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Review Article

The Evolution of Hearing from Fishes to Homo sapiens - A Chronological Review

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Abstract: The evolution of the human ear is a fascinating story of the formation and adaptation by trial and error of a primitive sound receptor. Human hearing is thus the end product of long and complex evolutionary steps, its primordium having first evolved from gill slits & jawbone of ancient fishes. Hearing is the most vital special sense organ to form the basis for communication by which civilization of the human race has taken place thus far. Knowing this evolutionary pathway will enable us to reason out the complex anatomy of human hearing in a better way. This review article is a synopsis from a number of scientific contributions in literature, which chronologically trace the origin & adaptations of the hearing apparatus from the era of fishes up to human life. It is paramount that the phylogeny & evolution of human hearing should be understood as it plays an important role in the understanding of the basis of congenital anomalies & inner ear pathophysiology. This knowledge will further help in propagation of evidence based clinical practice while managing various complex ear anomalies which we encounter in the present day.
Keywords: Evolution, Hearing, Phylogeny, Hyomandibula, Impedance Mismatch, Cochlea, Communication.

INTRODUCTION

Ernst Haeckel a German zoologist (1866) described 'The Theory of Recapitulation', whereby he quoted the Biogenetic law or Embryological parallelism, which highlights the basis of human evolution 'Ontogeny recapitulates phylogeny'. His theory lays emphasis that embryonal development of an individual organism (its ontogeny); follows the same path as the evolutionary history of its species (its phylogeny) [1]. This phenomenon is very apt while exploring the interesting entity of evolution of hearing and eventually the evolution of human communication. Hearing is the essence of civilization, since it was the first special sense to develop and was the primary stimulus for development of verbal skills and later organized lingual behavior and further evolution of speech and language in our ancestors [1].

The intricate hearing mechanism of human beings has phylogenetically supposed to have evolved primarily from the prehistoric fishes found in Paleozoic Age [1, 2]. In Paleozoic Jawless fish an underwater balancing device developed within the skull as a hollowed curve filled with fluid containing sensory cells that responded to movements in water & kept fish on an even keel. Soon evolved an air-sac, converting this original balancing organ into a hearing device and the evolution of hearing began since then. The scientific evidence for this origin is in the first fossil remains of a vestibular system (primordial ear bud) found in the earliest vertebrates of the Paleozoic age 'Agnathan fish' which evolved around 600 million years ago [3]. The basic steps in the phylogenic evolution of the ear are thus discernable from fossil evidence. In modern day, a few fish species continue have these air sacs which help them pick up underwater signals.

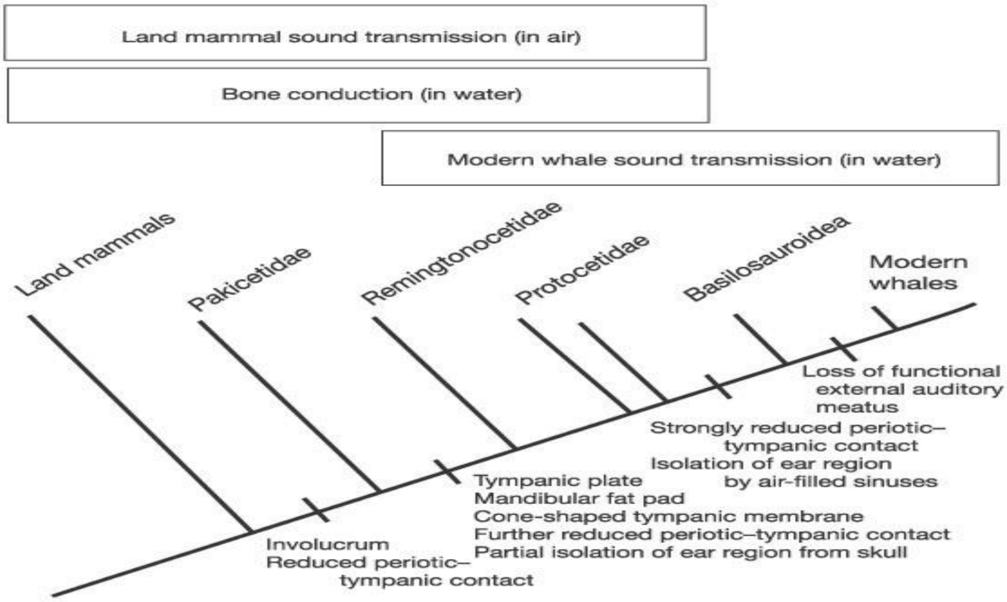

Fig-1: The Evolution of Hearing Apparatus
(Courtesy: The Evolutionary biology of hearing; Berlin: Springer-Verlag; eds: Popper AN, Webster DB, Fay RR, 1992)

