrane**.



The basilar membrane sits in the centre of the cochlea, and runs all the way from its **base** to its **apex** (top). In this diagram the cochlea has been uncoiled to reveal its longitudinal structure. By slicing through the uncoiled cochlea as illustrated we can take a look at its structure in cross-section.

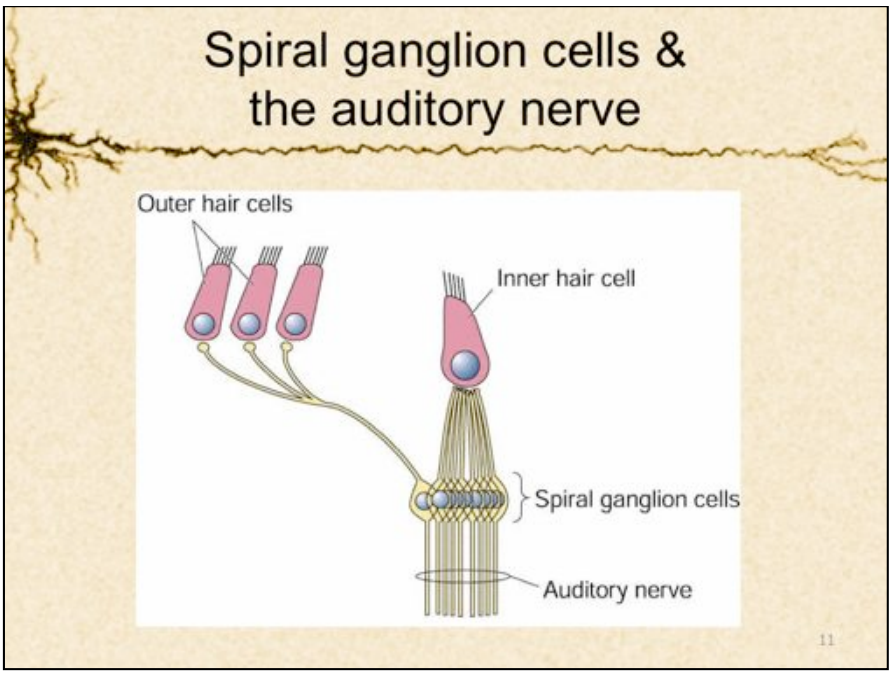


A cross-section taken across the longitudinal axis of the cochlea reveals three inner chambers, each of which is filled with fluid. On the floor of the centre chamber is a structure called the **Organ of Corti**, which runs all the way along the length of the cochlea. The Organ of Corti is composed of the **basilar membrane** at its base, receptors in the middle called **hair cells** (inner and outer), and a rigid shelf over the top called the **tectorial membrane** (recall from Lecture 4 that 'tectum' means roof).



This scanning electron micrograph shows a portion of the Organ of Corti. Where the tectorial membrane has been cut away it is possible to see the hair cells. Note that on top of the hair cells are tiny filaments called **stereocilia**.

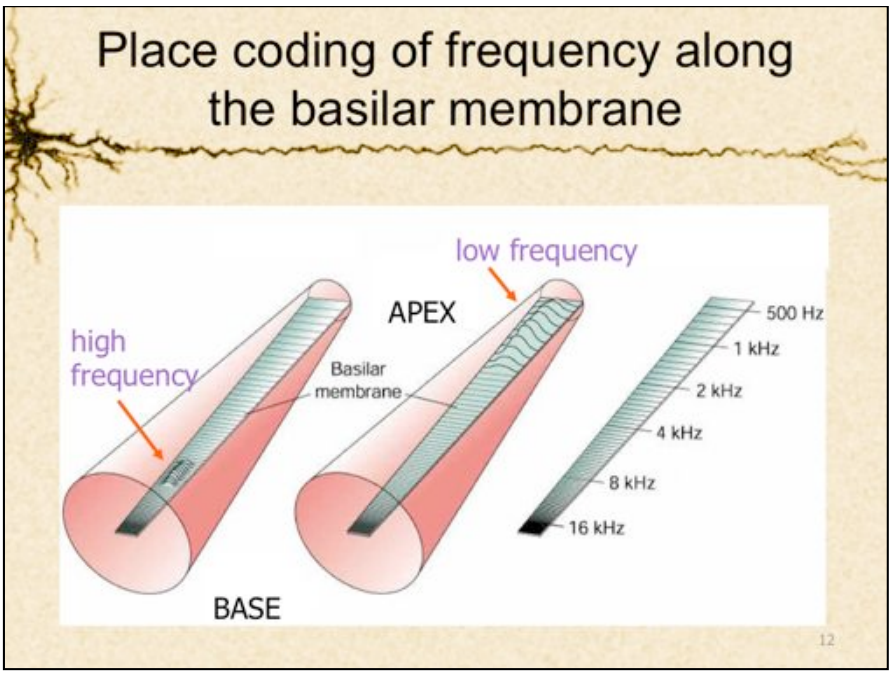
Sound waves cause the basilar membrane to move relative to the tectorial membrane above it. This motion effectively bends the stereocilia, either by direct contact with the tectorial membrane (in the case of outer hair cells), or by fluid motion induced by movement of the basilar membrane. Bending of the stereocilia of hair cells is what produces receptor potentials that convert sound waves into neural signals.



