

WHY IS THE COCHLEA ALWAYS CURLED?

Overview of The BIG IDEA of Hearing

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Appendix F

The cochlea of all tetrapods is coiled. Why? An analysis of the integrated neural system with a focus on hearing surfaces about five “Big Ideas.” This paper will focus on the most important big idea, *the cochlea of all tetrapods are curved for a reason*. It will also describe the convergence of a series of technologies in a beautifully integrated design using technologies unknown to man until at least the late 1970's, and only documented in a comprehensive analysis of that design during this decade.

There have been a significant set of unknowns related to how the cochlea operates that have vexed hearing researchers for many decades. These include,

1. How does the thimble size cochlea of humans manage to process auditory energy with wavelengths in air (and more crucially in water-based fluids) that are very much longer than the uncoiled length of the cochlea?
2. Why are cochlea curved into a logarithmic spiral, regardless of which family of tetrapods is of interest?
3. How is the acoustic energy projected into the labyrinthine organ, processed in order to serve the needs of the cochlea as a frequency dispersing mechanism?
4. How is dispersed energy converted into signals that can be manipulated within the hearing modality portion of the neural system?
5. How are the time delays associated with the signals derived from the sensory neurons spaced along the cochlea accommodated within the neural hearing system?

A first major problem exists because the cochlea of the hearing modality varies significantly in size. The length of the uncoiled human cochlea illustrates a most fundamental problem. It is nominally 35 mm long. That's the acoustic wavelength in air at a frequency of about 10,000 Hertz. In water, that acoustic wavelength would have a frequency of about 40,000 Hertz. Frequencies lower than that have wavelength very much longer than the uncoiled cochlea. Therefore some mechanism must be present within the cochlea that slows the flow of acoustic energy in order to provide physical separation of energy into spectral components that can be sensed neurally.

A second major problem revolves around the gelatinous character of most of the materials within the cochlea, even the muscle tissue. Those materials all exhibit a “stiffness” (Young's Modulus in engineering terms) that cannot support concepts of narrow frequency band resonant structures within the cochlea.

The following discussions will show that it is the integration of a variety of mechanisms and processes employing many different technologies that accomplish the remarkable performance of the cochlear mechanisms.

1 Brief Background

Hearing is one of about a half dozen sensory modalities sharing a common architecture within the neural system of the family Chordata (Vertebrata). These modalities are focused on creating a neural image of the external environment surrounding the animal. This abstract “neural image” is formed in a saliency map maintained by the central nervous system. Each modality employs a unique and specific sensory mechanism. These sensory mechanisms can generally be described by identifying a non-neural portion located prior to the sensory neurons, and also by the sensory neurons themselves. In vision, this non-neural part is primarily the lens of the eye and the structure maintaining the retina at the Petzval surface of the lens. In the case of hearing, the non-neural mechanism is more complex, particularly in the

case of terrestrial animals. In these animals, an external ear (typically labeled the pinna) is arranged to collect acoustic energy from the surrounding environment and deliver it to the tympanic membrane (eardrum). To achieve high auditory sensitivity in terrestrial animals, the difference in acoustic impedance between air and the fluid environment of the body requires the implementation of an impedance transformer, i.e. the middle ear.

The middle ear incorporates two diaphragms of different area (the tympanic membrane and the oval window) and a series of mechanical levers commonly labeled the ossicular bones (the malleus, incus and stapes). In the case of the human, and probably most species, these are known to be the smallest bones in the body.

The wetted surface of the oval window is built into the wall of the vestibule of the structure known as the labyrinth. The wetted surface of the oval window is frequently considered the beginning of the inner ear. However, the vestibule actually provides a common chamber shared by the sensory modalities associated with hearing and with the sensing of orientation relative to the earth centered inertial space.

Once delivered to the oval window, the path of the acoustic energy to the next major element of the hearing modality, the cochlea, has not been explored exhaustively. Only a portion of the acoustic energy introduced by the oval window into the vestibule actually excites the inner ear that begins at a structure known as the caecum of the vestibule. This structure is also known as the cul-de-sac of the cochlear duct in surgical circles. In hearing physiology, the cochlear duct is known as the scala media. It incorporates several critically important elements of the cochlea.

The cochlea is possibly the most technologically complex organ in the animal. It is most highly developed in the placental mammals, with its iconic curled shape first arising on earth during the cretaceous period (~50-100 million years ago). The non-placental (egg-laying) monotremes, birds and reptiles have a far less developed cochlea. [**Figure F.1.1-1**]

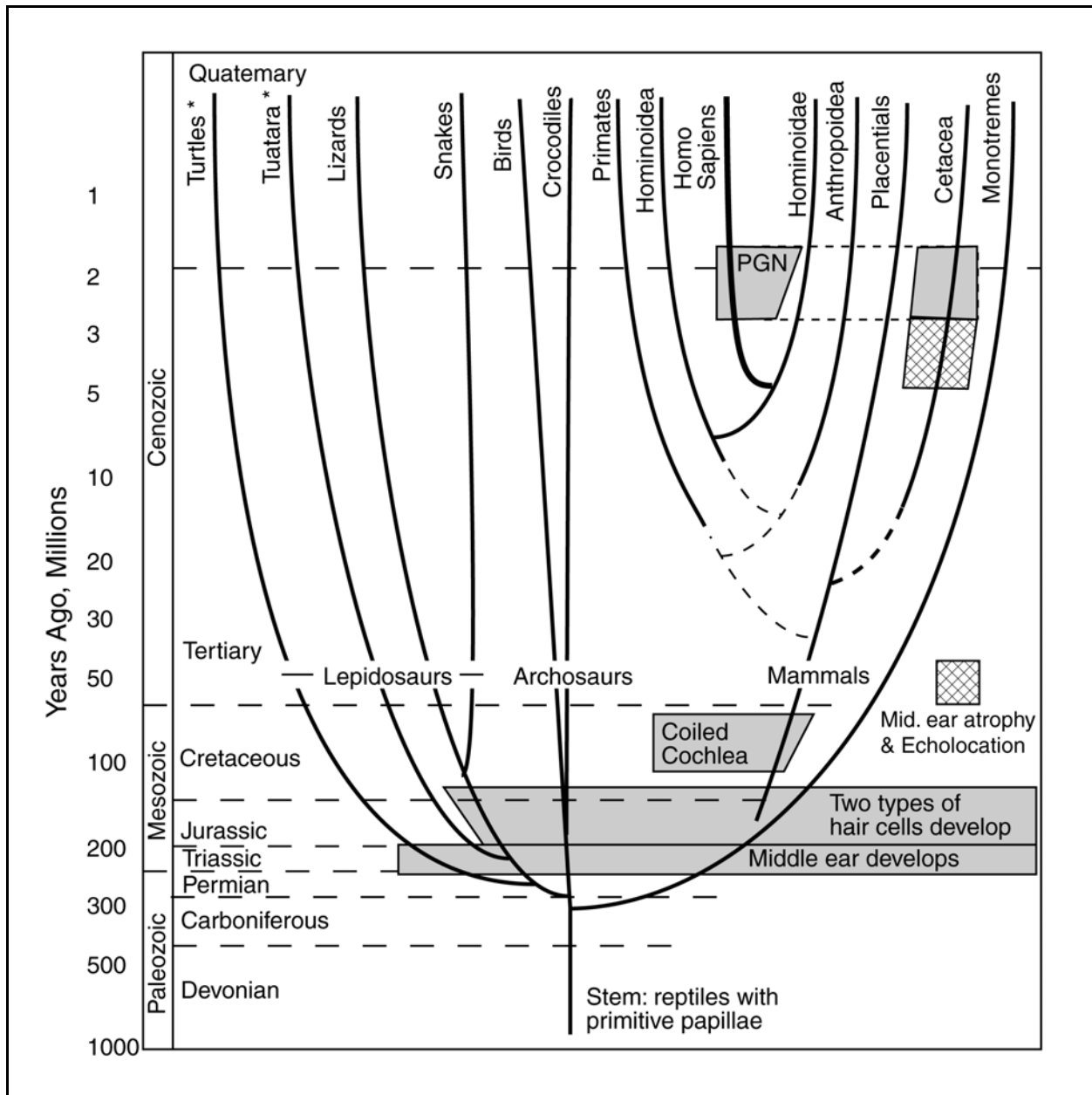


Figure F.1.1-1 A phylogenetic tree of the animal kingdom plotted versus geological time. The development of the middle ear and the differentiation into two types of sensory hair cells are said to have occurred multiple times. The evolution of the perigeniculate nucleus has apparently occurred only once. The monotremes on the right have 3/4 turn cochleae covering 2–6 kHz. The birds, including the parrots (Psittacines) have 1/8 to 1/4 turn cochleae, depending on definition, covering a range of 2 to 4 kHz. Atrophy of the middle ear among the marine mammals (Cetacea) appears widespread but as yet poorly documented. The coiled cochlea of the bottle-nosed dolphin shows specialization for echolocation. From Reformatted and expanded from Manly & Koppl, 1998.