Origin of the Hearing Organ in Prehistoric Fishes

The origin of sensory structures within the skull began with the epithelial ciliated cell 1.5 billion years ago in prehistoric life-forms. Cells acquired cilia to aid in locomotion and feeding, and later relayed information regarding the fluctuations of the surrounding prehistoric waters in which life first evolved. A segment of sensory epithelial ciliated cells became invaginated into the body to form a fluid-filled structure. This cystic structure allowed detection of the gravitational field of the earth, through movement of the entrained field triggering movement of lining sensory cilia forming 'Hair Cells'. This structure was expanded to include a variable number of fluid-filled semicircular canals and congregations of higher density material resting on the hair cells – 'Otoliths'. Later fish however evolved an air-sac that was used to regulate buoyancy and this sac converted the original balancing organ also into a hearing device [2, 3].

Osteichthyes fish evolved a diverticulum of the primitive labyrinth solely devoted to hearing called the “Lagena & Saccule”. Analysis of magnitude, direction and significance of auditory cues was necessary against the background noise from surf & underwater currents to utilize sound to best advantage. The lagena elongated getting closer in macroscopic structure to the contemporary cochlea, of which it is probably the antecedent. But, this hearing arrangement worked well only for fishes. The lagena & saccule which formed the primordial labyrinth later on evolved to give origin to the vestibule & cochlea and also formed the vestibulo-cochlear nerve in higher animals [4].

About 380 million years ago, as fish further evolved to migrate towards the land, there was a need for major modification to detect sound transmitted through air rather than water. Thus, when fish came to land they ran into an air-water impedance mismatch. This occurred due to a phase difference caused by the presence of two mediums for sound conduction, whereby sound waves in air had to cause a response in the receptor organ that was filled with fluid [4]. The solution for this came with the eventual development of three of the most delicate bones of the human body - the Ossicles which helped to provide the middle ear transformer mechanism for overcoming the phase difference induced by air and water media. Cochlear nerve endings within a tonotopically organized spiral Cochlea could then transmit sounds to the auditory cortex without loss of information. The 370-million-year-old Panderichthys, an intermediate species between fish and the first four-limbed animals to crawl onto land had small bones in its skull that appear to be early analogues of both ear canals and the gill system in some modern fish. The canals developed into true ears only after Panderichthys's descendants became air breathers, freeing up the former gill structures for sensory functions [1, 5].

