

WORLD CLASS EDUCATION

THE ANATOMY AND PHYSIOLOGY OF THE EAR AND HEARING

Hearing is one of the major senses and like vision is important for distant warning and communication. It can be used to alert, to communicate pleasure and fear. It is a conscious appreciation of vibration perceived as sound. In order to do this, the appropriate signal must reach the higher parts of the brain. The function of the ear is to convert physical vibration into an encoded nervous impulse. It can be thought of as a biological microphone. Like a microphone the ear is stimulated by vibration: in the microphone the vibration is transduced into an electrical signal, in the ear into a nervous impulse which in turn is then processed by the central auditory pathways of the brain. The mechanism to achieve this is complex. This module will deal mainly with the ear, first its structure and then its function, for it is the ear that is mainly at risk from hazardous sounds. The ears are paired organs, one on each side of the head with the sense organ itself, which is technically known as the cochlea, deeply buried within the temporal bones. Part of the ear is concerned with conducting sound to the cochlea, the cochlea is concerned with transducing vibration.

The transduction is performed by delicate hair cells which, when stimulated, initiate a nervous impulse. Because they are living, they are bathed in body fluid which provides them with energy, nutrients and oxygen. Most sound is transmitted by a vibration of air. Vibration is poorly transmitted at the interface between two media which differ greatly in characteristic impedance (product of density of the medium and speed of sound within it, c), as for example air and water. The ear has evolved a complex mechanism to overcome this impedance mis-match, known as the sound conducting mechanism. The sound conducting mechanism is divided into two parts, an outer and the middle ear, an outer part which catches sound and the middle ear which is an impedance matching device. Let us look at these parts in detail.

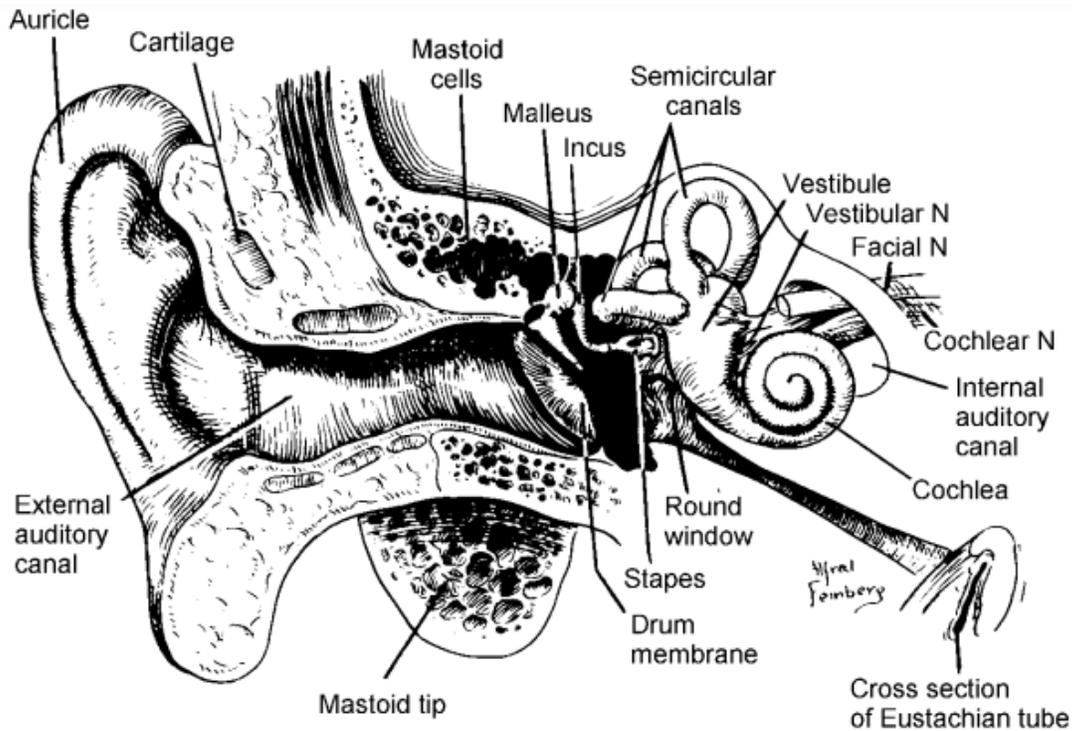


Figure 2.1. The pinna and external auditory canal form the outer ear, which is separated from the middle ear by the tympanic membrane. The middle ear houses three ossicles, the malleus, incus and stapes and is connected to the back of the nose by the Eustachian tube. Together they form the sound conducting mechanism. The inner ear consists of the cochlea which transduces vibration to a nervous impulse and the vestibular labyrinth which houses the organ of balance. (from Hallowell and Silverman, 1970)

