Basilar Membrane Vibration in the Gerbil Hemicochlea

CLAUS-PETER RICHTER, 2 BURT N. EVANS, 1 ROXANNE EDGE, 1 AND PETER DALLOS 1
1 Departments of Neurobiology and Physiology and Communication Sciences and Disorders, Auditory Physiology Laboratory (The Hugh Knowles Center), The Institute of Neuroscience, Northwestern University, Evanston, Illinois 60208; and 2 Zentrum der Physiologie, J.W. Goethe-Universität, Theodor-Stern-Kai 7, 60590 Frankfurt/Main, Germany

Richter, Claus Peter, Burt N. Evans, Roxanne Edge, and Peter Dallos. Basilar membrane vibration in the gerbil hemicochlea. J. Neurophysiol. 79: 2255–2264, 1998. Excised gerbil cochleae were cut along the mid-modiolar plane (hemicochlea). Along one-half turn of this preparation, fluorescent microbeads were placed on the basilar membrane (BM). The BM was vibrated with click stimuli (50 μs) produced mechanically by a piezo pusher. The stimulus delivery probe could be positioned either more apical or more basal from the beads. Vibration patterns were measured with a wide bandwidth photomultiplier from the movements of the beads. When the probe was positioned more basal, the responses to click stimuli were brief, damped sinusoids. According to the fast Fourier transforms (FFTs) of the averaged time wave forms, the best frequency between successive beads decreased toward the apex (0.8 octave/mm). Sharpness of tuning of the normalized FFT spectra (NQ_{on}) on average was 1.5. Response amplitude at a fixed input level, measured at different beads away from the stimulation site, dropped exponentially (58 dB/mm). In addition, for each individual bead, amplitude dropped linearly with decreasing stimulus intensity. In experiments where the stimulating probe was placed more apical, two major properties were observed: first, beads revealed only the spectral components present in the motion of the probe. Second, magnitude reduction of the displacement of the cochlear partition was greater, on average 155 dB/mm, indicating a lack of significant propagation in the reverse direction.

INTRODUCTION

Propagation of mechanical disturbances (traveling waves) along the basilar membrane in the cochlea has been studied experimentally for about half a century. As the traveling wave proceeds along the cochlea, from base toward apex, tones of different frequencies produce waves that rise in amplitude at different rates and attain their maxima at different locations before extinguishing. Thus the traveling wave functions as a spatial spectral analyzer. Further, the speed of transmission of the wave along the basilar membrane is slow compared with the propagation velocity of sound in fluid.

von Békésy (1928, 1960) first experimentally observed the traveling wave on the basilar membrane of human cadaver ears. Such waves also have been described for other classes. Beside mammals, a traveling wave has been found in birds (Gummer et al. 1987; von Békésy 1960) and alligators (Wilson et al. 1985). For mammals, the quantitative properties of traveling waves are now well established (Rhode 1971; Robles et al. 1986; Sellick et al. 1982; von Békésy 1960). For all cases, the direction of wave travel is from base to apex. Efforts to evoke wave travel towards the basal end of the cochlea, by moving the “stapes” to the apex, have not been successful. Regardless of the position of the stapes or artificial stapes, the wave propagation is in a base-to-apex direction (von Békésy 1928; Wever and Lawrence 1954). The explanation of this phenomenon is that no matter where acoustic energy is delivered into the cochlear fluids, traveling waves occur after the energy is transmitted to the inner ear fluids, and the direction of wave travel is determined by the mechanical properties of the basilar membrane (von Békésy 1928). The basilar membrane possesses exponentially graded stiffness, so that the base is some 100-fold stiffer than the apex (von Békésy 1960). Thus wave propagation is evidently unidirectional toward the more compliant region when input energy is delivered via the surrounding fluid.

The simple notion of resonance of the basilar membrane is based on the assumption that the longitudinal tension of the membrane is negligible. However, the question of whether longitudinal coupling is present in the basilar membrane is controversial (Völdrich 1978; von Békésy 1960). Existence of longitudinal coupling has been supported experimentally by von Békésy (1960) and has been considered in some cochlear models (Allen and Sondhi 1979; Wickersberg and Geisler 1985). Inclusion of longitudinal coupling in cochlear models broadens the tuning curve at its tip, as demanded by experimental observations. In other words, longitudinal coupling is incorporated to make modeling efforts conform more closely to physiological observations (Wickersberg and Geisler 1985). However, minimal longitudinal coupling in the basilar membrane has been observed experimentally (Völdrich 1978). Furthermore, other modeling efforts of the basilar membrane suggest that inclusion of longitudinal coupling reduces the tuning predicted by the model (Allen and Sondhi 1979).

