Basilar-membrane responses to tones at the base of the chinchilla cochlea

Mario A. Ruggero
The Hugh Knowles Center (Dept. of Communication Sciences and Disorders), and Institute for Neuroscience, Northwestern University, 2299 North Campus Drive, Evanston, Illinois 60208-3550

Nola C. Rich
1193 Liberty Church Road, Mocksville, North Carolina 27028

Alberto Recio and S. Shyamla Narayan
The Hugh Knowles Center (Dept. of Communication Sciences and Disorders), Northwestern University, Evanston, Illinois 60208-3550

Luis Robles
Departamento de Fisiología y Biofísica, Facultad de Medicina, Universidad de Chile, Santiago, Chile

(Received 24 June 1996; accepted for publication 13 September 1996)

Basilar-membrane responses to single tones were measured, using laser velocimetry, at a site of the chinchilla cochlea located 3.5 mm from its basal end. Responses to low-level (<10–20 dB SPL) characteristic-frequency (CF) tones (9–10 kHz) grow linearly with stimulus intensity and exhibit gains of 66–76 dB relative to stapes motion. At higher levels, CF responses grow monotonically at compressive rates, with input–output slopes as low as 0.2 dB/dB in the intensity range 40–80 dB. Compressive growth, which is significantly correlated with response sensitivity, is evident even at stimulus levels higher than 100 dB. Responses become rapidly linear as stimulus frequency departs from CF. As a result, at stimulus levels >80 dB the largest responses are elicited by tones with frequency about 0.4–0.5 octave below CF. For stimulus frequencies well above CF, responses stop decreasing with increasing frequency: A plateau is reached. The compressive growth of responses to tones with frequency near CF is accompanied by intensity-dependent phase shifts. Death abolishes all nonlinearities, reduces sensitivity at CF by as much as 60–81 dB, and causes a relative phase lead at CF. © *1997 Acoustical Society of America.* [S0001-4966(97)05104-7]

PACS numbers: 43.64.Kc, 43.64.Jb, 43.64.Ld, 43.64.Pg [RDF]

INTRODUCTION

Perhaps the most influential event in mammalian cochlear physiology during the last quarter century was Rhode's discovery of a basilar-membrane nonlinearity (Rhode, 1971). Rhode showed that, in relatively healthy cochleae, basilar-membrane responses to characteristic-frequency (CF) tones grow at compressive rates (less than 1 dB/dB) at moderate-to-intense stimulus levels. This discovery met with much initial skepticism, but the central findings have been subsequently replicated and refined in several laboratories (Sellick *et al.*, 1982; Robles *et al.*, 1986; Cooper and Rhode, 1992; Nuttall and Dolan, 1993; Murugasu and Russell, 1995). Nevertheless, there are many aspects of basilar-membrane responses to tones which, although already addressed by previous studies, could be usefully documented with greater quantitative detail in healthy cochleae. Among the issues that merit further investigation are (1) What is the magnitude of basilar-membrane vibration at neural-threshold levels?; (2) Do basilar-membrane responses to CF tones grow linearly at these threshold levels?; (3) How do the compressive rates of growth vary with stimulus intensity?; (4) Does the compressive rate of growth persist at intense stimulus levels?; (5) How does the compressive rate vary as a function of frequency?; (6) Is there a high-frequency magnitude plateau?; (7) Is there a phase plateau?

Rhode's finding of a basilar-membrane nonlinearity and its initial confirmations and extensions were obtained using the Mössbauer technique (Rhode, 1971, 1978; Sellick *et al.*, 1982; Robles *et al.*, 1986), which is time consuming, highly nonlinear, and probably deleterious to cochlear health (Kliauga and Khanna, 1983) and thus severely limits the extent and quality of the attainable data. More recently, most laboratories performing basilar-membrane measurements have adopted some form of laser interferometry. Application of this technique, which is essentially linear and offers other advantages over the Mössbauer technique (see Ruggero and Rich, 1991a), has permitted a detailed description of basilar-membrane responses to tones at the 18-kHz site of the healthy guinea pig cochlea (Nuttall and Dolan, 1996). The present account provides a comparable description for the 9–10 kHz basilar-membrane site of the chinchilla cochlea, updating a report that was based on the Mössbauer technique (Robles *et al.*, 1986) and addressing the questions posed above. A summary of the main results has been published in abstract form (Ruggero *et al.*, 1996c).

I. METHODS

A. Animal preparation

Basilar-membrane responses to tones were measured, using laser velocimetry, at a site of the chinchilla cochlea located 3.5 mm from the oval window. Chinchillas, anesthetized with sodium pentobarbital (initial dose: 65 mg/kg; injected intraperitoneally), were tracheotomized and intubated,

but forced respiration was usually not used. Normal body temperature was maintained by means of a heating pad servocontrolled by a rectal probe but no other precaution (e.g., heating of the headholder) was taken to maintain cochlear temperature. The left pinna was resected, the bulla was widely opened, and the tensor tympani muscle was cut. In many experiments, the stapedius muscle was detached from its anchoring. A silver-wire electrode was placed on the round window to record compound action potentials evoked by tone bursts (fundamental frequency: 500 Hz to 16 kHz, in 1/2 octave steps). Compound action potential (CAP) thresholds (sound-pressure levels—SPLs—required to elicit 10-μV $N1$ responses) served to monitor the physiological state of the cochlea. A small hole made in the basal turn of the otic capsule allowed direct visualization of the basilar membrane and placement on it of a few glass microbeads (diameter: 10–30 μm), which served as reflecting targets for the light beam of the laser velocimeter. In some experiments, basilar-membrane vibrations were measured after covering the hole in the otic capsule with a small window fashioned from slide coverslip glass.

B. Acoustic stimulation

Acoustic stimuli were produced under computer control by either a custom-built arbitrary waveform generator (Ruggero and Rich, 1983) or by a Tucker–Davis system, and were delivered through a Beyer DT-48 earphone. This was mounted on the back of a plastic speculum sealed to the bony ear canal by means of ear-impression compound. A Knowles (1842 or 1785) miniature microphone equipped with a probe tube was used to measure the sound pressure within 2 mm of the tympanic membrane. Single-tone stimuli were gated tones modulated at onset and offset by 1/2 period of a raised cosine waveform (1.16-ms rise/fall time). The tone bursts had durations of 5, 10, 25, or, exceptionally, 3 ms, and repetition periods of 25, 50, 100, or 15 ms, respectively. The use of large off-time/on-time ratios prevented the induction of threshold shifts by the repeated presentation of intense stimuli (see Fig. 16 and corresponding text). Tone stimuli were typically presented in steps of 1 kHz and 10 dB.

C. Laser velocimetry

Laser velocimetry measures the velocity of a vibrating object by detecting the Doppler frequency shift of light reflected from it. In our application of this method, the laser beam is reflected from glass microbeads placed on the basilar membrane. The velocimeter used in these experiments consisted of a 20-mW He–Ne laser (Spectra Physics 106-1), a Dantec 41X60 fiber vibrometer, and a Dantec 55N20 Doppler frequency tracker. The velocimeter head was coupled to a compound microscope (Olympus BHMJ) equipped with 5X and 20X ultralong working-distance objectives (Mitutoyo Plan Apo 5X, N. A. 0.14, and 20X, N.A. 0.42). The electrical output of the Doppler frequency tracker, a voltage (1–10 V) proportional to velocity, was frequency filtered with a pass band of 1–15 000 Hz (1–20 000 Hz exceptionally) before analog-to-digital conversion under computer control (typical sampling rate: 40 kHz; exceptionally: 100 or 166.6 kHz). Responses were usually averaged over 512 or 1024 stimulus repetitions (exceptionally: 64 repetitions) and velocity spectra were computed off-line by Fourier transformation. Response magnitudes are given throughout the paper as the peak amplitudes of velocity waveforms. For more details on the application of laser velocimetry to the measurement of basilar-membrane vibration in the chinchilla, see Ruggero and Rich (1991a).

