

Appendix N
Cochlear Mechanics Chronology
and
Falsification of the BM role in cochlear mechanics
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N.1 Introduction & Overview

The historical development of cochlear mechanics during the 20th Century began with von Bekesy's first major publication on the subject in 1928. The work was largely that of a communications engineer working with the largely empirical tools of that day. It lacked a strong mathematical foundation. It joined a large variety of earlier conceptual theories dating from the 19th Century. Wever tried to put all of these theories into perspective (page 41) in 1949¹ and provided a detailed critique of the theory of von Bekesy (pp 63-68). Wever also introduced his version of an alternate place-frequency theory. In 1971, Rhodes completed a Thesis employing what is today known as the Mossbauer technique of precision motion measurement to the study of the motions of the basilar membrane of the inner ear and the malleus of the middle ear. He highlighted many problems with the von Bekesy hypothesis but did manage to measure a traveling wave he associated with the BM, moving at between 9 and 12 meters/sec. Zweig took the data of Rhode in 1976 and reconstructed his interpretation of the motion of the BM fitting the von Bekesy hypothesis. The well known authority on fluid mechanics, Lighthill entered the field in 1981 with an initial paper that was somewhat cursory and failed to generate a large impact. It attempted to rationalize the work of von Bekesy, Rhode and Zweig noted above. He compared several alternate models in his Appendix A (p 167). At that time, he dismissed the one-dimensional cochlear model as unworkable in his Appendix C.

In 1989, Gulick et al. performed a major review of hearing theory and addressed the shortcomings of both the von Bekesy place approach and the Wever place frequency approach². They asserted the von Bekesy hypothesis was not an actual theory of hearing (pp 65-66), but was

- (1) merely a hypothesis of pitch discrimination,
- (2) failed to address the relationship between BM displacement and neural signal triggering,
- (3) did not offer a relationship between the receptor place along the BM and the neuron place and
- (4) suffered shortcomings in two specific areas based on clinical knowledge;
 - (a) it was inconsistent with the condition of presbycusis and
 - (b) it was inconsistent with high tone deafness as observed in the clinic.

Gulick et al. also found shortcomings with Wever's place-frequency hypothesis (pp 66-71); (1) a lack of parsimony, (2) a need for synchronism between sensory neurons, (3) a problem with the limited pulse rate of individual action potential streams generated in response to the sensory neurons, (4) insufficient localized response. After completing their survey, Gulick et al proceeded to regurgitate the caricatures of von Bekesy (pp 114 & 123) and calculated a variety of quality factors at the 10 dB level (p 128) for the BM of limited utility when compared to the available data from Robles et al. from 1986.

¹Wever, E. (1949) Theory of Hearing. NY: Wiley & Sons. (Republished by Dover in 1970, page numbers refer to the Dover edition)

²Gulick, W. Gescheider, G. & Frisina, R. (1989) Hearing: Physiological Acoustics, Neural Coding, and Psychocoustics. NY: Oxford Univ Press

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Gulick et al. did not consider the unique properties of the tectorial membrane. The potential of a liquid crystalline active surface on the tectorial membrane was not explored even though liquid crystalline technology was taking an important place in slow traveling waves of the surface acoustic wave (SAW) type (including Rayleigh and Lamb waves, known as modified Rayleigh waves) when combined on a shaped substrate capable of supporting SAW waves.

In 1991, Lighthill presented a masterful lecture on cochlear mechanics at an annual meeting of the American Society of Mechanical Engineers that was subsequently published in the *Journal of Vibration and Acoustics* (largely unknown to the hearing community—the article was cited only 28 times in 20 years). Contrary to his earlier assertion of 1981, he addressed the one-dimensional cochlear model in considerable detail in order to develop the thesis that a differential pressure across the basal BM led to the generation of a slowly traveling wave in at least the Stokes boundary layer of the fluids on each side of the BM due to the distensibility of the BM.

A common, but unproven assumption shared between the above material from von Békésy to Lighthill is that the data recorded beginning with Rhode is due to one unitary and continuous underlying function. The problems with this assumption will be addressed below. There is good data, from Kiang and others, to disavow this assumption.