When the sterocilia are moved ion channels are opened which in turn cause receptor potentials in the hair cells. The hair cells secrete a neurotransmitter that triggers action potentials in neurons called **spiral ganglion cells**. The axons of many thousands of spiral ganglion cells are grouped together to form the **auditory nerve**, which as we saw in Lecture 5 is the 8th cranial nerve.

The axons of auditory nerve neurons form synapses with neurons in the **medulla** (part of the brainstem), which in turn send their axons to other parts of the brain for further processing, as described later in the lecture.

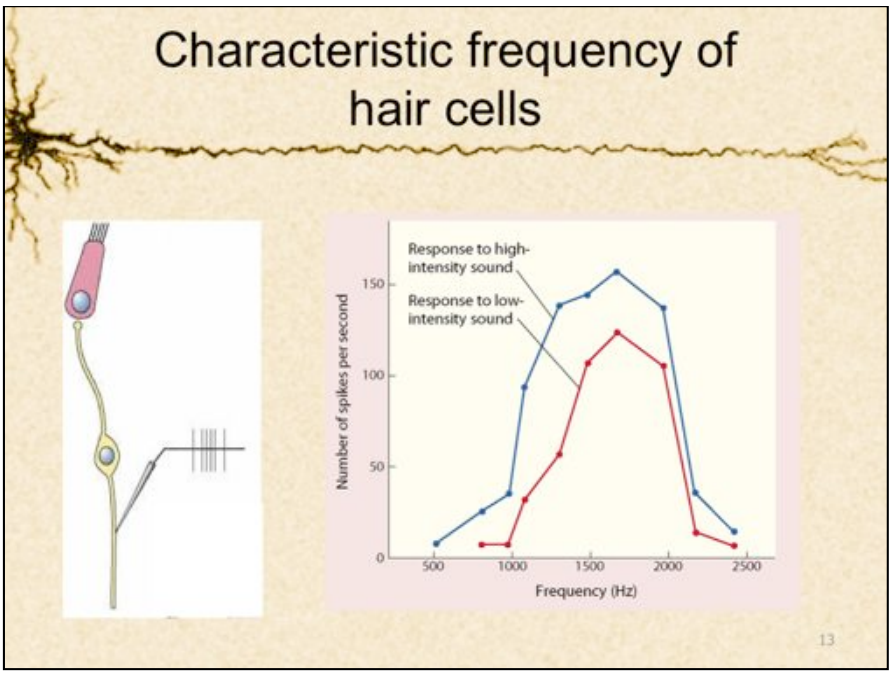
It is worth noting that about 95% of all axons of the auditory nerve form synapses with the inner hair cells, and just 5% do so with outer hair cells. In fact it is the inner hair cells that seem crucial for hearing. Animals and humans with inner hair cell damage have profound hearing losses. It is believed that the outer hair cells are not involved directly in hearing at all, but rather act as effector cells by changing the mechanical properties of the basilar membrane and thus modulating the effects of sound waves on the inner hair cells.



As outlined earlier, the perceptual dimension of pitch is determined by the physical dimension of frequency (of sound waves). In this lecture we shall focus on how the auditory system processes sound frequency, although there is obviously much more to hearing than pitch (e.g., loudness, timbre, spatial location).

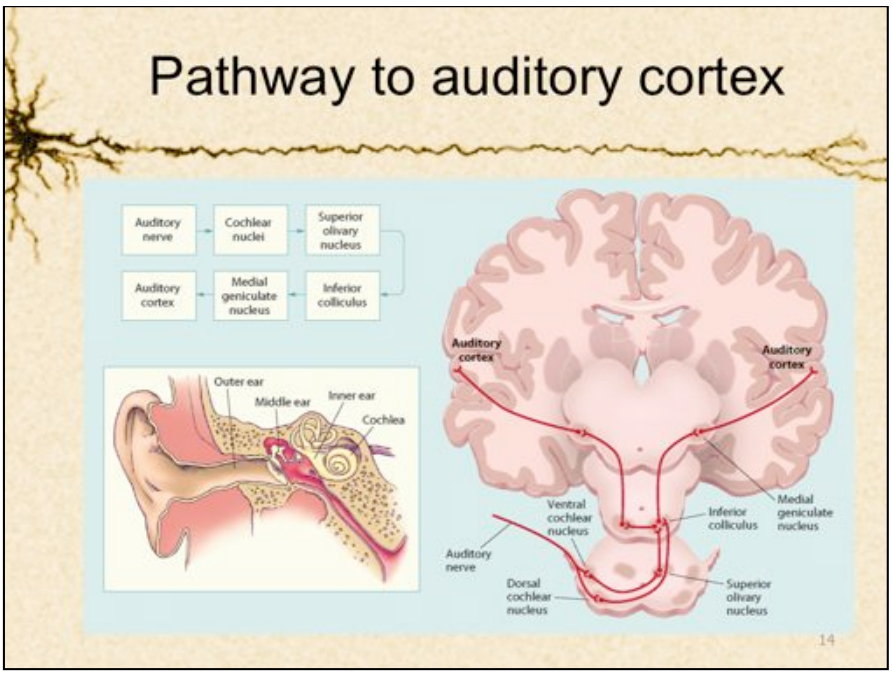
Sounds of different frequencies cause different regions of the basilar membrane to flex back and forth. Specifically, **higher frequencies** produce greater displacements of the basilar membrane toward its **basal end**, and **lower frequencies** produce more displacement at its **apex** (note the initially counterintuitive relationship between frequency and place on the basilar membrane).

