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The History of Physiological Acoustics

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When Neal Viemeister asked me to give a lecture on the history of physiological acoustics, I was reminded of a time when I was playing ball with my sons and their friends. One of the kids picked up my Stan Musial mitt and asked innocently "who is Stan Musial?" The question went right through me. Who wouldn't know about my childhood hero! Recently a graduate student in our lab had the temerity to ask, "who is Jerzy Rose?" That question struck even deeper, for I had only idolized Stan the Man from afar, but I had known Jerzy "up close and personal." The crowning blow came when a postdoc in our department told me he had thought that Nelson Kiang was my first student! Of course nearly the inverse was true—I was one of Nelson's early students. I realized that we were failing to pass on the rich historical perspective of our field to the next scientific generation, and so with some trepidation I accepted the invitation to give the lecture.

The first two papers that I could find in JASA that might be called "physiological acoustics" appeared in Volume 2 in 1930 and in more or less direct ways they portend the future of the field. A paper by Smith and Laird (Smith and Laird 1930) on effects of noise on stomach contractions could be considered an early precursor of the rapidly growing literature on cross-modality interactions in the system (Kanold and Young 2001). Firestone's analysis of interaural acoustic differences for tones in the same volume (Firestone 1930) gives rise to an enormous literature on this topic. The next paper was an invited talk by Hallowell Davis at the 1934 Meeting of the Society

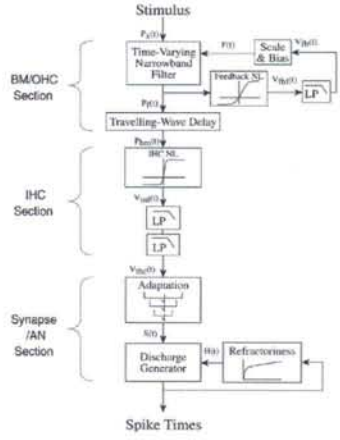


Figure 1. Model of stimulus processing in the peripheral auditory system. From (Carney 1993).

in Pittsburgh, published the next year in Volume 6 (Davis 1935). Davis presented some of his seminal observations on cochlear electrophysiology.

Throughout the history of the Society the primary focus of the *Journal* in physiological acoustics has been on the on the peripheral auditory system. In this review we focus on three parallel thrusts in the history of our understanding of the peripheral system. Figure 1 shows Laurel Carney's recent model of the peripheral system (Carney 1993). The first part of the review will look at the history of how the various stages of such a model have been fleshed out. The second part will focus on the neural encoding of sound in the auditory nerve (the output of the model), and the last will address how that code influences discrimination.

Unraveling Cochlear Mechanisms

The auditory nerve has long been considered a window on the biophysical mechanisms of cochlear transduction. The most carefully characterized aspect of the responses of single fibers has been the tuning curve, which is a plot of threshold versus frequency for tonal stimuli. The first tuning curves were reported by Galambos and Davis in 1943 (Galambos and Davis 1943), but they subsequently reported that they were probably recording from secondary cochlear nucleus neurons (Galambos and Davis 1944). The first tuning curve from an auditory-nerve fiber was probably the one reported by Tasaki in 1954 and shown in Fig. 2A (Tasaki 1954). Later, Yasuji Katsuki, in Japan(Katsuki, Sumi et al. 1958) and Nelson Kiang in Boston (Kiang, Watanabe et al. 1965; Kiang, Sachs et al. 1967) published tuning curves from many auditory-nerve fibers as shown in Fig.2B.

Perhaps the most intensively studied question in auditory theory is: "What are the cochlear mechanisms underlying the shapes of these tuning curves?" This question can be traced as far back as Helmholtz in the middle of the 19th century (Helmholtz 1863; Helmholtz 1954). It was originally less about auditory-nerve tuning curves and more about pitch discrimination. Georg von Békésy phrased the question in a 1956 paper in *Science* titled "Current status of theories of hearing" (Békésy 1956): "The words "theories of hearing" as commonly used are misleading...Theories of hearing are usually concerned with answering the question, how does the ear discriminate pitch? (But) we must know how the vibrations produced by a sound are distributed along the length of the basilar membrane before we can understand how pitch is discriminated and therefore theories of hearing are basically theories of the vibratory patterns of the basilar membrane and the sense organs attached to it."

As we all know, Georg von Békésy was the first to measure those patterns and he was awarded the Nobel Prize in 1961 for this work. A Physiological and Psychological Acoustics medal of this society bears his name.

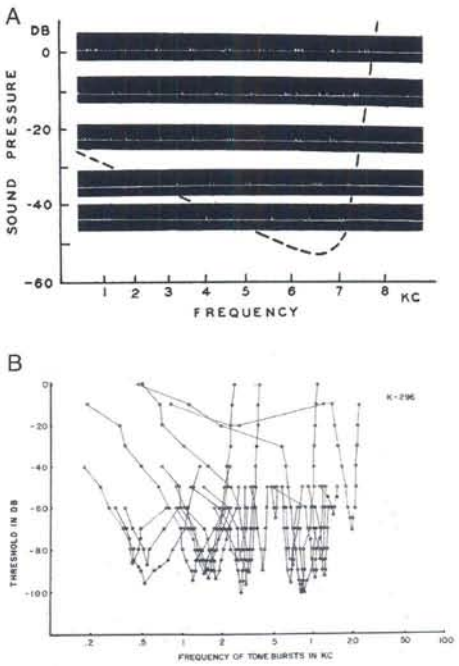


Figure 2. Auditory-nerve fiber tuning curves. A. from (Tasaki 1954); B: from (Kiang, Watanabe et al. 1965).

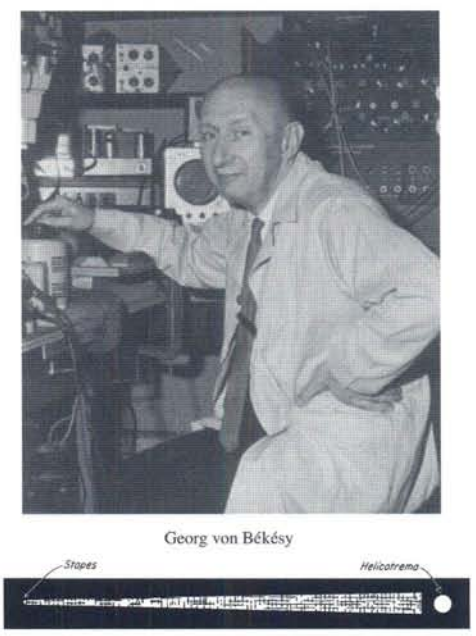


Figure 3. A. Photo of Georg von Békésy scanned from The Georg von Békésy Collection. (Békésy 1974). B. Basilar membrane model is a metal band with a slit cut in the shape of the basilar membrane and covered with an elastic membrane. From (Békésy 1960).

As illustrated in Fig. 3 Békésy was himself a great model builder, in the traditional sense of "builder," often simulating vibratory patterns on scaled up physical models of the cochlea. This model is a metal band with a slit cut in the shape of the basilar membrane and covered with an elastic membrane. When he got the thickness just right Békésy showed that intense sound caused circumscribed damage to the membrane at points progressively farther from the base as the frequency decreased. Figure 4A shows what may be the most famous of Békésy's observations, the traveling wave pattern along the basilar membrane of a human cadaver. It shows a wave whose amplitude grows as it travels toward the point of maximum displacement and decays rapidly beyond.

One of Békésy's many ingenious modeling efforts shown in Fig. 4B displays such a traveling wave pattern (Békésy 1960). In his own words from his Nobel Lecture (Békésy 1961): "...the final version of the model consists of a plastic tube filled with water, and a membrane 30 cm in length; when it is stimulated with a vibration it shows traveling waves of the same type as those seen in the normal human ear...I decided to go one step further and make a model of the inner ear with a nerve supply...so I simply placed my arm against the model. To my surprise, although the traveling waves ran the whole length of the membrane with almost the same amplitude, and only a quite flat maximum at one spot...I had the impression that only a section of the membrane 2-3 cm long was vibrating...Thus the century old problem of how the ear performs a frequency analysis—whether mechanically or neurally—could be solved; from these experiments it was evident that the ear contains a neuromechanical frequency analyzer, which combines a preliminary mechanical frequency analysis with a subsequent sharpening of the sensation area." Keep these words in mind as we survey the subsequent 40 year history of this idea.

Figure 5 (Békésy 1960) shows the tuning of the basilar membrane in the form of displacement versus frequency plots for four positions along the basilar membrane of guinea pig. In addition to his monumental work as a scientist, Békésy was also a serious collector of art and the inset is a 19th century Japanese print from the Békésy collection (Békésy 1974). These results of von Békésy stimulated a generation of basilar-membrane modelers, none more notable than Joe Zwislocki, (Fig. 6),

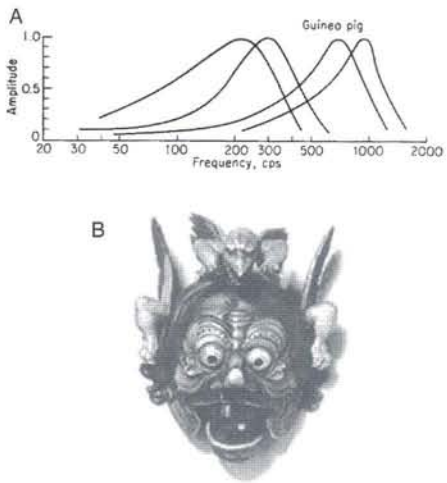


Figure 5. A. Displacement versus position functions for guinea pig basilar membrane. From (Bekesy 1960). B. Inro and netsuke, 18th-19th century, Japan. Selected objects from the collection of George von Békésy bequeathed to the Nobel Foundation. Edited by Jan Wirgin. Copyright © 1974 by The Nobel Foundation, Stockholm.