1.1 What is the cochlea

The cochlea is that portion of the hearing modality dedicated to accepting acoustic energy in a fluid environment and processing it into a phalanx of neural signals that can be used to extract information from the variations in that acoustic energy. An animal has two cochleae, one associated with each external ear. Binaural processing of the signals developed by each cochlea extracts additional information useful to the animal in perceiving its external acoustic environment.

The cochlea is extremely difficult to study in the laboratory because it is embedded in the temporal bone, which is generally an integral part of the cranium (skull). There is an interesting exception in the case of the active echo-locating members of Cetacea, particularly the well studied variety known as the bottle-nosed dolphin, *Tursiops truncatus*. In these animals, the cochlea is actually isolated from the skull and their sound generating mechanism.

While the cochlea is generally shown in texts using a caricature reminiscent of a snail shell (cochlea in latin), the cochlea does not have an external shape of its own. It can only be displayed in its true form by employing an impression made of the cavity it occupies within the temporal bone, using molding techniques.

The use of molding techniques is adequate for obtaining a replica of the outer extent of the cochlea, but most of the detail representing the internal structure of the cochlea is typically lost. To overcome this problem, extensive and highly invasive dissection and histological techniques have been used to determine the internal structure of the cochlea. The minute size and the gelatinous consistency of many of the structures inside the cochlea have made this process difficult (and largely inadequate with respect to understanding the dynamics and physiology of the cochlea). Such dissections and histological slicing have shown that the cochlea is divided into two major cavities separated by a structural element, known as the basilar membrane, and the scala media.

In 1992, Anson & Donaldson provided a replica of just the scala media of the cochlea. This replica allowed the detailed structure and geometry of the in-situ scala media to be studied in detail, including its location relative to the basilar membrane.

1.2 Historical background–What has been learned previously

Most of the early morphology and physiology of the cochlea was developed by one man during the 1930's and 1940's, Georg von Bekesy. The intellectual intensity of his work won him a Nobel Prize in 1961, although his work only provided a conceptual explanation of how the cochlea worked. The problem was the tools available to him; he was forced to try and drive a pin into gelatin using a sledge hammer. Paraphrasing another theory-oriented researcher, this work does not refute Bekesy's, rather this work extends Bekesy's into realms that Bekesy did not deal with.

From the 1950's until very recently, ever more sophisticated laboratory investigations of the cochlea sought to learn the secrets of its physiology with little progress. Most investigators pursued their laboratory investigations without benefit of the second half of the Scientific Method, a detailed null hypothesis of what they expected to find. Lacking a null hypothesis, such work must be characterized as exploratory research.

Between the 1950's and 1990's, much of the technology required to understand the physiology of the cochlea was not in the intellectual tool box of man. (1) The definition of the liquid crystalline state of matter was not recognized until the late 1960's, (2) the mechanism of energy dispersal employed in the cochlea was not discovered or documented until Marcatili in 1969, (3) an understanding of slow traveling waves in liquids (and liquid crystals) required to explain cochlear operation was not codified until Lighthill in 1978 and (4) the character of the sensory neuron was not developed until 1999 by Fulton, US Patent 5,946,185. The mechanism of transduction is still a subject of considerable detailed investigation.

The key to understanding the operation of the cochlea requires the assimilation of processes and mechanisms from each of these technologies into a coherent description.

2 The Big Ideas related to the physiology of the cochlea are;

1. To the extent one wants to focus on acoustics, anatomy, morphology and histology, the Marcatili Effect is the BIG IDEA.
2. To the extent one wants to understand the physical acoustics of the cochlea, one must understand the (slow) surface-bound acoustic traveling wave (SAW).
3. To the extent one wants to understand how the brain receives audio information, one must understand the electrolytics & architecture of the neural system
4. To the extent one wants to understand how humans interpret the audio information produced, one must understand how the brain manipulates the information extracted from neural signals.

This paper focuses on the combination of items 1 & 2, the Marcatili Effect manipulating the energy of a SAW traveling within the cochlea.

2.1 The physiology of the cochlea

The basilar membrane is a unique physical structure. It is a highly structured cellular membrane, supporting the sensory neurons (known historically as hair cells). It also supports a series of longitudinal structures, multiple nerves and multiple arteriolea. The membrane is stretched between two boney structures arranged in a helical form. The result is a very rigid structure similar to the helical automobile ramp in a parking garage. The basilar membrane acts as an inertial mass (seismic block) that supports the sensory neurons. **[Figure F.2.1-1]**

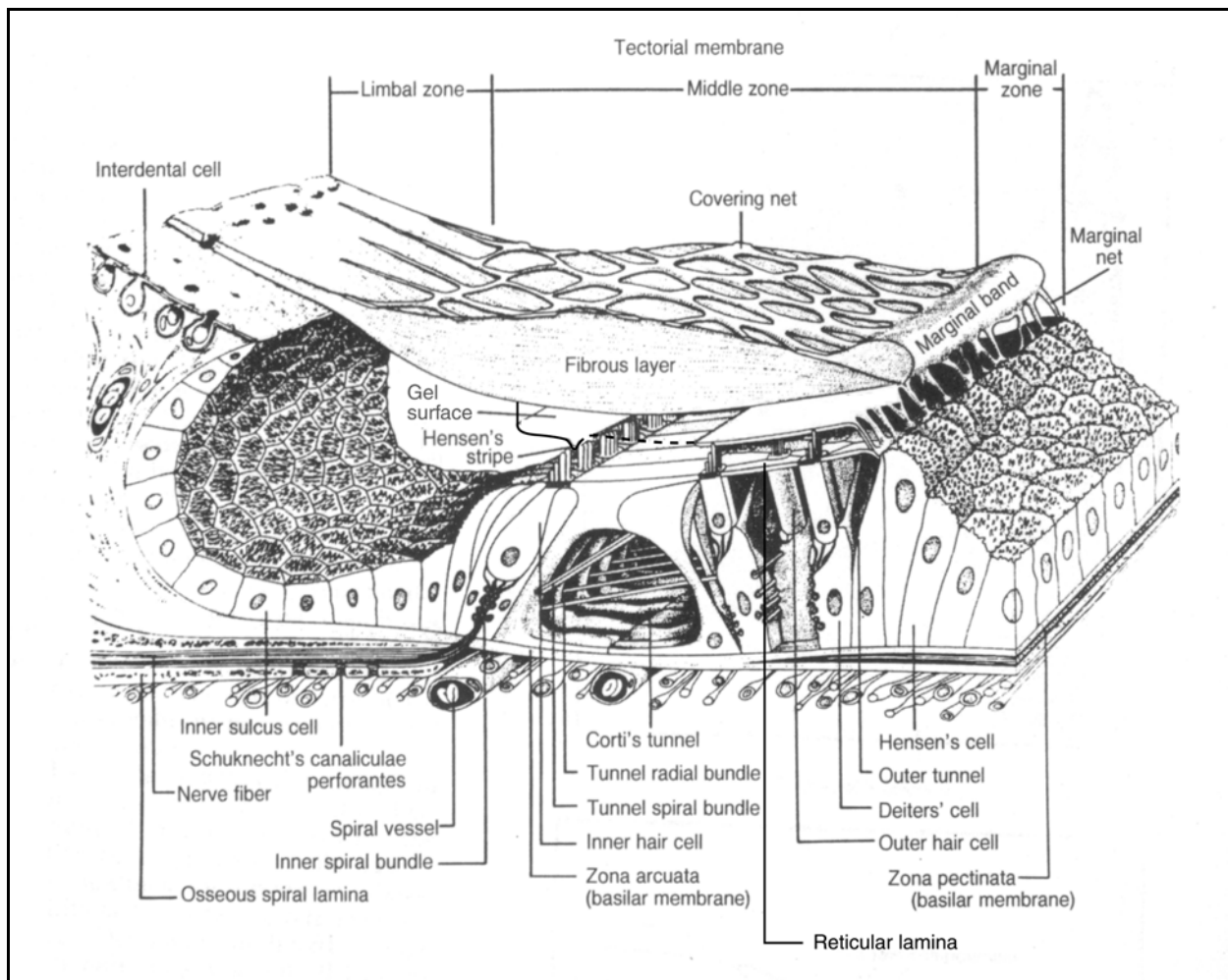


Figure F.2.1-1 Detail of the cochlear partition at the Organ of Corti. The gel (liquid-crystalline) coating on the underside of the fibrous layer of the tectorial membrane has been cut away to show the inner hair cells. Note Hensen's stripe (as opposed to Hensen's cells on right). All of the structure sitting on top of the basilar membrane tends to damp any oscillation by that membrane. Note the radial rigidizing structure, the Triangle of Corti. Note the longitudinal rigidizing (or at least hindering) structure of blood vessels and other tubular structures. The spiral/curved character of the basilar membrane stretched between bone also significantly rigidizes the membrane. Compare to Sally drawing in Allen, 1992.