Thus sounds of different frequencies are detected by means of a **place code** (i.e., a particular frequency of sound wave moves the basilar membrane maximally at a particular **place** along its length). Different frequencies of sound are therefore coded by the particular spiral ganglion cells that are active along the basilar membrane, and this information is transmitted via the auditory nerve to the brainstem and other parts of the brain.



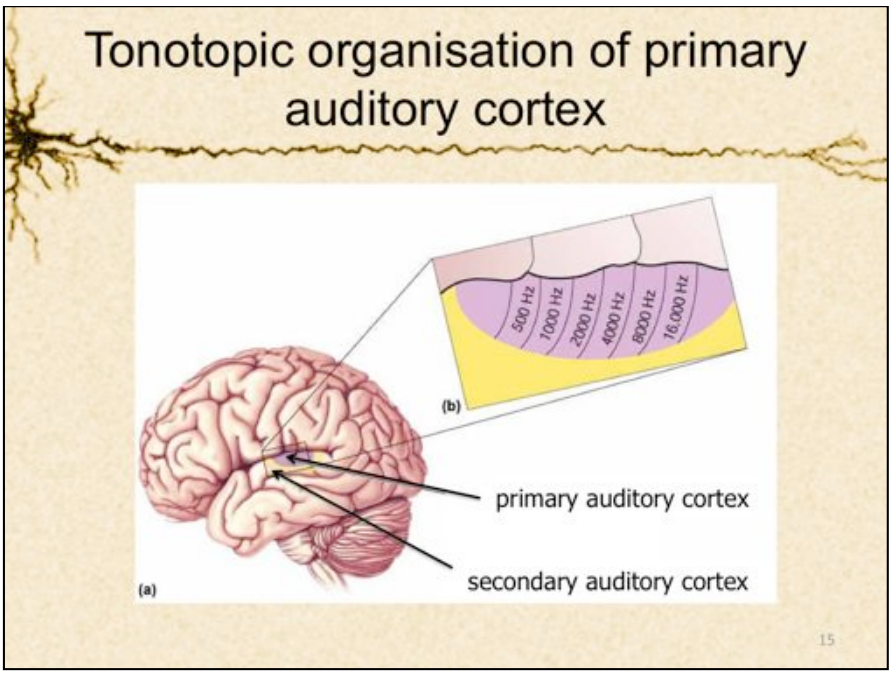
Recording extracellular membrane potentials from the axon of a spiral ganglion cell demonstrates the particular frequencies of soundwave to which that neuron responds best. This is shown by the tuning curve which shows the number of action potentials ('spikes') recorded from the neuron as a function of sound frequency.

This particular neuron has a preferred frequency of around 1600 Hz; note that the cell's firing rate declines rapidly for frequencies above and below 1600 Hz. Note also that this cell increases its overall firing rate in response to high-intensity versus low-intensity sounds, but the preferred frequency of 1600 Hz remains unchanged (i.e., the peaks of the functions are at the same frequency).



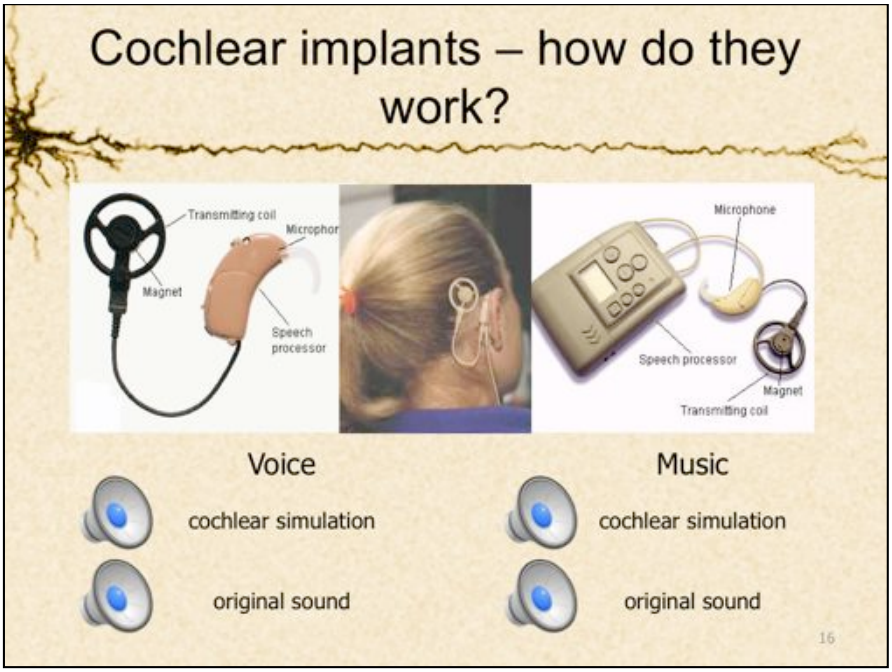
The auditory nerve carries neural information from the cochlea to the brainstem. Note that the auditory pathway to the primary auditory cortex is complex, and there are several synapses in various brainstem and midbrain structures along the way. It is not necessary to remember the names of all these structures, but you should bear in mind that auditory signals have already been through several stages of processing before they reach the primary auditory cortex.