In the midst of the above activity, Marcatili published new material on the spatial dispersion of Maxwellian energy applicable to a coiled cochlea in 1978. It was totally un-noticed by the hearing community until presented at the Keele Workshop on Cochlear Mechanics in 2008 and published in 2009 in the record of that meeting³.

The Marcatili Effect;

- supports the requirement for a coiled cochlea in all terrestrial vertebrates with hearing.
- defines the exponential relationship between acoustic frequency and spatial position along the cochlea,
- defines the extremely high attenuation within the cochlea at frequencies above cutoff, and
- accounts for the unique suppression of backward propagation of acoustic energy at frequencies above the BF location of the OAE stimulus.

At the end of the 20th Century, the hearing community is left with a conventional wisdom based on a one-dimensional model of cochlear mechanics that is totally dependent on an unrealizable variation in anisotropic basilar membrane stiffness (reciprocal of compliance). The longitudinal stiffness must remain at a negligible value over the entire length of the cochlea while the lateral stiffness must vary over a range of at least four orders of magnitude (Lighthill's value) to six orders to accommodate non-human species with a wider acoustic hearing range.

Even a four order range of stiffness exceeds the material range available between that of diamond and gelatin. The lateral stiffness at the basal end of the Organ of Corti must be compatible with diamond in order to achieve resonance at a frequency above 15 kHz while being sufficiently distensible to satisfy Lighthill's description of slow wave generation.

The emerging model is totally different and relies upon a coiled structure known as Hensen's stripe, not on the BM but an element of the tectorial membrane (TM), that forms a microstrip type of energy transporter (a single "conductor" above a ground plane) rather than a coaxial cable. The microstrip disperses energy according to the Marcatili Effect from Hensen's stripe to the outer hair cells where transduction occurs without the need for auxiliary amplification. The Marcatili Effect also controls what stimulated otoacoustic emissions (StOAE) generated at a discontinuity along the cochlea can be backward propagated to be observed as distortion product otoacoustic emissions (DPOAE) at the vestibule and

³Fulton, J. (2009) Modeling Hensen's stripe as a topographic waveguide that defines the roles of the OHC and IHC *In* Cooper, N. & Kemp, D. eds. *Concepts and Challenges in the Biophysics of Hearing*. London: World Scientific pp 269-275

ultimately at the ear canal.

N.2 Steps in the development of the archaic model of the cochlea based on von Bekesy

While the von Bekesy model of the cochlear mechanics of hearing is the predominant one today, its justification lies on a very select group of investigations. These investigations are cited and synopsised below.

N.2.1 The 1971 investigation of BM motion by Rhode

Rhode provided results from a very early investigation (1971) of the properties of the BM using the Mossbauer Technique⁴. The Mossbauer technique employs a radio active isotope to provide a Doppler measurement of BM motion tied to the rate of nuclear particle emission. The experiments were clearly exploratory, but extensive. He investigated the BM of the squirrel monkey, using nearly 150 live specimens. Sections of the five micron thick foil of the cobalt-57 source were used with sizes ranging from 40 x 50 microns to 80 x 80 microns. The measurements were made from only one location on each BM of each subject. The lateral location of the sample, and the precise longitudinal location along the BM were not determined. However, the samples were introduced to an area of less than 2 mm diameter exhibiting a peak displacement at frequencies between 6.5 and 7.5 kHz.

Figure N.2.1-1 is important to the following discussion. It has been modified only to show the direction of energy flow along the cochlea and to show an extension of the slope in (c). The maximum effective frequency is indicated by the small vertical arrows. It can be assumed the Mossbauer source straddled those locations. Note the major difference in the horizontal scales. Note also that the high frequency skirt of the amplitude response is quite steep, indicating the energy at higher frequency has been removed prior to reaching this point. Figure 6 of the paper indicates this skirt had a slope of at least -65 dB/oct. and reached -110 dB/oct in these experiments. Rhode noted higher slopes were measured but all appeared to be limited by the capability of the test equipment. These slopes are far higher than can be achieved by a single stage tuned circuit formed by the BM.