[xxx May switch to simpler Figure 2.3.4-3 of Figure 4.3.3-6, Fulton harrison88pg16.]

The cilia at the free end of the each sensory neuron act like the phonograph needle sensing the variations in the groove of a phonograph record. They penetrate a reticular membrane and contact the underside of the tectorial membrane on the opposite side of the scala media. It is the underside of the tectorial membrane that combines a variety of unique features implementing the BIG IDEA of the cochlea.

It is the surface between the non-cellular (liquid crystalline) layer of the tectorial membrane and the endolymph of the scala media that is unique. This surface is ideally structured to support what Lighthill defined as a capillary type Surface Acoustic Wave (SAW). This type of SAW is ideal in that it is not dependent on the orientation of the gravity vector like the similar gravity type surface acoustic waves. Because of this difference, the ear works just fine upside down.

2.2 The SAW on the tectorial membrane surface

It should be noted before continuing, Lighthill also showed the bulk properties of a fluid like water cannot support a slow acoustic wave. It can only do so in conjunction with a surface shared with a material of different bulk properties, in this case the liquid crystalline surface of the tectorial membrane.

The velocity of the SAW wave traveling along the tectorial membrane at the fluid interface has been predicted and measured at about 6 meters/sec (a factor of 250 times slower than a conventional acoustic wave). As a result, a sine wave at 15000 Hertz exhibits a wavelength of only 0.4 mm; a sine wave at 100 Hertz exhibits a wavelength of only 60 mm. While it is not particularly relevant as developed below, all of the frequencies between these two values have a half-wavelength less than the length of the cochlea.

The liquid crystalline surface of the tectorial membrane is found to consist of a ridgeline, called Hensen's Stripe and a nearby flat plane. It is the curvature of this ridgeline that is the critical element in the operation of the cochlea. As is well documented in SAW filter technology, an acoustic wave can be made to travel along this ridge at negligible loss as long as it is reasonably straight. In the case of the cochlea it is not, its curvature changes continuously in accordance with a Hankel Function.] [Figure F.2.2-1]

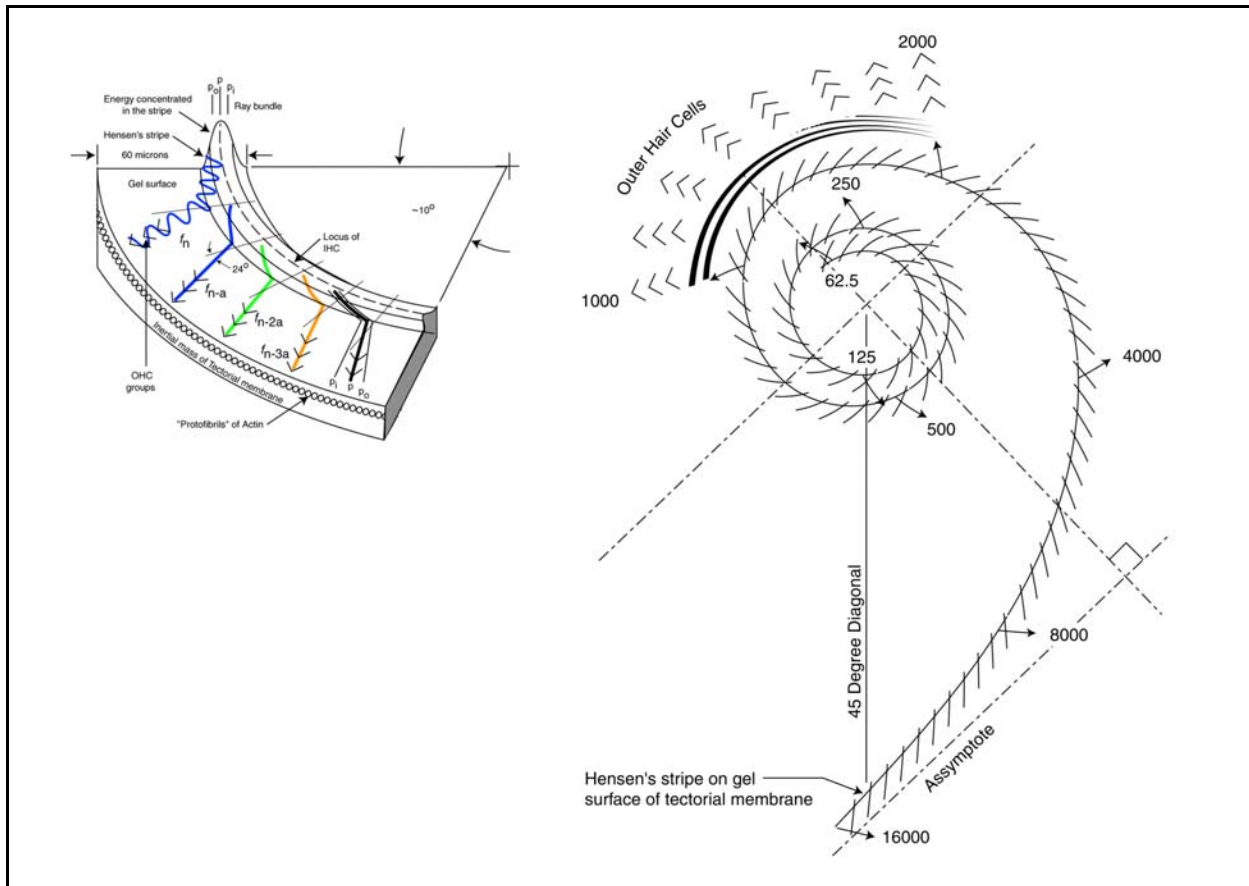


Figure F.2.2-1 Standardized frequency selective spatial dispersion along Hensen's stripe. Left; the dispersion of the energy traveling along Hensen's stripe out onto the flat region of the liquid crystalline surface of the tectorial membrane, where it is intercepted by the "triplet" groups of outer hair cells. Note the locus of inner hair cells along the peak of Hensen's stripe. This is the key application of the Marcatili Effect. Right; plan view of the coiled cochlea showing the dispersion of acoustic energy as a function of the curvature of Hensen's stripe. Location of Hensen's stripe does not always coincide with the location of the basilar membrane. This is the key geometry of the cochlea.

To achieve the desired dispersion of acoustic energy into the appropriate sensory neurons, it is important that Hensen's stripe be curved in a systematic manner. This is the second key to the operation of the cochlea. Hensen's stripe (and not the basilar membrane, the tectorial membrane or the cochlea) must exhibit a characteristic curvature. This is in fact the curvature observed in all cochleae. For humans, this curvature is described by a progressive Hankel Function, a two-dimensional Bessel Function formed into a corkscrew of decreasing radius.

The number of turns (or partial turns) of this corkscrew is indicative of the range of acoustic frequencies that can be heard by a specific animal species. In some cases, Hensen's stripe diverges from a nominal Hankel Function in order to provide either enhanced frequency resolution or to skip over frequency bands not of ecological interest for that species. This condition is easily demonstrated using available data from the mustached bat and the bottle-nosed dolphin, both employing active echo-location techniques.

In human hearing, and apparently that of many other species, the Hankel Function is modified near the apex (the low frequency region) into what can be called a modified Hankel Function. The reason for this modification is not obvious, but may be to avoid excessive crowding of the nerves leaving the cochlea.

2.3 The Marcatili Effect & the Hankel Function predict the auditory response of the cochlea

Enrique Marcatili, retired from Bell Laboratories, was winner of the IEEE's Baker Prize in 1975. Marcatili has been described as "a pioneer in optical fiber research," and he is a member of the National Academy of Engineering.

Marcatili researched the reason light energy leaked out of a curved fiber optic cable. He developed a very precise theory for this loss for a variety of cable configurations. However, he did not explore a continuous change in curvature of the cable. Later investigators did and the continuously curved cable is now widely used in sophisticated commercial dispersion filters for fiber optic cables.