Note also that signals from the auditory nerve of each ear are transmitted to **both** cerebral hemispheres. Thus, unlike the primary visual cortex which processes information exclusively from the contralateral visual field, the primary auditory cortex processes sounds from both ears and both sides of space. In fact processing of inputs from the two ears (**binaural processing**) is essential for localising sounds in space.



The **primary auditory cortex** is located in a region of the temporal lobe called the **superior temporal gyrus** (as you will recall from Slide 23 in Lecture 4). Much of this cortical region is buried inside the deep fold of the **lateral fissure**, and is therefore not visible from a lateral view of the brain.

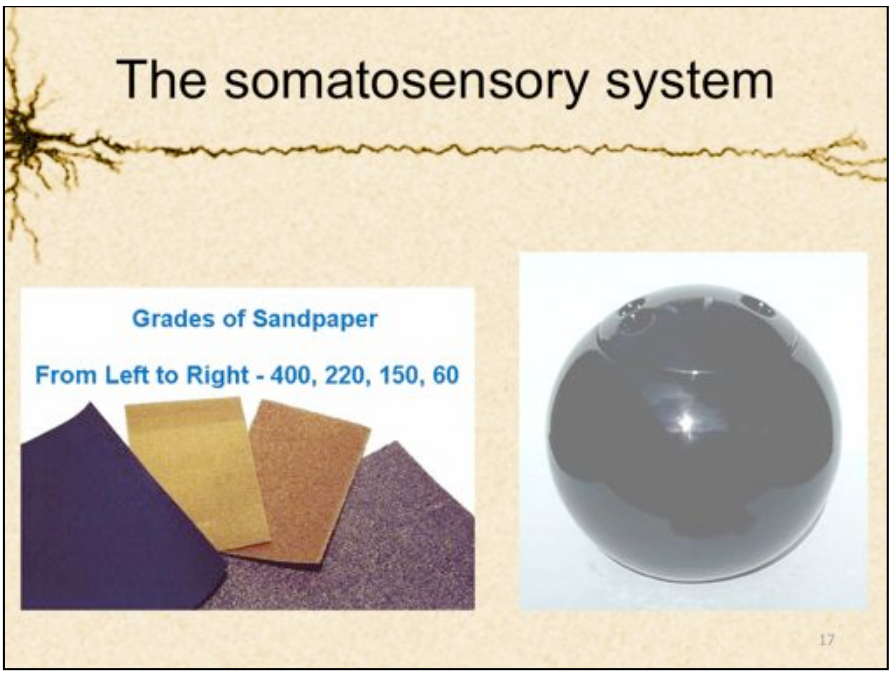
Just as the basilar membrane represents different frequencies along its length, so the primary auditory cortex is organised as a **tonotopic map**, with lower frequencies represented more anteriorly and higher frequencies more posteriorly.



Having considered the brain structures and processes underlying normal hearing, it is possible to understand the various reasons for hearing loss, and the recent attempts by scientists to find ways to restore hearing.

For individuals with damage to the hair cells, typically due to a congenital abnormality, one approach to restoring hearing is to use a **cochlear implant**. The cochlear implant has several key components. On the outside of the head, a microphone sits behind the pinna and detects sounds in the environment. It feeds inputs to an electronic signal processor. On the inside, a surgeon implants a tiny array of electrodes into the cochlea so that it follows the snail-like curl and rests against the basilar membrane along its length. Each electrode in the array stimulates a particular part of the basilar membrane. The electrodes receive their inputs from the external signal processor, via a circular transmitter fitted to the scalp.

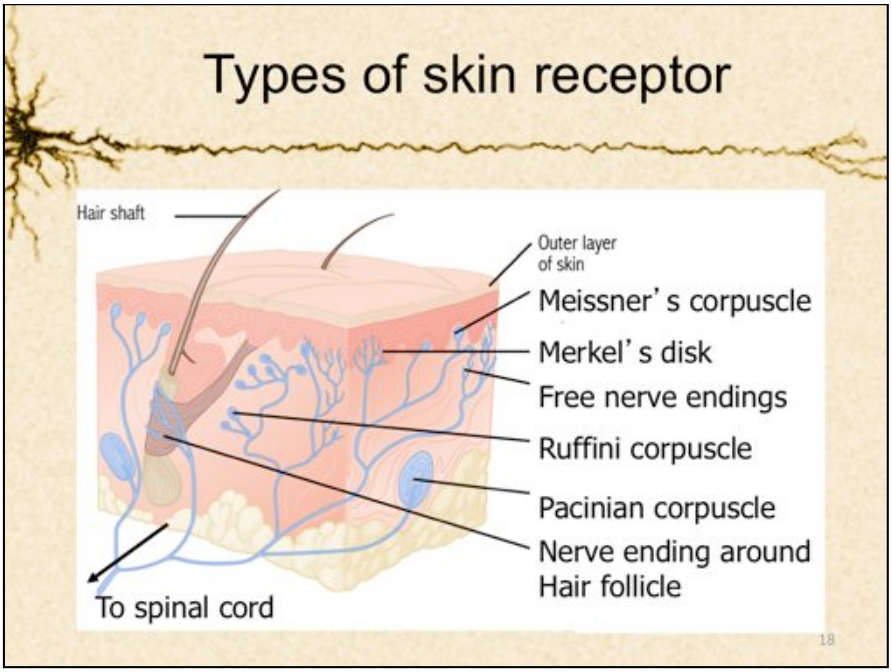
The main aim of cochlear implants is to help the individual to understand speech. The sound information provided by such an implant certainly achieves this aim in most individuals, but the quality of the signal is still well below what people with normal hearing are used to.