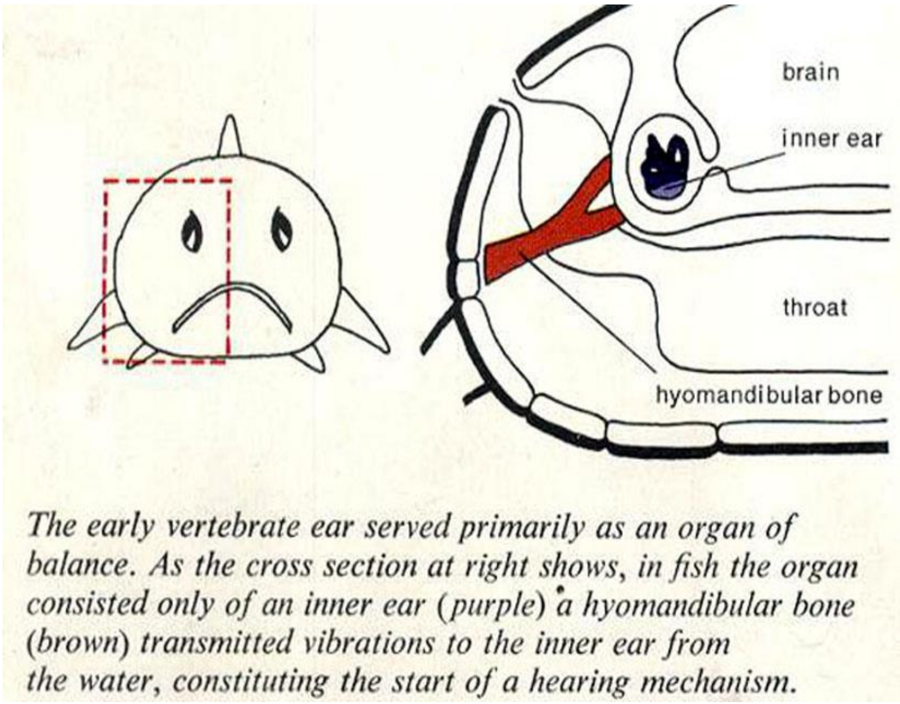

Fig-2: Hearing in Ancient Fish
(Courtesy: Bioacoustics - a comparative approach; London Acad Press; ed. B. Lewis, 1983)

Hearing in Amphibians

In the primitive amphibians, the region behind the head was formed of a number of arches, each comprising a pouch-like gill for breathing and muscles to ventilate the primitive lungs. Around 300 million yrs ago, these regions of the anterior gill arches ossified and evolved into skull components. But, Amphibians had inadequate primitive arrangement of their hearing organ. Hence, Amphibians continued to lay flat on the ground for a further thirty million years, using fins to scuttle around, and during this time the 'Hyomandibula' continued to adapt to its new additional function of transmitting sounds from the land [5].

The early amphibian ear was attuned to high amplitude low frequency sounds which transmit well through the ground. Hence, when early amphibians lay on the ground, these vibrations would cause vibration of the jaw, the hyomandibular bone, the cranium with the contained auditory receptor (basilar papilla in amphibians) where these sounds were ‘heard’. The axial skeletons configuration in supporting the animal shifted on land, meaning that the ribs and inter-costal muscles could take on a new role in expanding one of the more posterior gills, which became lungs. This was ventilation as opposed to the gill pumping action for gas exchange that had preceded and was far more efficient at gas exchange.

An air-filled structure of relatively fixed volume, like a redundant gill, was potentially an excellent method of sound amplification. Compressing such a structure with sound-waves over a relatively large area caused an increase in its internal pressure and this high pressure could then be transmitted to something of smaller surface area to amplify the original source of sound. Hences, the hyomandibula receded to create a wider ear opening in early land animals such as the tetrapod Acanthostega (now part of the middle ear in humans and other mammals). In living species of amphibia, the saccule acts like an auditory organ. Frogs are believed to use their saccules to detect the source of a sound by positioning their front legs to triangulate from where the sound is coming. Many of the larger reptiles have massive ossicular stapes; it seems likely that the dinosaurs heard by detecting their own body movements. In mammals, the saccule has been relegated to a vestibular organ associated with maintaining balance [4, 5].

Rise of the Reptiles

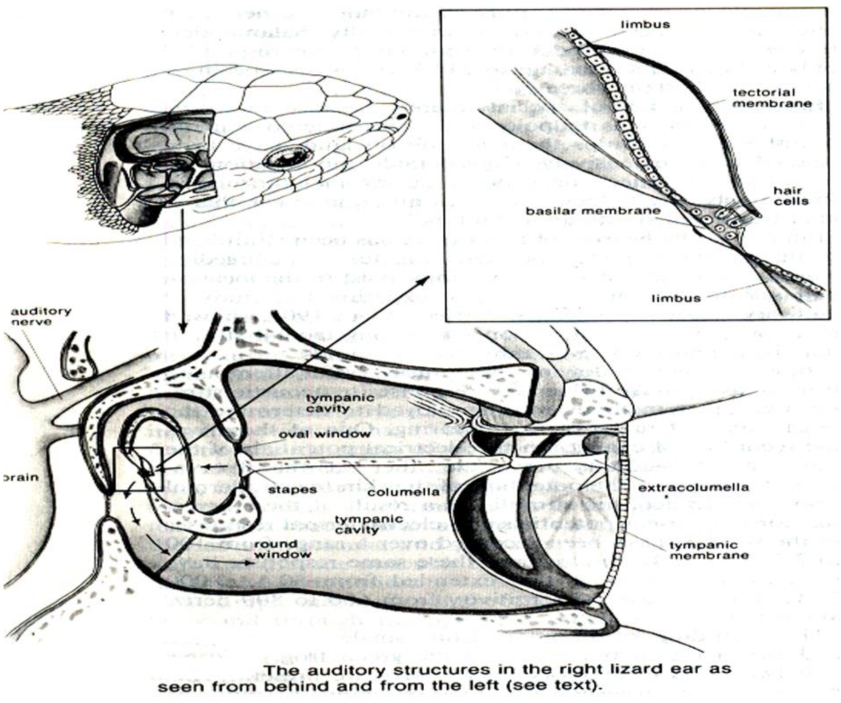

Fig-3: The Reptilian Ear
(Courtesy: Manley G.A. A review of the auditory physiology of the reptiles Progr Sens Physiol, 1981)

