Different forms of energy require different means of transduction. The human ear is divided into three distinct parts.

The **outer ear** consists of the visible ear (the pinna), the auditory canal, and the eardrum, which responds to sound waves gathered by the pinna and channeled into the canal.

The **middle ear** is a tiny air-filled chamber behind the eardrum, containing the ossicles—the hammer, anvil and stirrup bones—all of which create a lever that mechanically transmits and intensifies vibrations from the eardrum to the inner ear.

The **inner ear** contains the spiral-shaped cochlea, a fluid-filled tube that is the organ of auditory transduction.

The **basilar membrane** of the inner ear is the structure that undulates when vibrations from the ossicles reach the cochlear fluid. Its wave-like movement stimulates thousands of tiny hair cells, specialized auditory receptor neurons embedded in this membrane.

The **hair cells** release neurotransmitter molecules, initiating a neural signal in the auditory nerve that travels to the brain. Memorize auditory transduction for the next exam.
Hearing

There are three physical dimensions of sound waves that correspond to auditory perception: frequency, amplitude & complexity. (Table 4.3)

Frequency: perception of pitch, measured in cycles per second or Hertz

Amplitude: perception of loudness, measured in decibels

Complexity: perception of timbre, which allows us to distinguish two sources with the same pitch and loudness

Memorize Fig. 4.20 Anatomy of the Human Ear for the next exam, especially the areas of the brain dedicated to auditory perception

Sound is converted to neural impulses in the inner ear.

Cochlea: fluid-filled tube containing cells that transduce sound vibrations into neural impulses

Basilar membrane: structure in the inner ear that moves up and down in time with vibrations relayed from the ossicles, transmitted through the oval window
**Primary Auditory Cortex**

- **Place code**: different frequencies stimulate neural signals at specific places along the basilar membrane. Fig. 4.21

  Bekesy, 1960 found that movement of the basilar membrane resembles a traveling wave; the frequency of the stimulating sound determines the wave's shape.

  When the frequency is low, the apex (wide floppy tip) of the basilar membrane moves the most; when the frequency is high, the base (narrow stiff end) moves the most.

  The movement of the basilar membrane causes hair cells to bend, initiating a neural signal in the auditory nerve. Axons fire the most in the hair cells along the area of the basilar membrane with the most motion. The brain processes the information about which axons are the most active.

- **Temporal code**: registers relatively low frequencies (up to about 5000 Hz) via the firing rate of action potentials entering the auditory nerve. Action potentials from the hair cells are synchronized in time with the peaks of the incoming sound waves. Fig 4.22

  This process provides the brain with very precise information about pitch that supplements information provided by place code.

  The firing rate of individual neurons is only of limited relevance, since typically information is coded across groups of cells.
Perceiving Pitch, Loudness, Timbre, Location

Location: like binocular vision, location is not perceived directly, but calculated by using different cues

Monaural cues for location: the intricate folds of the pinna alter sounds, emphasizing some frequency components over others depending on where the sound is coming from.

Sounds arrive sooner at the ear nearer to the source than at the far ear.

The time difference is effective for indicating the location of lower frequency components of a sound even when it is as brief as a few microseconds.

The higher frequency components of a sound are more intense in the ear closer to the sound, because the listener's head blocks the higher frequencies.

Turning your head to locate the source of a sound changes the relative intensity and timing of sound waves arriving in your ears and collecting better information about the likely source of the sound.

Turning your head also allows you to integrate vision and sound to locate the source of the sound, and 'vision is king' in the sensory system, simple by the greater amount of neural matter it is built on.
Perceiving Pitch

- From the inner ear, action potentials in the auditory nerve to the thalamus and ultimately to an area of the cerebral cortex called **area A1**, a portion of the temporal lobe that contains the primary auditory cortex.

- Auditory areas in the left hemisphere analyze sounds related to language and in the right hemisphere rhythms and music.