Investigators following Marcatili, demonstrated that the SAW energy of a specific frequency cannot sustain itself along the ridgeline such as Hensen's stripe if the curvature exceeds a certain specific value. It will descend down the side of the ridgeline and travel away from the ridgeline along the flat plane of the tectorial membrane. It is this dispersion of acoustic energy by the curvature of Hensen's stripe (the Marcatili Effect) that is THE BIG IDEA in the Cochlea and in hearing. It is key to the operation of cochlea. As the slowly traveling Surface Acoustic energy is dispersed in fans of different frequencies, small portions of this fan are captured by the individual cilia of a first set of sensory neurons, known as the outer hair cells (OHC), acting as styli triggering neural signals. Thus the OHC located along a specific radial of the helix formed by Hensen's stripe deliver a narrow band neural signal characteristic of a center frequency.

The key feature of the Marcatili Effect is the presence of an exponential in the attenuation term of the loss equation for the energy in a waveguide of constant curvature. The result was an equation involving an exponential of an exponential (a previously unknown mathematical configuration in waveguide phenomena Figure 4(top)).

$$\text{Amplitude} = 1 - \exp(\alpha x)$$

$$\alpha = c_1 \cdot \exp(-c_2 \cdot (r/R)) \quad R = \text{critical radius of curv.}$$

$$\int_0^f \exp k \cdot \exp^{-W_x} dx \quad \text{where } W_x = \frac{M \cdot x^{0.5}}{R}$$

OR

$$\int_0^f \exp k \cdot \exp^{-\underbrace{M \cdot x^{0.5}}/R} dx$$

Figure F.2.3-1 Attenuation versus frequency equations for Marcatili Effect. Top; original form for R fixed and the local radius of curvature, r, also fixed. The exponential of an exponential is a rare form. Bottom; form showing r expressed by a Hankel Function of length x. *This is the key equation of the cochlea.* The difficulty of integration should be obvious. Integration by parts, and the conversion of the integrand into a series, gave similar results.

If the curvature of the waveguide is continuously changing, the resultant equation can be expressed as a function of distance along the curve, and becomes even more complex.

Before proceeding, it is useful to consider what happens to the acoustic energy that continues past the point of specific curvature. This is a broad spectrum of energy except it is periodically reduced in high frequency content. This energy is sensed by a second set of sensory neurons, known as the inner hair cells (IHC), and arranged on the basilar membrane so their cilia contact the top of the ridgeline and act as a second set of styli. It is the neural signals from the IHC that provide a set of broadband signals that are critically important in the sensing of direction in a binaural system.

[Figure F.2.3-2] describes the relationship between sensed acoustic frequency and sensor neuron position along Hensen's stripe within the cochlea. The predicted (dashed line) line overlays the measured data of the cat quite precisely and suggests the remarkable ability of the theory to predict (and/or accommodate) the extended frequency response of the cat, the macaque and the active echo-locating bats and dolphins.

As shown, it overlays the measured human response quite well if specific parameters are modified to move it down and slightly to the left.

The confluence of the theoretical and empirical auditory responses shown in **[Figure F.2.3-2]** is strong support for the validity of the Marcatili Effect as the dominant mechanism determining the audio frequency resolution of the cochlea.

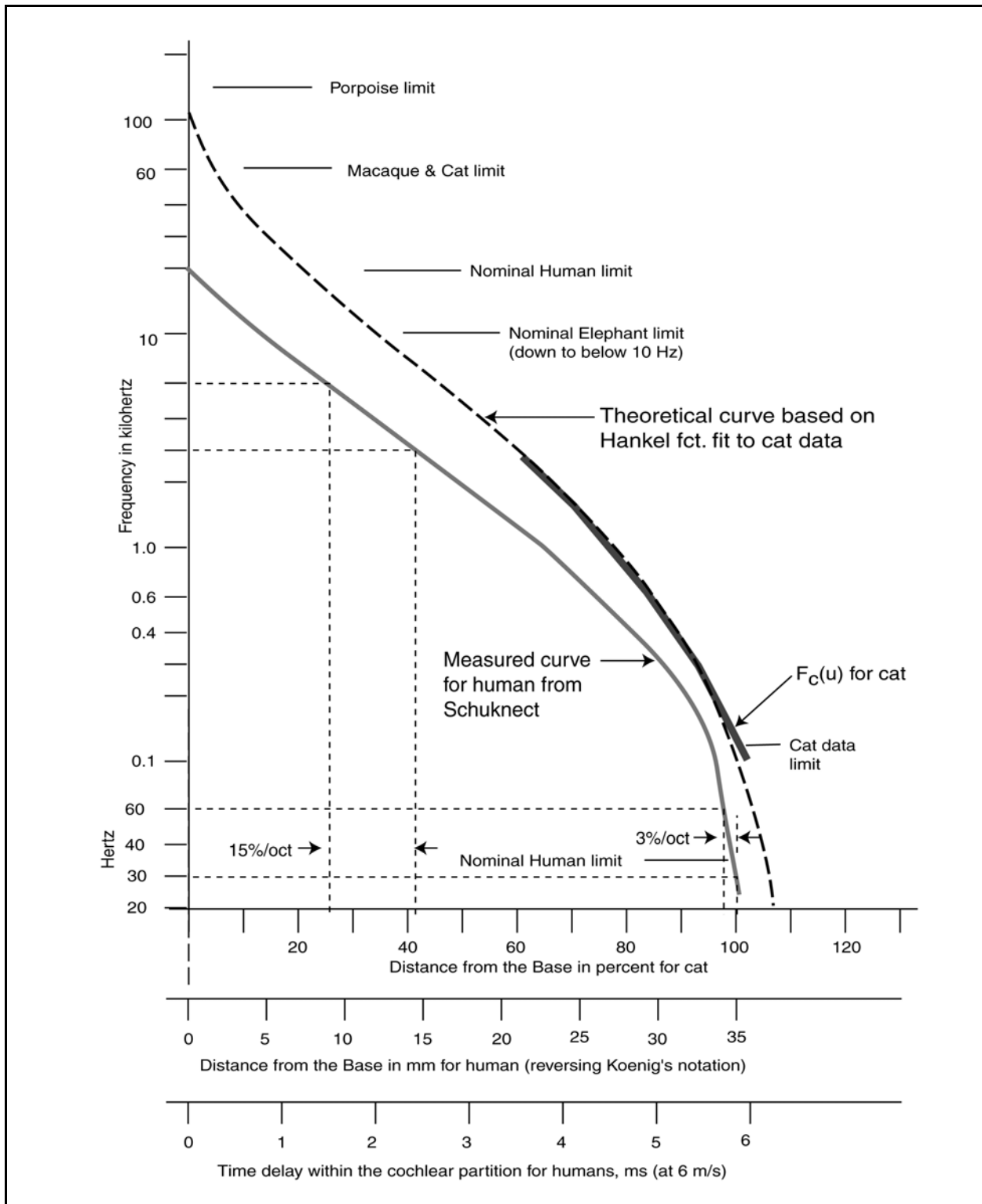


Figure F.2.3-2 Proposed place-frequency-delay characteristic of the cochlear partition. Solid line; humans based on a propagation velocity of 6 meters/sec. Dashed line, theoretical place-frequency-delay characteristic. *This is the key performance relationship within the cochlea.* Heavy solid line, measured data for the cat. Also shown, the limits of hearing in various animals as they relate to the theoretical curve. The bottom two scales indicate how the cochlea acts as a transversal filter.

2.4 The Marcatili Effect explains the attenuation found in hearing

An explanation has long been sought for the remarkably high attenuation in the skirts of the neural signal passband of both the inner and outer hair cells. The attenuation is far higher than in any previously known electrical or mechanical filter phenomenon, whether associated with resonance or not. The Marcatili Effect generates just such high skirt attenuation. The attenuation associated with this Effect is given by the line integral of the Hankel Function. The line integral itself is a little known mathematical function. However when used in conjunction with the Hankel Function, a remarkable mathematical form results, the integral of an exponential of an exponential [Figure 4(bottom)]. The result is an attenuation coefficient that continues to increase exponentially with frequency (rather than remaining constant). The resulting attenuation is nominally 180 dB/decade (55 dB/octave) at 50 db below peak response. This value is compatible with the attenuations of between 100 and 1000 db/octave measured by multiple investigators. [Figure F.2.4-1]