SOUND CONDUCTING MECHANISMS

The Outer Ear

The outer ear transmits sound to the tympanic membrane. The pinna, that part which protrudes from the side of the skull, made of cartilage covered by skin, collects sound and channels it into the ear canal. The pinna is angled so that it catches sounds that come from in front more than those from behind and so is already helpful in localizing sound. Because of the relative size of the head and the wavelength of audible sound, this effect only applies at higher frequencies. In the middle frequencies the head itself casts a sound shadow and in the lower frequencies phase of arrival of a sound between the ears helps localize a sound. The ear canal is about 4 centimetres long and consists of an outer and inner part. The outer portion is lined with hairy skin containing sweat glands and oily sebaceous glands which together form ear wax. Hairs grow in the outer part of the ear canal and they and the wax serve as a protective barrier and a disinfectant. Very quickly however, the skin of the ear canal becomes thin and simple and is attached firmly to the bone of the deeper ear canal, a hard cavity which absorbs little sound but directs it to the drum head (eardrum or tympanic membrane) at its base. The outer layer of the drumhead itself is formed of skin in continuity with that of the ear canal.

In life, skin sheds and is continuously renewing. Ear canal skin grows like a fingernail from the depths to the exterior so that the skin is shed into the waxy secretions in the outer part and falls out. This is the reason for not using cotton buds to clean the ear canal because very frequently they merely push the shed skin and wax deep into the canal, impacting it and obstructing hearing. The ear canal has a slight bend where the outer cartilaginous part joins the bony thin skinned inner portion, so that the outer part runs somewhat backwards and the inner part somewhat forwards. This bend is yet another part of the protective mechanism of the ear, stopping foreign objects from reaching the tympanic membrane. However it means that to inspect the tympanic membrane from the outside, one must pull the ear upwards and backwards. The tympanic membrane separates the ear canal from the middle ear and is the first part of the sound transducing mechanism. Shaped somewhat like a loudspeaker cone (which is an ideal shape for transmitting sound between solids and air), it is a simple membrane covered by a very thin layer of skin on the outside, a thin lining membrane of the respiratory epithelium tract on the inner surface and with a stiffening fibrous middle layer. The whole membrane is less than a 1/10th of millimetre thick. It covers a round opening about 1 centimetre in diameter into the middle ear cavity. Although the tympanic membrane is often called the ear drum, technically the whole middle ear space is the ear drum and the tympanic membrane the drum skin.

The Middle Ear

The middle ear is an air filled space connected to the back of the nose by a long, thin tube called the Eustachian tube. The middle ear space houses three little bones, the hammer, anvil and stirrup (malleus, incus and stapes) which conduct sound from the tympanic membrane to the inner ear. The outer wall of the middle ear is the tympanic membrane, the inner wall is the cochlea. The upper limit of the middle ear forms the bone beneath the middle lobe of the brain and the floor of the middle ear covers the beginning of the great vein that drains blood from the head, the jugular bulb. At the front end of the middle ear lies the opening of the Eustachian tube and at its posterior end is a passageway to a group of air cells within the temporal bone known as the mastoid air cells.

One can think of the middle ear space shaped rather like a frying pan on its side with a handle pointing downwards and forwards (the Eustachian tube) but with a hole in the back wall leading to a piece of spongy bone with many air cells, the mastoid air cells. The middle ear is an extension of the respiratory air spaces of the nose and the sinuses and is lined with respiratory membrane, thick near the Eustachian tube and thin as it passes into the mastoid. It has the ability to secrete mucus. The Eustachian tube is bony as it leaves the ear but as it nears the back end of the nose, in the nasopharynx, consists of cartilage and muscle. Contracture of muscle actively opens the tube and allows the air pressure in the middle ear and the nose to equalize. Sound is conducted from the tympanic membrane to the inner ear by three bones, the malleus, incus and stapes. The malleus is shaped like a club; its handle is embedded in the tympanic membrane, running from its centre upwards.