II. RESULTS

The initial preparations for basilar-membrane recordings were performed in 129 chinchillas but useful data were obtained in only 43. Judging from elevations in compound action potential (CAP) thresholds at near-CF frequencies, all experimental cochleae were damaged to some extent by the surgical procedures involved in opening the otic capsule. The present paper is largely based on the analysis of data from the six cochleae that yielded the most sensitive basilar-membrane responses to CF tones. Two of these cochleae, which yielded an extensive sampling of basilar-membrane responses to tones as a function of stimulus frequency and intensity, are highlighted throughout the paper. These responses were selected for presentation because: (1) they were exceptionally stable (remaining invariant over several hours of recording); (2) they were collected in near-normal cochleae (surgically induced CAP threshold elevations at CF of 6–12 dB); and (3) they were especially sensitive.

All the recordings were obtained at a region of the basilar membrane located about 3.5 mm from the oval window (Robles *et al.*, 1986). At the beginning of the recording sessions (and usually also at later times throughout the sessions) basilar-membrane responses to clicks were measured at several intensities. Responses to low-intensity clicks provided for rapid estimation of CF and basilar-membrane sensitivity. Responses to tones were then measured as a function of intensity and frequency, typically in 10-dB and 1-kHz steps. CFs were always in the range 8–11 kHz, most often 9 or 10 kHz.

A. Waveshape and spectrum of responses to tones

Figure 1 illustrates basilar-membrane velocity recordings from a cochlea in which the preparatory surgery caused only small (6 dB) elevations of the CAP thresholds for stimulus frequencies (8 and 11.3 kHz) closely flanking the CF (10 kHz) of the recording site. The traces show the averaged responses to 10-kHz tone bursts presented at 30–70 dB SPL. The responses to the lower-level stimuli resemble the stimulus waveforms, which have symmetric envelopes. At higher stimulus levels, the response offsets are longer than the onsets and the traces exhibit ''ringing'' that persists well after the end of the stimulus. At even higher stimulus intensities (not shown), response asymmetry is often accompanied by overshoot-like irregularities with instantaneous frequency equal to CF regardless of the stimulus frequency. Asymmetry and ''overshoots'' are usually present in the responses of sensitive cochleae to intense tones with frequency near to or higher than CF, but are absent from responses to tones with frequency well below CF or, at any frequency, in insensitive cochleae.

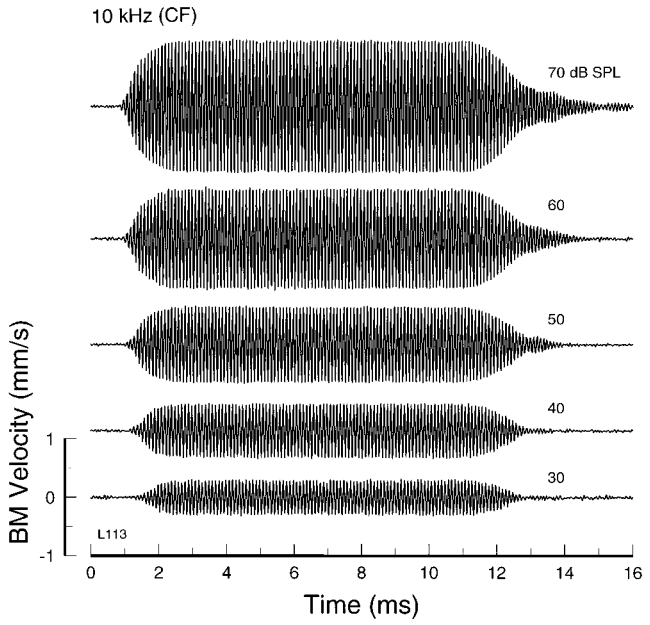

FIG. 1. Basilar-membrane velocity responses to 10-kHz (=CF) tones. Each waveform represents the average of 512 responses. Stimulus intensity is indicated at right. Zero time corresponds to the onset of the electrical input to the earphone. Data recorded in cochlea L113.

Although the waveforms of Fig. 1 are not visibly distorted, their Fourier transforms (not shown) do contain even-order harmonics. In general, responses to tones, regardless of frequency, are symmetric (i.e., they are devoid of dc components) and exhibit very low levels of harmonic distortion. Second-harmonic components occasionally reach levels as high as −20 to −30 dB relative to the fundamental. Such distortion, which is generally accompanied by a small dc shift, appears to arise as an artifact in the velocimeter system. The presence of even-order distortion is typically associated with poor recording conditions (when little light is reflected from the target) and/or with a large fundamental signal and high-sensitivity settings of the Doppler-frequency tracker. Under such circumstances, decreasing the sensitivity setting dramatically reduces the magnitudes of both the second harmonic and the dc shift.

B. Magnitude of responses to CF tones as a function of intensity

The steady-state amplitudes of velocity traces such as those of Fig. 1 were measured by means of Fourier transformation. Figure 2 displays velocity-intensity functions for basilar-membrane responses to CF tones in six sensitive cochleae. The CFs (determined to the nearest kHz) are: 8 kHz (L126), 9 kHz (L13 and L125), or 10 kHz (L57, L113, and L110). Response amplitudes generally grow monotonically with stimulus intensity, with remarkably little variation among different cochleae in the intensity range 20–70 dB SPL. To a first approximation, in the 20–70 dB range all the velocity-intensity curves lie close to a single straight line in log–log coordinates, defining velocity as a simple power function of stimulus pressure. However, all curves grow more steeply at the lowest stimulus intensities (<20 dB) than

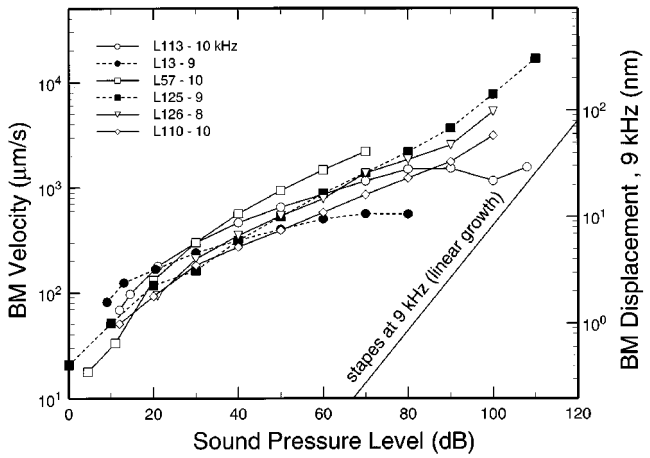

FIG. 2. Velocity-intensity functions for basilar-membrane responses to CF tones. The steady-state peak velocities of waveforms such as those of Fig. 1 are plotted for six relatively healthy cochleae against stimulus intensity. The straight line at right indicates the average motion of the stapes in response to 9-kHz tones (measured by Ruggero *et al.*, 1990). The right ordinate indicates basilar-membrane displacement. This scale is exact for responses to 9-kHz tones but approximate for responses to 8 or 10 kHz.

at moderate intensities (40–80 dB). At the highest stimulus intensities (>80 dB), the curves tend to diverge. Two velocity-intensity functions (L13 and L113) reach asymptotic velocities of 0.6 and 1.6 mm/s (10 and 25 nm), but three curves show increased rates of growth between 90 and 110 dB, reaching velocities of 3–8 mm/s (60–140 nm) at 100 dB SPL.