A lack of longitudinal coupling in the basilar membrane would not permit propagation of energy in the basilar membrane itself. Consequently, in this case, all acoustic energy has to be coupled through the cochlear fluids. Interesting questions of how energy corresponding to internally generated signals, such as otoacoustic emissions is back-propagated to the stapes or how combination tones are distributed remain largely unanswered.

In the case of combination tones, it is assumed that energy is generated at one place on the basilar membrane and propagates as a traveling wave to the basilar membrane site with a characteristic frequency equal to that of the combination tone (Goldstein 1968; Siegel et al. 1982; Smoorenburg 1972b; Zwicker 1955). The interesting question is whether propagation of energy through the basilar membrane might play a role and whether the propagation is unidirectional.

Questions of bidirectional propagation of energy and of...
longitudinal coupling in the basilar membrane are addressed in the present experiments. A suitable preparation for these investigations is the "hemicochlea." A cochlea, cut in two along the mid-modiolar plane (Hu et al. 1995), allows access to the basilar membrane at the more basal or more apical cut edges of an individual half-turn. Fluorescent spheres, located along a half-turn of the hemicochlea, can be used to evaluate response properties at different locations along the basilar membrane while the latter is driven mechanically either at a more basal or more apical site. The advantage of the preparation, in comparison with in vivo measurements, is the possibility of evaluating the propagation of energy along the basilar membrane in two directions, from base to apex and vice versa. Furthermore, it is possible to obtain measures of vibratory patterns at several locations in the same preparation. The drop in response amplitude of the vibration pattern measured by the photomultiplier was proportional to the distance by which the fluorescent beads moved in and out of the aperture of the photomultiplier.

For testing the photomultiplier, a calibration pipette with a fluorescent bead glued to its tip was mounted to a piezo pusher (PZL 007, Burleigh) and was placed on the microscope stage. The displacement of the pipette was parallel to the optical plane.

During the experiments, the hemicochleae were attached to a ball-joint manipulator. The ball-joint manipulator then was transferred into a stable metal hemisphere filled with HBSS and placed into a hole on the microscope stage. Initially the surface of the metal hemisphere and the surface of the microscope stage were parallel. The cochlea on the ball joint manipulator then was oriented so that the basilar membrane was parallel to the optical axis and perpendicular to the surface of the microscope stage (radial view). The ball-joint manipulator then was fixed tightly with a set screw. This, however, did not allow monitoring the vibration patterns of the beads except at the cut edge of the hemicochlea and necessitated reorientation for beads further away from the cut edge.

Final adjustments in orientation of the preparation were achieved by tilting the metal hemishell. The hemishell was angled such that beads close to the probe and beads further in were visualized at the same time (Fig. 2). An imaginary line perpendicular to the surface of the basilar membrane and parallel to the surface of the hemishell was used to determine the angle for the trigonometric correction. The angle $\beta$ was measured between the surface of the microscope stage and the surface of the hemishell. Then $\alpha = \pi/2 - \beta$ (Fig. 2). Trigonometric corrections were made to obtain the transverse component of basilar membrane vibration $c$ from the measured oblique motion of the beads relative to the optical axis of the microscope $a$; $c = a/\sin\alpha$. Rotation around the optical axis was minimal and was not considered in the corrections. Once the preparation was oriented, the stimulation probe was brought to the basilar membrane until the bead at the tip of the glass pipette contacted the subsurface of the basilar membrane (facing scala tympani). The basilar membrane reflected the light emitted from the fluorescent bead at the tip of the electrode. Thus contact of the probe to the basilar membrane could be detected easily by visual inspection while advancing the probe. The angle of the stimulation probe was almost perpendicular to the subsurface of the basilar membrane in the experiments.

For measurements, the aperture of the photomultiplier was placed over half of the surface image of the beads. Transverse motion of the basilar membrane lead to maximum light intensity change by the bead moving in and out of the aperture. Positioning was achieved by moving the entire microscope stage in the optical plane. The orientation of the slit then could be optimized by rotation of the photomultiplier around the optical axis.