The elevation of the body off the ground had far-reaching consequences for amphibians. Their adaptation to land helped in the formation of the middle ear. Their gill pouch migrated upwards to lie closer to the cranium and so formed the middle-ear cleft, retaining its respiratory epithelium and a connection to the pharynx as the eustachian tube [6]. Around the same time, the first articulation between the jaw and the cranium formed in reptiles alleviating the hyomandibula bone from some of its need to suspend the jaw. The upper end of the hyomandibula could increasingly take on its purpose in sound transmission and eventually separated off from the remainder of the bone to lie inside the new middle ear cavity as a strut called the 'Columella'. The columella adapted the ear to transmission of higher frequency sound and gave direction to such transmission. The columella is the precursor of the human stapes [7, 8]. The post-dentary bones were freed of a role in mastication and they had already to some extent been involved in hearing as ground vibrations had been transmitted through them to the hyomandibula earlier in evolution. A mutation in regulatory genes allowed some of the post-dentary bones to migrate up into the middle ear. The lateral part of the middle ear conductive mechanism was essentially a modified jaw.

The lower end of the hyomandibula bone was left to continue in suspending the jaw muscles as the hyoid bone but with the new jaw joint, many of the muscles were now redundant in their original role; they have migrated forwards in humans to form muscles of facial expression. A muscle that originally elevated the upper hyomandibula – 'levator hyoidei' was now attached to the columella and became adapted to tense this bone in the presence of loud noise as the early stapedius muscle (supplied by the nerve of the hyoid arch – the facial nerve). The soft tissues lateral to the middle ear cavity thinned to improve sound transmission and formed an early tympanic membrane.

The basilar papilla of the amphibian inner ear elongated and responded increasingly to higher frequency air-borne sounds, forming the reptilian cochlear duct. This is the structure of the ancient reptilian ear and is still to be found in most extant reptiles [7, 8]. The reptilian ear is comparable to that of humans, but it lacks the malleus, incus and external ear structure. These refinements came with the arrival of mammals around 230 million years ago. Today, with a few exceptions, the hearing of non-mammalian species (reptiles, birds, & amphibia) is optimized to detect acoustic frequencies between 2 KHz & 14 KHz, while some can hear even ultrasonic frequencies [5, 18].

Avian Hearing

High frequency hearing capacity developed once the animals took to the air. This mechanism depended upon the individual hair cells in the hearing organs acting as selective filters, each of which relays information about different frequencies to the brain. In these hair cells, conducting ion channels are built into the cell membrane to ensure that the hair cells resonate electrically at only one frequency. This tonotopicity prevailed through evolution in higher animals.

The birds required to specifically hunting for food based on frequency specific acoustic stimuli and their hearing got fine tuned to the higher frequencies which they could perceive from great heights while in flight [9]. Supersonic hearing in snow owls & vampire bats have been well known to function as an echo locating sonar which serves as their most vital sensory organ for food, communication, navigation & exist as their primary mode of survival [9]. The barn owl has amazing hearing abilities, relying on its ears for navigation and can detect its prey accurately within a range of a few centimeters, even from a great distance [10].

Mammalian Hearing

Mammals first appeared around 230 million years ago, evolving from a branch of reptiles known as ‘Synapsids’ [11]. The first mammals were in general much smaller than the preceding reptiles and had a smaller distance between their ears. The vertebrate auditory system was more refined and had developed special tasks like acoustic feature discrimination, sound source localization, frequency analysis and auditory scene analysis in coordination with the visual inputs. These sorts of capabilities arose very early in the evolution of the vertebrates and have been modified by selection in different species [12, 13, 16]. Refinements to the ear in Mammals occurred rapidly due to multiple episodic genetic evolution of 'prestin' - the functional motor protein of cochlear outer hair cells providing robust hearing capacity and this may have been the reason for mammals to adapt and dominate over other species [14, 15].