Figure 3 displays the slopes of the input–output functions of Fig. 2. Growth rates are highest, approaching linearity, at intensities lower than 20 dB SPL. Growth rate is compressive (<1 dB/dB) at all intensities higher than 20 dB. In the range 40–90 dB, rates are relatively stable for any single cochlea but vary across cochleae between 0.2 and 0.5 dB/dB. Probably not coincidentally, the lowest rates of growth (<0.3 dB/dB) in the mid-intensity range belong to cochleae (L13 and L113) that produced the largest responses at low stimulus levels (Fig. 2).

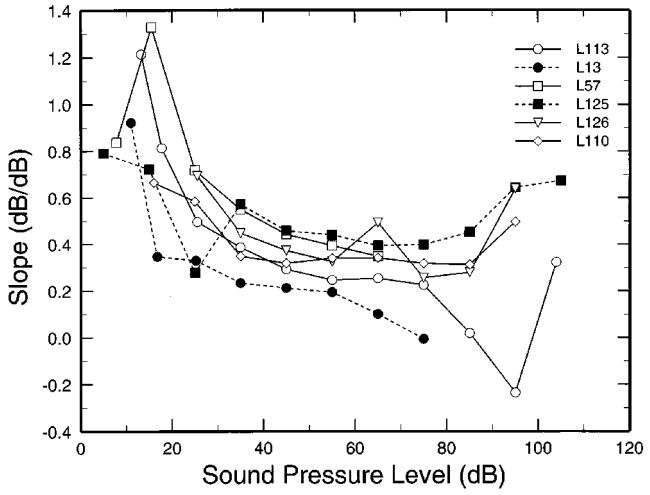

FIG. 3. Slopes of basilar-membrane responses to CF tones, plotted against stimulus intensity. The slopes of the CF input–output functions of Fig. 2 are expressed in units of dB (velocity)/dB (pressure).

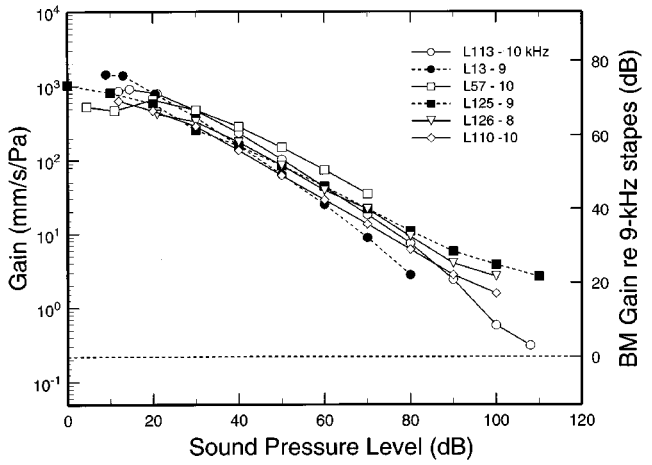

FIG. 4. Gain of basilar-membrane responses to CF tones, plotted against stimulus intensity. Basilar-membrane gains were computed by dividing the peak response velocities shown in Fig. 2 by the corresponding stimulus pressures (left scale). The right scale indicates the gain (in decibels) of basilar membrane motion relative to stapes motion (horizontal dash line, Ruggero *et al.*, 1990). This scale is exact for responses to 9-kHz tones but approximate for responses to 8 or 10 kHz.

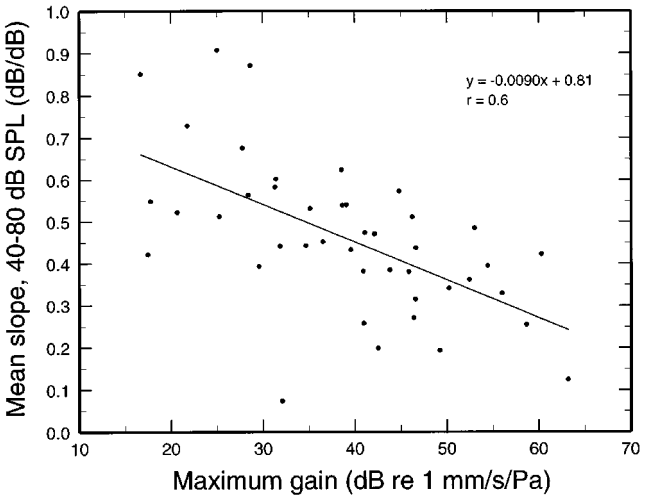

FIG. 5. Relationship between the sensitivity and the nonlinear growth of basilar-membrane responses to CF tones. The scatter diagram plots, for each of 43 cochleae, the maximal gain of basilar-membrane vibration (e.g., Fig. 4) against the average slope of the velocity-intensity function (e.g., Fig. 3) measured between 40 and 80 dB SPL.

In all cochleae represented in Fig. 3, the nonlinear growth of basilar-membrane motion persists even at the highest of physiologically relevant stimulus intensities. In the two most sensitive cochleae (L13 and L113), the rates of growth dip down to zero or negative values at the highest stimulus intensities. In other cochleae, growth rates climb to values of 0.5–0.7 dB/dB at intensities higher than 90 dB. In even less sensitive cochleae (not shown) that nevertheless retain some degree of nonlinearity, responses to intense CF tones can reach nearly linear growth rates (0.8–0.9 dB/dB). This suggests that the increase in the slope of response growth at high stimulus levels varies directly with the extent of surgically induced cochlear damage and may be smaller (or even absent) in completely normal cochleae.

Figure 4 illustrates the systematic decrease in gain (i.e., velocity per unit pressure) that basilar-membrane responses to CF tones undergo with increasing stimulus intensity. At 100–110 dB SPL, basilar-membrane gain can be as much as 69 dB lower than at intensities <20 dB. The right scale (the magnitude of basilar-membrane motion relative to stapes motion; Ruggero *et al.*, 1990), indicates that at low stimulus levels basilar-membrane vibrations are enormously larger than stapes motion, amounting to gains of 66–76 dB. Basilar-membrane vibration exceeds stapes motion even at stimulus levels as high as 110 dB SPL.

It was noted above that, among the cochleae represented in Figs. 2–4, the two with the most compressive rates of response growth (Fig. 3) were also among the most sensitive ones (Figs. 2 and 4). We explored the relationship between sensitivity and nonlinear growth in a sample of 43 cochleae (Fig. 5) by correlating the maximal gains (Fig. 4) with the average slopes of velocity-intensity functions in the range 40–80 dB SPL (Fig. 3). These quantities (gain: dB *re*: 1 mm/s/Pa; slope: dB/dB) were significantly and negatively correlated, with $r=-0.60$, slope of -0.0090 (dB/dB)/(dB *re*: 1 mm/s/Pa) and y intercept of 0.81 dB/dB. Applying the regression-line equation to the measured maximal gains at CF in cochleae L13 and L113 (63 and 59 dB *re*: 1 mm/s/Pa) yields slopes of 0.24 and 0.28 dB/dB, respectively. If one takes into account sensitivity losses due to surgery (12 and 6 dB, respectively, in cochleae L13 and L113) the predicted slopes (based on corrected maximal gains of 75 and 65 dB *re*: 1 mm/s/Pa) are 0.14 and 0.23 dB/dB. Thus, one expects that velocity-intensity functions for CF tones in entirely normal cochleae have slopes of approximately 0.2 dB/dB in the 40–80 dB intensity range.