The **somatosensory system** is responsible for representing what is happening to the outer surface of the body and inside it.

The somatosensory system incorporates the **cutaneous senses** (those pertaining to touch), **kinaesthesia** (information about the positions of the limbs), and the **organic senses** (information about the state of internal organs). In this lecture we will focus on the cutaneous senses. We shall consider kinesthesia in a later lecture on the sensorimotor system.

The cutaneous senses respond to many different aspects of stimuli that impinge directly or indirectly on the skin: **pressure**, **vibration**, **heating**, **cooling**, and noxious stimuli that damage the skin and cause **pain**.



The skin is a vital organ of the body, and one that we cannot survive without. Although extensive damage to the visual and auditory systems may be detrimental to our everyday behaviour, extensive burns to the skin are often fatal.

The skin is essential for maintaining fluid balance, and for thermoregulation (e.g., sweating cools the body, constriction of surface blood vessels conserves heat). The appearance of the skin varies widely across different body sites, from the hairy skin of our scalp, arms and legs to the smooth, glabrous (i.e., hairless) skin of the palms and soles of the feet.

The skin consists of several different types of receptors, each of which performs a specific role in transmitting cutaneous information.

Hairy skin contains the following receptors:

Ruffini corpuscles respond to indentation of the skin.

Pacinian corpuscles respond to rapid vibrations. These are relatively large receptors (up to 1 mm in diameter), made up of many onion-like layers wrapped around the dendrite of a single axon.

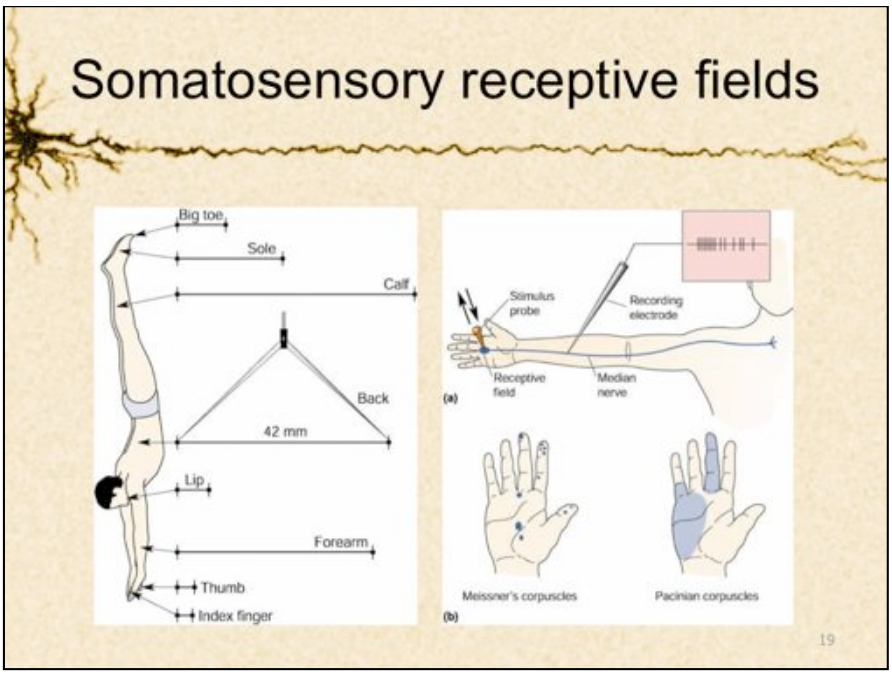
Free nerve endings, which are located near the outer layer of the skin, detect painful stimuli and changes in temperature. Free nerve endings are also found around hair follicles, and are responsible for detecting movements are the hairs.

Glabrous skin has a more complex array of receptors, which probably reflects the fact that we use these surfaces (fingers, palms) to actively explore objects in the environment. By contrast, hairy skin surfaces are normally passive recipients of information from objects that come into contact with them. In addition to the receptors already listed above, glabrous skin also contains:

Meissner's corpuscles, which respond to taps and low-frequency vibrations.