Note the reported phase shifts are all measured at the location of the indicated best frequency, near the basal end of the cochlea. The shift of $+1.6$ radians at minimal frequency does not apply to the phase of the signal when sensed by the appropriate sensory neurons near the apex. It indicates that $+1.6$ radians (~ 90 degrees) of phase shift existed between the observation point and the reference source.

⁴Rhode, W. (1971) Observation of the vibration of the basilar membrane in squirrel monkeys using the Mossbauer technique *J Acoust Soc Am* vol 49, pp 1218-1231

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The data in (b) was obtained by subtracting the two data sets in (a). The interpretation of the resulting data is highly dependent on the model assumed. Both Rhode, and later Lighthill assumed the curve is indicative of the energy passing from the malleas to the BM directly.

An alternate interpretation arises if the energy is being propagated along Hensen's stripe. In this case, a broad coupling exists between the energy sensed by the inner hair cells (resulting in the 6dB/oct portion of the curve) and an additional coupling exists between the energy dispersed to the OHC where most, but not all of it, is absorbed. That not absorbed is transferred to the BM and presented as the excess amplitude. This interpretation is compatible with more detailed measurements made by Kiang et al⁵ in 1986. They noted a notch or "Kiang's seam" where the curve deviates from the 6 dB/oct line that is also seen in the phase response (but not in the Rhode graph of (c) because of its coarseness). See also **Section 4.6.3** of Fulton, 2008.

The data in (c) shows a maximum phase difference at a very low frequency, estimated as 200 Hz. At higher frequencies, the curve exhibits a slope of 2.2 radians/kHz (corresponding to a group velocity of 12 m/sec) until reaching 5.5 kHz where the slope increases abruptly to a nominal five radians per kHz (group velocity of 9 m/sec) for the squirrel monkey. Rhode chose to associate this data with the constant velocity (non-dispersive) propagation hypothesized by Zwislocki (1965) and Tonndorf (1970).

As in the case of (b), further interpretation of this data depends on the model used.

Lighthill interprets the data as showing dispersive propagation while this work interprets the data as showing non dispersive propagation based on later data (Such as that of Ghaffari et al⁶.) and a different model (**Section 4.3.3**)

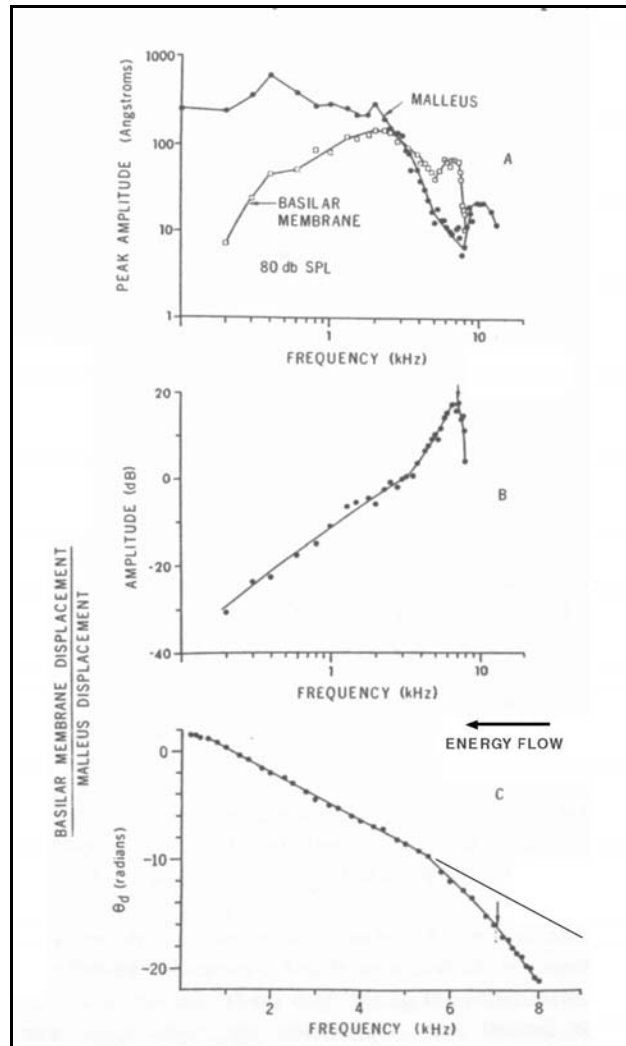


Figure N.2.1-1 Mossbauer data collected from the squirrel monkey by Rhode. (a); amplitude of vibration of the malleus and of the basilar membrane as a function of frequency. (b); input-output ratio for the malleus and the basilar membrane. (c); phase differences between the motion of the basilar membrane and the motion of the malleus. See text. From Rhode, 1971.