C. Variation of velocity-intensity functions with stimulus frequency

Figure 6 presents a family of velocity-intensity functions for responses of a single basilar-membrane site to tones with frequency equal to and higher than CF (10 kHz). Responses to 11-kHz tones grew at rates slightly more compressive than

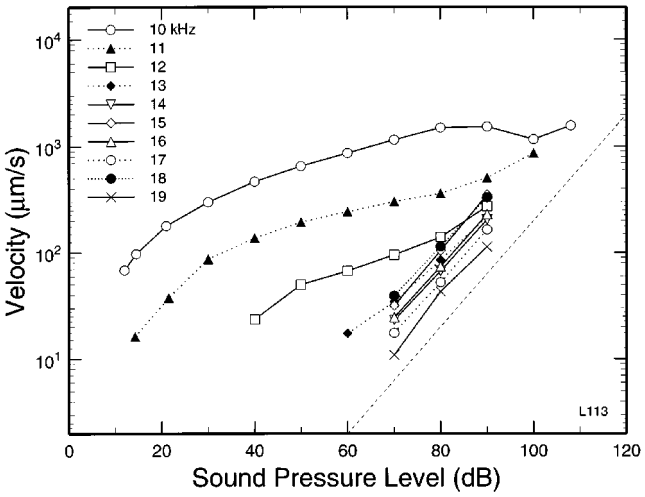

FIG. 6. Velocity-intensity functions of basilar-membrane responses to tones with frequency equal to and higher than CF (10 kHz). The straight dashed line at right has a linear slope (1 dB/dB). The data were recorded in cochlea L113.

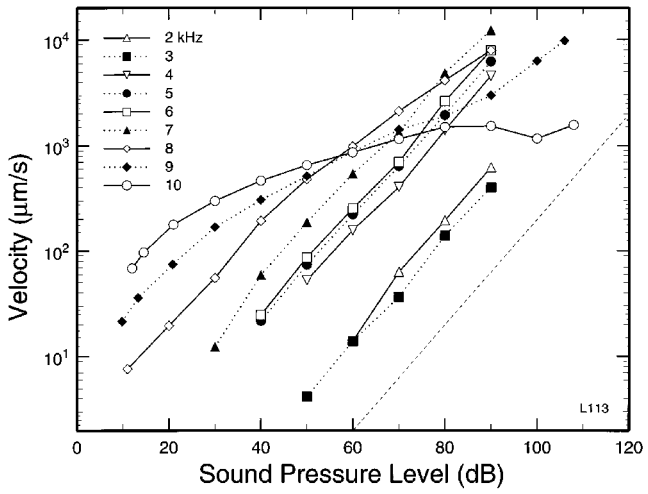

FIG. 7. Velocity-intensity functions of basilar-membrane responses to tones with frequency equal to and lower than CF (10 kHz). The straight dashed line at right has a linear slope (1 dB/dB). The data were recorded in the same cochlea (L113) represented in Fig. 6.

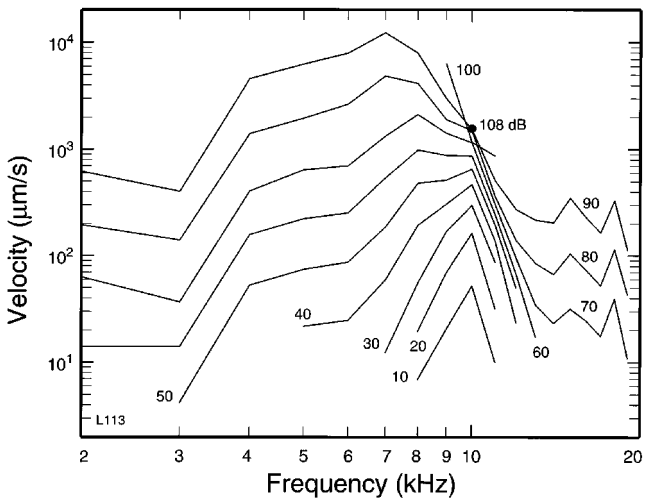

FIG. 8. A family of isointensity curves representing the velocity of basilar-membrane responses to tone pips as a function of frequency (abscissa) and intensity (parameter, in dB SPL). The isointensity curves represent the same data of Figs. 6 and 7.

responses to CF tones at intensities of 40–80 dB but grew at higher rates (closer to linear) at intensities lower than 30 dB SPL and higher than 80 dB. Responses to 12-kHz tones also displayed a central compressive region flanked by less nonlinear regions at lower and higher intensities. In this case, however, the highly compressive region was restricted to a narrower range, 50–80 dB. Responses to tones with frequency higher than 13 kHz were linear.

Figure 7 shows velocity-intensity functions at the same cochlear site for tones with frequency of 10 kHz (=CF) and lower. Responses to 9-kHz tones grew nonlinearly but at rates higher than responses to CF. Thus, although 9-kHz responses were some 7.3 dB smaller than at CF for 10-dB stimuli, they surpassed CF responses at 60 dB SPL and were some 6 dB larger at 90 dB. Responses to 8-kHz tones grew linearly between 10 and 50 dB, displayed a mildly nonlinear rate of growth between 50 and 90 dB, and exceeded CF responses by some 14 dB at 90 dB. Responses to tones with frequencies lower than 7 kHz were linear and, in the range 4–7 kHz, larger than responses to CF tones at 90 dB. For frequencies near CF, the slopes of the velocity-intensity functions varied systematically with frequency (not shown explicitly). For example, in the 40–80 dB range the slopes for tones with frequency of 6, 7, 8, 9, 10, 11, and 12 kHz were 0.99, 0.94, 0.66, 0.41, 0.25, 0.21, and 0.37 dB/dB, respectively.

D. Variation of isointensity functions with stimulus intensity

The variation of response velocity as a function of stimulus frequency and intensity can be viewed comprehensively by recasting the data of Figs. 6 and 7 into a family of isointensity functions (Fig. 8). For tones with frequency well below CF, isointensity curves for stimuli 10 dB apart are separated by velocities that differ by a ratio of 3.1 (i.e., 10 dB), indicating linear growth. Response growth became increasingly compressive as stimulus frequency approached CF. Responses to CF tones (10 kHz) grew linearly between 10 and 20 dB SPL but grew at highly compressive rates at higher intensities. (The 10-dB curve in Fig. 8 has been extrapolated linearly from responses to stimuli presented at slightly higher levels; see Figs. 6 and 7.) The most nonlinear growth rates were those for tones with frequency (11 kHz) just above CF. At stimulus frequencies of 14 kHz and higher, responses grew linearly and reached a plateau.