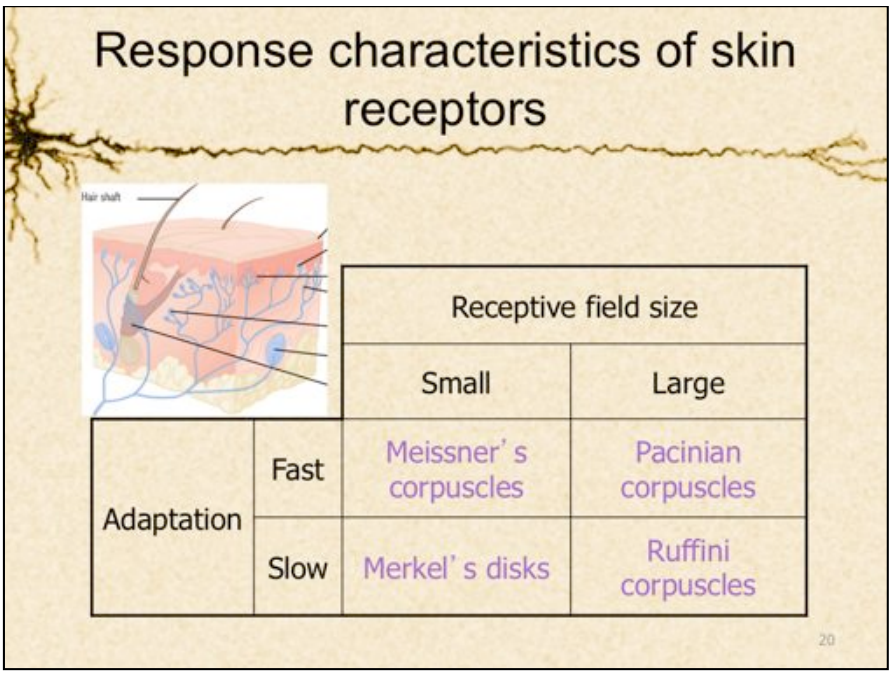
Merkel's disks, which respond to indentation of the skin.

The cell bodies of neurons whose dendrites are present in the skin are located in the dorsal root ganglia of the spinal cord.



By placing a microelectrode into a single axon carrying information from the skin to the dorsal root ganglia of the spinal cord, it is possible to measure the **receptive field** of the neuron concerned (i.e., the region of the skin surface over which it responds to its preferred stimulus, such as indentation, vibration, etc.).

The size of the receptive fields for the various receptor types varies considerably for different regions of the skin surface. In regions where the receptive fields are small and densely packed, the ability to discriminate between two points is much higher than in regions where the receptive fields are large and more sparsely distributed. Thus, our threshold for discriminating two points on the index finger is around 2 or 3 mm, whereas our threshold on the back is more than 40 mm.

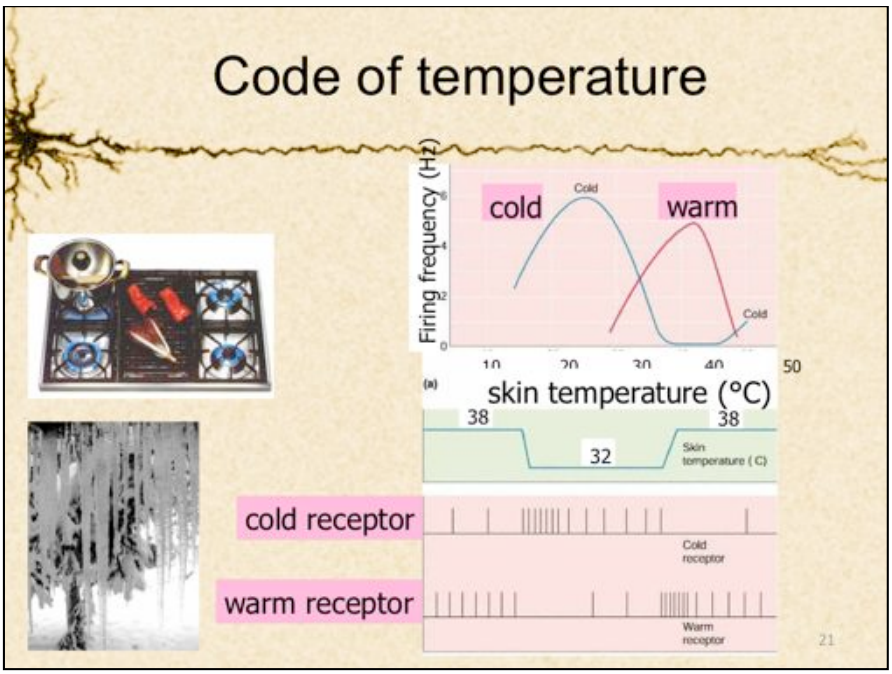


The different types of skin receptor can be characterised by two functional properties:

1) **Receptive field size** (small, large)
2) **Adaptation** (fast, slow)