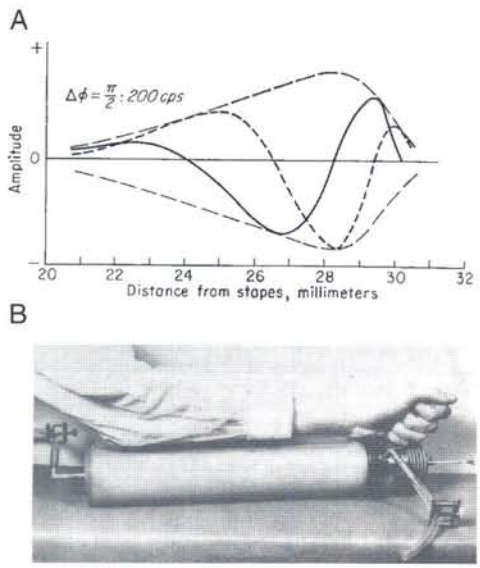


Figure 4. A. Traveling wave patterns on the basilar membrane. From (Bekesy 1960). B. Mechanical model of the inner ear. From (Békésy 1961).

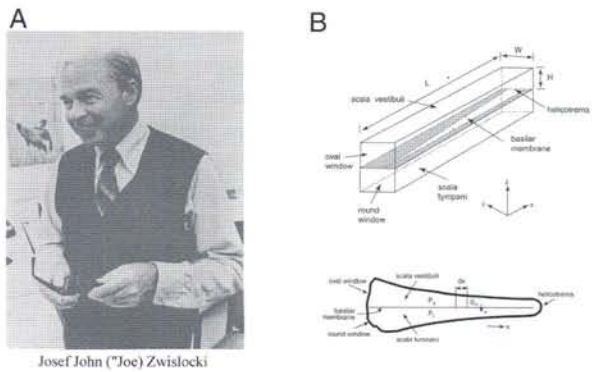


Figure 6. A. Photo of Josef J. Zwislocki. From Abstracts of the 1988 Midwinter Meeting of the Association for Research in Otolaryngology. B. Geometry of Zwislocki model of basilar membrane motion. From (Zwislocki 1965).

who was awarded the first von Békésy Medal by this Society in 1985. Until the 1970's models of basilar-membrane mechanics represented all cochlear structures as linear and passive. The motion of such a system is governed by the laws of classical fluid dynamics. In the late 1940's Zwisloski developed the prototype model based on these concepts of fluid dynamics, and the idealized model of cochlear geometry shown in Fig. 6. The model has been widely applied and with the advent of modern computing the model has been made progressively more precise with regard to cochlear structure (Sondhi 1978; Steele and Taber 1979).

Although such models can reproduce the Békésy data very well, they by no means answer the question of what determines the shapes of auditory nerve tuning curves. Figure 7A from a paper by Pat Wilson from the University of Keele in 1974 (Wilson 1974) compares mechanical and neural tuning curves in guinea pig. The dashed curves are the resonance curves from Békésy, and the dotted curve is a mechanical tuning curve from guinea pig from J.P. Wilson and J.R. Johnstone (Wilson and Johnstone 1975). The mechanical tuning is much broader than the neural tuning curves. In particular, the mechanical curves lack the sharp tips seen in the neural curves.

This discrepancy between neural and mechanical tuning led to one of the most exciting and controversy-filled times in the history of physiological acoustics. Barely noticeable in Fig. 7A, but of enormous importance, are mechanical tuning curves for squirrel monkey measured by Bill Rhode (Rhode 1971). In 1971, Rhode published a paper that was to reverberate throughout the auditory research world for years. Figure 7B shows that resonance curves for the basilar membrane in the squirrel monkey can be considerably sharper than had been thought. But as the level of tone used to measure the contours increases the tuning broadens and at the highest level the displacement function takes on the low-pass filter shape seen in the guinea pig data of Wilson and Johnstone (Fig. 7A). This broadening reflects a strong nonlinearity in the basilar membrane mechanics. At and just above the best frequency the functions are highly compressive, that is, as stimulus level increases the ratio of displacement to stimulus level decreases.

These data are the first indication of a non-linear basilar membrane and really set the community on its collective ear. Quoting from a 1952 paper by Békésy (Békésy 1952): "When the traveling waves along the cochlear partition were first observed, it was possible to show that a decrease of the stimulus to half its magnitude did not alter the pattern of vibration. The cochlea therefore is a linear system." Linear or non-linear became a central question of auditory research and controversy raged well into the 1980's, when it would become clear that the basilar membrane is highly non-linear.

In the early 1970's, when issues of basilar membrane tuning were still very much unresolved, Ted Evans and his colleagues at the University of Keele in England proposed a so-called second filter between basilar membrane motion and auditory nerve discharges. In a review paper Ted, shown in Fig. 8 with the then Minister of Health of the UK Patrick Jenkin, says: "On occasions when recordings were made under conditions where the cochlear blood supply was impaired... the (neural) tuning curves obtained had high thresholds, were broadly tuned and resembled the basilar membrane curves...These findings suggest that the sharpening of the frequency selectivity of the cochlea may be vulnerable to certain deleterious influences such as anoxia." (Evans 1975) The data in Fig. 8 show that the normal low-threshold sharply tuned segment of the neural tuning curve can be lost after a few minutes' respiration in 5% O^2. Again quoting Evans: "It seems unlikely that the mechanics of the basilar membrane would be so severely affected by brief periods of hypoxia". However, more recent studies by Shyam Khanna and his colleagues (Khanna and Leonard 1982) have shown that basilar membrane mechanics are extremely sensitive to subtle metabolic influences.

Early on, some thought was given to the idea that sharpening of neural tuning may involve the innervation patterns of the auditory nerve fiber endings in the cochlea. In 1933 Lorente de No, then at the Central Institute for the Deaf in St. Louis, published a paper (Lorente de No 1981) that was for thirty years the accepted view of cochlear innervation (Fig. 9). Lorente describes the now familiar radial and spiral fibers. Over the course of the next thirty years there were numerous attempts to find a correlation between these two types of afferent fibers and the response patterns of auditory-nerve fibers (Goblick and Pfeiffer 1969). For example, Nelson Kiang's 1965 monograph (Kiang, Watanabe et al. 1965) shows that fibers with the same best frequencies may have very different thresholds. Tasaki (Tasaki 1954) suggested that fibers connected to inner hair cells may have higher thresholds

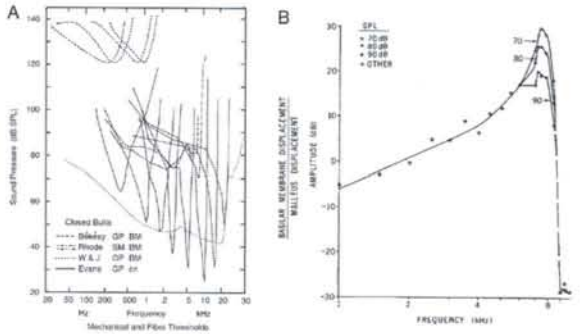


Figure 7. Comparison of neural and mechanical tuning curves. From (Wilson 1974). B. Basilar membrane displacement functions from squirrel monkey. From (Rhode 1971).

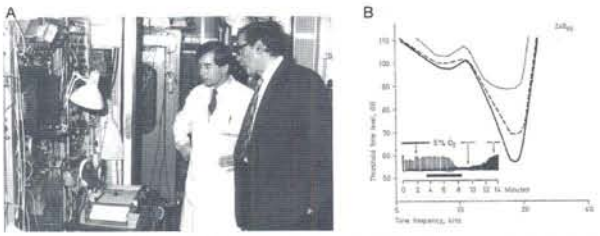


Figure 8. A. Photo of E.F. (Ted) Evans (in white lab coat). Courtesy Dr. Evans. B. Effects of hypoxia on auditory-nerve fiber tuning curves. From (Evans 1978).

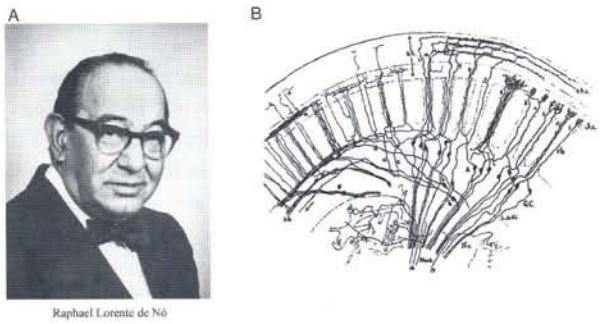


Figure 9. A. Photo of Raphael Lorente de No. From Abstracts of the 1986 Midwinter Meeting of the Association for Research in Otolaryngology. B. Innervation patterns in the cochlea. From (Lorente de No 1981).

than fibers connected to outer hair cells which sit on a place on the basilar membrane that appears less firmly attached to bone. With vintage (and I should say often appropriate) Kiang skepticism, Kiang says of Tasaki's and other hypotheses: "Our own data do not support any of these previous suggestions. It might be prudent to defer speculation on this topic until some unsettled anatomic questions have been answered, for example, "what are the relative numbers of radial and spiral fibers? Do the spiral fibers innervate hair cells all along their course after crossing the tunnel of Corti?" (Kiang, Watanabe et al. 1965) A landmark paper by Hendrik Spoendlin (Spoendlin 1968) answered these and many other questions about the afferent innervation. Spoendlin showed (Fig. 10) that 90% of the afferents are radial and innervate a single inner hair cell. Spiral fibers are unmyelinated and form synapses with 10-20 outer hair cells. Because of their small size and number there are few if any documented recordings from these spiral fibers. It is no surprise, then, that no real correlations were found between anatomical and physiological response types.