The head of the club lies in a cavity of the middle ear above the tympanic membrane (the attic) where it is suspended by a ligament from the bone that forms the covering of the brain. Here the head articulates with the incus which is cone shaped, with the base of the cone articulating with the head of the malleus, also in the attic. The incus runs backwards from the malleus and has sticking down from it a very little thin projection known as its long process which hangs freely in the middle ear. It has a right angle bend at its tip which is attached to the stapes (stirrup), the third bone shaped with an arch and a 3.

THE SOUND TRANSDUCING MECHANISM

The Inner Ear

Structure

The bony cochlea is so called because it is shaped like a snail shell. It has two and a half turns and houses the organ of hearing known as the membranous labyrinth surrounded by fluid called the perilymph. The cochlea has a volume of about 0.2 of a millilitre. In this space lie up to 30,000 hair cells which transduce vibration into nervous impulses and about 19,000 nerve fibres which transmit the signals to and from the brain. It is easiest to think of the membranous labyrinth by imagining the cochlea to be straightened out as a bony tube closed at the apex and open at the base with the round and oval windows and a connection to the vestibular labyrinth (see Figure 2.2). It is in continuity with the vestibular labyrinth or organ of balance which in technical terms acts as both a linear and angular accelerometer, thus enabling the brain to know the position of the head in relationship to gravity and its surroundings. The organ of balance will not be dealt with any further. The foot plate covers the oval window, an opening into the vestibule of the inner ear or cochlea, with which it articulates by the stapedio-vestibular joint.

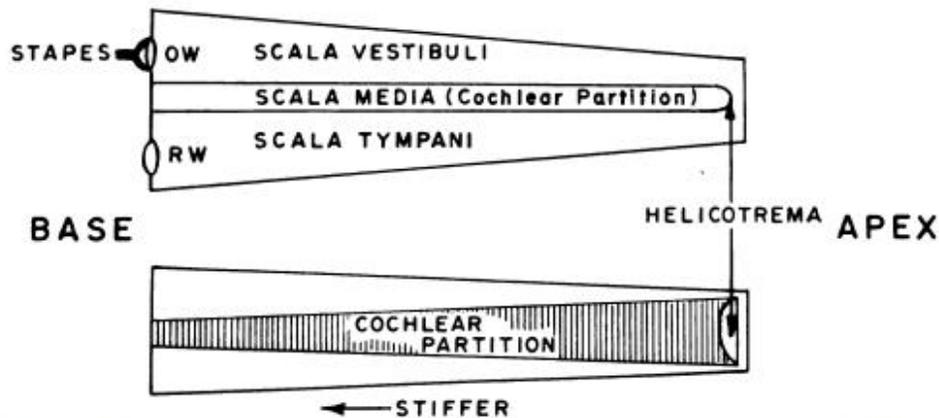


Figure 2.2. The cochlea is a bony tube, filled with perilymph in which floats the endolymph filled membranous labyrinth. This separates the scala vestibuli from the scala media. (from Hallowell and Silverman, 1970)

Vibration of the foot plate of the stapes vibrates the perilymph in the bony cochlea. This fluid is essentially incompressible. Therefore, there has to be a counter opening in the labyrinth to allow fluid space to expand when the stapes foot plate moves inwards and in turn to move inwards when the stapes foot plate moves outwards. The counter opening is provided by the round window membrane which lies beneath the oval window in the inner wall of the middle ear. It is covered by a fibrous membrane which moves synchronously but in opposite phase with the foot plate in the oval window. The membranous labyrinth is separated into three sections, by a membranous sac of triangular cross section which run the length of the cochlea. The two outer sections are the scala vestibuli which is connected to the oval window, and the scala tympani which is connected to the round window. The sections are filled with perilymph; they connect at the apex by a small opening known as the helicotrema which serves as a pressure equalizing mechanism at frequencies well below the audible range. They also connect at the vestibular end with the fluid surrounding the brain, through a small channel known as the perilymphatic aqueduct. The membranous labyrinth, also known as the cochlear duct, is filled with different fluid called endolymph. On one side it is