The frequency-specific compressive nonlinearity caused a systematic reduction of the most effective stimulus frequency as a function of increasing stimulus intensity. At intensities equal to or lower than 50 dB SPL, the peak responses occurred at 10 kHz; at 60 and 70 dB the largest responses were elicited by 8-kHz tones; at 80 and 90 dB SPL, the peak response shifted to 7 kHz, equivalent to a frequency decrease of 0.51 octave relative to CF. Peak re-

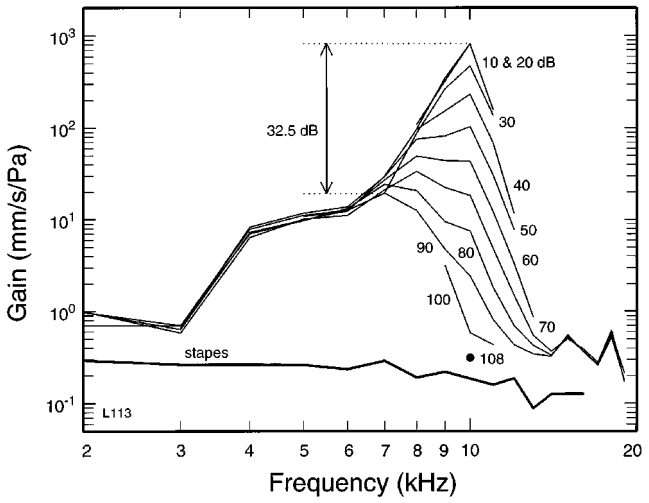

FIG. 9. A family of isointensity curves representing the gain (velocity divided by stimulus pressure) of basilar-membrane responses to tone pips as a function of frequency (abscissa) and intensity (parameter, in dB SPL). The isointensity curves represent the same data of Figs. 6–8, recorded in cochlea L113. The thick line at bottom indicates the average motion of the stapes (Ruggero *et al.*, 1990).

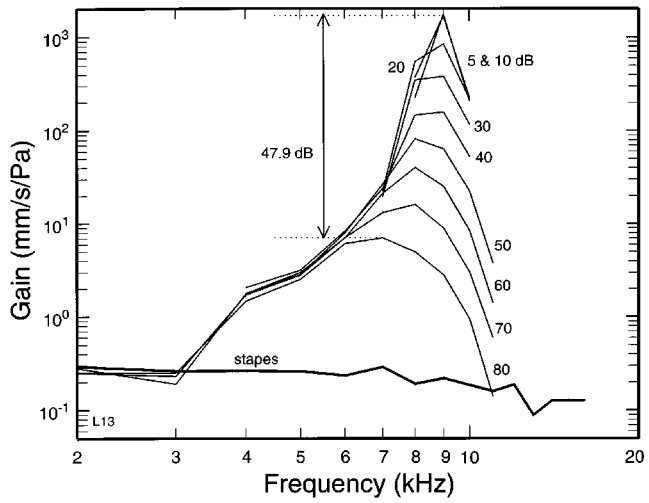

FIG. 10. A family of isointensity curves representing the gain (velocity divided by stimulus pressure) of basilar-membrane responses to tone pips as a function of frequency (abscissa) and intensity (parameter, in dB SPL). The thick line at bottom indicates the average motion of the stapes (Ruggero *et al.*, 1990). Data recorded in cochlea L13.

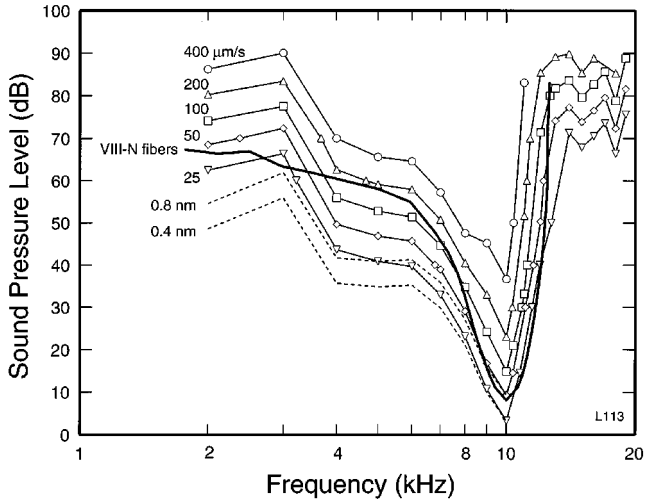

FIG. 11. Basilar-membrane and auditory-nerve tuning curves. The data of Figs. 6–9 are presented as isovelocity contours for responses of 25, 50, 100, 200, and 400 μm/s (thin solid lines) and isodisplacement (0.4 and 0.8 nm) contours (dashed lines). The thick solid line is an average frequency-threshold tuning curve computed from the rate thresholds of 50–274 chinchilla auditory-nerve fibers with CFs of 8–12 kHz and high spontaneous activity.

sponses in another sensitive cochlea (L13; see Fig. 10) changed from 9 kHz (CF) at low stimulus levels to 7 kHz at 80 dB, amounting to a decrease of 0.36 octave relative to CF. Another trend of the variation of isointensity functions with stimulus intensity consists of a systematic broadening of the response bandwidth: Whereas for 20-dB stimuli the 10-dB bandwidth in this cochlea is 2.5 kHz, at 90 dB the 10-dB bandwidth is 5 kHz.

The data of Fig. 8 are replotted in Fig. 9 after normalization to stimulus intensity, thus yielding gains (velocity per unit stimulus pressure). Had responses grown linearly with stimulus intensity, the isointensity gain curves would superimpose. In fact, the curves superimpose only at frequencies removed from CF, i.e., below 7 kHz and above 13 kHz. At near-CF frequencies, gain grows systematically larger as a function of decreasing stimulus level, except between 10 and 20 dB, in which range responses grow linearly and gains attain a maximal (asymptotic) value. The change in gain associated with nonlinear growth at CF cannot be expressed as a single value because compressive growth prevails even at levels higher than 100 dB (compare 10-kHz gains at 100 and 108 dB SPL). Thus, it is only possible to specify a *minimum* change in gain (e.g., 69 dB in cochlea L113, measured between 20 and 108 dB SPL; see also Fig. 4). However, it is possible to specify a single value for the difference between the maximal sensitivity at CF and the peak sensitivity for responses that grow linearly or nearly so (i.e., at 7 kHz). In cochlea L113, this difference between the peak gain at low (10–20 dB) and high (90 dB) stimulus levels amounts to 32.5 dB (Fig. 9). Taking into account that cochlea L113 had experienced a 6-dB sensitivity loss at CF during the preliminary surgery (as judged by CAP threshold elevations at 8 and 11.3 kHz), one can estimate that the difference in the intact cochlea would have amounted to 38.5 dB.

Figure 10 presents another family of isointensity functions normalized to stimulus intensity. The basilar-membrane responses in cochlea L13 resembled those of L113 but were more sensitive at low stimulus levels. CF responses grew linearly between 5 and 10 dB SPL but exhibited strongly compressive growth between 10 and 80 dB. The change of response gain at CF as a function of stimulus level was 55.6 dB (measured between 10 and 80 dB SPL). As previously noted in the case of L113, the change of response gain would presumably have been even larger had responses been available for higher stimulus intensities. The difference between the peak gains for low-level (5 or 10 dB) and intense (80-dB) stimuli was 47.9 dB. Corrected for the surgically induced deterioration of the preparation (12 dB, estimated from CAP threshold elevations at 8 and 11.3 kHz), the corresponding value is 59.9 dB.

E. Tuning curves

For comparison with responses to sound at more central stages of cochlear processing (e.g., hair cells, auditory-nerve fibers), it is convenient to present basilar-membrane magnitude data in the form of isoresponse contours (i.e., ''tuning curves''). Figure 11 shows tuning curves for velocities of 25, 50, 100, 200, and 400 μm/s (thin solid lines), derived by interpolation from the velocity-intensity curves for a single cochlea (L113: Figs. 6 and 7), and isodisplacement tuning curves (dashed lines) for displacement values of 0.4 and 0.8 nm (derived from the isovelocity curves at 25 and 50 μm/s, respectively). On the high-frequency side, isovelocity tuning curves have slopes averaging 260 dB/octave between 40 and 70 dB SPL. On the lower-frequency side, the slopes are much lower, in the order of -52 dB/octave. Q_{10} values (CF divided by 10-dB bandwidth) for the 25-, 50-, 100-, 200-, and 400-μm/s curves are 5.3, 5.6, 6.1, 7.1, and 5.2, respectively. Q_{20} values (CF divided by 20-dB bandwidth) are 3.2, 3.3, 3.3, 3.4, and 2.9, respectively.