In an elegant series of papers in the late 70's and early 80's Charlie Liberman and his colleagues did demonstrate a correlation among the radial afferents with wide ranging implications (Liberman 1978). Liberman focused on spontaneous rate as a parameter and subdivided fibers

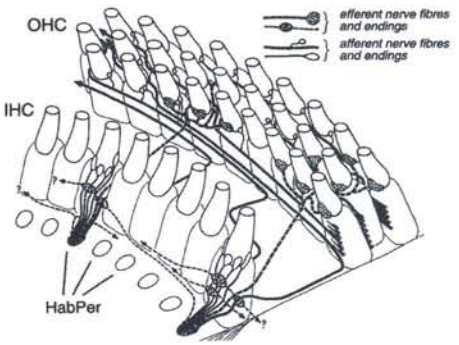


Figure 10. Innervation patterns in the cochlea. From (Spoendlin 1978).

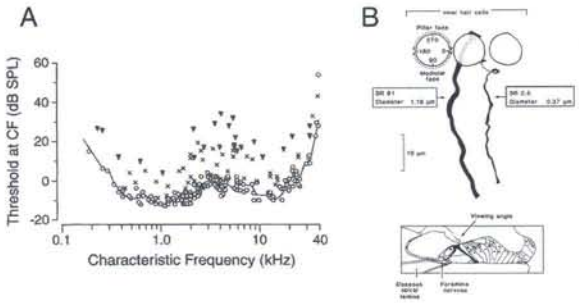


Figure 11. A. Threshold versus best frequency for auditory-nerve fibers categorized by spontaneous rate: circles, triangles and x's correspond to high, medium and low rates respectively. From (Liberman 1978). B. Hair cell innervation pattern of a high and a low spontaneous rate fiber. From (Liberman 1982).

into three groups: low, medium and high spontaneous rate fibers (Fig. 11A). One of Liberman's most important observations was that spontaneous rate is correlated with fiber threshold, that is low spontaneous fibers have the highest thresholds at any BF and high spontaneous fibers have the lowest thresholds. Taking advantage of newly developed techniques for marking neurons (Fig. 11B) Liberman showed that all radial fibers innervate only one inner hair cell, that low and high spontaneous rate units actually innervate different sides of the same hair cell and that details of the synaptic endings of the two spontaneous classes are different (Liberman 1982). We will return to the functional implications of these classes of fibers later.

So, most of the afferents innervate inner hair cells. Then what is the function of outer hair cells? Figure 12 shows that by the mid-1980's the question of basilar membrane tuning had been largely resolved. As shown by the superimposed mechanical and neural tuning curves Mario Ruggero and others (Robles, Ruggero et al. 1986) showed that basilar membrane and neural tuning

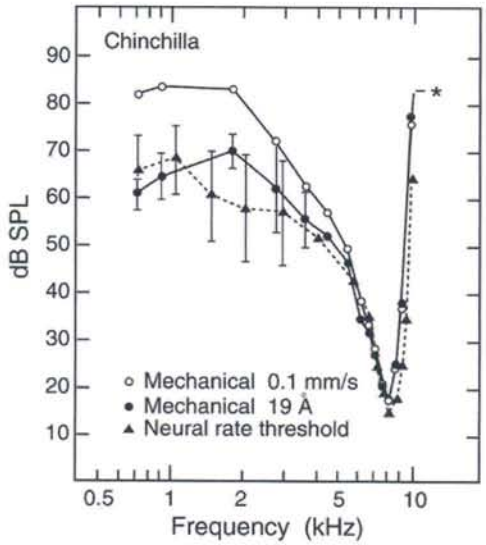


Figure 12. Comparison of neural and mechanical tuning curves. From (Robles, Ruggero et al. 1986).

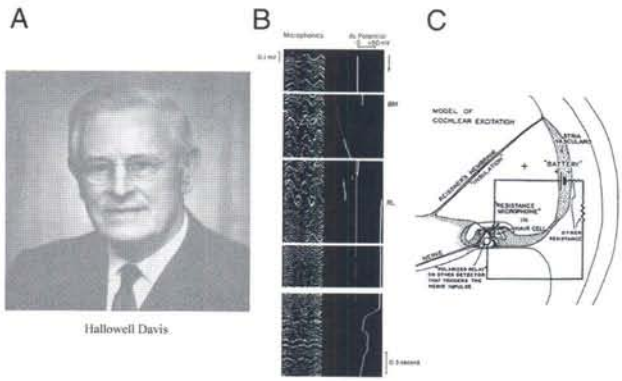


Figure 13. A. Photo of Hallowell Davis. From Abstracts of the 1982 Midwinter Meeting of the Association for Research in Otolaryngology. B. DC (right) and AC (left) potentials recorded as a microelectrode is advanced from scala tympani through scala media into scala vestibuli. From (Tasaki, Davis et al. 1954). C. The "Davis model" of cochlear electroanatomy. From (Davis 1965).

were at least very similar. For reasons that we will explore later, at about this time the idea that outer hair cells might play a role in sharpening basilar-membrane tuning began to emerge.

But the quest to find a role for the outer hair cells really begins much earlier. I quote from The Professional Memoirs of Hallowell Davis (Davis 1991): " the new era in auditory physiology really began in 1930 with the publication by E.G. Wever and C.W. Bray of a paper in *Science* "Auditory Nerve Impulses." "In 1929 he (Wever) undertook to determine the frequency of impulses in the cat's auditory nerve with an instrument capable of dealing with high audio frequencies. The instruments chosen were the telephone and the ear of an observer. A rather large electrode was placed on the auditory nerve in the internal auditory meatus of a decerebrate cat in a quiet experimental room and another member of the team listened to the signals in a telephone in a distant quiet room. Voices of the experimenters could not be heard directly, but in the telephone the listener could hear clearly any words spoken near the cat. Transmission ceased with the death of the animal." Wever and Bray had launched a new era of cochlear electrophysiology, and Davis and his colleagues carried it forward. Hallowell Davis (Fig. 13), born in 1896, was a giant in this society and keenly active virtually until his death at age 96 in 1992. He was awarded the Society's gold medal in 1965 and the National Medal of Science in 1975.

Continuing to quote from the Davis memoirs: "In 1933 Derbyshire and I submitted for publication our definitive study of the electric response of the cochlea, based chiefly on recordings from the round window of cat. The cochlear response differs fundamentally from the action potential of nerve and muscle: It shows no characteristic wave form of its own, but reproduces that of the stimulus. We have also confirmed that this response is absent in albinic cats which on histologic examination are found to lack the organ of Corti. We have ventured the hypothesis that the sensory cells of this organ are responsible for the electrical change". i.e., they had described the cochlear microphonic and correctly hypothesized its source.

Techniques for differential recording between scala vestibuli, scala tympani and scala media later allowed for the measurement of highly localized cochlear potentials. Figure 13B from a 1954 paper by Tasaki and his colleagues (Tasaki, Davis et al. 1954) shows both dc and ac potentials as a microelectrode is advanced from scala tympani through scala media into scala vestibuli. Note that as the electrode penetrates the reticular lamina there is a positive jump in the DC potential, corresponding to the endocochlear potential that had first been identified by Békésy in 1952 (Békésy 1952) and the phase of the ac component (the CM) reverses. This strongly suggested to Tasaki that the source of the CM is at the reticular lamina, i.e., at the hair-bearing end of the hair cells. We will see that this hypothesis was confirmed later by Jim Hudspeth (Hudspeth 1982).

On the basis of measurements like these, Davis (Davis 1965) proposed what has become known as the Davis variable resistance model (Fig. 13C). In the model the transducer channel is represented by the ciliary displacement-dependent conductance and current through it is driven by the endocochlear potential. Virtually all cochlear transduction models start with some variation on this Davis model.

Detailed studies of cochlear potentials in the 50's,

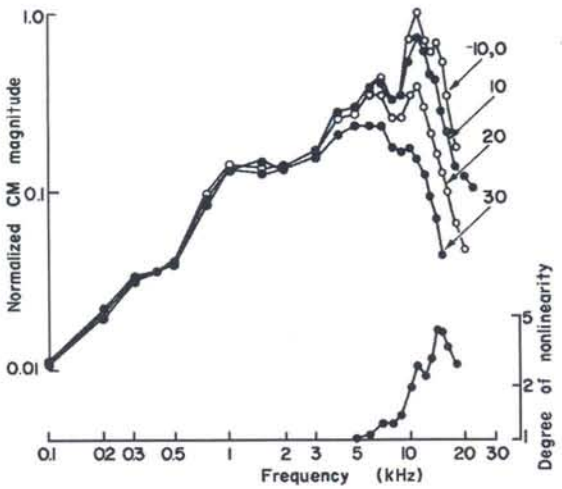


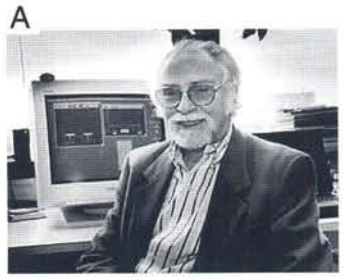
Figure 14. Cochlear microphonic potential versus frequency showing nonlinear behavior at and above the best frequency. From (Dallos, Cheatham et al. 1974).

60's and into the 70's led to a detailed picture of the electroanatomy of the cochlea. Certainly among the most quantitative of these came from Peter Dallos and his colleagues (Dallos 1973). For example, Fig.14 (Dallos, Cheatham et al. 1974) shows nonlinear behavior in cochlear microphonic (CM) that is similar to the mechanical nonlinearity of Rhode. Dallos cautions that while "it is tempting to associate the pronounced frequency dependent nonlinearity of the CM with the somewhat similar nonlinearity that Rhode has observed in the basilar membrane motion, militating against this temptation are numerous observations supporting the claims that the dominant CM nonlinearity arises from hair cell processes" (Dallos, Cheatham et al. 1974). It became clear later that these two nonlinearities were at the very least intimately related. In this regard, it is important that Dallos has shown that most of the cochlear microphonic is generated by the outer hair cells.