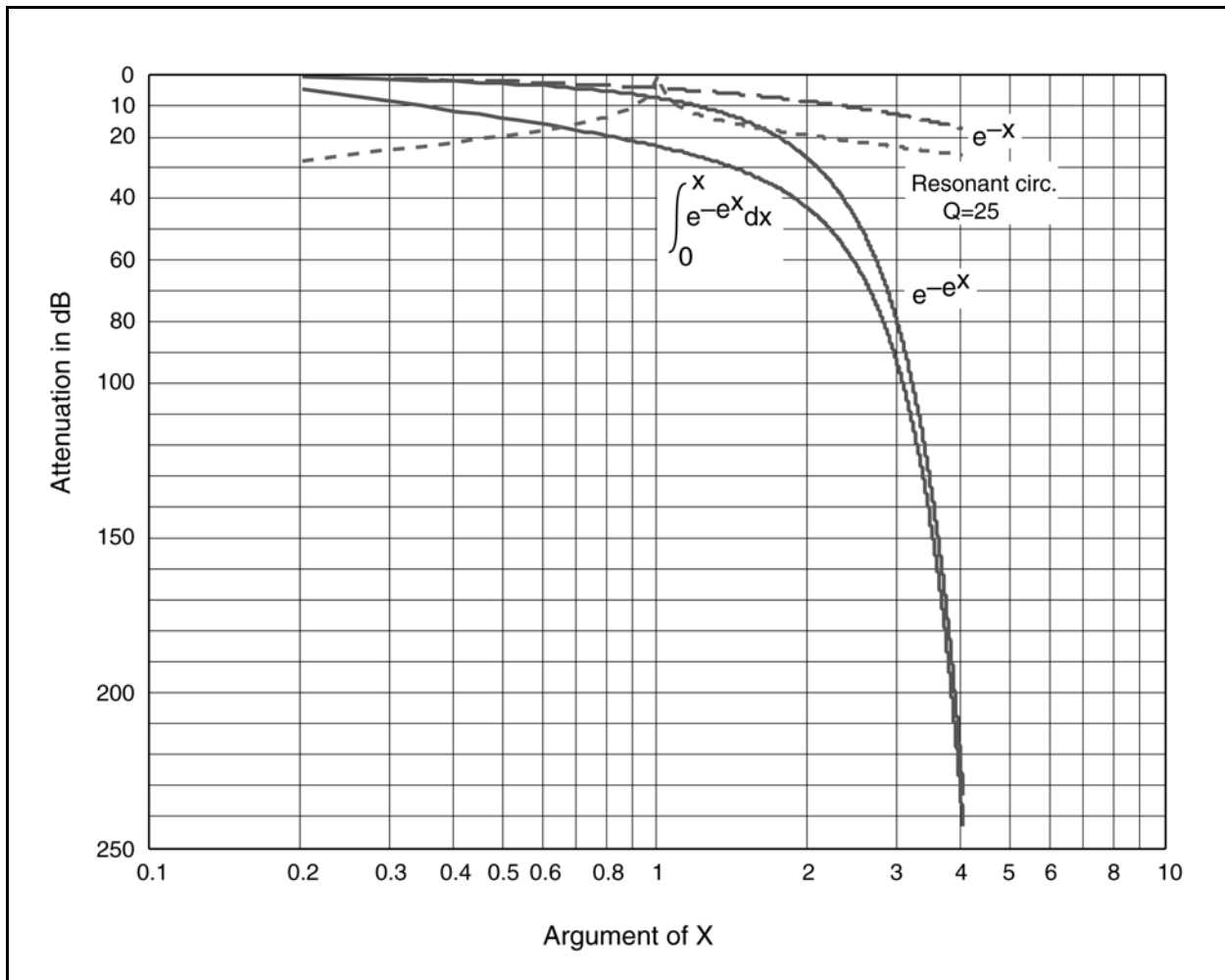


Figure F.2.4-1 The attenuation of exponential and resonant functions. Solid lines; the local and integrated exponential of an exponential function. A simple exponential and a resonant circuit are shown for comparison. The resonant circuit has a $Q = 25$. It is difficult to achieve even 60 dB with a crystal filter. The attenuation of the “exponential of an exponential” is dramatic while the exponential of an exponential easily achieves 100 to 1000 dB. The curves have been normalized to a common maximum.

The Marcatili Effect correctly describes the extreme attenuation characteristics of the cochlea without involving any other attenuation mechanism associated with the hair cells. No other theory of cochlea operation has even offered a suggestion as to the source mechanism of those very high measured attenuation levels.

3 Animated depictions of cochlea operation

<http://neuronresearch.net/hearing/files/animation.htm> offers a variety of individual animations describing the operation of the cochlea.

4 The BIG IDEA leads to significant changes in our understanding of the cochlea

The above analysis leads to a different interpretation of how the cochlea works in at least four areas.

4.1 The energy diagram removes the need for an acoustic amplifier

The hearing community has been struggling with a “floating model” of the cochlea that has accepted very large coupling losses between the energy level at the oval window of the vestibule and the energy level of the basilar membrane. This model has required a large amount of amplification of the mechanical signal to adequately stimulate the cilia of the sensory neurons [Dashed path in **Figure F.4.1-1**].

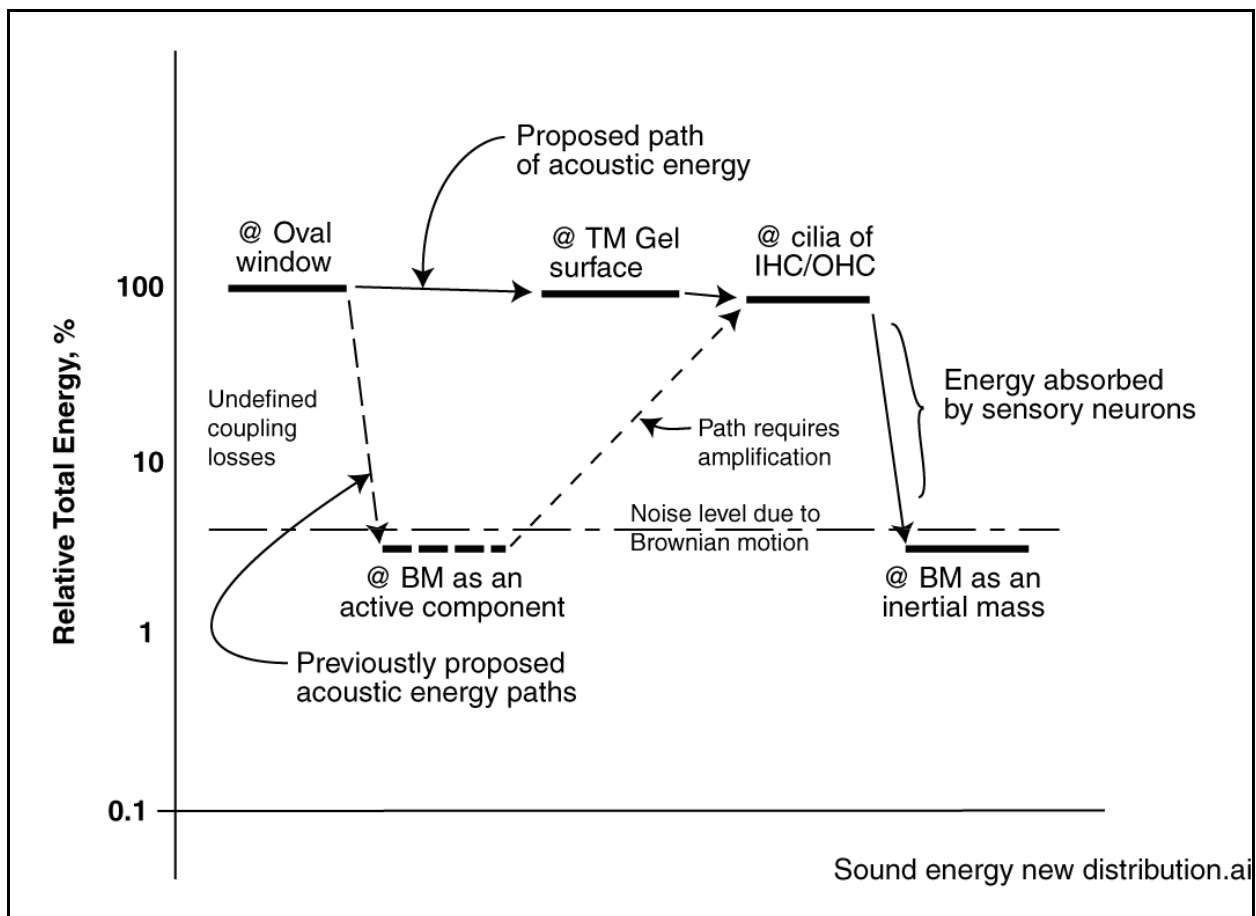


Figure F.4.1-1 Potential signal paths within the cochlear partition (Organ of Corti). Solid arrows show paths proposed in this theory. Nearly all of the energy at the oval window is delivered to the sensory neurons. The basilar membrane takes on its appropriate role of an inertial mass. Dashed arrows represent the earlier proposals. After encountering major unexplained losses, earlier proposals require a mechanical cochlear amplifier to raise the signal level above the measured level of the basilar membrane. These proposals require an undocumented connection between the scala vestibuli and the vestibule of the labyrinth.