**Photomultiplier**

Frequency response properties and sensitivity of the system were determined respectively with a light emission diode (LED) and a fluorescent bead (90 $\mu$m diam) attached to the tip of a micropipette. The micropipette was fixed to a piezo pusher (PZL 007, Burleigh) and could be displaced by known amounts (between 2 mm and 5 $\mu$m).

**FREQUENCY RESPONSE PROPERTIES.** A red LED was focused on the photomultiplier using the upright Leitz microscope. The signal for the LED was forward biased by a DC voltage of 2.5 V and modulated by a ternary noise stimulus (100-nV peak).
The response of the photomultiplier to the stimulus was measured to determine magnitude and phase properties of the system. A pseudorandom ternary noise sequence with a flat magnitude, and zero phase response up to roughly half of the sampling rate of 90 kHz (Möller 1981; Zierler 1959) was generated via a programmable waveform generating board (Metabyte, AWFG-2). The ternary noise used here was generated with three amplitude levels (−a, 0, a) and a recursive algorithm with memory (n = 6), resulting in 728 (or 3^n − 1) amplitude level transitions per period. The fast Fourier transform (FFT) was performed with 728 points and resulted in n = 182 nonzero odd frequency components. The (182) even frequency components were zero, reflecting the odd (inverse-repeat) character of the waveform around the middle of the sequence (i.e., the 2nd half of the waveform was the same as the 1st one but of the opposite sign). For the frequency range (0.13–22 kHz), no drop in magnitude (Fig. 3A) and no phase shift of the response signal could be detected (Fig. 3B). This indicates flat frequency response behavior of the measuring system, at least ≈ 22 kHz. The corner frequency of the measuring system was determined by the rise-time of the response of the photomultiplier to a voltage step applied to the LED. The time to reach 63% of the maximum response was 1.5 μs which corresponds to a corner frequency of ≈ 106 kHz.

MINIMUM DETECTABLE RESPONSE AND LINEARITY. The amplitude of the photomultiplier response to a sinusoidal movement (100 Hz) of the fluorescent bead decreased linearly down to ≈ 10 nm with decreasing motion of the bead (Fig. 4).

**Stimulus**

A micropipette with a 90-μm fluorescent bead attached to its tip with acrylic was mounted on a piezo stepper (PZL 007, Burleigh) and used to deliver mechanical stimuli almost perpendicular to the plane of the basilar membrane. A micromanipulator was used to advance the piezo and the stimulation probe to the basilar membrane until mechanical contact was observed. Subsequently, during the experiments, the basilar membrane was moved by mechanical pulses of the probe toward scala vestibuli. Time waveform of the displacement for one probe, loaded by the basilar membrane, is shown in Fig. 8A. The corresponding frequency spectrum is plotted in Fig. 8B. The maximal amplitude of the probe movement when electrical square pulses (50 μs, 1–3 V) were applied to the pusher was between 0.4 and 1.2 μm.

**Data analysis**

Responses measured by the photomultiplier were fed into an anti-aliasing Bessel filter (corner frequency 20–30 kHz). Subsequently, the filtered response was sampled by a DAS50 board at a sampling rate of 1 MHz. Off-line analysis included visual inspection of the time waveforms and determination of frequency response using a FFT of the analogue signal. The FFTs were normal-
were exposed and cut in the mid-modiolar plane. These procedures took ~30 min. Thereafter, fluorescent beads were placed on the basilar membrane at different locations along a half-turn. The placing of the beads, the positioning of the preparation on the microscope stage and the placing of the probe to vibrate the basilar membrane took on average 154 min (range: 30–390 min; standard deviation: 39 min). After the hemicochleae were placed, the data were acquired within an average time interval of 75 min (range: 16–151 min; standard deviation: 12 min).

REPEATED MEASUREMENTS. Repeated measurements which were done within the time interval of 1 h did not show changes in the best frequency. However, there was variation in the amplitude obtained (Fig. 5). Here two examples are shown, HCoRev1 and HCoRev2. They revealed a scatter in peak-to-peak amplitude of 0.48 ± 0.16 μm [characteristic frequency (CF) changed from 2,750 to 2,500 Hz, which equals 0.14 octaves] and 0.36 ± 0.06 μm (no CF change was detected). Examples of FFTs of the time waveforms are shown in Fig. 5. In example HCoRev1, the amplitude decreased after the first trial but then remained almost constant. However, in HcoRev2, the amplitude was initially constant but the last trial showed an increase. One reason for the observed changes in amplitude might be due to possible changes in light intensity from the mercury lamp used to excite the fluorescent light. Despite the scatter in amplitude found in repetitive measurements, the results did not show a systematic increase or decrease in vibration amplitudes.