To this point, the nature of hair cell function had to be inferred from recordings of extracellular potentials like the CM. The first direct recordings from hair cells came not from the mammalian cochlea but from the amphibian lateral line in 1970 by Harris, Frishkopf and Flock (Harris, Frishkopf et al. 1970). The first auditory hair cell recordings were from the auditory papilla of the alligator lizard by Tom Weiss and his colleagues at MIT in 1974 (Weiss, Mulroy et al. 1974). Some aspects of this end organ make it especially attractive for studies of hair cell function. For example, as illustrated in Fig. 15 hair cells on opposite sides of the dorsal region of this organ are morphologically polarized in opposite directions (as defined by the eccentric position of the kinocilium). On the basis of responses to clicks, Weiss and his colleagues developed a detailed version of the Davis model in which motion of the cilia toward the kinocilium causes a large nonlinear increase in the hair cell conductance (Fig. 15B, bottom left). In the model, the opposite morphological polarization of hair cells on two sides of the papilla leads to the opposite polarity click responses as observed experimentally in these cells (waveforms at bottom of left and right columns). These results confirm the hypothesis relating morphological polarization and response polarity put forth by Flock and Wersall in 1962 on the basis of microphonic recordings from the lateral line organ of fish (Flock and Wersall 1962).

In 1977 Jim Hudspeth mechanically stimulated ciliary bundles on individual bullfrog saccular hair cells while recording intracellularly within the same cell, as in Fig. 16 (Hudspeth and Corey 1977). His results confirmed that displacement toward the kinocilium leads both to a hair cell depolarization as well as an increase in conductance. The input/output functions for the cells were highly rectifying (Fig. 16B).

Then in 1984 Jim Pickles discovered tip links shown in Fig. 17 (Pickles, Comis et al. 1984; Hackney, Fettiplace et al. 1993), fine strands that connect the tops of a shorter stereocilium with the lateral wall of its taller neighbor. Hudspeth had demonstrated in 1982 that transducer current flowed through the stereocilia tips (Hudspeth 1982).



Thomas F. Weiss

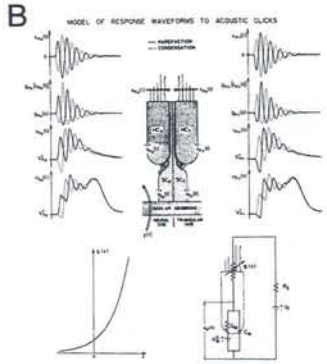


Figure 15. A. Photo of Thomas Weiss. (Courtesy Dr. Weiss.) B. Hair cells morphologically polarized in opposite directions produce oppositely polarized response to clicks. In detailed version of the Davis model motion of the cilia toward the kinocilium causes a large nonlinear increase in the hair cell conductance. From (Weiss, Mulroy et al. 1974).

These two discoveries led to the currently accepted notion of a spring-loaded trapdoor mechanism of hair cell excitation (Gillespie 1995). Changing tension in the tip link is hypothesized to change the conduction probabilities of a cation-conducting channel.

In 1978 Ian Russell and Peter Sellick at the University of Sussex published results of the first intracellular recordings from inner hair cells in the mammalian (i.e., guinea pig) cochlea (Russell and Sellick 1978). Subsequently Dallos and his group were able to record from outer hair cells (Dallos, Santos-Sacchi et al. 1982; Dallos 1985). Both inner and outer hair cells are sharply tuned and have tuning curves very similar to that of the basilar membrane at the same place in the cochlea. But, as Geisler emphasizes in his recent book *From Sound to Synapse* (Geisler 1998), "... it would be wrong to assume that hair cells in the mammalian cochlea are simply passive recorders of basilar membrane vibrations. They are not." One line of research that led to this conclusion involves the efferent innervation of the cochlea, which had been carefully described in 1946 by Grant Rasmussen (Rasmussen 1946) and further characterized by Bruce Warr, John Guinan and their colleagues in the late 1970s (Rasmussen 1946; Warr and Guinan 1979), who showed that the efferents that Spoendlin shows terminating on outer hair cells (Fig. 10) have a separate brainstem origin from those that synapse on the afferent neurons under the inner hair cells. In 1956 Bob Galambos, then at Walter Reed Medical Center, had demonstrated that stimulating the efferents where they cross the midline of the brainstem suppresses the whole nerve action potential recorded from the auditory nerve (Fig. 18, Galambos 1956). Figure 19 from Mike Wiederhold's work in the late 1960's shows the strong suppression effect in single auditory nerve fibers (Wiederhold and Kiang 1970). There is very strong evidence that stimulating in the floor of the fourth ventricle activates only the efferents that innervate the outer hair cells (Brown, Nuttall et al. 1983). But recall that Spoendlin had shown that almost all of the auditory-nerve fibers innervate the inner hair cells. Thus we have a crucial anomaly: the afferent fibers, from which virtually all of our recordings come, innervate only inner hair cells and yet stimulating efferents that go only to the outer hair cells affects auditory nerve responses in a major way.

In the late 1970's evidence began to mount that the outer hair cells might play a role in an active, energy-

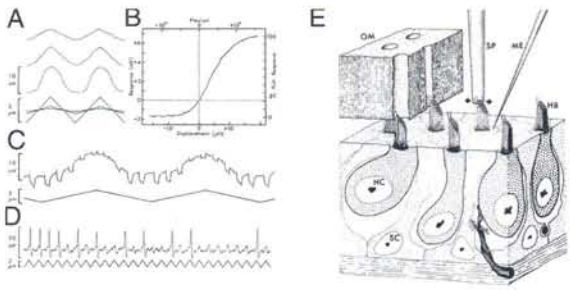


Figure 16. Effects of stimulating ciliary bundles on individual bullfrog saccular hair cells while recording intracellularly within the same cell (as in E). Displacement toward the kinocilium leads both to a hair cell depolarization (A and B) as well as an increase in conductance as measured with constant current pulses (C). Spikes are generated in innervating fibers on the depolarizing phase (D). From (Hudspeth and Corey 1977).

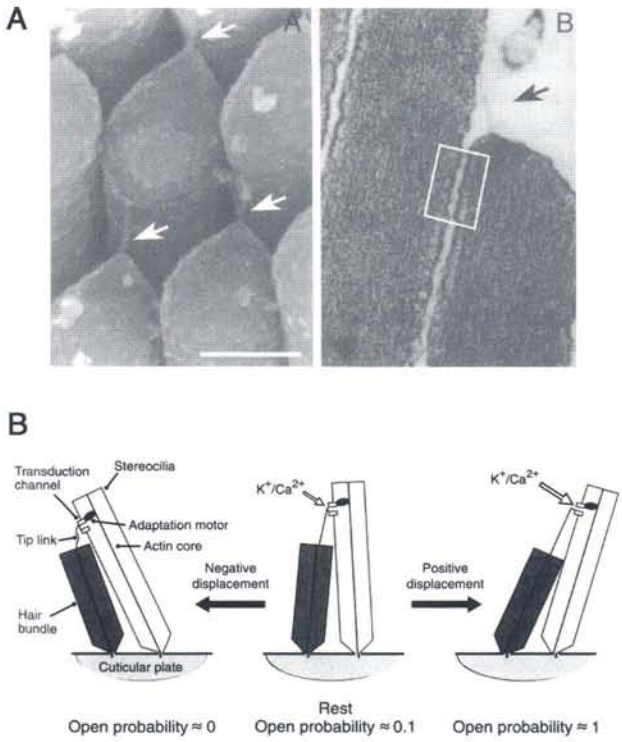
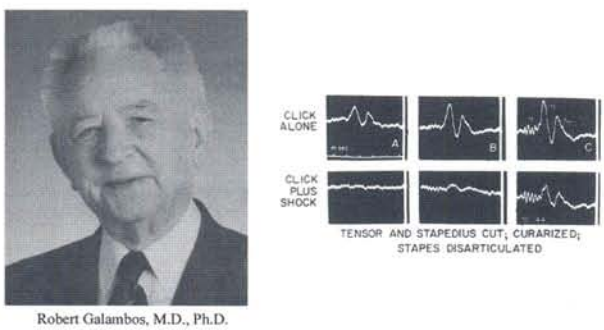


Figure 17. A. Electron micrographs showing tip links (arrows). From (Hackney, Fettiplace et al. 1993). B. Spring-loaded trapdoor mechanism of hair cell excitation. From (Gillespie 1995).



Robert Galambos, M.D., Ph.D.

Figure 18. A. Photo of Robert Galambos. From Abstracts of the 1998 Midwinter Meeting of the Association for Research in Otolaryngology. B. Suppression of whole nerve-action potentials by stimulation of efferent fibers to the cochlea. From (Galambos 1956).

generating mechanism in the cochlea—the so-called cochlear amplifier. The first clue to the identity of the cochlear amplifier came in 1975 when Ryan and Dallos (Ryan and Dallos 1975; Dallos and Harris 1977) showed that destruction of outer hair cells in chinchillas drastically elevated behavioral thresholds and thresholds of auditory-nerve fibers. In 1978 David Kemp, reported that faint sounds could be recorded coming out of human ears being stimulated with acoustic clicks (Kemp 1978); these so-called otoacoustic emissions were assumed to be generated actively by the basilar membrane (Zweig and Shera 1995). Then in 1980 David Mountain showed that stimulating the COCB or changing the endocochlear potential could alter the otoacoustic emissions (Mountain 1980). Both of these results argued for electrical feedback from outer hair cells onto the basilar membrane.