In addition to basilar-membrane tuning curves, Fig. 11 depicts an average frequency-threshold tuning curve com-

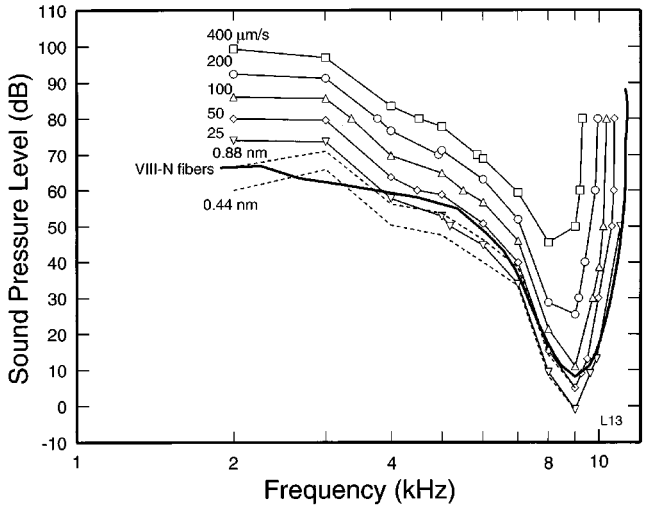

FIG. 12. Basilar-membrane and auditory-nerve tuning curves. The data of Fig. 10 are presented as isovelocity contours for responses of 25, 50, 100, 200, and 400 μm/s (thin solid lines) and isodisplacement (0.44 and 0.88 nm) contours (dashed lines). The thick solid line is an average frequency-threshold tuning curve computed from the rate thresholds of 50–274 auditory-nerve fibers with CFs of 8–12 kHz and high spontaneous activity.

puted from the rate responses of chinchilla auditory-nerve fibers with CFs in the range of 8–12 kHz and spontaneous activity higher than 18 spikes/s. The tuning curve is a detailed composite of the features of 58–274 fibers (depending on frequency) in 86 animals (Temchin *et al.*, 1997). For frequencies near CF, the averaged features were the frequencies corresponding to stimulus intensities sampled in 3–5 dB steps between CF threshold and 70–80 dB SPL. For ''tail'' frequencies, the averaged features were the SPLs corresponding to frequencies sampled in 0.25 octave steps (relative to CF). The average frequency-threshold curve has a CF threshold of 8 dB SPL, which corresponds to a velocity of 39 μm/s or a displacement of 0.62 nm in cochlea L113. The neural tuning curve has high- and low-frequency slopes of 318 and −117 dB/oct, respectively, and its Q_{10} is 4.6. The

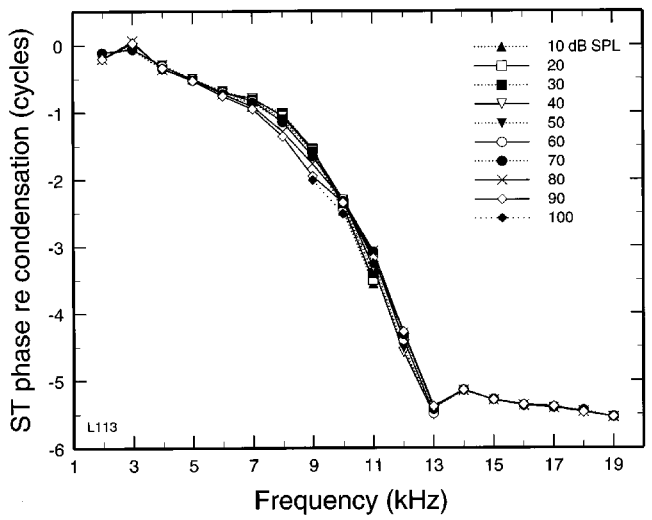

FIG. 13. The variation of basilar-membrane response phases as a function of frequency. Phases—displacement toward scala tympani relative to condensation at the eardrum—were computed from the responses of cochlea L113, whose magnitudes are represented in Figs. 6–9 and 11. Each curve represents data for a single stimulus intensity (legend).

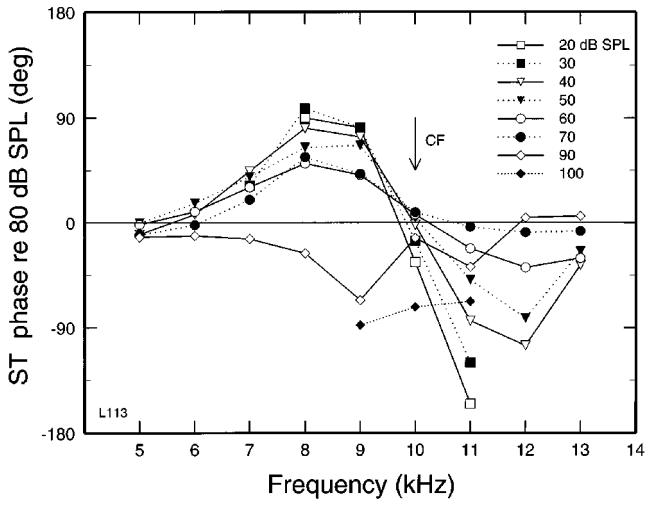

FIG. 14. Intensity dependence of basilar-membrane response phases. The phases represented in Fig. 13 have been normalized to those at 80 dB SPL. Positive phases indicate leads relative to responses at 80 dB.

neural and mechanical tuning curves resemble each other closely at near-CF frequencies but the resemblance is weaker at frequencies well below CF. In the range 2–10 kHz, the neural curve most closely approximates the 50-μm/s isovelocity curve.

Figure 12 shows isovelocity and isodisplacement tuning curves for another cochlea (L13). For the 50–200 μm/s isovelocity curves, high- and low-frequency slopes average 589 and −125 dB/oct, respectively. For the same curves, Q_{10} values average 6.0. The CF threshold from the average auditory-nerve frequency-threshold curve (8 dB SPL) corresponds in cochlea L13 to a basilar-membrane velocity of 73 μm/s or a displacement of 1.3 nm. In this case, one isodisplacement curve (0.88 nm) provides a better match to the neural tuning curve than the isovelocity curves.