- There is also evidence that the auditory cortex is composed of two distinct streams, roughly analogous to the dorsal and ventral streams of the visual system. Note this is DTI at work.

- Spatial (where) auditory features allow the location of the source of a sound in space, and are processed by areas toward the caudal (back) part of the auditory cortex.

- Non-spatial (what) features, which allow identification of a sound are processed in the ventral (lower) part of the auditory cortex.

- All of hearing, however, depends on temporal aspects.

- Neurons in the area A1 respond to simple tones, and successive auditory areas in the brain process sounds of increasing complexity.

- The human ear is most sensitive to frequencies around 1000 to 3500 Hz.

- The human ear has two mechanisms to encode sound waves, one for high frequencies and one for low frequencies.
Localizing Sound Sources

- The placement of our ears on opposite sides of the head gives us stereophonic hearing. The sound arriving at the ear closer to the source is louder than the sound in the farther ear, mainly because the listener's head partially blocks the sound energy.

- This loudness difference decreases as the sound source moves away from a position directly to one side (maximal difference) to straight ahead (no difference).

- Another cue to a sound's location arises from timing. Sound waves arrive sooner at the near ear than at the far ear. The timing difference can be as brief as a few microseconds but together with the intensity difference, it is sufficient to allow us to perceive the location of a sound.

- When the sound source is ambiguous, you might turn your head from side to side to locate it.

- By doing this, you are changing the relative intensity and timing of sound waves arriving in your ears and collecting better information about the likely source of the sound.
Hearing Loss

- **Conductive hearing loss** arises because the eardrum and ossicles are damaged to the point that they cannot conduct sound waves effectively to the cochlea. The cochlea itself is normal, making this a mechanical problem with the moving parts of the ear (hammer, anvil, stirrup, eardrum).

- **Sensorineural hearing loss** is caused by damage to the cochlea, the hair cells, or the auditory nerve.

- A **cochlear implant** may offer some help; it is a device that replaces the function of the hair cells. The external parts of the device include a microphone and a speech processor, worn behind the ear. The implanted parts include a receiver just inside the skull and a thin wire containing electrodes inserted into the cochlea to stimulate the auditory nerve.

- What matters is age at implantation. See 'Big Technology for Little Ears', page 157

- Sound picked up by the microphone is transformed into electronic signals by the speech processor; the signal is then transmitted to the implanted receiver which activates the electrodes in the cochlea.

- Infants who have not yet learned to speak are especially vulnerable because they may miss the **critical period** for language learning. Without auditory feedback at this time, normal speech is nearly impossible to achieve. Early use of cochlear implants had been associated with improved speech and language skills for hearing-impaired children.
Music Training

- Musicians have greater plasticity in the motor cortex than non-musicians; they also have increased gray matter in motor and auditory brain regions compared with non-musicians.

- Musicians show differences in brain responses to musical stimuli compared with non-musicians.

- Musical training also extends to auditory processing in non-musical domains; they show enhanced brain responses when listening to speech compared with non-musicians.

- Musicians also exhibit an improved ability to detect speech when it is presented in a noisy background; this effect has been demonstrated even in children, who typically have serious problems preceiving this kind of speech.

- Correlation or causation? Individual genetic differences may lead some people to become musicians; recent experiments however, suggest a causal role. Learning to play an instrument demands attention to precise details of sounds.
Haptic Perception

- **Memorize Fig. 4.23 for the next exam**: the tactile receptive field, a small patch of skin that relates information about pain, pressure, texture, pattern, or vibration to a receptor.

- Haptic perception is the active exploration of the environment by touching or grasping objects with our hands. Four types of receptors located under the skin's surface enable us to sense pressure, texture, pattern, or vibration. Thermoreceptors are nerve fibers that sense cold and warmth. Memorize the figure 'Touch Receptors for the next exam.