In 1985 Bill Brownell and his colleagues made one of the most far-reaching observations in the modern history of physiological acoustics (Brownell, Bader et al. 1985). While on sabbatical in Switzerland Brownell developed an *in vitro* isolated hair cell preparation and showed that when outer hair cells are electrically stimulated they are capable of mechanical deformations at acoustic frequencies. They suggested that this so-called electromotility was the connection between outer-hair cell membrane potential and cochlear mechanics. They argued on the basis of the microanatomy of the cochlea shown in Fig. 20 that a decrease in outer hair cell length results in a decrease in the separation between the basilar membrane and the reticular lamina. The past 15 years have seen this electromotility characterized in detail from the level of the whole cell to the level of the so-called molecular motor that drives the motility. Recently Dallos and colleagues have isolated the putative motor protein, which they designated prestin (Zheng, Shen et al. 2000).

Exactly how the electromotility influences basilar membrane motion is unknown at this time but so-called micromechanical models have been very helpful in advancing our understanding. In these models the microstructures in the cochlear partition are driven by the macromechanical motion of the basilar membrane and in turn, via electromotility feed back energy into the mac-

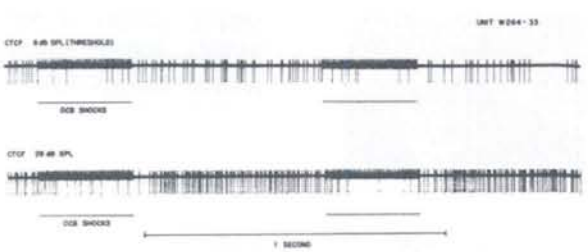


Figure 19. Suppression of activity in single auditory-nerve fibers by stimulation of efferent fibers to the cochlea. From (Wiederhold and Kiang 1970).

romechanical motion to sharpen tuning. A key aspect of the micromechanical processes is the conversion from macromotion of the basilar membrane into radial shear on the inner hair cell stereocilia as was originally envisioned by ter Kuile in 1900 as illustrated in Fig. 21A from Hallowell Davis (Davis 1965). Over the past 15 years, many detailed models of the micromechanics have been produced. Jont Allen considered the simplified model of the cochlear duct shown in Fig. 21B (Allen 1977, 1980). Both Zwislocki and Allen advanced the idea that the tectorial membrane has a resonance of its own near the resonant frequency of the basilar membrane and represented by the mass, spring and dashpot shown here (Zwislocki and Kletsky 1979; Allen 1980; Zwislocki 1990). The effect of this resonance is to place a zero just below the best frequency in the resonance curve of the stereocilia. Such models do produce sharp tuning in the stereocilia, and thus act as a second filter. However, the macromotion of the basilar membrane is unaffected and feedback from hair cells to basilar membrane displacement must be incorporated to produce sharp basilar-membrane tuning. Several investigators have shown directly that electrical stimulation of the cochlea can produce motion of the basilar membrane (Xue, Mountain et al. 1995; Nuttall, Guo et al. 1999). A general schematic of this feedback system is shown in Fig. 21C (from (Geisler 1998)). Cochlear partition forces deflect the cilia, which produces a transducer current and a corresponding change in outer hair cell membrane potential. This outer hair cell membrane potential change is reverse-transduced into an electromotile force on the cochlear partition.

We have toured the history of this outer hair cell feedback model of basilar membrane motion and we have touched on the transduction mechanisms of the inner hair cell in non-mammalian species. More direct measurements of input/output functions of cochlear hair cells by Dallos, Russell and others confirm the halfwave

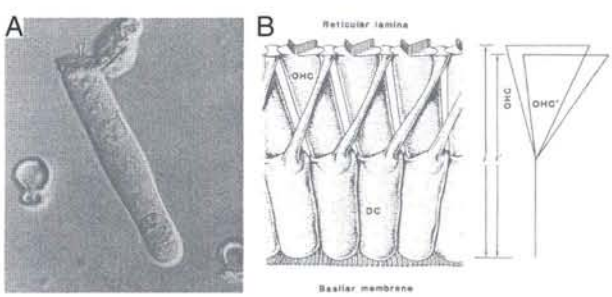


Figure 20. A. An isolated outer hair cell. B. Drawing of cochlear partition geometry showing how shortening of outer hair cells could cause a decrease in the separation between the basilar membrane and the reticular lamina. From (Brownell, Bader et al. 1985).

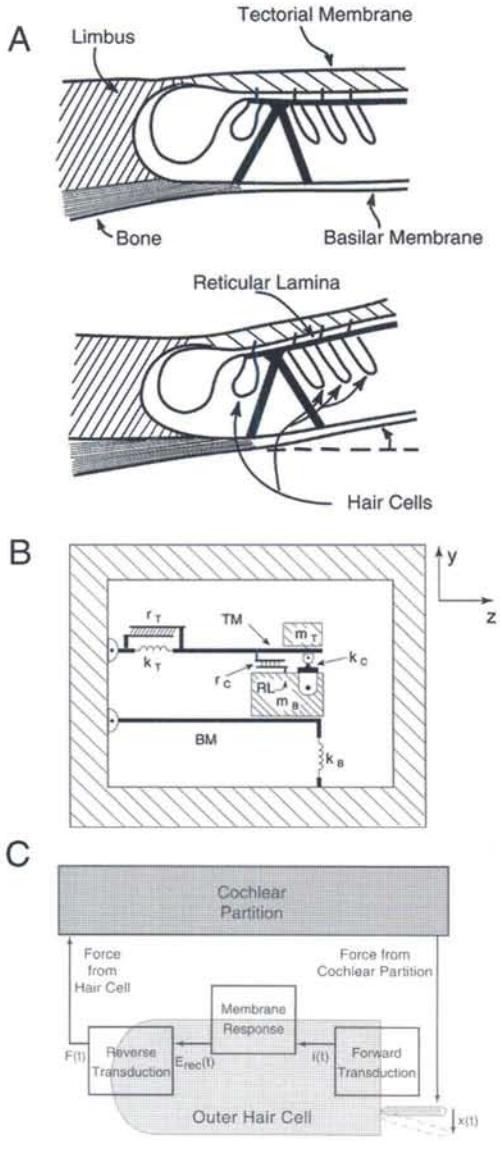


Figure 21. A. Conversion from macromotion of the basilar membrane into radial shear on the inner hair cell stereocilia as was originally envisioned by ter Kuile. From (Davis 1965). B. Diagram of model for cochlear micromechanics. From (Allen 1980). C. Schematic diagram of conceptual model for outer hair cell feedback onto the cochlear partition. From (Geisler 1998).

rectifying nature of the transduction process in both inner and outer hair cells as shown in Fig. 22 from a 1986 paper by Dallos (Dallos 1986). Also shown here is another contribution of the Dallos group to this Society—the Bekesy medal, which Peter won in 1995, was designed by Peter's wife Joan.

The final stage in the peripheral model of Fig.1 is synaptic transmission from the inner hair cell to the innervating auditory nerve fibers. The basis for our current models of this stage are found in the extensive and detailed studies of adaptation in the auditory nerve fiber responses to tones by Bob Smith and his colleagues at Syracuse University (Smith and Zwislocki 1975; Smith and Brachman 1982). As illustrated in Fig. 23 (Geisler 1998), the underlying principle of synaptic models is that neurotransmitter flows into a reservoir at a steady rate and stored for release to the afferent neuron at a rate determined by the membrane potential.

Stimulus encoding in the auditory nerve

So much for the cochlear mechanisms underlying the response properties of auditory-nerve fibers. There has been an intimately related but parallel history of our knowledge of how those patterns represent the information in an acoustic stimulus. Because the inner hair cell acts as a half-wave rectifier, we expect that there should be an ac component of the auditory nerve fiber responses to tones. Jerzy Rose and his colleagues Joe Hind, David Anderson and John Brugge studied this ac component in a landmark paper in 1967 (Rose, Brugge et al. 1967). The photo in Fig. 24 shows their team during an early auditory nerve recording session. In addition to the notable people in the photo we see one of the great technologi-

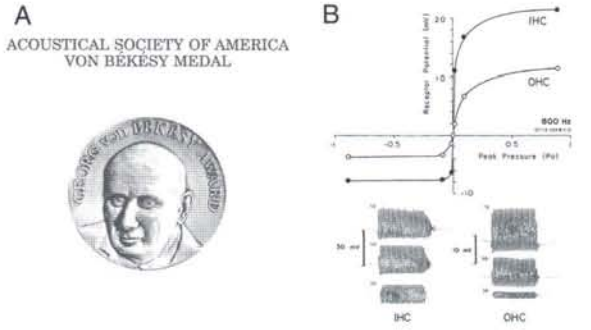


Figure 22. A. The Georg von Bekesy Medal in Physiological Acoustics. B. Input/output functions for inner and outer hair cell. From (Dallos 1986).

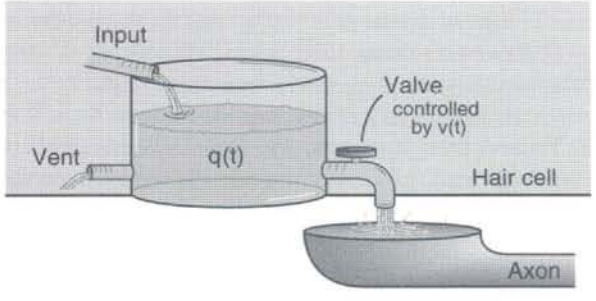


Figure 23. Representation of a model for hair cell synaptic transmission. From (Geisler 1998).

cal leaps forward in neurophysiology. The equipment rack contains an original LINC computer assembled by Joe and Dan Geisler at MIT as part of an NIH sponsored project that brought on-line computing to neurophysiology. Among other things, the LINC permitted on-line display of the ac component of the auditory nerve response in the form of a period histogram. The a.c. or so-called phase-locked response is shown by the peaks in the period histograms. Phase locking has been studied in great detail by many investigators since this early work of the Rose group. An interesting aspect of this body of work is that it involved some important advances in statistical estimation theory, which have since found applications in a number of other fields including medical imaging (Miller and Mark 1992; Johnson 1996).