In the mammalian ear, smaller inter-aural distance predisposed to better localization of high frequency sounds and helped further significant improvements in the design and abilities of their hearing function. This arrangement has also led to the ultrasonic hearing abilities of bats, whales & the cat family [18, 20]. In primates, the inner ear further evolved allowing the resolution of complex patterning of frequency and timing of auditory information that underlies comprehending human language [16, 21, 23]. The addition of two more bones to the middle ear, together with adaptations to the cochlea, created an ear responding to sound frequencies greater than 10 KHz, which is a defining characteristic of the mammalian ear. The mammalian middle ear possesses three ossicles with a unique transformer mechanism, by which these sound waves are delivered onto the labyrinthine windows with minimal loss of energy. The inner ear is formed as an intricate spiral with three chambers with tonotopically arranged organ of corti, which filters sounds at different frequencies & transmits it onto the auditory cortex via a sequential relay of specialized neurons.

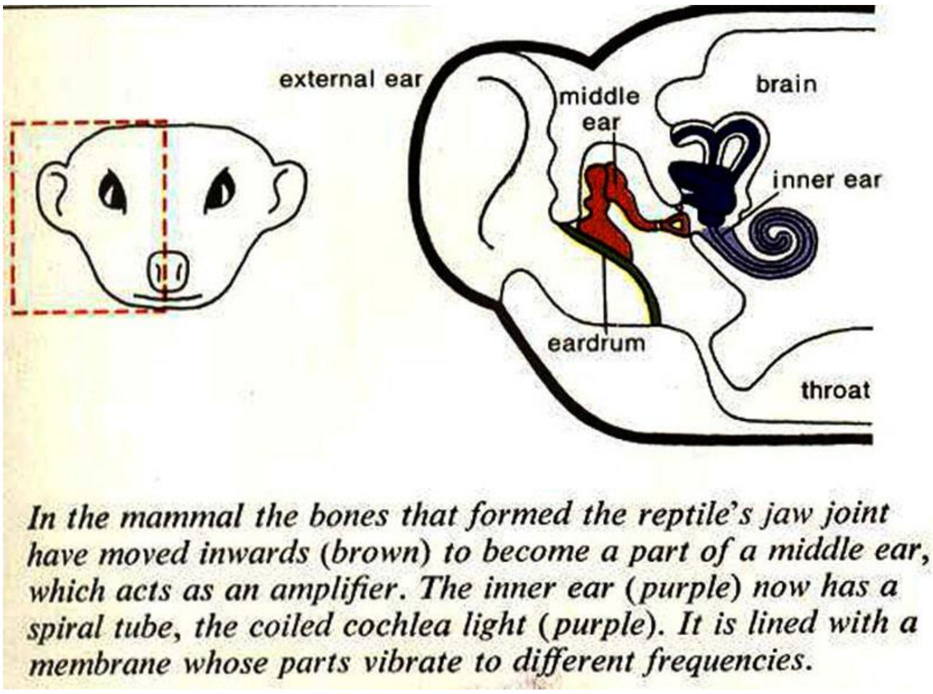

Fig-4: The Mammalian Ear
(Courtesy: Bioacoustics - a comparative approach; London Acad Press; ed. B. Lewis, 1983)

The mammalian ear is thus the best developed among all vertebrate ears, with an intricate anatomical framework supported by a delicate physiological function [17, 19]. The mammalian cochlea, elongated as its discriminatory power improved, ending curled up into a snail shape to fit into the cranium. The coiled structure of the cochlear duct is a uniquely mammalian development. With increasing information coming from the cochlea, new brain (neo-cortex) was able to undertake auditory analysis of sounds. In the nearest mammalian relatives (e.g. in monotremes) and in non-mammals the cochlea is straight. The coiling is not important for the physics of sound propagation in the cochlear fluids, but it does provide for an efficient and compact packing of the duct in the skull [18].

Surprisingly, the architecture of the mammalian cochlea does not vary as much between different species. The basic structure of the cochlea has not changed with the diversity of modern mammals nor does the cochlea scale change significantly with brain size or body mass. This may be a factor why we find that cochlea is fully developed to adult size even at birth. The basilar membrane in a mouse is about 10 mm long and occupies the volume of a small lentil, yet in an Elephant, the membrane is only six times longer. In the human inner ear the basilar membrane is 34 mm long and is coiled into a cochlea the size of a baked bean [21].