VARIABLE LOAD OF THE BASILAR MEMBRANE. In three experiments, the influence of a change in the load on the vibration probe by the basilar membrane was tested. For this purpose, the location of the probe, which initially was positioned by eye, was changed by altering the DC voltage to the piezo pusher. Thus the position was changed relative to the initial position. Increasing the tensioned to their maximum amplitude. The frequency of the maximum of the ratio between beads’ FFT and probe’s FFT was designated the ‘‘best frequency.’’ To measure the bandwidth of the obtained FFT spectra, a normalized sharpness (NQ10dB) has been defined (best frequency of the FFT spectrum/bandwidth of the normalized FFT spectrum at a magnitude of 0.32 peak).

The logarithmic decrement δ of the vibration patterns of the cochlear partition was calculated as described by von Békésy (1960, page 458): δ = ln (i2/i1), where i2/i1 denotes the amplitude ratio between successive response cycles.

RESULTS

These experiments were performed to study basic mechanical vibration properties of the BM. Therefore, mechanical pulse stimuli were applied directly to the BM in 22 hemicochleae. Responses to such stimuli were used to determine filter properties and damping of the BM vibration at different locations along a hemitim. The stimulus probe was placed either at the basal cut edge (n = 17; cut edge closer to the basal end of the cochlea) or the apical cut edge (n = 9; cut edge closer to the apical end of the cochlea). Thus energy propagation and drop in response magnitude could be studied in two directions.

Reliability of measurements

DATA ACQUISITION. As described in METHODS, both bullae were removed after killing the animals and the cochleae were exposed and cut in the mid-modiolar plane. These procedures took ~30 min. Thereafter, fluorescent beads were placed on the basilar membrane at different locations along a half-turn. The placing of the beads, the positioning of the preparation on the microscope stage and the placing of the probe to vibrate the basilar membrane took on average 154 min (range: 30–390 min; standard deviation: 39 min). After the hemicochleae were placed, the data were acquired within an average time interval of 75 min (range: 16–151 min; standard deviation: 12 min).

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The NQ_{10dB} of the obtained response curve was between 0.6 and 2.7, on average 1.5. A small, nonsignificant decrease in NQ_{10dB} was attained with increasing distance from the base of the BM (n = 32). Response amplitudes to stimuli of different intensities obtained from individual beads dropped linearly (Fig. 9).

Reduction between successive peaks of a given sinusoidal response was measured and the logarithmic decrement (\(\delta\)) was computed. \(\delta\) was between 0.16 and 1.8, on average 0.6 (n = 30). The decay of the amplitude at different beads away from the stimulation location could be described as an exponential drop of ~58 dB/mm (Fig. 11A).

To determine whether energy is mainly propagated via the fluids or the BM, a hole was made into the arcuate zone (between stimulus delivery and measurement sites) using a glass pipette. If energy is propagated by the BM, this “cutting” of the BM should decrease the vibration amplitude significantly. This manipulation lead to an immediate drop of the response amplitude by 7.8 dB beyond the cut. A bigger decrease in response magnitude is expected if pectinate zone and tectorial membrane could be separated as well. FFT spectra of the sinusoidal responses showed the same frequency distribution before and after the cut of the basilar membrane. Only the magnitude of the FFT spectra decreased.

Interestingly, beads placed in four hemicochleae revealed no tuning. Aside from magnitude scaling, time waveforms and FFTs at the different beads were essentially identical to the responses obtained from the stimulation probe. For these

Stimulus is basal to site of measurement

Examples of time responses and FFTs are shown for three preparations in Figs. 7 and 8. Impulse responses appeared as brief, filtered damped sinusoids. The frequency of this sinusoid was specific to a given fluorescent bead’s location. The time waveforms obtained from different beads revealed a decrease in frequency of the oscillations with increasing distance of the beads from the stimulation probe (Figs. 7A and 8A). Corresponding FFTs showed that the vibration pattern at any bead was tuned, reflecting a distinct best frequency (Figs. 7B and 8B). According to the FFTs of the time waveforms, the shift in best frequency between successive beads was between 0.3 and 1.7 octaves/mm, on average 0.8 octave/mm (n = 20). A slight, nonsignificant decrease of the CF-shift was found with increasing distance from the base. The NQ_{10dB} of the obtained response curve was between 0.6 and 2.7, on average 1.5. A small, nonsignificant decrease in NQ_{10dB} was attained with increasing distance from the base of the BM (n = 32). Response amplitudes to stimuli of different intensities obtained from individual beads dropped linearly (Fig. 9).