The dc component of the inner hair cell receptor potential produces changes in average rate of innervating auditory-nerve fibers as is shown by the PST histogram in Fig. 25 from Kiang's 1965 monograph (Kiang, Watanabe et al. 1965). The photo shows Nelson, Walter Rosenblith and Bill Peake, taken at about the same time. Walter founded the Communications Biophysics Group at MIT, which spawned many eminent auditory physiologists, including Peake and Kiang. A standard question in doctoral qualifying exams is "why use tones to study the auditory system?" The obvious answer is that sinusoids are useful in describing the responses of linear systems. But we have seen that the cochlea is highly nonlinear at virtually every level and there are many auditory-nerve reflections of cochlear non-linearities, perhaps the simplest of which is the saturation of discharge rate with sound level, first demonstrated by Katsuki (Katsuki, Sumi et al. 1958) and Kiang (Kiang, Watanabe et al. 1965). In 1974 Sachs and Abbas (Sachs and Abbas 1974). showed that low threshold fibers saturate completely over about a 30 dB range of sound levels but that high threshold fibers do not saturate completely at reasonable sound levels, and rate can continue to increase over a range of more than 80 dB (Fig. 26A). In the same paper, they showed that this behavior is easily reproduced by a simple cochlear model in which the non-linear basilar membrane is followed by a simple saturating hair cell/synapse complex (Fig. 26B). Although this model was subject of controversy at the time in light of debate over basilar-membrane nonlinearity (Palmer and Evans 1980; Sachs, Winslow et al. 1989; Sokolowski, Sachs et al. 1989), in a more recent series of extremely careful and elegant papers, Graham Yates, Robert Patuzzi, Don Robertson and their colleagues in Perth have confirmed this model and actually used it to predict basilar membrane displacement functions in the guinea pig (Yates, Winter et al. 1990).

This relatively simple picture sometimes breaks down at very high stimulus levels. Kiang and his colleagues showed (Fig. 27) that in some instances the functions have a saturating low level component separated from a high level component by a sharp notch (Kiang, Liberman et al. 1986). A sharp shift in the phase of the response is associated with the notch. Kiang and his colleagues and others have attempted to associate the two components with interactions between inner and outer hair cells.

Studies with two-tone stimuli demonstrate even

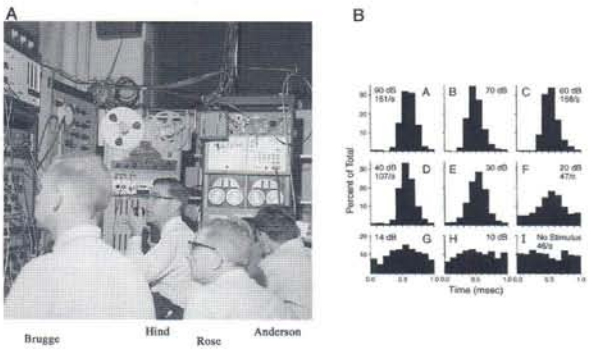


Figure 24. A. Rose, Hind, Anderson and Brugge team. (Courtesy Dr. Brugge.) B. Period histograms showing auditory-nerve fiber phase-locked responses to tones. From (Rose, Brugge et al. 1967).

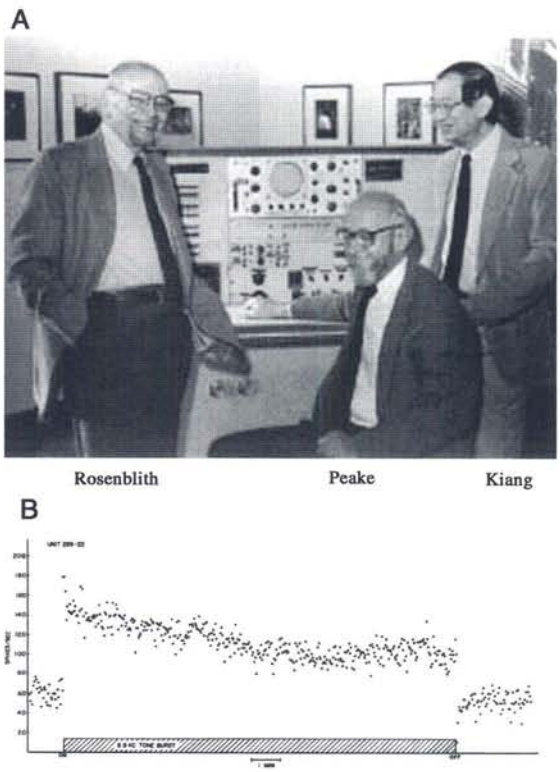


Figure 25. A. Photo of Walter Rosenblith, Bill Peake and Nelson Kiang. B. Post stimulus time histogram showing rate response of an auditory-nerve fiber. From (Kiang, Watanabe et al. 1965).

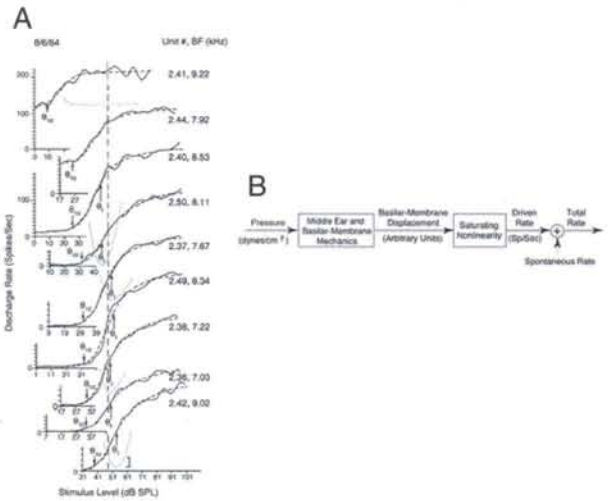


Figure 26. A. Rate versus level functions for auditory-nerve fibers with similar best frquencies. From (Sachs, Winslow et al. 1989). B. Model relating discharge rate to basilar membrane displacement that is the basis for the dashed curves in A. From (Sachs and Abbas 1976).

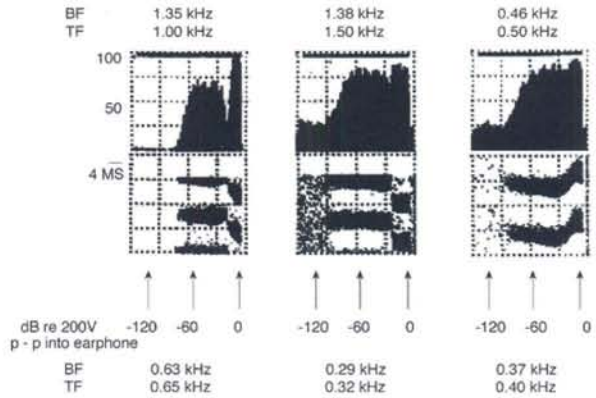


Figure 27. Rate-level functions (top) and corresponding phase plots for three auditory-nerve fibers, showing notches and phase shifts at high levels. From (Kiang, Liberman et al. 1986).

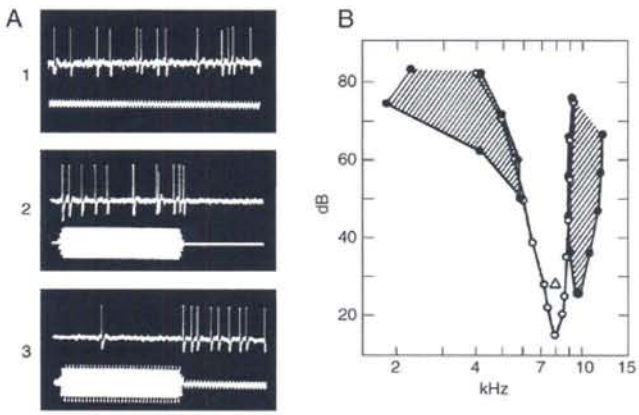


Figure 28. A. Suppression of responses to BF tones by off-BF tones. B. Suppression areas for a single auditory-nerve fiber. From (Arthur, Pfeiffer et al. 1971).

more dramatically the nonlinear behavior of the auditory-nerve encoding process. A phenomenon called two-tone suppression is shown in Fig. 28 by the decrease in rate to a BF tone by simultaneous presentation of another tone (Sachs and Kiang 1968; Arthur, Pfeiffer et al. 1971). The general characteristics of two tone suppression are often displayed in the form of suppression areas. Two-tone suppression has been characterized in great detail by numerous groups and there is very strong evidence that suppression is a reflection of a basilar membrane nonlinearity similar to that first observed by Bill Rhode and studied extensively by Mario Ruggero and his colleagues at Universities of Minnesota and Northwestern (Robles, Ruggero et al. 1991; Rhode and Cooper 1993). Non-linearities are also evident in the phase-locked responses to two tones as was shown by the Wisconsin group in 1969 (Brugge, Anderson et al. 1969). For example, the phase-locked responses to one tone can be suppressed by the simultaneous presentation of a second tone.