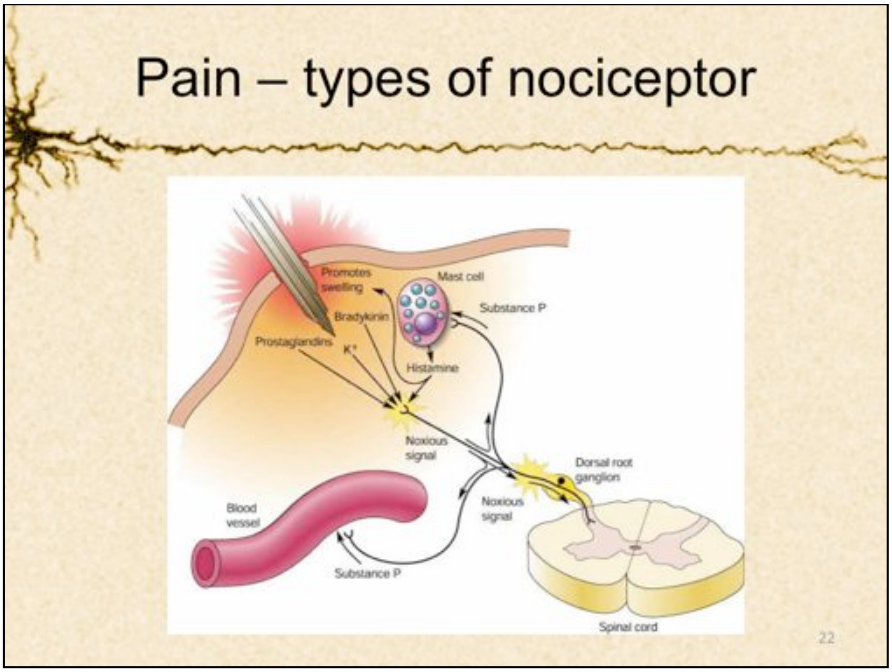
Constant, non-painful stimulation of the skin tends not to be very effective in evoking skin sensation. For example, when sitting still we are not aware of the skin sensations associated with the band of a wristwatch or of our clothes. The skin responds to **changing**, rather than static stimulation.

The reason for the lack of sensation to static stimuli is that the skin receptors readily **adapt** to a constant stimulus. Meissner's corpuscles and Pacinian corpuscles are fast adapting, and hence tend to encode rapid vibration (which translates to the perceptual dimension of **roughness**). Merkel's disks and Ruffini corpuscles are slow adapting, and encode indentation of the skin.



Temperature is encoded by free nerve endings in the skin.

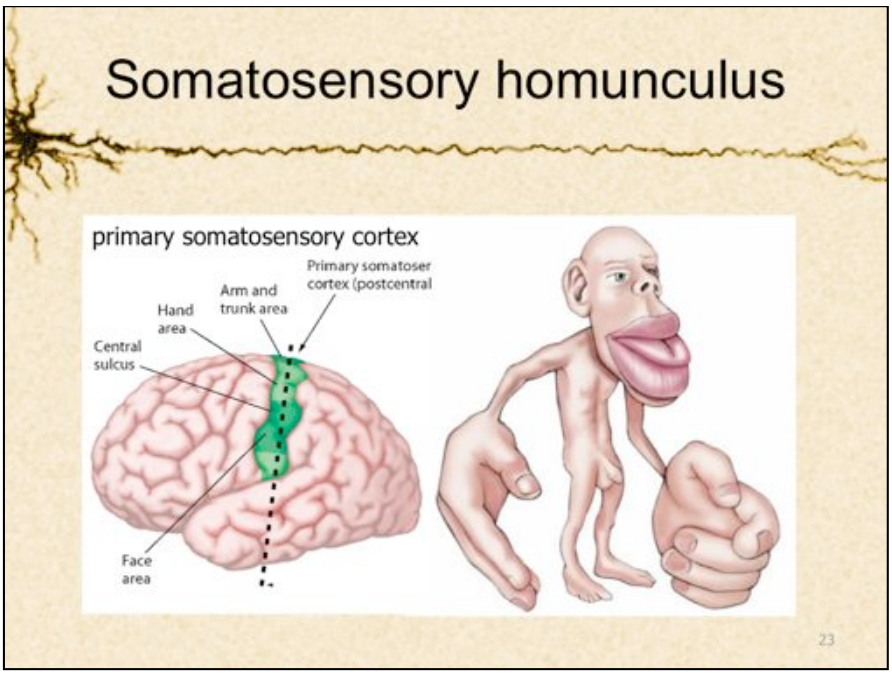
Sensations of warmness and coolness are **relative** rather than absolute. Thus, whether a particular region of skin feels warm or cool depends on the immediately prior thermal stimulation of that region. Cold receptors and warm receptors respond to **changes** in skin temperature.



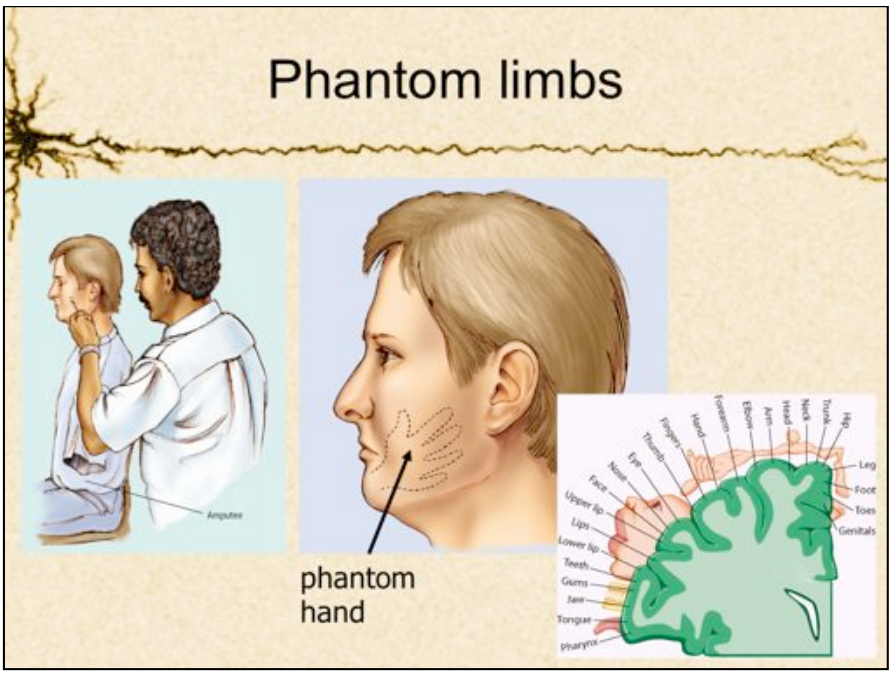
Pain sensation is also encoded by free nerve endings. There are three types of pain receptors (**nociceptors**) in the skin:

1) **High-threshold mechanoreceptors**, which encode striking, stretching or pinching.
2) **Capsaicin receptors**, which respond to extreme heat, acid and capsaicin (the fiery ingredient in chilli peppers)
3) **ATP receptors**, which respond when a muscle is damaged or blood supply is interrupted (these fibres are most likely responsible for the pain associated with muscle injury and migraine). [Recall that ATP, or adenosine triphosphate, is the fuel for cell metabolism.]

The axons from pain receptors have their cell bodies in the dorsal root ganglia of the spinal cord.



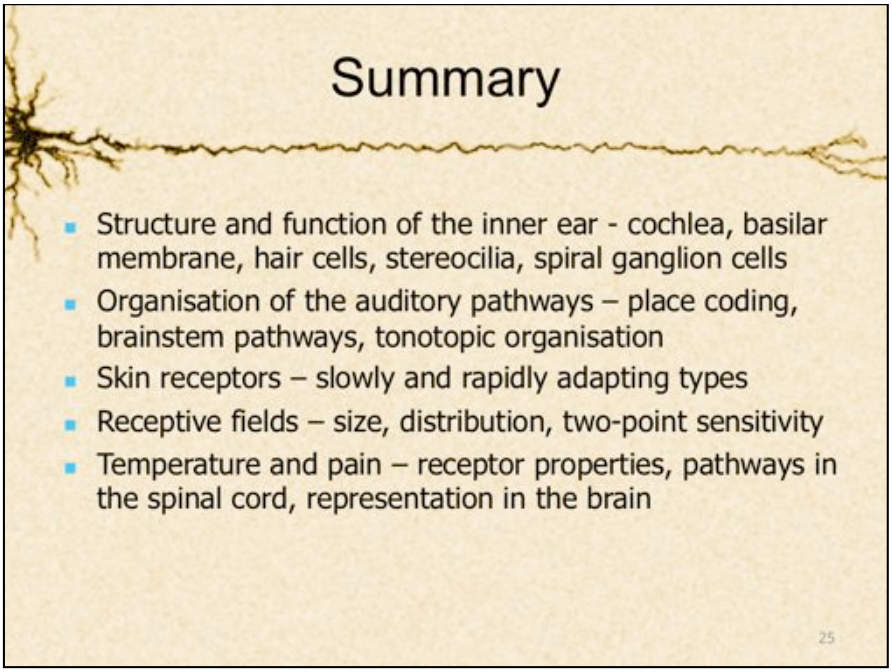
Recall that the primary somatosensory cortex is organised in such a fashion that it forms a **somatotopic map** of the skin surface (see Slide 20, Lecture 4). The amount of somatosensory cortex devoted to representing particular areas of skin is not reflected by their surface area, but rather by their sensitivity. The somatosensory homunculus ('little man') provides a graphical interpretation of the relative amount of the somatosensory cortex that is devoted to different regions of the skin (see Slide 21, Lecture 4). Note the oversized hands, fingers, lips and tongue.



One interesting aspect of the somatosensory cortex is that it often continues to function after the skin that innervates it has been removed, either by surgical or accidental amputation (e.g., of a limb).

Phantom limbs are the sensations that arise from a limb that is no longer present. They occur in about 70% of patients with limb amputations. Phantom limbs are very real to the perceiver, and can often be quite painful. People can move their phantom limbs, and many manoeuvre themselves to avoid knocking their phantom against a chair or doorframe. In fact all of the sensations that can be experienced with a normal limb are experienced in phantoms limbs, including pain, pressure, warmth, cold, wetness, and itchiness.

Occasionally the phantom limb may ‘migrate’ so that it is felt as part of another region of the skin. For instance, when touched on the same side of the cheek as the missing limb, individuals often report feeling the stroking sensation on their phantom limb as well. The most likely explanation is that adjacent areas of the cortex represent the face and hand, and that the region of cortex that once subserved the limb alone now represents skin sensations from the face as well. This kind of phenomenon provides an example of remarkable **plasticity** in the functional organisation of the adult somatosensory system.


Summary
Structure and function of the inner ear - cochlea, basilar membrane, hair cells, stereocilia, spiral ganglion cells
Organisation of the auditory pathways – place coding, brainstem pathways, tonotopic organisation
Skin receptors – slowly and rapidly adapting types
Receptive fields – size, distribution, two-point sensitivity
Temperature and pain – receptor properties, pathways in the spinal cord, representation in the brain
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