separated from the scala vestibuli by Reissner's membrane, and on the opposite side from the scala tympani by the basilar membrane (see Figure 2.3). The basilar membrane is composed of a great number of taut, radially parallel fibres sealed between a gelatinous material of very weak shear strength. These fibres are resonant at progressively lower frequencies as one progresses from the basal to the apical ends of the cochlea. Four rows of hair cells lie on top of the basilar membrane, together with supporting cells. A single inner row is medial, closest to the central core of the cochlea. It has an abundant nerve supply carrying messages to the brain. The three outer rows, which receive mainly an afferent nerve supply, are separated from the inner row by tunnel cells forming a stiff structure of triangular cross section known as the tunnel of Corti (see Figure 2.3). Any natural displacement of the cochlear partition results in a rocking motion of the tunnel of Corti and consequently a lateral displacement of the inner hair cells.

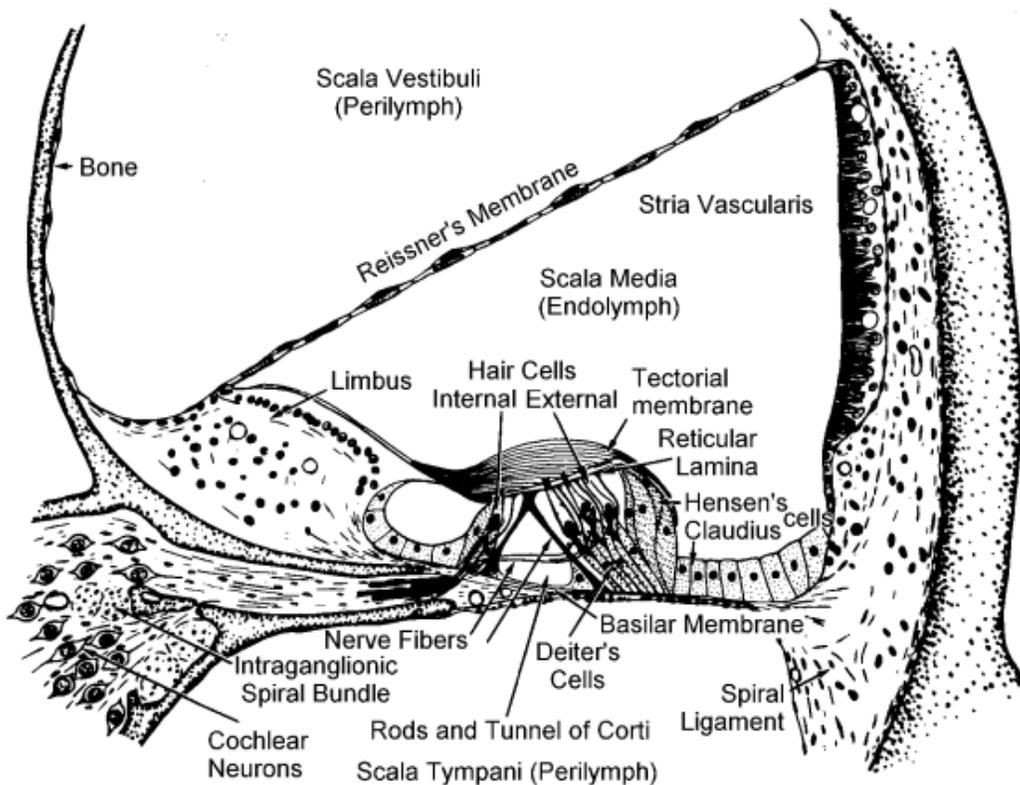


Figure 2.3. A cross section of one turn of the cochlea showing details of the membranous labyrinth. (from Hallowell and Silverman, 1970)

The hair cells derive their name from the presence at their free ends of stereocilia which are tiny little stiff hair like structures of the order of a few micrometers long (Figure 2.4). The stereocilia of the hair cells are arranged in rows in a very narrow cleft called the subtektorial space formed by the presence above the hair cells of the radially stiff tectorial membrane. The cilia of the outer hair cells are firmly attached to the tectorial membrane while the cilia of the inner hair cells are either free standing or loosely attached to the tectorial membrane. In summary then, anatomically, the ear consists of a sound conducting mechanism and a sound transducing mechanism. The sound conducting mechanism has two parts, the outer ear consisting of the pinna and ear canal, and the middle ear consisting of the tympanic membrane. The middle ear air space is connected to the nose by the Eustachian tube and to the mastoid air cells housing the ossicular

chain, the malleus, stapes and incus. The inner ear, or cochlea, transduces vibration transmitted to the perilymph via the ossicular chain into a nervous impulse which is then taken to the brain where it is perceived as sound.