In 1971, at the time of the publication of Rhode's results, Russ Pfeiffer proposed a model that has influenced the thinking about the nature of the cochlear nonlinearity ever since (Pfeiffer 1970). Russ (photo in Fig. 29A) was Nelson Kiang's student before moving to Washington University in the late 60's. He became associate editor of JASA and made numerous creative contributions to Physiological Acoustics before his tragic death in an automobile accident in 1975. Central to the model is the basilar membrane compressive nonlinearity (Fig. 29B). It is trivial to show mathematically that such a nonlinearity can generate combination tones and that it produces suppression of the ac response at one frequency by simultaneous presentation of a second frequency. However the compression may not produce the equivalent of rate suppression, i.e., a decrease in the rms value of the signal output, because of a strong output response component at the suppressor frequency. In order to produce rate suppression Pfeiffer used a bandpass nonlinearity, as shown in Fig. 29C. The first filter in this model determines the suppression area boundaries, the compressive nonlinearity produces the suppression and the narrow second filter tuned to BF reduces the output component at the sup-

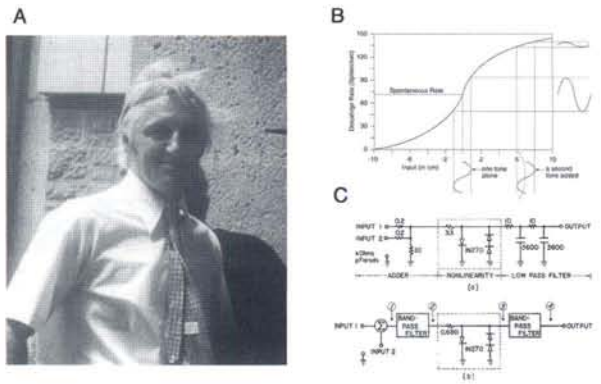


Figure 29 A. Photo of Russ Pfeiffer. (Courtesy Dr. D.O. Kim.) B. Saturating nonlinearity showing suppression of ac response component to a high frequency tone bya addition of a lower frequency tone of greater amplitude. From (Geisler 1998). C. Bandpass nonlinearity model for two tone suppression. From (Pfeiffer 1970).

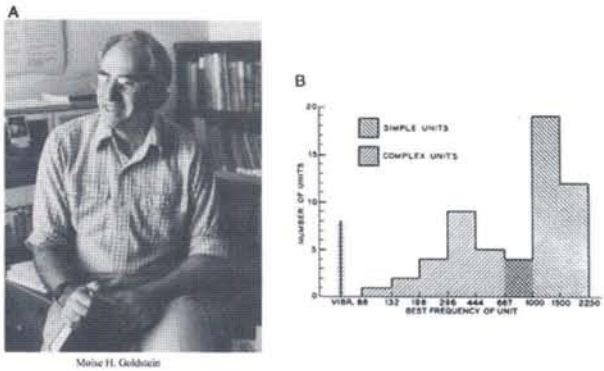


Figure 30. A. Photo of Moise Goldstein. (Courtesy Dr. Goldstein.) B. Histogram of best frequencies in bullfrog auditory nerve. From (Frishkopf and Goldstein 1963).

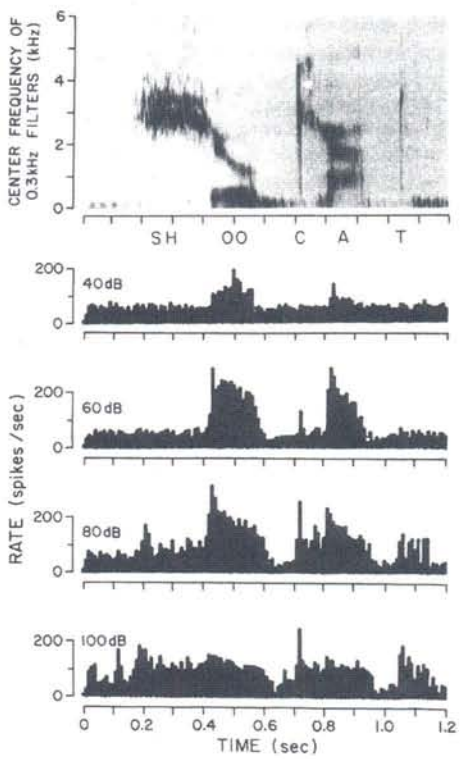


Figure 31. Spectrogram and corresponding PST histograms of auditory nerve responses for the phrase "shoo cat". From (Kiang and Moxon 1974).

pressor frequency, thus allowing rate suppression to occur. The BPNL model in its various realizations provides a qualitatively reasonable representation of many aspects of auditory nerve two-tone responses (Goldstein 1990).

Success in describing the detail the responses of auditory nerve fibers to tones and combinations of tones led several groups in the late 70's and early 80's to look at the neural encoding of speech. Earlier, animal communication sounds had been studied in a number of animals (Frishkopf and Goldstein 1963; Konishi 1969; Hoy 1978). For example, Larry Frishkopf and Moise Goldstein showed in 1963 (Frishkopf and Goldstein 1963) that there are two populations of fibers in the frog's auditory nerve coming from different end organs (Fig. 30) The BFs of the two populations correspond to two peaks in the vocal spectrum of the frog. While these and numerous other studies have important implications for animal communications, their specialized nature limit the possible extrapolations to human speech.

Perhaps the most catchy speech stimulus was used by Kiang and Moxon in their 1974 paper where they show (Fig. 31) PST histograms of single cat auditory-nerve fiber responses to the phrase "Shoo cat" (Kiang and Moxon 1974). However, it is clear that in studying the encoding of sounds as complex as speech, we need to consider not the responses of single fibers but the responses of the whole population of auditory-nerve fibers. In another of his innovative contributions, Russ Pfeiffer in a 1975 paper with Duck Kim provided the tool we needed to look at populations of fibers (Pfeiffer and Kim 1975). As shown in Fig. 32 over the course of several days they recorded responses to the same tones from several hundred single fibers in the same cat and plotted the responses as a function of characteristic frequency. The result was their estimate of the traveling-wave envelope for these tones, both in amplitude and phase. In an elegant series of papers Kim, Charlie Molnar and their colleagues (Kim and Molnar 1979) applied this population technique to describe the cochlear distribution of responses to one and two-tone stimuli, and in doing so laid the groundwork for population studies of the encoding of speech. Charlie, who died in 1996, was a close friend and colleague

of Russ, both at MIT and Washington U. and a scientist of enormous breadth and creativity. He was one of the developers of the LINC computer.

In 1979 Eric Young and I published the first population studies of speech coding (Sachs and Young 1979; Young and Sachs 1979). We showed that for a vowel with a formant structure as shown in Fig. 33 plots of discharge rate versus BF, called rate-place profiles, reflect the presumed distribution of basilar membrane amplitude and therefore provide a beautiful representation of the speech spectrum. A potentially more precise spectral representation results if instead of rate we plot a measure of the phase-locked response to speech as in Fig. 34 (Young and Sachs 1979). The principle underlying the so-called temporal representation is that, because of basilar membrane filtering, fibers phase-lock to stimulus energy near their BF. The temporal representation is so precise, in fact that Alan Palmer showed that two vowels with different pitches can be separated on the basis of the representation (Palmer 1990). Several groups have pursued both rate and temporal representations of speech over a wide range of speech stimuli (Delgutte 1980; Sinex and Geisler 1983; Geisler 1988).

We would be remiss in not paying tribute to another of this Society's giants. Ken Stevens, who by the way is alive and as active as ever. Ken earned both the Gold Medal of the Society and the National Medal of Science.

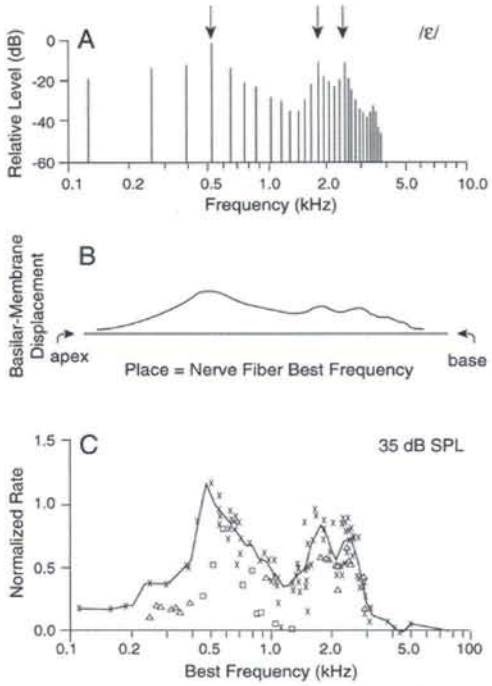


Figure 33. Rate versus best frequency for a population of auditory-nerve fibers (C). Stimulus is vowel /Σ / whose spectrum is shown in (A). Hypothetical basilar membrane displacement shown in (B). From (Sachs and Young 1979).

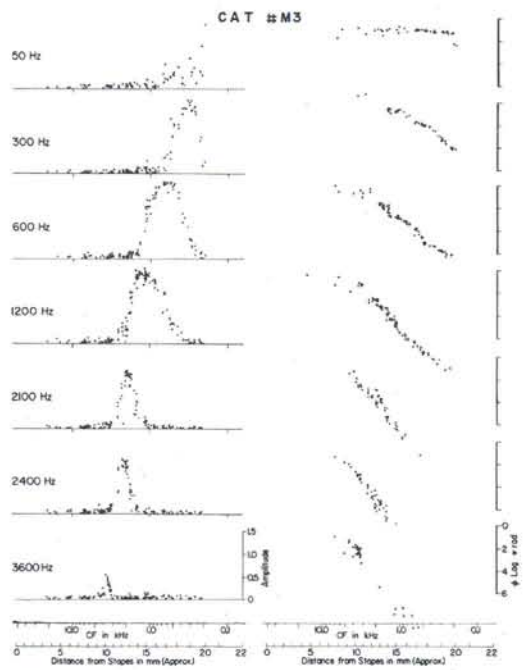


Figure 32. Amplitude and phase of response plotted versus best frequency for a population of auditory-nerve fibers for 7 tone frequencies. From (Pfeiffer and Kim 1975).