In mammalian species, and in those animals where high frequency hearing is critical, frequencies are selected not by the electrical properties of the individual hair cells but by the intrinsic mechanical properties of the whole cochlea. In these cases, the mechanical excitation pattern activates appropriate subpopulations of hair cells. In the mammalian cochlea it is believed that the separation of frequency information is carried out only by the mechanics of the cochlea fluids and the basilar membrane. This is similar to the mechanism proposed by Helmholtz in 1862 and subsequently elaborated by Von Bekesy in the 1930s.

The ear structure of each mammalian species is specialized for its specific needs and ear is the organ of survival in many species even today. Hearing is more important than vision for Dolphins, seen in the murky waters of Yangtze River of China & Megong River of Thailand. It is the primary organ of survival for dolphins who are near blind due to high content of alluvial soil deposits in the water of their ecosystem, causing near zero visibility. They utilize acoustic impulses to study their underwater terrain & to perceive their prey or predator [20, 21]. Elephants have large ears that are sensitive to the very low-frequency sounds they use to communicate over long distances. Bats have minute middle ear structures that are sensitive to the high frequencies used in their echo-locating sonar. The ears of these two species are so different that there is little overlap in their auditory range [22].

The acoustic range in modern day mammals extends over four to nine octaves when measured as in the range of a musical instrument. Although the lowest frequencies detectable by the mammalian ear do vary between species, the biophysics of cochlear mechanics requires, very approximately, a fixed length of basilar membrane per octave analyzed for obtaining comprehensive auditory coverage [23].

Hearing in the Homo sapiens

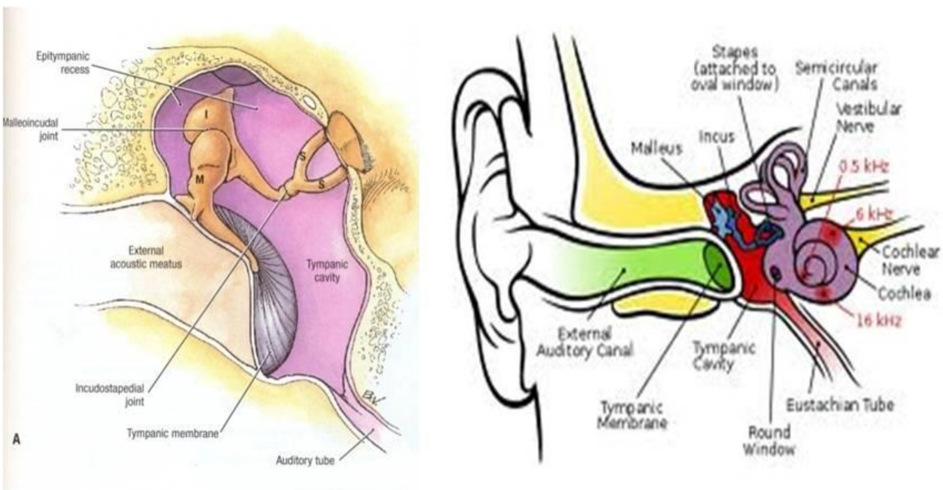

Fig-5: The Human Hearing Apparatus
(Courtesy: Manley GA. Evolutionary paths to mammalian cochleae. J Assoc Res Otolaryngol, 2012)

Hearing is the most ancient special sense in humans. In lower animals it provided a sense of location to find prey & protect them from predators. Later, it distinctly evolved further in humans to encompass the special functions of listening & communication [24].

The middle ear ossicles comprehensively overcame the impedance to hearing by their unique transformer mechanism, by which all transmitted sound energy was concentrated onto a small labyrinthine window & it was carried further into the inner ear which is a vibrant entity with tonotopically organized sensory organ of Corti. This integrity of signals was transmitted in a relay to other principal synaptic stations of the auditory pathway. Thus, the human ear possesses an intricate anatomical framework & delicate physiological function [24, 25].