N.2.2 The 1976 reconstruction of Rhode data by Zweig

⁵Kiang, N. Liberman, M. Sewell, W. & Guinan, J. (1986) Single unit clues to cochlear mechanisms *Hear Res* vol 22, pp 171-182

⁶Ghaffari, R. Aranyosi, A. & Freeman, D. (2007) Longitudinally propagating traveling waves on the mammalian tectorial membrane *PNAS* vol 41, pp 16510-16515

Zweig provided a major analysis⁷ of von Békésy's hypothesis involving the reconstruction of his proposed energy flow along the BM based on the laboratory measurements of Rhode. While the paper is well structured semantically, its tone is pedagogical rather than rigorous in its development. It frequently relies upon statements beginning with "it can be shown" or "it has been shown (unpublished notes of the author)" that are unconvincing.

The one-dimensional analysis requires zero mechanical coupling between adjacent lateral strips of the BM in order to achieve a reasonable Q (quality ratio) of resonance in the BM acting as a substrate. In that regard, Zweig uses an attenuation on the high frequency side of Rhodes data reaching 300 dB/oct based on the Zweig mathematical model (figure 8). The attenuation on the low frequency skirt never approaches this high value (and appears to remain below 24 dB/oct).

In developing his thesis, Zweig notes a fundamental conflict in the hypothesis of von Békésy supported by Rhode. According to their theory,

"traveling waves are localized along the basilar membrane because the mechanical properties of the cochlea are continuously changing along its length. The more rapid the changes, the sharper the envelope of the wave, and the more precise the correspondence between frequency and position. If the changes are too rapid, however, the traveling wave is reflected, and a standing wave is formed."

He closes by reiterating this basic conflict,

"The suppression of reflections is in direct conflict with the requirement that the cochlea provide the sharpest possible frequency analysis."

He proceeds to develop a "compromise" within his mathematical model in that the product $N \cdot (\delta)^{0.5} \approx 1.0$ where N is "defined as the number of cycles of the asymptotic high-frequency phase shift" and δ is the damping coefficient of the decoupled oscillators associated with individual lateral slices of the BM.

N.2.3 The 1976 followup paper by Zweig et al.

Zweig et al. provided an analysis⁸ contemporaneous with the Zweig 1976. Their abstract begins;

"It is conjectured that the design of the cochlea is influenced by two conflicting requirements: (1) the cochlea should act as a precise frequency analyzer and (2) waves propagating along the basilar membrane should be transmitted without reflections. Accurate frequency analysis is possible only if the mechanical properties of the cochlea change rapidly with distance along the basilar membrane. Reflections of waves traveling on the basilar membrane will be negligible, however, only if these same mechanical properties change slowly."

They then propose, "A compromise between these two requirements is possible if a loss constant related to the sharpness of response of the basilar membrane to a pure tone is related to the number N of wavelengths of the wave on the basilar membrane."

After a review of previous work, they state,

"Békésy found (von Békésy, 1960) that waves on the basilar membrane traveled only in one direction, from the stapes towards the helicotrema. Waves traveling in both directions simultaneously would have given a more complicated pattern of displacement. The present paper applies an approximation technique, based on Békésy's observations, to a transmission line model of cochlear mechanics. The central assumption is that energy transmitted down the line is not

⁷Zweig, G. (1976) Basilar Membrane Motion *Cold Spring Harbor Laboratory for Quantitative Biology* vol XL, pp 619-633

⁸Zweig, G. Lipes, R. & Pierce, J. (1976) The cochlear compromise *J Acoust Soc Am* vol. 59(4) pp 975-982

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reflected during propagation, i.e., a wave traveling in one direction will not set up waves traveling in the opposite direction.