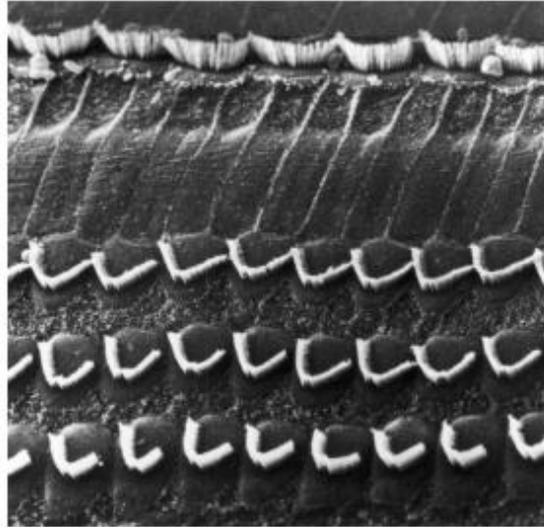


Figure 2.4. A surface view looking down on the top of the hair cells; note the three rows of outer hair cells and the one row of inner cells.

Function Transduction of vibration in the audible range to a nervous impulse is performed by the inner hair cells; when the basilar membrane is rocked by a travelling wave, the cilia of the inner hair cells are bent in relation to the body of the cell, ion passages are opened or closed in the body of the cell and the afferent nerve ending which is attached to the hair cell base is stimulated. As mentioned earlier, the basilar membrane responds resonantly to highest frequencies at the basal end nearest the oval window and to progressively lower frequencies as one progresses toward the apical end. At the apical end the basilar membrane responds resonantly to the lowest frequencies of sound. A disturbance introduced at the oval window is transmitted as a wave which travels along the basilar membrane with the remarkable property that as each frequency component of the travelling wave reaches its place of resonance it stops and travels no further. The cochlea is thus a remarkably efficient frequency analyser. The cochlea has an abundant nerve supply both of fibres taking impulses from the cochlea to the brain (afferent pathways) and fibres bringing impulses from the brain to the cochlea (efferent fibres). When stimulated the inner hair cells trigger afferent nervous impulses to the brain. Like virtually all neural-mechanisms there is an active feedback loop. The copious nerve supply to the outer hair cells is overwhelmingly efferent, although the full function of the efferent pathways is not yet fully understood. It has been suggested that the purpose of the active feedback system which has been described is to maintain the lateral displacement of the stereocilia in the sub tectorial space within some acceptable limits.

THE PHYSIOLOGY OF HEARING

The Outer and Middle Ears

Let us deal first with the sound conducting mechanism. The range of audible sound is approximately 10 octaves from somewhere between 16 and 32 Hz (cycles per second) to somewhere between 16,000 and 20,000 Hz. The sensitivity is low at the extremes but becomes much more sensitive above 128 Hz up to about 4,000 Hz when it again becomes rapidly less sensitive. The range of maximum sensitivity and audibility diminishes with age. The head itself acts as a natural barrier between the two ears and thus a sound source at one side will produce a more intense stimulus of the ear nearest to it and incidentally the sound will also arrive there sooner, thus helping to provide a mechanism for sound localization based on intensity and time of arrival differences of sound. High frequency hearing is more necessary than low frequency hearing for this purpose and this explains why sound localization becomes difficult with a high frequency hearing loss.

The head in humans is large in comparison to the size of the pinna so the role of the pinna is less than in some other mammals. Nonetheless, its crinkled shape catches higher frequency sounds and funnels them into the ear canal. It also blocks some higher frequency sound from behind, helping to identify whether the sound comes from the front or the back. The ear canal acts as a resonating tube and actually amplifies sounds at between 3000 and 4,000 Hz adding to the sensitivity (and susceptibility to damage) of the ear at these frequencies.