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FIG. 7. A: normalized time waveforms obtained at beads located in the 1st turn (preparation HCo116) and 2nd turn (preparation HCo142) of 2 different gerbil hemicochleae. Distances from the basal end of the cochlea. Distance of the probe from the basal end of the basilar membrane was 3.5 mm (HCo116) and 7.6 mm (HCo142). B: FFTs of the time waveforms shown in A. Magnitudes are normalized to the maximum value. A reduction of response amplitude of 15 dB/mm was observed.

FIG. 8. A: example of nonnormalized time waveforms obtained at beads located in the 1st turn of a gerbil hemicochlea (preparation HCo112). Distances are from the basal end of the cochlea. B: FFTs of the time waveforms shown in A.

FIG. 9. Stimulus intensity vs. vibration amplitude measured at several beads. Data for 5 representative preparations are shown. Thick line represents linear response.

Stimulus more apical to site of measurement

Time waveforms obtained from 26 different beads placed in nine different cochleae reflected the properties of the stimulation probe. A shift in frequency of the oscillations with increasing distance of the beads from the stimulation probe was not observed (Fig. 10). The reduction of the amplitude was on average 155 dB/mm (Fig. 11B).

Beads in a glass tube

Experiments to mimic fluid properties in the hemicochlea in the basal turn were carried out. Beads were placed in a glass tube (length: 3 mm; diameter: 0.68 mm) and immersed in a dish of HBSS. A probe similar to that used in the hemicochlea experiments was placed in front of the opening of one end of the glass tube. Again, electrical square pulse stimuli were applied to the piezo pusher. A mechanical click response was produced by the stimulus delivery probe. The beads located along the longitudinal axis of the glass tube showed a reduction of response amplitude of 15 dB/mm (Fig. 11C) with increasing distance from the probe. This is in reasonable agreement with responses from beads obtained in the hemicochlea which did not show tuning (19 dB/mm).

Therefore, for the latter cochleae, it is surmised that the beads were only loosely attached to the basilar membrane and did not reflect its vibratory properties.
that found by von Békésy, between 1.4 and 1.8. Ruggero et al. (1992) showed a $\vartheta$ of $\sim 0.09$ in a living animal and a $\vartheta$ of $\sim 0.5$ post mortem and at high sound pressure levels. Because the logarithmic decrement increases with post mortem time, the $\vartheta$ might be a measure for assessing the condition of the preparation.

A frequency place map for the hemicochlea has been developed using the FFT results of the bead responses and the distances of the beads from the basal end of the basilar membrane (Fig. 12). Compared with in vivo frequency place maps based on horseradish peroxidase (HRP) staining of single fibers with determined CF of adult animals (Echteler et al. 1989; Müller 1996), the frequency place map in the hemicochlea was shifted $\sim 1.4$ octaves toward lower frequencies. According to the literature, the frequency place map in a dead cochlea shifts $\sim 0.5–0.9$ octaves (Rhode 1973; Rhode and Robles 1974; Ruggero et al. 1992). These data were obtained within the first hour after death. However, a decrease in the characteristic frequency as a function of time after death has been described in BM vibration amplitudes (Rhode 1973; Rhode and Robles 1974) with a shift

**DISCUSSION**

*Overview*

Experiments in the hemicochlea revealed some of the passive mechanical properties of the gerbil inner ear. Direct mechanical vibration of the BM with mechanical pulse inputs showed band-pass responses for different beads located along the BM. The responses to broadband stimuli were brief highly damped sinusoidal waveforms with different frequencies. Normalized sharpness of the response curves ($\text{NQ}_{10\text{dB}}$, on average 1.5), shift in best frequency (on average 0.8 mm/octave), and logarithmic decrement (on average 0.6) were determined from the responses. From cochleae in poor condition or from in vitro cochlear preparations, similar results have been obtained by others [guinea pig: best frequency: 0.8 kHz, $\text{NQ}_{10\text{dB}}$: 0.94] (Rhode 1973); squirrel monkey: best frequency: 8 kHz, $\text{NQ}_{10\text{dB}}$: 1.4 (Rhode and Robles 1974); guinea pig: best frequency: 8 kHz, $\text{NQ}_{10\text{dB}}$: 0.94 (Rhode and Cooper 1993); chinchilla: best frequency: 10 kHz, $\text{NQ}_{10\text{dB}}$: 1.8–2.0 (Ruggero et al. 1992)]. Thus aspects of the present findings coincide with the results of other groups, reflecting the operation of the passive cochlea. However, the logarithmic decrement $\vartheta$ was better in the present set of data (0.6) than