If there were reflections, some of the power that could otherwise excite the hair cells (the transducers that convert mechanical deformation into electrical potential) would instead be turned back towards the stapes. Ideally, the power flow should continue undiminished until it reaches a place, characteristic of the exciting frequency, where it is converted into neural impulses.”

Such reverse propagation is a hallmark of OAE generation as it is currently understood and frequently encountered in the clinical setting as well as in virtually all terrestrial vertebrates.

They continue,

“If the cochlea is uncoiled and approximated by two fluid-filled rigid-walled compartments separated by an elastic sheet (Fig. 1) then it may be represented by a transmission line when the wavelength of a wave on the sheet is larger than the height of the compartments (Zwislocki, 1946, 1948).”

They make the customary but unrealizable assumption,

“that adjacent regions of the basilar membrane are not mechanically coupled together. Loosely speaking, the basilar membrane is assumed to act like a Beautyrest mattress whose coils move independently of each other. (The stiffness of these coils will change exponentially from foot to head). Models which couple adjacent regions by assuming that the membrane acts like a beam have difficulty localizing the response (Steele, 1974).”

They conclude the cochlea acts as a common transmission line with modestly varying properties and a critical parameter supporting a compromise between opposing requirements.

N.2.4 The 1991 Rayleigh Lecture by Lighthill

The 1991 Rayleigh Lecture before the ASME in San Francisco by Lighthill was beautifully presented to an elite audience not particularly knowledgeable in the hearing modality. It employed much more rigorous mathematics than is typical in the field. However, it was based on a number of arbitrary principles.

- It required the presence of a basilar membrane beneath the Organ of Corti, even though no BM is present in the cochlea of amphibians with otherwise normal hearing hearing via its basilar papilla (one of two).
- It requires the Organ of Corti remain centered over the BM, even though it is known the OC is frequently found on the shelf to either side of the BM.
- It continues to employ cartoons rather than faithful photographic records of the relevant cochlear structures (specifically the relationship between the oval window and the scala vestibuli in figure 2).
- It ignores the capillary wave term in his equation of surface acoustic waves, the dispersion relationship, at a fluid/fluid interface (1978, eq. 49).
- It arbitrarily narrows the human auditory spectrum (to 200 Hz to 20kHz) in order to reduce demands on the range of the BM stiffness, although any useful theory must accommodate the full human range of 20 Hz to 20kHz (or the even greater reported range of 200 Hz to 45 kHz in the squirrel monkey of Rhode).
- It requires zero coupling between incremental segments of the BM along its longitudinal extent.

It accepted the hypothesis of von Békésy and the reconstruction of his predicted energy concentration function as reconstructed by Zweig (1976) based on the laboratory investigation of Rhode (1971).

As a result, it develops a logical operational description of an unrealistic physical model. It describes a concentration of acoustic energy of a specific frequency at a given location of resonance along the BM. At such locations, the propagation velocity of the energy at that appropriate frequency is predicted to go to zero. The description employs the term “piles up” to describe this effect (a less than scientific

metaphor).

- The coiling of the cochlea and the constraint provided by the “essentially rigid” spiral ligament,
- The longitudinal structure on the underside of the BM, and
- The longitudinal bracing of the outer hair cells along the tunnel of Corti

all contribute to the longitudinal stiffness of the BM in opposition to the founding characteristics incorporated into the Lighthill hypothesis.

Lighthill accepts the need for an amplification of the energy level within the cochlea, particularly in support of the OAE mechanism. The need for this amplification appears to be to raise the low level of the physical signal measured at the BM back to the much higher level at the malleus, without accounting for why the BM energy level is so low..

N.3 Falsification of the basilar membrane as a major element of hearing

The conventional wisdom with regard to the role of the basilar membrane in hearing is that the acoustic energy is propagated along this membrane in response to a differential pressure applied between the scala vestibuli and the scala tympani at the base of the cochlea.

There is an alternate model, wherein the tectorial membrane is the main substrate for acoustic energy propagation within the cochlea. It provides a more parsimonious mathematical description, a less constrained model of cochlear mechanics and a model compatible with a broader range of evidence.