Early humans evolved the anatomy needed to hear each other and respond, at least 350,000 years ago. This suggests that some rudimentary form of speech developed early on in our evolution, but there is no clarity on their ability for formal conversations, which occurred much later. The skeletal anatomy in hominids is compatible with a human-like pattern of sound power transmission through the outer and middle ear at frequencies up to five kHz, suggesting that they already had auditory capacities similar to those of living humans in this frequency range. These ancestral human's hearing sensitivity approached that of modern humans, suggesting that they too could distinguish speech. Binaural sound sensitivity & discrimination developed in the earliest stages of man's lineage and has remained relatively unchanged since the simian level [24].

In the Cainozoic age, the ear of man and primates developed fully. Interestingly, semicircular canals of humans have a higher ratio of the size of anterior & posterior canals versus lateral canal when compared to apes due to bipedal locomotion [1, 5, 24]. Changes in the size of these canals have been traced through our hominid ancestors by high-resolution CT scans of fossil skulls to infer when humans adapted bipedal locomotion. The frequency of the lowest threshold has declined in man's lineage - the greatest drop probably occurring during the Eocene. The total area of the audible field increased until the Eocene and has decreased since then. The auricular muscles are rudimentary as localization became less vital. The connection between the Temporal lobe & the Amygdala was the most crucial evolutionary step in giving emotional content to hearing & probably developed quite late in evolution – but reached its zenith in the Homo sapien brain [25].

Origin of Communication

The human auditory cortex is the most advanced of any species, and the cochlea is very elongate. Surprisingly however, the human cochlea has regressed in its range of frequency response – perhaps to concentrate analysis on frequencies produced by human vocal cords. This integration probably leads to intricate refinements in the temporal cortex which processed vocalizations and thereby triggering the evolution of speech and later language skills in our ancestors. Speech developed in Neanderthal man 1.5 million yrs ago as he descended from the trees, became a hunter & made noises to hunt prey & for protection. Descent to ground was due to prominence of Lateral Semicircular Canal in Homo Habilis and Homo erectus. There is convincing fossil evidence those 30,000 yrs ago in Mesopotamian civilization began the origin of the linguistic & caligraphic modern man [18].

The speech centre has large neural representation in the cerebral cortex. Human speech is complex and involves > 100 muscles (more than any other human mechanical activity) and is the fastest discrete motor activity that humans perform. Speech requires unusually complex breath control to produce long utterances on a single out-breath. The ratio of inhalation time: exhalation time is 1:1.2 for normal (rest) breathing & ≥ 1:8 for speech. The Evolutionary Adaptations for Speech are implicated to the Descent of larynx and lengthening of Laryngo-pharynx (vocal tract shape); Size of Hypoglossal canal (tongue function); Size of Vertebral canal (respiratory function); specialized muscle types and the special coding of genes (FOXP2) [19, 25]. Adult human larynx is lower in the throat than that of non-human primates and human infants, while Non-human primate tongue is flat in mouth (Fig-6). Human tongue is curved, and the VT is divided into 2 cavities with a right-angle bend. This anatomical configuration and tongue mobility permits articulation of point vowels [a i u] and thus language development began [18].