**Fig. 10.** Time waveforms (A) and corresponding FFT spectra at beads located in the 1st turn when the stimulation probe was placed more apical to the measuring site. For these experiments, energy propagation from the apex to the base was studied. Spectral response properties obtained at all beads reflected that of the stimulation probe. Drop in vibration amplitude for this preparation was $\sim 140$ dB/mm, but interestingly $\sim 190$ dB/mm from probe to 1st bead.

**Fig. 11.** Drop in peak to peak amplitude of the time waveforms vs. distances of the beads from the stimulation probe. A–C: each data point represents 1 bead used for measurements, each type of symbol represents 1 preparation. A: stimulus probe was located at the more basal cut edge of the hemicochlea. B: probe was located more apical. For the symbols with a downward arrow, no response could be measured. Each point with a downward arrow shows the noise amplitude obtained at the beads’ location. C: small symbols represent beads that only reflected the spectral properties of the stimulation probe (thick line). Large open diamonds show beads in a glass tube (thin broken line).
of ~1.4 octaves toward lower frequencies. In the present experiments, the mean shift of 1.4 octaves of the BM frequency place map, then might be explained by the times after death for the measurements, which were usually 3.0 h (range: 1.0–6.5 h) after killing the animal. The scatter of the data presented for one location (same distance of the bead from the basal end of the basilar membrane) also may be caused by the differing times between killing the animal and data acquisition.

For an isolated preparation, the cochlear amplifier is probably not active. In the present experiments, a linear magnitude response versus stimulus intensity was found (Fig. 9). Therefore the nonlinear behavior of basilar membrane vibration patterns is missing. This finding is in agreement with cochleae in poor condition or excised cochleae (Khanna and Leonard 1986; Rhode and Robles 1974; Ruggero et al. 1992).

**Direction of energy propagation**

In the present preparation, propagation of energy on the basilar membrane from base toward apex and vice versa could be investigated. As shown, tuned BM vibration patterns were observed if the basilar membrane was stimulated more basal than the location the vibration of which was measured by the behavior of the beads. In none of our experiments could we detect a tuned vibration pattern of the BM if energy propagated from the apex to the base. The question, whether a traveling wave from apex to base is sustainable in the cochlea was addressed by von Bekesy (1928). He moved the stapes to more apical positions in the cochlea, but he never saw a traveling wave running from apex to base. However, in his experiments, he investigated the whole cochlea, including at least the fluids and the basilar membrane properties. The acoustic energy in his experiments was coupled to the basilar membrane through the fluids. No matter where introduced, this acoustic energy propagates in the scalae with the speed of sound and thus provides an essentially instantaneous pressure gradient across the basilar membrane. This pressure gradient sets the membrane in motion and a well-behaved traveling wave results as an aftereffect. Direct experimental investigation of wave travel for the case when energy is directly conveyed to the basilar membrane has been lacking. Thus potential reverse propagation properties only have been investigated partially. In the present experiments, based on direct mechanical input, no locally tuned vibration of the BM could be observed if energy propagated toward the base of the basilar membrane. As a consequence, one may surmise that in the case of otoacoustic emissions of any sort, direct propagation of energy through the basilar membrane seems unlikely. Local sources of vibration on the basilar membrane could probably couple directly into the scala vestibuli fluids and the resulting pressure would drive the stapes footplate. Delay times for evoked otoacoustic emissions of >10 ms (for review see Probst et al. 1991) remain unexplained, inasmuch as they cannot incorporate a ‘‘reverse traveling wave’’ time delay.