N.3.1 The conventional wisdom on participation of the basilar membrane

The justification for this is based on very early laboratory investigations of von Békésy using primitive tools, followed by his hypothesis of a poorly defined resonating phenomenon dependent on dispersive propagation of energy along a BM of continually changing substrate properties. These changes were in proportion to the square of the ratio of high to low frequency limits of that species hearing. The required ratio between the properties leading to physical resonance exceeds one million to one in the human (rather than the demanding 10,000:1 noted by Lighthill). As noted by Zweig and by Zweig et al., the specific ratio between specific terms in the resonance equation are quite demanding and conflicting. Simultaneously, the generation of a slow wave due to differential pressure between the boundary layers of fluid in the scala vestibuli and the scala tympani, supported by Lighthill, requires a different set of mechanical properties for the basilar membrane acting as a substrate in order for the energy related to a specific frequency to “pile up” at a given location.

All of these analyses were based on the application of one-dimensional mathematical equations that required the coiled cochlea performing the same as an uncoiled cochlea that is not constrained by the spiral ligament. They also demand the total uncoupling of lateral strips of the BM from each other (on a scale of microns), in order to achieve negligible compliance between the mechanical properties of the BM, while simultaneously achieving the extremely high ratio between high and low compliance of the BM in the lateral direction indicated by the above ratio of nominally one million to one.

The above set of conditions have not been shown to exist in practice. In addition the two-way propagation of acoustic energy along the cochlea is now well documented in otoacoustic emission research.

Finally, the equations of Lighthill described a mechanism involving only a specified number of break points in the amplitude and the phase responses. Ruggero et al. showed data from a similar experiment⁹, except employing Fourier transforms of click responses exhibiting an additional break point not

⁹Ruggero, M. Rich, N. & Recio, A. (1992b) Basilar membrane response to clicks *In* Cazals, Y. Demany, I. & Horner, K. eds. Auditory Physiology and Perception, vol 83 of Advances in Biosciences. Oxford: Pergamon Press pp 85-89

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accounted for in Lighthill's analysis, **Figure N.3.1-1 from his figure 2**. Ruggero apparently was measuring differential phases over a nominal distance of 3.5 mm between some portion of the eardrum and a location within the cochlea while Rhode measured differential phases between a location at the cochlea and the malleus specifically. Ruggero et al. gives these second slopes as -560 microseconds for the 107 dB stimulus and -680 microseconds for the 57 dB stimulus although neither appears to be statistically valid. Compare this figure with frame (c) of Section N.2.1.