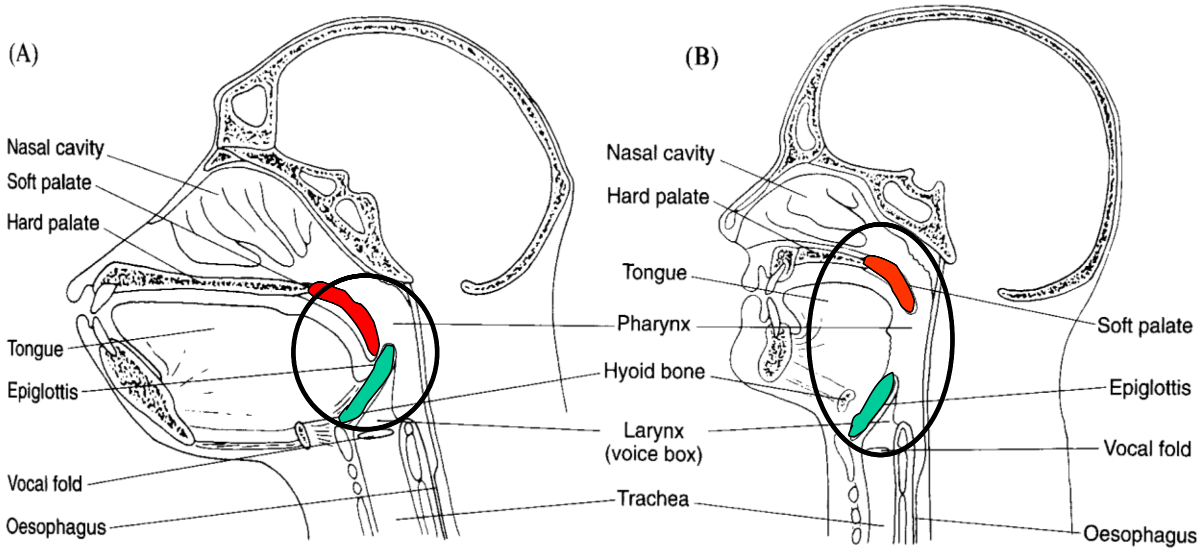

Fig-6: Phylogenetic Differences in the Oral Anatomy of Apes versus Humans
(Courtesy: Amniote Pale biology: perspectives on the evolution of mammals, birds, and reptiles: Eds: Carrano MT, Gaudin TJ, Blob RW, Wible JR. Chicago Univ Press, 2006)

A fair degree of evidence is available today to support both speech and symbol capacity in Neanderthals. Common ancestor of us and Neanderthals lived about 500,000 years ago and most likely age of some form of speech evolved about 400,000 years ago. Firm limit from common ancestor of modern man with writing skills & symbolic civilized behavior occurred around 100,000 years ago in Homo Heidelbergensis and later in Homo erectus. The Neanderthal man (Hominids extinct 30,000 years ago), were found to have some intelligible communication skills. Lieberman and Crelin reconstructed Neanderthal vocal tract and proposed, Neanderthals had a higher larynx than modern humans, which would not have permitted them to articulate the point vowels. This and other speech inadequacies probably contributed to their eventual extinction [18].

Human communication is thus the end product of long and complex evolutionary steps in hearing & speech with natural occurrence of genetic mutations & further refining of anatomy through the tides of time to best suit the modern man to rule this planet today.

Phylogenetic Relevance of Evolution of Hearing in the Present Day

Human brain has special characteristics, unique to itself, thus leading to total dominance over other animals, in the present day world. Neural "plasticity" is the ability of the central nervous system to be programmed to learn a task and this is unique to the human brain. Deprivation of auditory input causes structural changes in brainstem auditory nuclei and the primary auditory cortex. Auditory neural plasticity fades rapidly after a 'critical age for acquisition' as other senses begin to scavenge the auditory deprived brain. Hence any auditory intervention must be done as early as possible to take advantage of this phenomenon of neural plasticity to retrain the brain to hear.

PET scans have shown that a phenomenon of neural scavenging goes on actively in the brain where unused territory in the brain is 'taken over' by other functions. Loss of auditory information to the brain, eventually leads to loss of speech development and language acquisition. If the lost function is restored in time, then the 'lost territory' has to be regained after a struggle. This territorial war is interesting as it gives the physical basis for neural plasticity.

CONCLUSION

The climax of this evolutionary story is its clinical relevance in the present day. By occurrence of natural mutations, clinicians face a multitude of congenital and hereditary anomalies in the hearing apparatus like congenital aplasia / hypoplasia of the cochlea, labyrinth and auditory nerve or cochlear anomalies like in Michels' / Mondini's deformities. It is possible with today's technological advancements to screen for hearing in the foetus and at Birth. Modern day science delves deeply into the nuances of genetic basis for these phylogenetic hearing defects, to explore a possible way to overcome the problem at an embryonal level.

Necessary and timely intervention to restore hearing in congenitally deaf children should be undertaken at an early age, in order to provide them the necessary auditory inputs to develop normal speech and language. This is possible as the auditory system is unique in its organization which gives it the opportunity to receive & integrate external electronic circuits. This has given us, for the first time, the ability to intervene & modify the function of the central nervous system with auditory neural prosthesis like cochlear Implantation & auditory brainstem implantation.

The advent of such bionic hearing, has in the present day helped bypass a few of the phylogenetic defects leading to hearing loss and has paved a way to restore hearing in congenitally deaf individuals. Knowing the evolutionary history & embryonal anatomy of the human ear will provide the wisdom to rationalize their optimal management in modern day clinical practice.

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