Recognizing that the acoustic energy applied to the oval window is efficiently transferred to the liquid crystalline surface of the tectorial membrane provides a different model. An efficient path is provided leading to the dispersal of the energy to the hair cells at high efficiency. The sensory neurons absorb most of the energy; some residual energy is delivered to the basilar membrane acting as an inertial mass [Solid path in **Figure F.2.4-2**].

The proposed mode of acoustic energy dispersal negates the need for an “acoustic amplifier” to excite the hair cells.

4.2 There is no longer a requirement for a flexible basilar membrane

Recognizing that the acoustic energy is not applied to the basilar membrane directly also eliminates another long standing conceptual problem. How could the complex and rigidized structure of the basilar membrane provide compliance typical of fluids in order to support the acoustic isolation of adjacent hair

cells? The question becomes irrelevant if the acoustic energy is actually propagated along the liquid-crystalline surface of the tectorial membrane.

4.3 The dual character of the neural paths to the brain is explained

Looking again at the physiology of the cochlea above, it is seen that two distinct sets of neural signals are generated as a function of position along the cochlea. Because of the slow propagation velocity of the signals traveling down Hensen's stripe, they are also dispersed in time. These two sets are of totally different character. Thus, the cochlea is acting as a dual channel transversal filter. The one set of transversal signals represent the broadband signals created by the inner hair cells associated directly with the ridge of Hensen's stripe. These signals are delivered to the medial olivary complex (MOC) of the cochlear nucleus in their time dispersed format. The other set of transversal signals represent the narrowband signals created by the outer hair cells associated with the inner liquid crystalline surface of the tectorial membrane. These signals are delivered to the lateral olivary complex (LOC) of the cochlear nucleus in their time dispersed format.[**Figure F.4.3-1**]

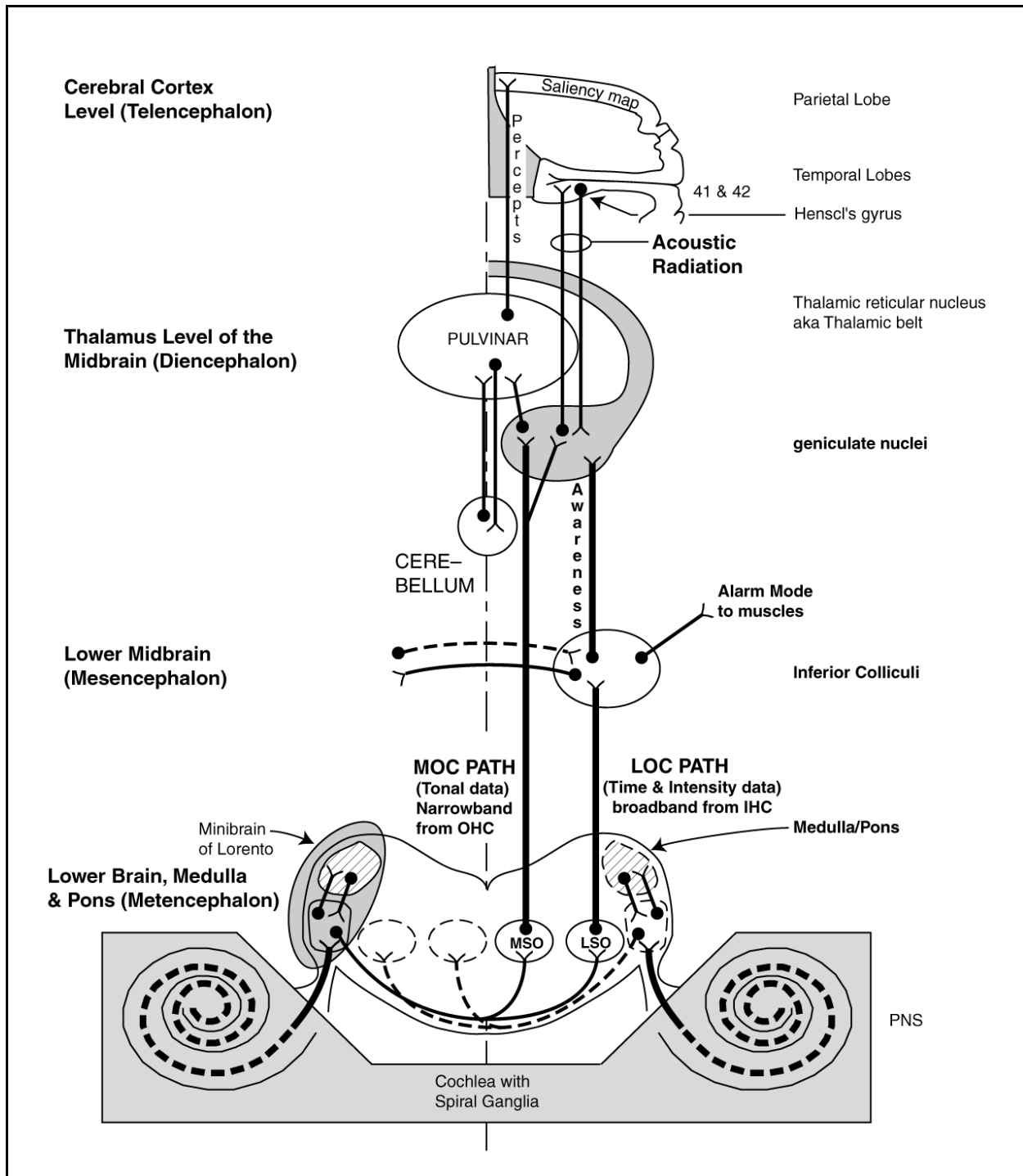


Figure F.4.3-1 Top level schematic of the circuits of the auditory system within the human cranium. Figure represents a “reduced mesh” of the complete schematic. MSO & LSO; medial and lateral superior olives. MOC; channel supporting tonal aspects of speech and music. LOC; channel supporting source location and fricative aspects of speech and music.

The MOC path, named after its emanation from the medial olivary complex (MOC) of what Lorento in 1981 called the mini-brain of hearing, supports the multiple narrowband, or tonal, channels of the hearing modality. The mini-brain is more formally the cochlear nucleus. It is located in the wall of the cylindrical old brain, frequently labeled the brainstem, leading to the spinal chord. The LOC path, named after its emanation from the lateral olivary complex (LOC) of the mini-brain supports the multiple wideband, or time and intensity, channels of the hearing modality.

It is interesting to note the bandwidth characteristics of the LOC and MOC channels as they are generated at the output of the sensory neurons. [**Figure F.4.3-2**]