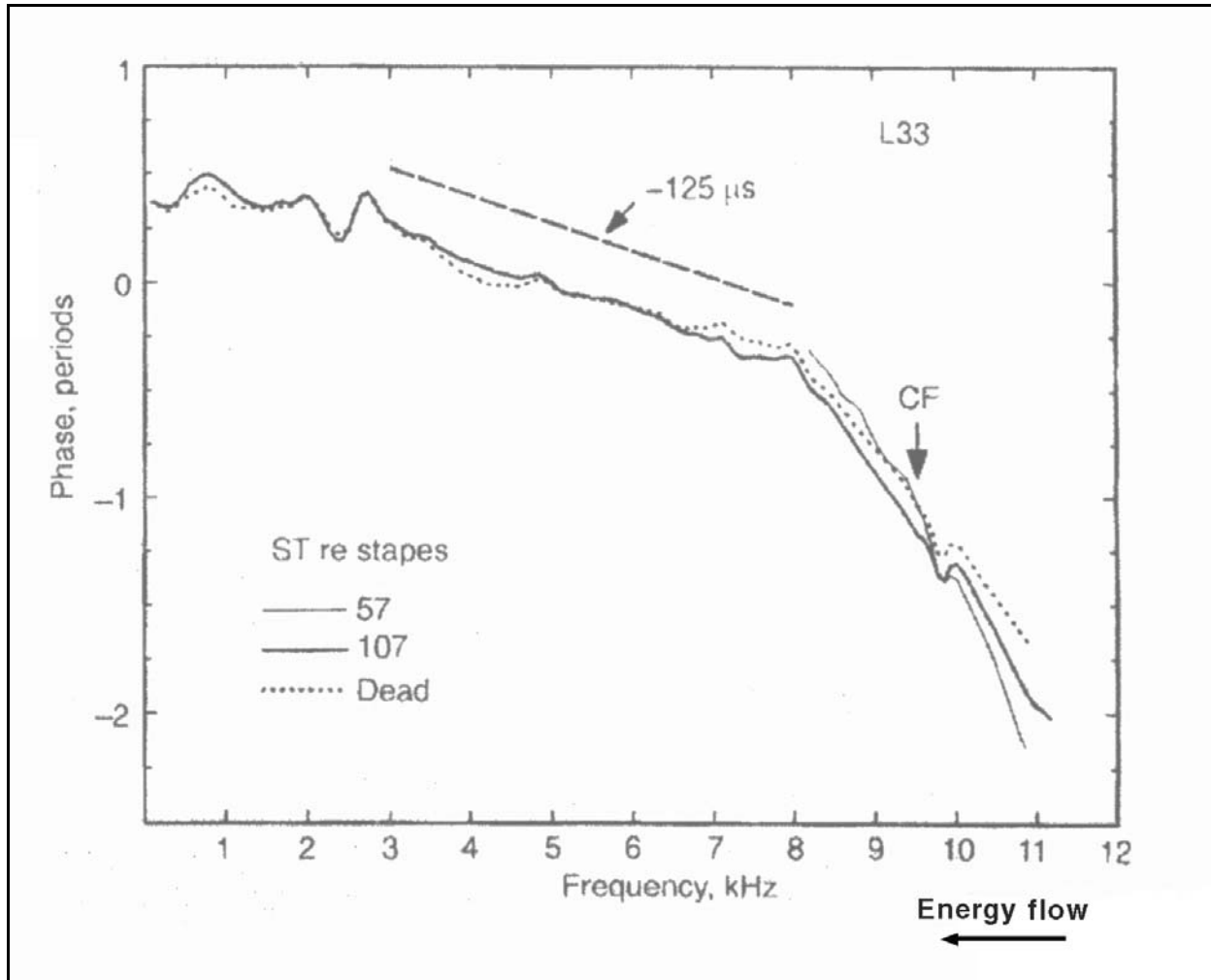


Figure N.3.1-1 Differential phases of basilar-membrane responses to *pseudo-clicks* in chinchilla cochlea, a large number of live specimens (continuous lines) and postmortem (dotted line). Phases, computed by Fourier transformation of a set of temporal waveforms resulting from a non-impulse and structured click stimulus. 57 and 107 refer to the db level used in the stimulation. Duration after death was not given. Note the direction of energy flow within the cochlea. From Ruggero, 1992.

The waveforms presented in figure 1 of the 1994 paper are clearly not the total responses of the BM to a impulse type click. They are the filtered (narrow band) responses at a specific location of the BM in response to a synthetic stimulus at a similar clock frequency with a long clocked tail (over two milliseconds). The location appears to have been underneath the OHC corresponding to the CF location for 9.5 kHz in the chinchilla (3.5 mm from the oval window (fenestra vestibuli)).

This figure and similar ones in the literature show three segments to the phase response, “a low-frequency (zero slope) segment which extends between DC and 1-3 kHz; a mid-frequency segment, with shallow, constant slope between 1-3 kHz and frequencies just below the characteristic frequency, and a high-

frequency segment, with steep slope, around and beyond the characteristic frequency.” Such a characteristic does not appear compatible with the analysis of Lighthill. Ruggero, in response to questions from the floor in Ruggero et al. showed an awareness that the phase versus frequency response in their figure 4 might be due to two underlying mechanisms, one for the segment below the CF and one for the segment including the CF. He also noted they did not have sufficient data to interpret the non-monotonic waveforms in their figure 1.

The hypothesis of the basilar membrane acting as a substrate with uniquely optimized properties supporting acoustic energy propagating in only one direction within the cochlea is therefore falsified.