F. Variation of response phases as a function of stimulus frequency and intensity

Figure 13 shows the phases of responses in cochlea L113, corresponding to the magnitudes of Figs. 6–9. Each phase curve, which indicates displacement toward scala tympani relative to condensation at the eardrum, represents one stimulus intensity. The curves show phase lags that increase monotonically as a function of increasing frequency. In order to resolve 360-deg ambiguities in unfolding the phases, we have taken advantage of recordings of responses to clicks (not shown), whose spectral phases match fairly closely those of responses to tones (Ruggero *et al.*, 1992a). The slopes of the curves become steeper as CF is approached. For stimulus frequencies 4–7 kHz, for which response magnitudes grow linearly or nearly so (Figs. 7–9), the slope varies little with stimulus intensity, averaging −1.15 rad/kHz, equivalent to a group delay of 183 μs. Near CF, the slopes vary systematically with stimulus intensity: Group delays range from 0.99 ms for 10-dB tones to 0.61 ms for 90-dB tones. The phase slope is steepest at frequencies just higher than CF. Measured between 10 kHz (CF) and 12 kHz, the group delays are 1.1–1.3 ms. The rapid increase of phase lag

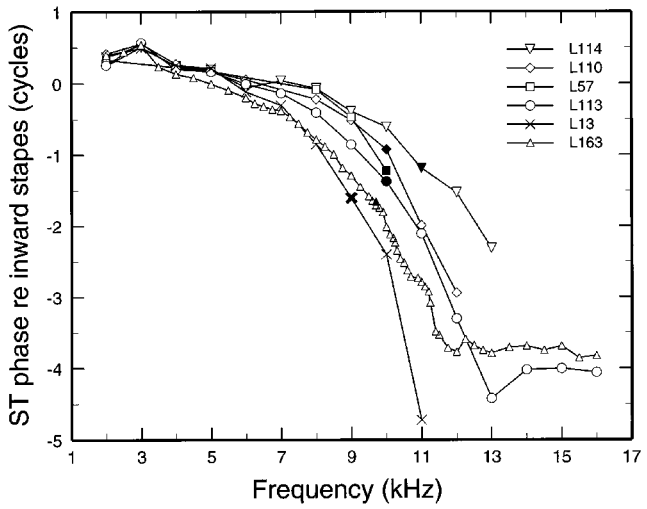

FIG. 15. Phase-versus-frequency curves, relative to stapes motion, of basilar-membrane responses to 70- or 80-dB tones in several cochleae. The filled symbols indicate phases at the CF frequencies.

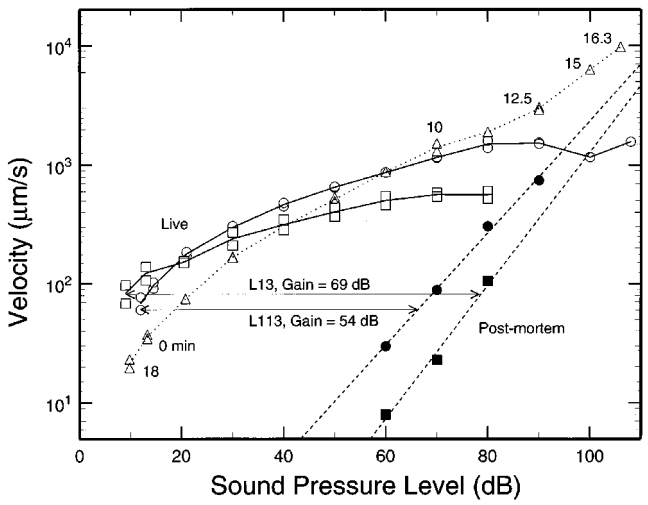

FIG. 16. Stability and vulnerability of responses to CF and near-CF tones. The open symbols depict the peak velocities of responses to CF tones (L13: squares; L113: circles) and 9-kHz tones (L113: triangles) recorded in the sensitive cochleae of two live chinchillas. The filled symbols represent the CF responses recorded immediately after (within minutes of) death. Responses to CF tones in both cochleae (and also responses to 9 kHz in cochlea L113) were measured both early in the experiment and 160–240 min later. The numbers next to the 9-kHz data points indicate the relative times (in min) of the early recordings.

with stimulus frequency is interrupted at frequencies higher than 12 kHz, at which the phase lags essentially reach a plateau.

At near-CF stimulus frequencies, where response magnitudes grow nonlinearly, response phases vary with stimulus intensity. The phases are displayed in Fig. 14 after normalization to the responses to 80-dB tones. In the intensity range 30–80 dB, responses to CF tones (arrow) change little with stimulus intensity. In the same intensity range, response phases for frequencies lower than CF systematically lag phases for lower-intensity stimuli. The lags are largest (>100 deg between 30 and 80 dB) for responses to 8 kHz and diminish at lower frequencies, becoming insignificant below 6 kHz. Response phases for tones with frequency just higher than CF systematically lead the phases for lower-intensity stimuli. For any given intensity, the largest leads (exceeding 90 deg) occur for tones with frequency of 11–12 kHz. The systematic leads do not persist at levels of 90 and 100 dB. At these intensities, regardless of stimulus frequency, response phases lag responses to lower-level stimuli. Thus, for frequencies lower than CF, responses to intense tones can be nearly antiphase relative to responses to low-level tones (e.g., 9 kHz). A dependence of response phase on stimulus intensity similar to that depicted in Fig. 14 also characterized the near-CF basilar-membrane responses in other sensitive cochleae, including L13 (see Figs. 10 and 12). The phase effects appeared to be extremely dependent on the state of the cochlea, since only small phase shifts could be demonstrated in many less-sensitive cochleae that nevertheless retained substantial nonlinearity.

Phase-versus-frequency curves for basilar-membrane responses to 70- or 80-dB tones in several cochleae are plotted in Fig. 15 after normalization to stapes displacement. The curve for L163 was normalized using stapes data collected in the same animal. The other curves were normalized using average stapes data (''open'' curve in Fig. 11 of Ruggero *et al.*, 1990). All the phase curves contain a low-frequency segment, with relatively shallow slope, and a near-CF segment, with steep slope. The phase lags at CF amount to 0.9–1.6 cycles. The transition frequency between the two segments seems to increase as a function of increasing CF. The low-frequency segments of the phase-versus-frequency curves have similar group delays (i.e., slopes), averaging 144 μs. The segments with frequency just higher than CF have group delays that may grow larger with decreasing CF (e.g., 1.6, 1.0, and 0.56 ms for L13, L113, and L114, with CFs of 9, 10, and 11 kHz, respectively).

Two of the phase curves of Fig. 15 exhibit plateaus at frequencies higher than CF. One curve (L163) was obtained with small frequency steps and therefore it was not subject to phase ambiguities. In the case of the other curve (L113), a 2π phase ambiguity at frequencies of 12 kHz and higher was resolved using phase-versus-frequency curves computed from responses to clicks in the same cochlea. [The phase-versus-frequency curves for responses to clicks closely resemble those of responses to tones (Ruggero *et al.*, 1992a).] In both cochleae, the plateaus hovered around phase lags of 3.7–4.1 cycles relative to inward stapes displacement.

G. Response stability and the effects of death

Basilar-membrane responses to near-CF tones often deteriorated with the passage of time, becoming less sensitive and more linear. However, responses in several cochleae retained their initial sensitivity and nonlinearity over several hours. Figure 16 shows two velocity-intensity functions (open circles) for the responses of cochlea L113 to 10-kHz (CF) tones, one recorded early in the experiment and the other about 4 h later, after recording the responses depicted in Figs. 6–9, 11, 13, and 14. The two velocity-intensity functions were very similar. The responses of another cochlea, L13, to CF tones (open squares) were measured some 2 h and 40 min apart, before and after the recordings illustrated

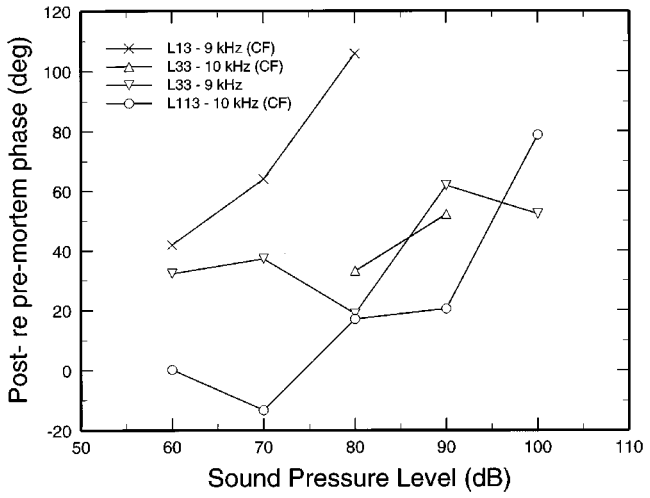

FIG. 17. The effects of death on the phases of responses to near-CF tones, plotted as a function of stimulus intensity. The phases for the responses to CF tones in live animals (open circles and squares in Fig. 16) were subtracted from the post-mortem response phases (filled symbols). Thus, positive phase values indicate relative phase leads of the post-mortem responses. Also shown are the net post-mortem phase changes for 10-kHz (CF) and 9-kHz tones in another cochlea.

in Figs. 10 and 12. As in the case of L113, the responses remained quite stable. The stability of the responses to CF tones in these two cochleae convincingly demonstrates that the frequency specificity of the magnitude and phase nonlinearities illustrated in Figs. 6–14 is not an artifact of recordings obtained under dissimilar physiological conditions (see Khanna, 1984, p. 216).