The ear is very sensitive and responds to sounds of very low intensity, to vibrations which are hardly greater than the natural random movement of molecules of air. To do this the air pressure on both sides of the tympanic membrane must be equal. Anyone who has their ear blocked even by the small pressure change of a rapid elevator ride knows the truth of this. The Eustachian tube provides the means of the pressure equalization. It does this by opening for short periods, with every 3rd or 4th swallow; if it were open all the time one would hear one's own every breath.

Because the lining membrane of the middle ear is a respiratory membrane, it can absorb some gases, so if the Eustachian tube is closed for too long it absorbs carbon dioxide and oxygen from the air in the middle ear, thus producing a negative pressure. This may produce pain (as experienced if the Eustachian tube is not unblocked during descent of an aeroplane). The middle ear cavity itself is quite small and the mastoid air cells act as an air reservoir cushioning the effects of pressure change. If negative pressure lasts too long, fluid is secreted by the middle ear, producing a conductive hearing loss.

The outer and middle ears serve to amplify the sound signal. The pinna presents a fairly large surface area and funnels sound to the smaller tympanic membrane; in turn the surface of the tympanic membrane is itself much larger than that of the stapes foot plate, so there is a hydraulic amplification: a small movement over a large area is converted to a larger movement of a smaller area. In addition, the ossicular chain is a system of levers which serve to amplify the sound. The outer and middle ears amplify sound on its passage from the exterior to the inner ear by about 30 dB.

The Inner Ear

The function of the inner ear is to transduce vibration into nervous impulses. While doing so, it also produces a frequency (or pitch) and intensity (or loudness) analysis of the sound. Nerve fibres can fire at a rate of just under 200 times per second. Sound level information is conveyed to the brain by the rate of nerve firing, for example, by a group of nerves each firing at a rate at less than 200 pulses per second. They can also fire in locked phase with acoustic signals up to about 5 kHz. At frequencies below 5 kHz, groups of

nerve fibres firing in lock phase with an acoustic signal convey information about frequency to the brain. Above about 5 kHz frequency information conveyed to the brain is based upon the place of stimulation on the basilar membrane. As an aside, music translated up into the frequency range above 5 kHz does not sound musical. As mentioned above each place along the length of the basilar membrane has its own characteristic frequency, with the highest frequency response at the basal end and lowest frequency response at the apical end. Also any sound introduced at the oval window by motion of the stapes is transmitted along the basilar membrane as a travelling wave until all of its frequency components reach their respective places of resonance where they stop and travel no further. For example, a 1 kHz tone induces resonance at about the middle of the basilar membrane. Any frequency components lower than 1 kHz must travel more than half the length of the basilar membrane, whereas high frequency components, greater than 1 kHz must travel less than half the length of the basilar membrane.

Evidently the brain must suppress high frequency information in favour of low frequency information as the travelling wave on the basilar membrane passes through places of high frequency resonant response. An explanation is thus provided for the observation that low frequency sounds, for example traffic noise, are very effective in masking high frequency sounds, for example the fricatives of speech, making telephones near busy streets difficult to use. How does the brain cope with intensity? The physiological range of intensity of the normal ear is huge. As a matter of interest it is the same as that of the eye when the responses of the cones and rods are considered together; thus the visual analogue is appropriate. It is as wide as seeing a candle flicker on a dark night at a hundred meters to looking indirectly into a bright sun.

The range is so great that only the logarithmic response characteristic of variable rate processes and thus favoured by anatomical systems, is capable of encompassing it. The normal range of human hearing is from 0 to 100 dB(A), before sound becomes uncomfortably loud. Mounted on the basilar membrane close to the end nearest the central core of the cochlea are a single row of inner hair cells followed by three rows of outer hair cells which are separated from the single row of inner hair cells by a stiff structure of triangular cross section known as the tunnel of Corti. Any natural displacement of the cochlear partition results in a rocking motion of the tunnel of Corti and consequently a lateral displacement of the inner hair cells. The ear has evolved a very intriguing mechanism to cope with the large range in sound intensity encountered in the environment. Only the inner hair cells initiate nervous impulses which are heard as sound.