The situation that energy has to be somehow propagate from apex to base in the cochlea might be similar for distortion products. In this case, two tones of frequency \( f_1 \) and \( f_2 \) \((f_1 < f_2)\) are applied simultaneously to the ear, generating intermodulation distortion (colloquially called combination tones), including \( f_2-f_1 \), \( 2f_1-f_2 \), and \( 2f_2-f_1 \) (for a historical review, see Goldstein and Kiang 1968; Plomp 1965; Smoorenburg 1972a). The component \( 2f_1-f_2 \) is audible in a restricted frequency region below \( f_1 \) (Goldstein 1967; Plomp 1965; Smoorenburg 1972a; Zwicker 1955), and it is highly dependent on the frequency separation of \( f_1 \) and \( f_2 \) (Goldstein 1967). There is experimental evidence that combination tones are generated at one place on the basilar membrane and propagate to the basilar membrane site with characteristic frequency equal to that of the combination tone (Goldstein 1967; Siegel et al. 1982; Smoorenburg 1972b; Zurek and Sachs 1979). Such an origin is consistent with the presence of combination tones in recordings of cochlear microphonics (Gibian and Kim 1982), responses of cochlear nerve fibers (Buunen and Rhode 1978; Goldstein and Kiang 1968; Kim et al. 1980; Siegel et al. 1982), and basilar membrane measurements (Nuttal et al. 1990; Rhode and Cooper 1993; Robles et al. 1990). In these cases, judging from the present set of data, the dominant coupling of energy is through the fluids and not via the basilar membrane. The findings of the present experiments showed a drop in vibration amplitude of 155 dB/mm from an apex to base direction. Thus propagation of energy through the basilar membrane from apex to base is unlikely. Interestingly, and in harmony with the above, in a simple transmission line model it has not been possible to set up a traveling wave running in the direction of high to low compliance.

In four of the cochleae, no tuned response properties at the different beads were obtained. For these cochleae, the drop in response amplitude of the beads with increasing span from the vibration probe was similar to the drop in response amplitude of beads placed in a glass tube. The suggestion is that these beads were not attached to the basilar membrane and therefore did not reveal its vibration properties. Rather, the beads were attached loosely or floating, reflecting the
vibration patterns of the stimulation probe transmitted by the fluid. Drops in vibration amplitude for the beads placed in a tube or in a hemicochlea without tuned behavior were similar, 15–19 dB/mm. In contrast to this slope, the attached beads showed a decrease in response magnitude of 58 dB/mm (probe more basal) or 155 dB/mm (probe more apical). The latter two values are significantly greater than the small attenuation provided by the fluids alone. It is likely that the numbers reflect mainly basilar membrane properties. Although longitudinal coupling is present, it behaves as if it were small and unidirectional. In other words, mechanical energy within the basilar membrane propagates more efficiently toward the apex than toward the base, but in either case with significant attenuation.

Another interesting question is, whether the asymmetric drop in BM vibration amplitude can be used to improve modeling efforts? As pointed out by de Boer (1996): “a most important point which has not been clarified satisfactorily, concerns the mutual mechanical coupling of elements of the organ of Corti in the longitudinal direction.” Longitudinal coupling has been neglected for the cochlear partition in the “classical” models. However, existence of longitudinal coupling in the basilar membrane has been supported experimentally by von Békésy (1960) and has been considered in some cochlear models (Wickesberg and Geisler 1985). Inclusion of longitudinal coupling in cochlear models broadens the tuning curve at its tip as demanded by experimental observations. Poor results in some modeling efforts, when longitudinal coupling is present, may be due to the fact that coupling in the BM has been assumed too high. Based on the present results, it is conceivable that small longitudinal coupling has to be considered to improve modeling.

In summary, the hemicochlea is a novel preparation, useful for the study of certain passive mechanical properties of the mammalian cochlea. These experiments showed spectral maxima of different frequency along the cochlear partition but only for propagation in the direction from base to apex. This is true, independent of whether the acoustic energy has been fed through the fluids (von Békésy 1928) or directly by vibrating the basilar membrane (present experiments). Propagation of acoustic energy through the basilar membrane appears possible because small longitudinal coupling was observed on the basilar membrane. This energy propagation via the basilar membrane itself can be demonstrated when the energy coupled via the fluids is negligible. Due to the open scala, the fluids in the hemicochlea are effectively “grounded.” Interestingly, the propagation of energy is greater toward the apex compared with propagation of energy toward the base. This is undoubtedly due to the graded impedance of the basilar membrane, whereby energy flow can occur only from less compliant regions toward more compliant ones. Even in the favored direction, longitudinal coupling is small as ascertained from the decrease in vibration amplitude with a rate of ~58 dB/mm.

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Address for reprint requests: C.-P. Richter, Northwestern University, Frances Searle Building, 2299 North Campus Dr., Evanston, IL 60208.

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