- High acuity is defined as more of the tactile brain is devoted to parts of the skin surface where sensitivity to fine spatial detail (acuity) is greatest, such as fingertips and lips.

- There is mounting evidence (again from DTI) for a distinction between 'what' and 'where' pathways in touch analogous to vision and sound. 'What' system provides information about the properties of surfaces and objects; 'Where' system provides information about a location in external space that is being touched or a location on the body that is being stimulated.

- FMRI evidence suggests that the 'what' and 'where' touch pathways involve areas in the lower and upper regions of the parietal lobe, respectively.

- Tissue damage is also transduced by A-delta fibres, which register the initial sharp pain, and the C-fibres which transmit the longer-lasting duller pain.
Kinesthesia

One aspect of sensation and perception is knowing where parts of your body are at any given moment, or *proprioception*. Receptors in the muscles, tendons, and joints signal the position of the body in space, whereas information about balance and head movement originates in the inner ear.

Muscle, joint, and tendon feedback about how your arms are moving can be used to improve performance through learning (primarily in the cerebellum).

Maintaining balance depends primarily on the *vestibular system*, the three fluid-filled semi-circular canals and adjacent organs located next to the cochlea in each inner ear. The semicircular canals are arranged in three perpendicular orientations and studded with hair cells that detect movement when the head moves or accelerates. The bending of hair cells generates activity in the vestibular nerve which is then conveyed to the brain.

Vision also helps us keep our balance. Bertenthal et. al. (1997) experimented with the visual aspect of balance by placing people in rooms that can be tilted forward and backward. If the room tilts enough, people will topple over as they try to compensate for what their visual system is telling them.

When a mismatch between the information provided by visual cues and vestibular feedback occurs, motion sickness can result.

But that is not nearly as interesting as the emerging phenomenon of *cyberpuke*.

Pain

- Pain indicates damage (or potential damage) to the body. Congenital insensitivity to pain is a rare and dangerous disorder; children who experience this disorder are at increased risk of dying during childhood.

- **Chronic pain** is defined as pain that has persisted after the affected tissue has had time to heal. It is estimated to afflict 20% of the population. It consumes a large proportion of health care resources in Canada.

- Tissue damage is transduced by pain receptors; researchers distinguish between fast-acting A-delta fibres, which transmit the initial sharp pain, and the slower C-fibres, which transmit the longer-lasting duller pain that persists after the initial injury. Both the A- and C-fibres are impaired in congenital pain insensitivity.

- Neural signals for apoin travel to two distinct areas in the brain and evoke two distinct psychological experiences. One pathway sends signals to the somatosenary cortex, the 'where' of the pain, and the 'what' sort of pain; the second pathway sends signals to the emotional and motivational brain cortices—such as the hypothalamus and the amygdala—and to the frontal lobe. **Memorize Fig 4.24 for the next exam**

- Pain typically feels as if it comes from the site of the tissue damage that caused it.

- **Referred pain**, however, comes from around bones, muscles and internal organs, though it feels as if it were on the surface of the body. This pain occurs when sensory information from internal and external areas converges on the same nerve cells in the spinal cord.
Pain intensity cannot always be predicted from the extent of the injury; for example turf toe. A more accurate predictor is the amount of neural 'real estate' in the somatosensory cortex dedicated to that body part. That is why damage to the torso and legs is not as painful as damage to the lips or nose.

Gate-control theory holds that signals arriving from pain receptors in the body can be stopped, (or gated) by interneurons in the spinal cord via feedback from two directions. Pain can be gated, for example, by rubbing the affected area, activating skin receptors.

Pain can also be gated from the brain by modulating the activity of pain-transmission neurons. This neural feedback is elicited not by the pain itself, but rather by activity deep within the thalamus.

This neural feedback comes from a region in the midbrain called the periaqueductal grey (PAG). Under extreme conditions such as high stress, naturally occurring endorphins can activate the PAG to send inhibitory signals to neurons in the spinal cord that then suppress pain signals to the brain. PAG is also activated through the use of opiate drugs such as morphine.