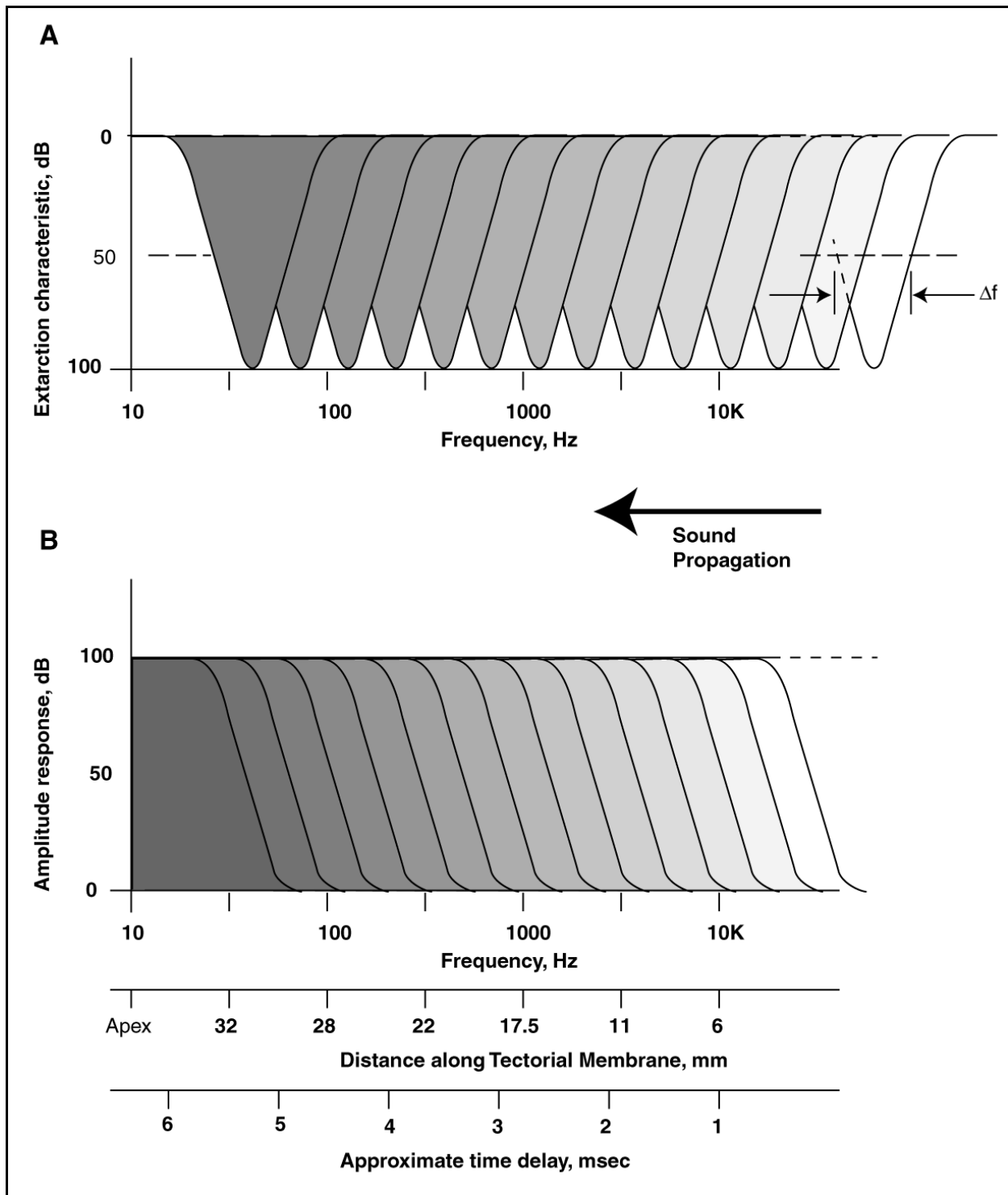


Figure F.4.3-2 Caricature of signal extraction by the SAW filter of a human cochlea. A; nominal signal extraction profile for OHC beginning on the right. Each extraction occurs sequentially. Each extraction has a nominal bandwidth (at xxx) as shown by the arrows. The Q of the extraction is given by the median frequency divided by the bandwidth. B; the residual signal bandwidth of the SAW filter sensed by the IHC at a given point along the tectorial membrane.

Note the skirts of each of these channels exhibits the very steep attenuation provided by the Marcatili Effect upon which the cochlea depends. Note also the two scales present, the neural signal sources of these channels are dispersed in both position along the cochlea (which equates to time due to the transversal filter mentioned above) and frequency.

A feature of the neural system that will not be addressed here is its use of computational anatomy. Computational anatomy allows the system to perform complex signal transformations without employing transcendental mathematics (integration particularly). In the case of the transversal signals traveling along the MOC and LOC paths, the signals can be brought back into time synchronism by merely adjusting the lengths of the individual neuron paths.

4.4 The Marcatili Effect dominates the human Audiogram of ISO 226:2003

The acoustic frequency response of human hearing is difficult to quantify because the ultimate measure of performance is a psychological phenomenon. A unit of perceptual loudness has been identified and defined as the phon. A condition of equal loudness must be determined by using a two-frequency test, where the more distant the two frequencies, the more difficult the perceptual comparison. This situation results in an equal loudness contour that is precise for adjacent frequencies but suffers from a potential run-out error as the frequencies become farther apart. The determination of the equal-loudness-level contour as a function of frequency is found to also be subject to the state of adaptation of the hearing modality (and the performance of the Eustachian tube. Thus, tests have been used to determine the statistical mean sensitivity (energy required to achieve a constant loudness across the audio frequency band) of the human auditory modality under various states of adaptation. The statistical variation in these protocols is quite high, resulting in high standard deviations in the reported data.

The normal equal-loudness-level contours of human hearing have been standardized by the International Standards Organization based on a consensus among investigators using data from multiple laboratories. The ISO, and earlier standards, have been revised several times as laboratory evaluation techniques have improved and the resulting consensus has changed. Changes as large as 15 dB were made between the low frequency values of the 1987 and 2003 revisions of the Standard. However, the standard deviations remain in the +/- 5dB range between 20 and 10,000 Hertz in the 2003 revision. **[Figure F.4.4-1]** At higher frequencies the standard deviations remain to be stated officially.

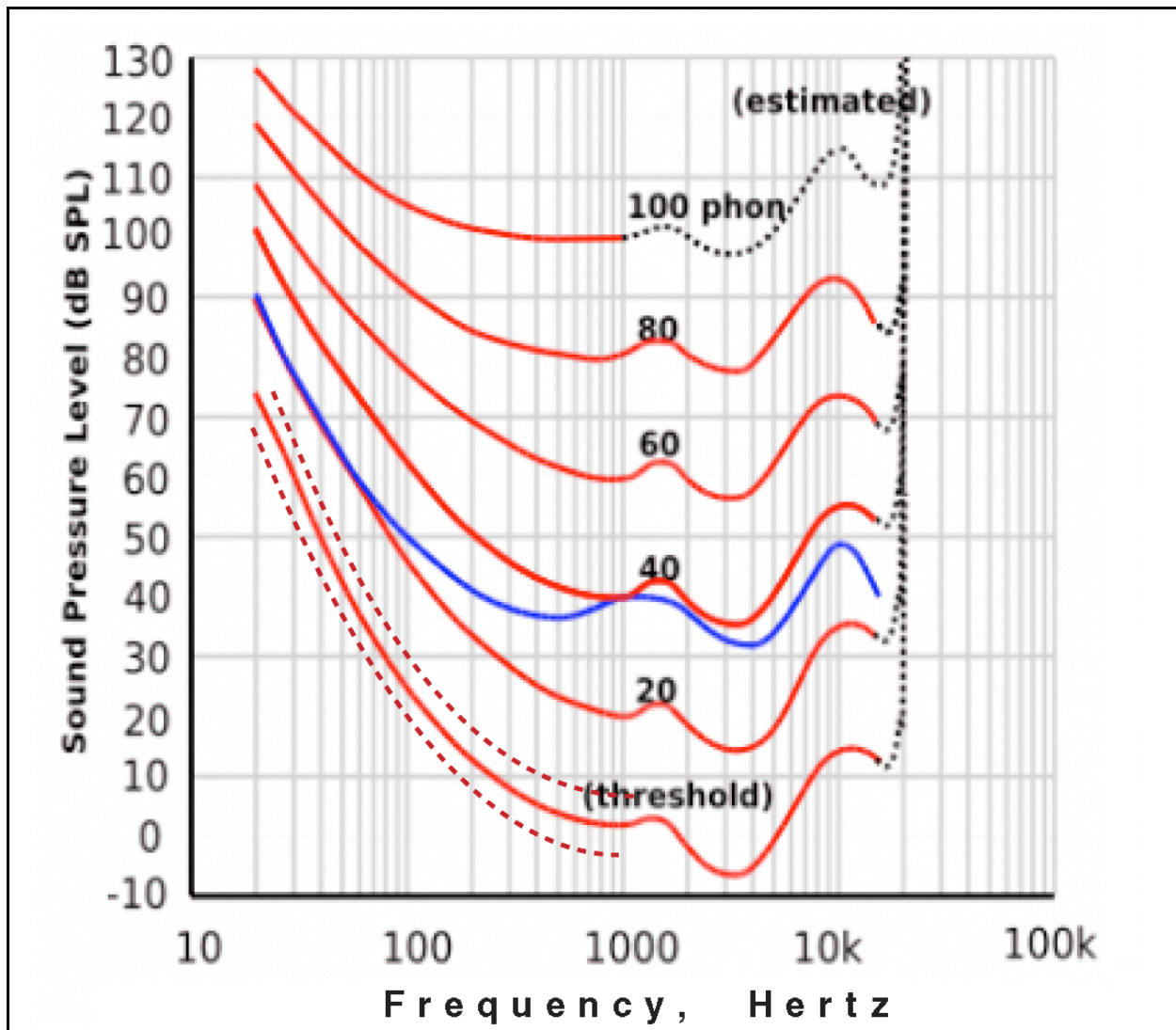


Figure F.4.4-1 Accepted ISO 226 Standards of 1987 at 40 phons (blue) and 2003 (red) showing significant differences. The Standards are based entirely on empirical data. Standard deviations associated with the 2003 threshold (dashed red). Variations of ± 10 dB are common in psychophysical experiments.

The audio frequency characteristics of the outer, middle and inner ear can be calculated from the available attenuation data. Whether the neural processing associated with the MOC or LOC channels is dominant in this calculation is difficult to say unequivocally. However, the audio attenuation associated with the tonal or LOC channel appears to be dominant. Under this assumption, the envelope of the audio spectrum is determined predominantly by the inner ear. The result is a middle region of constant sensitivity, bounded by roll-offs at high and low frequencies due to the Marcatili Effect.