Other arguable, but not provable, factors are,

- the lack of any evidence that a slow traveling wave can be associated with the boundary layer in the fluid on each side of a structure as structurally complex as the BM (is the boundary layer between the BM and the reticular lamina or outside of it?). Even the authority on fluid dynamics, Lighthill, failed to offer any theory in this area.
- any discussion of frequency dispersion at auditory frequencies is highly dependent on a detailed model of the flow of energy involved, something sorely lacking in the case of the basilar membrane as a host^{10,11}.
- the limited laboratory evidence on the variation in the stiffness of the BM over its length, a factor of only about 3:1. This is far below the value suggested by Lighthill, much less the even higher value needed to support human hearing.
- None of the above investigators demonstrated the proposed amplitude versus frequency response of Rhode was due to a single mechanism associated exclusively with the basilar membrane.
- It is not obvious that Ruggero et al. factored out the extended duration stimulus pulse from the response at the CF location before taking their Fourier transforms in order to obtain the correct transfer function.
- The group delay of Ruggero et al. and of Lighthill should have been determined from the middle portion of the phase versus frequency response and not the total response.

N.3.2 The recent accumulation of information related to the tectorial membrane

The accumulation of more recent laboratory data, beginning with Kiang et al. strongly suggests the data of Rhode (used by Zweig and by Lighthill) is not due to a unitary mechanism but is the sum of two distinct mechanisms. This mechanism consists of energy propagating along the tectorial membrane (TM) in a non-frequency--dispersive mode as a modified Rayleigh wave (velocity given by the slope of the extended phase versus frequency graph in frame b of Rhode). See **Section 4.6** for the development of this model. At a given point, the sensing of the total energy in the signal by the inner hair cells (IHC) results in an unabsorbed residual energy being transferred to the BM at a point below the IHC (Hensen's stripe) that exhibits a non-dispersive wideband character. At an adjacent point, the spatial dispersion of the energy associated with the best frequency for that location, based on the Marcatili Effect, to the location of the outer hair cells (OHC), and the less than 100% absorption of that energy by the OHC, results in the transfer of residual narrow band energy to the BM below the OHC. As a result of these two mechanism, the summary motion of the BM recorded by a probe depends on the specific lateral location of the probe relative to the BM. This motion of the BM in response to stimulation via two separate paths from the tectorial membrane has been documented by Nilsen & Russell¹² as caricatured in **Section 4.6.3.1** of

¹⁰Ramo, S. & Whinnery, J. (1953) *Fields and Waves in Modern Radio*. NY: McGraw-Hill pp 46-48

¹¹Stratton, J. (1941) *Electromagnetic Theory*. NY: McGraw-Hill pp 330-340

¹²Nilsen, K. & Russell, I. (1999) Timing of cochlear feedback: spatial and temporal representation of a tone across the basilar membrane *Nature Neurosci* vol. 2(7), pp 642-648

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Chapter 4 of the Fulton, 2008, text. They used laser interferometry to obtain BM motion data at a finer spatial resolution and at more specific lateral locations than previously available.

A more complete understanding of the operation of the cochlea based on the tectorial membrane based model can be obtained by combining **Figures 4.6.3-1 & 9.11.3-2**, and noting how the measurements of BM displacement at a given location documents the residual motion of the BM after the vast majority of the acoustic energy has been absorbed by the OHC or passed along to a location more remote from the vestibule. The residual motion of the BM is due to the summation of residual motion due to imperfect energy absorption by both the IHC and the OHC at a given location. The measured residual motion is a function of the lateral location of the sensing mechanism at the BM.

The spatial dispersion of energy by the Marcatili Effect does not involve any resonance mechanism or any frequency dispersion factor.

When measuring the total response in the frequency domain, the measurement at the BM sums the components from the IHC and OHC in phase. Since the BM acts as an imperfect seismic block. A measurement of the signal from the OHC sensory neuron shows the difference between the phase of the signal dispersed from Hensen's stripe minus the residual motion of the BM. The resulting composite signal shows a notch due to this phase reversal, known as "Kiang's seam." See **Section 4.6.3.2**.

Only the middle portion of the phase versus frequency characteristic should be used to calculate the group delay of the cochlea. The group velocity, calculated from this group delay, approaches the constant phase velocity of the energy as the frequency–dispersion factor approaches zero.

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