There is also a pain-facilitation signal that increases the sensation of pain when we are ill (for example influenza).

Finally it should be noted the gate-control theory is challenged by the perception that pain is a two way street: bottom-up (eg. skin surface) versus top-down (brain).

Fig. 4.24 will be on the next exam.
Olfaction is the least understood sense and the only one directly connected to the forebrain & amygdala. Remember that the other senses connect through the thalamus. This indicates how ancient this neural pathway must be. **Memorize Fig. 4.25 for the next exam**

This mapping indicates that smell has a close relationship with areas involved in emotional and social behavior. Memorize the figure 'Anatomy of a Smell' for the next exam.

Terms to remember: **olfactory receptor neurons (ORN); odorant molecules; olfactory epithelium; glomerulus.**

Groups of ORNs send their axons from the olfactory epithelium into the olfactory bulb, a brain structure located above the nasal cavity beneath the frontal lobes. Humans possess 350 different ORN types, allowing us to discriminate between 10,000 odorants, as each one has a unique pattern of neural activity. Some dogs have 100 times more ORNs than do humans.

Humans can sense some smells in extremely small concentrations, such as **mercaptan**, at 0.0003 ppm.

Odour perception includes both information about the identity of the odour, as well as the emotional response. The **object-centred** approach suggests that information about the identity of the 'odour object' is quickly accessed from memory, triggering an emotional response.

The **valence-centred** approach suggests that the emotional response comes first, providing a basis for determining the identity of the odour. Research presently suggests that odour perception is guided first by memory and then by emotion.

Smell also exhibits sensory adaptation. Smells fade after a few minutes; reducing sensitivity allows us to detect new smells after the initial evaluation.

Top down: fMRI evidence indicates that the **orbitofrontal cortex** responds more strongly to smells labeled as 'pleasant' rather than 'unpleasant'. 
In a PET study (Savic et. al. 2005), heterosexual woman, homosexual man and heterosexual man were scanned as they were presented with each of several odours.

During the presentation of a testosterone-based odour, there was significant activation in the hypothalamus for heterosexual women and homosexual men, but not for heterosexual men.

An estrogen-based odour activated the hypothalamus in in heterosexual men but not in heterosexual women. Strikingly, homosexual men responded to this odour the same way that heterosexual women did.

Other common odours unrelated to sexual arousal were processed similarly by all three groups.

In a follow-up study (Bergund, Lindstrom & Savic) lesbians responded to the testosterone and estrogen odours largely similar to heterosexual men.

Taken together, the two studies suggest that some human pheromones are related to sexual orientation.
The tongue is covered with thousands of papilla, within each are hundreds of taste buds. Memorized the 'Taste Bud' figure for the next exam. Each taste bud contains 50 to 200 taste receptor cells. **Memorize Fig 4.26 for the next exam.**

- Taste perception fades with age; half of the taste receptors are lost by age 20.

- The test system contains only five main types of taste receptors: salt, sour, bitter, sweet, savoury (high proteins like meat and cheese (Yamaguchi, 1998)).

- Microvilli react to **tastant** molecules: salt to NaCL; sour to acids; bitter has 50 to 80 distinct binding sites; sweet to sugars and others.

- Savoury (umami) receptors respond to glutamate, an amino acid in protein foods. Glutamate is a major excitatory neurotransmitter, hence monosodium glutamate (MSG) is often used to flavour Asian foods.

- Taste & smell collaborate to produce flavour.

- Taste experiences also vary widely across individuals. About 50% of people (tasters) report a mildly bitter taste caffeine (for example), whereas 25%(non-tasters) do not.

- Bartoshuk, 2000 reported that the remaining 25% are super-tasters who find dark green vegetables bitter to the point of being inedible. **Super tasters** also tend to avoid fatty, creamy foods.