The acoustic transfer function of the outer ear has been well reported by Weiner & Ross, and it exhibits considerable irregularity. The acoustic transfer function of the middle ear is very difficult to measure and little information is available in the form required. Most investigators ignore the presence of the Eustachian tube and only stimulate the ear canal. Under these conditions, the middle ear is generally reported to act as a low pass filter (dashed line at low frequencies). The data available from Rosowski

shows the complete middle ear acts as a bandpass filter. In both cases, the human ear is found to roll-off at a frequency near 15 kHz. [Figure F.4.4-2]

Combining the measured attenuation characteristics of the outer and middle ears with the theoretical characteristic of the inner ears shows the audio spectrum of human hearing is dominated by the Marcatili Effect, except for two situations, the ripples in the response at frequencies above 1000 due to the outer ear and the variation in attenuation at low frequencies due to variability in Eustachian tube performance. Comparing this response with the ISO 226 standard shows the empirical standard is tracking the theoretical response at high frequencies and is within the predicted theoretical envelope at low frequencies. [Figure F.4.4-3]

This is the same phenomenon, the empirical ISO sanctioned Equal-Loudness Level standard approaches the underlying theoretical performance as laboratory evaluation techniques improve, that is occurring in the ISO sanctioned Uniform-Chromaticity-Scale (UCS) visual Chromaticity Diagram.

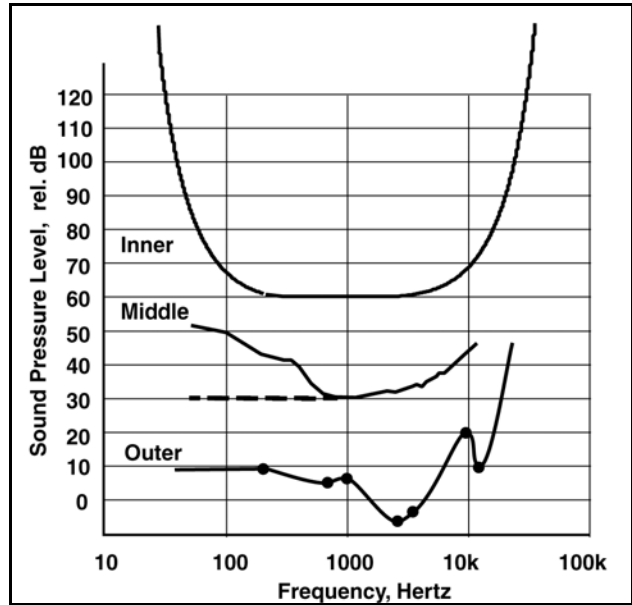


Figure F.4.4-2 Contributions of outer, middle and inner ears to the audiogram of humans for free field acoustic stimulation from the front. Middle ear shown with Eustachian tube functional (solid line).

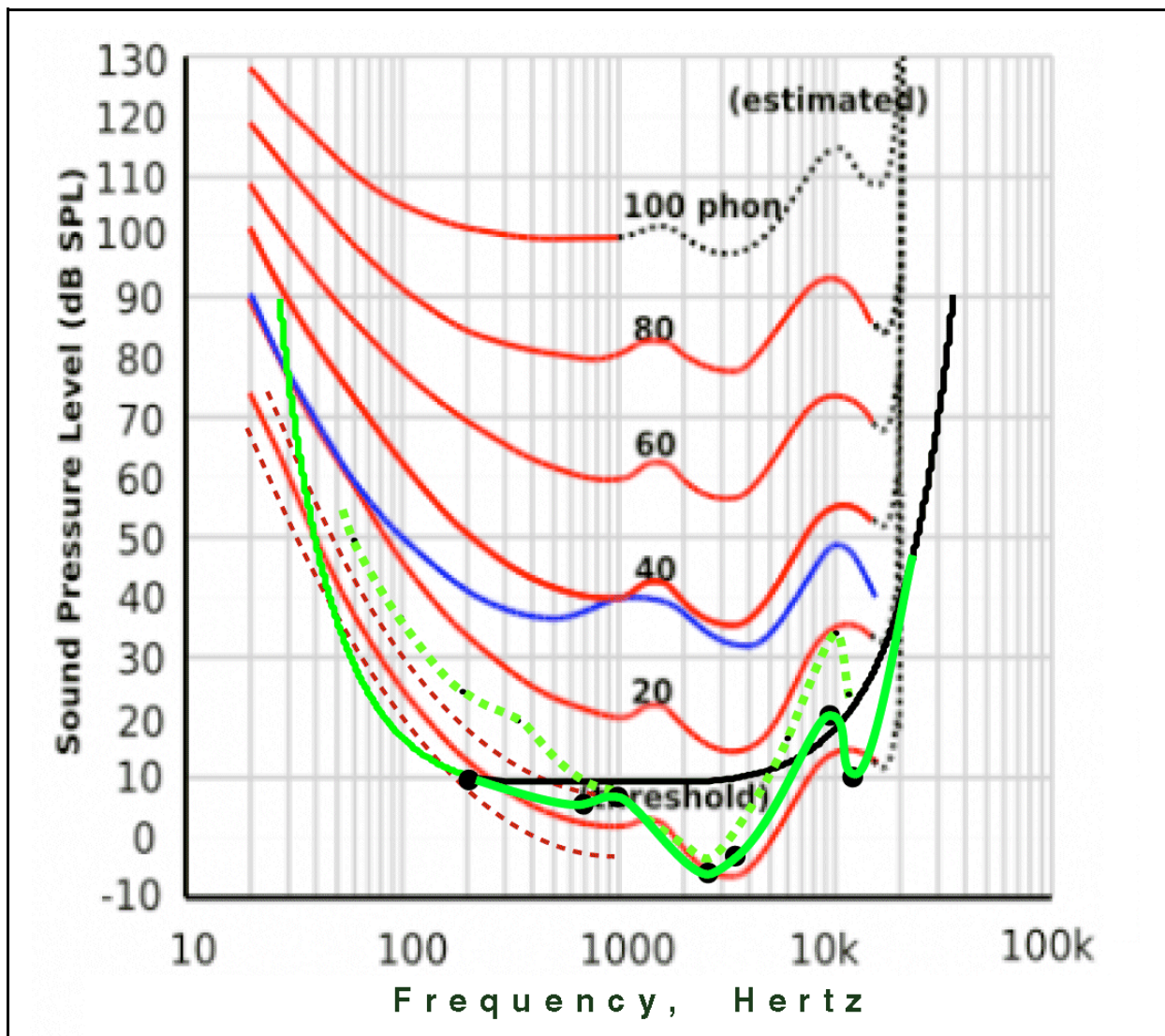


Figure F.4.4-3 The latest ISO 226:2003 standard versus theory. Solid red lines; the Standard. Dashed red lines; one standard deviation from the mean of the Standard. Blue lines; the previous (1987) standard at 40 Phons. Black line; the transfer function of the cochlea (inner ear) based on the Marcatili Effect. Solid green line; transfer function of the complete ear with Eustachian path open. Dashed green line, transfer function of complete ear with Eustachian path obstructed.

4.5 Summarizing the impact of the Marcatili Effect on hearing research

Application of the Marcatili Effect to the theoretical understanding of the hearing modality has a significant impact on the past literature and future research. The Effect, combined with the slow surface acoustic wave (SAW) filter of the tectorial membrane coiled into a modified Hankel Function shows the cochlea employs a dispersive filter with the properties associated with a multi-channel spectrometer. As a result, the cochlea;

1. does not rely upon any traveling wave within the bulk contents of any element of the cochlea.
2. does not rely upon any “tuned circuits” or any resonance phenomenon within the auditory system.
3. does not rely upon any regenerative amplification process within the cochlea.

4. does not rely upon any positive feedback system within the cochlea.

The cochlea does generate two distinct sets of neural signals of the time dispersed form suggested by its acting as the initial portion of a transversal filter. Each set is used for a totally different purpose, the MOC set is used for perceiving frequency patterns. The LOC set is used for perceiving transient events, particularly those related to acoustic source location. Both sets contribute to the understanding of speech, as illustrated by the typical spectrogram of speech.

Fully referenced and detailed support for this paper is available in both printed and electronic form at www.neuronresearch.net/hearing. A printed version, "Hearing: A 21st Century Paradigm is available on the website or from book dealers; ISBN 142516065-4. The same material in electronic form, along with many animations, is also available from the website.

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Color overlays will be added to the PowerPoint version to show;

1. humans use the entire length of Hensen's stripe shown (0.06 to 16 kHz),
2. the monotremes use only the 1 to 6 kHz region,
3. the birds use only the 2 to 4 kHz region.
4. The echolocating bats and dolphins rescale the coil to achieve performance over the range of 2 to- 3 kHz up to 120-150 kHz.