They are not particularly sensitive but they are rugged and they are placed at the inner edge of the basilar membrane which is relatively immobile. The point where the basilar membrane vibrates most is about its middle so that the inner hair cells are spared the most violent vibration of very intense sound. The question then arises, how do the inner hair cells respond to slight or moderate amounts of stimulation? Here the outer hair cells play a major role. When they are stimulated by the travelling wave they respond actively and physically contract. They have muscle proteins in their wall and literally shorten. Because they are attached both to the Reissner's membrane and the basilar membrane, this produces an additional shear movement of the membranous labyrinth, which amplifies the travelling wave at the point of maximal stimulation. This amplified movement is transmitted to the inner hair cells which then respond. If the amount of movement of the basilar membrane is slight, the amount of outer hair cell contracture adds significantly to the basilar cell movement; if the amount of movement is large the contracture adds nothing to the already great displacement of the membranous labyrinth.

If the outer hair cells are damaged they no longer contract in response to slight sounds and the inner hair cells are not stimulated. This produces a hearing loss for low intensity sound. If the sound is more intense, the inner hair cells are stimulated directly and they respond normally so that the ability to hear louder

sounds remain unimpaired. This is a common phenomenon known as loudness recruitment. The inner hair cells are much "tougher" than outer hair cells and much less likely to be damaged by ageing, noise or most ototoxic drugs, so ageing, noise and ototoxic drugs usually only produce hearing loss but not deafness. It was noted earlier that the ear is most sensitive to sounds between approximately 3000 and 4000 Hz, in part because of the amplifying mechanism of the ear canal. Thus, the most intense stimulus is produced at these frequencies and the outer hair cells which respond to these frequencies are most at risk from damage. Prolonged exposure to loud sounds damages these hair cells and thus explains the hearing loss from noise which occurs first at 3 to 4 kHz.

CENTRAL AUDITORY PROCESSING

The nervous impulses are carried along the 8th (statio-acoustic nerve) from the cochlea to the brain stem. Here the nerve fibres reach nuclei where they relay with other nerve fibres. The fibres from each auditory nerve split, some passing to one side of the brain, others remaining on the same side. Thus, as auditory stimuli pass up each side of the brain from both ears, unilateral hearing loss cannot be caused by a brain lesion. The fibres pass up the hind brain to the mid brain and the cerebral cortex.

The Ability to Block Out Unwanted Sounds.

In a crowded noisy room a young person with normal hearing can tune in and out conversations at will. This is known technically as the cocktail party effect. The brain quite automatically adjusts time of arrival and intensity differences of sound from different signal sources so that the one which is wanted passes to the cortex and all others which do not meet these criteria are suppressed by feedback loops. This requires both good high frequency peripheral hearing, two ears and an additional central mechanism. Even in the presence of normal bilateral peripheral hearing, the elderly lose part of the central mechanism and find it difficult to listen in crowded rooms. This is compounded if there is some hearing loss.

Spatial Localization.

A normal human can localize quite accurately the source of the sound. One knows from what direction the sound is coming; one knows where to turn one's head to look for a speaker; as one knows where to look for an aeroplane or a bird. There are specific neurones which deal with this in the mid brain.

On and Off Sounds

Hearing has an alerting function especially to warning signals of all kinds. There are brain cells which respond only to the onset of a sound and others which respond only to the switching off of the sound, i.e. a change. Think only of being in an air conditioned room when the air conditioner turns on, one notices it. After a while it blends into the background and is ignored. When it switches off, again one notices it for a short time and then too the absence of sound blends into the background. These cells allow the ear to respond to acoustic change - one adjusts to constant sound - change is immediately noticeable. This is true too with machinery and a trained ear notices change.

Interaction of Sound Stimuli with Other Parts of the Brain

Sound stimuli produce interaction with other parts of the brain to provide appropriate responses. Thus, a warning signal will produce an immediate general reaction leading to escape, a quickening of the heart rate, a tensing of the muscle and a readiness to move. A baby's cry will alert the mother in a way it does not alert

others. The sound of martial music may lead to bracing movement of those to whom it is being played and induce fear and cowering in the hearts and minds of those at whom it is being played. Certain sounds can evoke anger, others pleasure. The point is that the sensations produced by hearing are blended into the body mechanism in the central nervous system to make them part of the whole milieu in which we live.