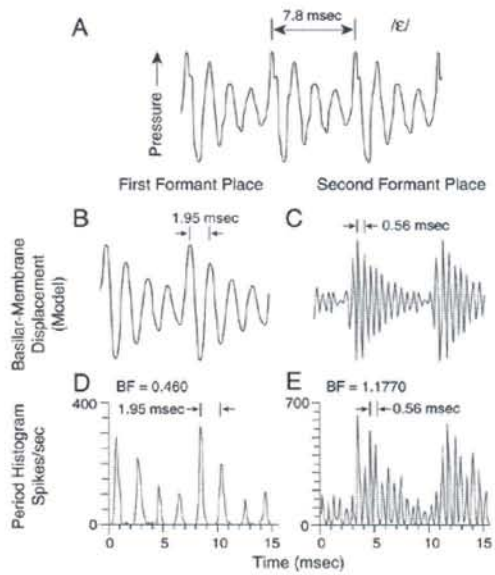


Figure 34. A. Time waveform of vowel /Σ /. B. Response to /Σ / of basilar membrane model at the 512 Hz (= first formant) place. D. Period histogram for response to /Σ / for auditory-nerve fiber with best frequency near the first formant. C. and E. Same foor second formant. Data replotted from (Young and Sachs 1979).

His monumental work in all aspects of speech had an enormous impact on those of us who studied the encoding of speech in the auditory system.

Models of auditory discrimination

An unanswered question in auditory theory is whether the brain actually uses the rate-place code, the temporal code or some combination. The search for answers to this question has been the focus of another thrust of physiological acoustics, namely the relationship between patterns of spike trains in the auditory nerve and human performance in auditory detection and discrimination tasks. This thrust has been the glue that has bound Physiological and Psychological Acoustics together in one technical committee of the Society. In 1968 Bill Siebert at MIT first articulated a framework that became the prototype that still finds wide applications not only in auditory research but also in other sensory systems (Siebert 1968). He began by noting that there are certain fundamental limitations on the precision with which auditory-nerve fibers can transmit stimulus information. These limitations come about because of the noisy (stochastic) nature of the auditory-nerve fiber spike trains and because of resolution limits in the cochlear mechanisms that generate the spike trains, e.g., limited frequency resolution of the cochlear filters and limited dynamic range of auditory-nerve spike rates.

Siebert introduced an extremely simple model (Fig. 35), which is remarkable in the depth of the insights that it provided despite the simplicity. In the model, the displacement of the stapes is converted into basilar-membrane displacement by an array of linear filters. The tuning curves of the basilar membrane are linear in log-log coordinates and the slopes are taken to approximate auditory-nerve tuning. In order to avoid dealing with phase-locking in this early model, Siebert converts the rms value of displacement into the average rate of a Poisson model of the auditory nerve spike trains via a highly simplified expression for the measured rate-intensity functions. Siebert analyzed this model in terms of signal detection theory and statistical estimation theory. Associating the jnd with the standard deviation of the model estimate of intensity or frequency, Siebert obtained jnd vs. sound level functions that were similar to those that had been measured psychophysically at the time. One of the striking features of these functions is that for high stimulus levels the jnds are independent of level. Siebert shows that because of rate saturation this level independence in the model depends on the rate changes at the edges of the stimulated region of the cochlea.

But subsequent psychophysical results shed some doubt on this idea that the central processor must use responses of off-frequency fibers in frequency or intensity discrimination at high stimulus levels. For example, Neal Viemeister showed (Fig. 36) that subjects do quite well at intensity discrimination in a background of notched noise where presumably the off-frequency fibers with BFs outside the notch are saturated by the noise (Viemeister 1983). Bill Shofner showed that one way around this dilemma lay in the low spontaneous high threshold units, which are not saturated by the background noise (Shofner and Sachs 1986; Delgutte 1990). Viemeister, Ber-

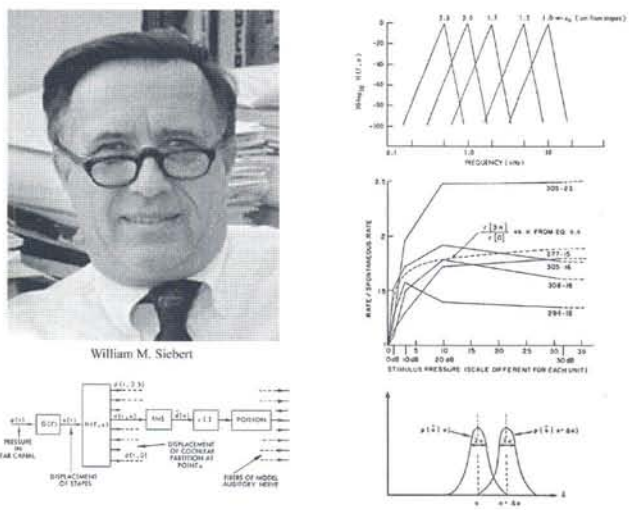


Figure 35. Photo of Bill Siebert (Courtesy MIT Research Laboratory of Electronics). Siebert's peripheral auditory system model. From (Siebert 1968).

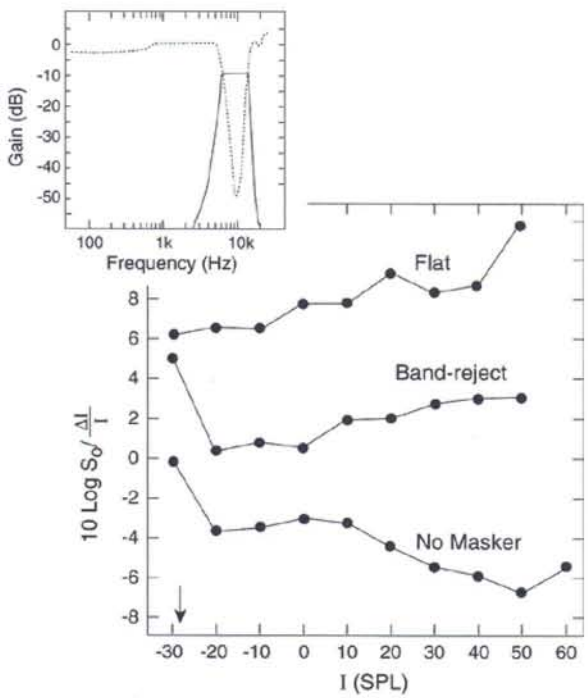


Figure 36. Tone detection in masking noise. From (Viemeister 1983).

trand Delgutte and others have shown that combining rates of low, medium and high spontaneous rate fibers in a Siebert-like model does go a long way to explaining intensity discrimination in situations where spread of excitation is eliminated (Viemeister 1988; Delgutte 1990).

There is another way around the saturation problem that was explored by Siebert in a 1970 paper (Siebert 1970). There he developed a similar model based on auditory nerve phase-locking responses and showed that frequency jnds could be explained on the basis of only a few fibers tuned to the stimulus frequency, independent of stimulus level. Although in the intervening years there have been numerous models based on Siebert's phase-locking ideas including models for interaural phase discrimination by Steve Colburn and his colleagues (Colburn 1973; Goldstein 1973) and speech and frequency discrimination by Julius Goldstein and his colleagues, it is fair to say that the question of whether the brain uses the simple rate-place code, the temporal code or some combination remains largely unanswered.

Summary

We have followed the histories of three related themes in Physiological Acoustics as they have evolved throughout the history of this Society. At this point I had intended to summarize the progress we have made by picking a few titles from each of the Society's three quarter-centuries. Much to my initial surprise the topics have not changed very much in those 72 years but the substance has changed significantly. For example, we saw an article on the acoustics of the external ear in volume 2 of JASA in 1930 and again the same topic appears in 1990. Not that there hasn't been progress. The 1930 paper reports rather crude measurements on human ears, while the 1990 paper presents extremely precise measurements of the head related transfer function in the cat, which has stimulated a whole new direction of research in the peripheral and central mechanisms of sound localization (Musicant, Chan et al. 1990; Rice, May et al. 1992).

So instead of summarizing what I have said about the past 75 years, I will give my limited vision of the next quarter of the Society's first century. What might the next 25 years hold?

Clearly although the topics might not change all that much we are going to know a lot more about them. Our models of the peripheral auditory system will be informed by all that modern genetics, molecular biology and sensor technology has to offer us. We will undoubtedly know in detail the molecular mechanisms of electromotility and its effect on basilar membrane mechanics. We will fully understand how the hair cell functions. As a result we will be able to construct cochlear models at a level of biophysical precision unimaginable not only when Bekesy and Zwislocki were first building models of cochlear mechanics, but even 30 or 40 years later.

And the applications of this knowledge and these models are potentially breathtaking. From designing new generations of hearing aids based on cochlear mechanisms, to optimizing the application of stem cell technology and hair cell regeneration to cure rather than treat deafness, the quantitative, mechanisms-oriented approach that characterizes the vast majority of the work that appears in JASA is going to make the future even richer than the past. I hope that we all enjoy its full potential.

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Psychological and Physiological Acoustics Timeline

1928 •••• Founding meeting of ASA.

1929 •••• First volume of JASA.

1930 •••• Measurement of "auditory impulses" (Wever and Bray).

1931 •••• Estimate of just detectable changes in frequency (Shower and Biddulph).

1933 •••• Estimate of absolute threshold (Sivian and White).

1938 •••• Pitch of the Residue: evaluating the role of temporal analysis in pitch perception (Schouten).

1943 •••• Physiological tuning curves (probably cochlear nucleus, Galambos and Davis).

1948 •••• Binaural Unmasking (Hirsh).

1953 •••• **Elucidation of the "Cocktail-party" problem (Cherry).**