Also shown in Fig. 16 are responses to 9-kHz tones (open triangles) in cochlea L113 that demonstrate that the repeated presentation of intense near-CF stimuli did not lead to changes in response sensitivity (such as noted in some Mössbauer studies: Sellick *et al.*, 1982; Patuzzi *et al.*, 1984). Two velocity-intensity functions were recorded, one early in the experiment and the other nearly 4 h later. At each stimulus intensity, 512 repetitions of 10-ms tone bursts were presented every 50 ms. Responses for the curve obtained earlier were measured with tones presented at systematically increasing intensity, from 13 to 106 dB SPL, followed immediately by a presentation at 10 dB. Comparison of the response magnitudes at the latter intensity shows that they are nearly identical, thus demonstrating that the repeated presentation of 106-dB tone bursts did not alter the sensitivity of responses to low-level stimuli. Presumably the threshold shifts reported in some Mössbauer studies (Sellick *et al.*, 1982; Patuzzi *et al.*, 1984) resulted from the presentation of long-duration tones.

Figure 16 allows a comparison of velocity-intensity functions for CF tones in cochleae L13 and L113 before (open circles and squares) and after death (solid symbols). Death produced large decreases in the sensitivity and nonlinearity of responses. For low-level CF stimuli, death diminished sensitivity by 54 (L113) or 69 dB (L13). Taking into account that the pre-mortem responses were measured in cochleae that had suffered (surgically induced) sensitivity losses of 6–12 dB, it is likely that the net effect of death in intact cochleae would have amounted to 60 dB in L113 and 81 dB in L13.

Whereas the slopes of the intensity functions at moderate stimulus levels were originally lower than 0.3 dB/dB (see Fig. 3), the post-mortem curves had essentially linear slopes (dashed lines; L13: 1.12 dB/dB; L113: 0.95 dB/dB). Although no post-mortem responses are available for intensities higher than 80 or 90 dB, linear extrapolation suggests that the latter became larger than pre-mortem responses at stimulus levels higher than 100 dB SPL in both cochleae.

The post-mortem reductions in the magnitude of responses to CF tones were accompanied by relative phase leads (Fig. 17). The phase leads were small at stimulus intensities <70 dB but tended to grow with intensity. For the two cochleae illustrated in Fig. 16, the phase leads amounted to 79–105 deg at stimulus intensities of 80–100 dB. Post-mortem phase changes for responses to 10-kHz (CF) and 9-kHz tones were similar but somewhat smaller in another, less-sensitive, cochlea (L33; see Ruggero *et al.*, 1992a and Ruggero, 1994).

III. DISCUSSION

A. Evaluation of laser-velocimetry recordings: Contamination by a fluid-depth artifact

Cooper and Rhode (1992) have described an artifact that must be taken into account in interpreting basilar-membrane recordings obtained using laser velocimetry. These authors noted that a laser velocimeter cannot distinguish Doppler shifts caused by motion of the laser-beam target (the beads on the basilar membrane) from frequency shifts caused by changes of the path length of the laser beam due to alterations in the depth of the fluid in scala tympani. The latter are certain to exist as result of stapes vibration. When the stapes is pushed inward, the fluid meniscus overlying the recording site must bulge out of the otic capsule, causing an increased beam path length. When the stapes is pulled outward, the path length must be shorter. Thus, when basilar-membrane motion is small in comparison with the variation in fluid depth, the velocimeter output should grow in proportion to stapes velocity rather than in proportion to basilar-membrane velocity.

The effect of fluid-meniscus motion is most conspicuous for low stimulus frequencies, which elicit the largest middle-ear responses and the smallest basilar-membrane vibrations (e.g., Ruggero *et al.*, 1990; Cooper and Rhode, 1992). Indeed, we have strong evidence that responses to tones with frequencies lower than 2–3 kHz actually reflect stapes motion. At such frequencies, stapes and ''basilar-membrane'' motion can have comparable magnitudes (Figs. 9 and 10; see also Fig. 19 of Ruggero *et al.*, 1990) and the response phase (out-of-phase with stapes inward displacement) differ from those previously recorded with the Mössbauer technique (Ruggero *et al.*, 1986) but are consistent with those expected from the artifact (Cooper and Rhode, 1992; p. 176). Most convincingly, when measurements at the chinchilla cochlea are performed after covering the hole in the otic capsule with a glass window, responses for low stimulus frequencies are selectively reduced relative to those recorded without the

window (Recio *et al.*, 1997). Therefore, in this paper we have not presented data for stimulus frequencies lower than 2 kHz and view responses to 2–3 kHz tones with caution.

Fluid-meniscus motion could conceivably also contaminate responses to near-CF stimuli at sufficiently high levels, when the linear growth of the artifact might overtake the slower (compressive) growth of basilar-membrane responses. In such a case, responses should grow linearly and their gain should be comparable to that of stapes motion. In fact, responses to CF tones had magnitudes that exceeded stapes vibration even at intensities of 100 dB or higher (Fig. 2) and their growth remained substantially nonlinear even at intensities of 100–110 dB (Fig. 3). Perhaps most telling, the magnitude of basilar-membrane responses to CF tones exceeded stapes vibration even in cochleae that yielded insensitive and nearly linear responses (not shown) as a result of surgical damage.

Finally, it is worth considering whether the high-frequency magnitude plateau (Figs. 8 and 9) reflects the fluid-depth artifact. Although this hypothesis seems to be supported by the linearity and the insensitivity of responses at the plateau, we tend to discount it because a plateau with identical characteristics has also been demonstrated at the same site of the chinchilla cochlea using the Mössbauer technique (Robles *et al.*, 1986). Gamma rays are far more penetrating than visible-light photons and thus are minimally refracted at the air-perilymph interface. Therefore, changes in perilymph depth should translate into insignificant changes in effective path length.

B. Waveshape and spectrum of basilar-membrane responses to tones

Because of the inherent severe nonlinearity of the Lorentzian function that relates gamma-ray counts to velocity (Rhode, 1971; Ruggero and Rich, 1991a), studies that used the Mössbauer method (e.g., Sellick *et al.*, 1982, 1983b; Robles *et al.*, 1986; Ruggero *et al.*, 1986) could not address effectively the question of whether basilar-membrane responses to tones contain harmonic distortion. The present chinchilla data concur with laser velocimetry recordings in guinea pig (see Fig. 20 of Cooper and Rhode, 1992) in showing that basilar-membrane responses to tones, regardless of CF, are largely free of harmonic distortion, even though their rate of growth with intensity may be highly compressive.

C. Magnitude and rate of growth of basilar-membrane responses to near-threshold CF tones

Mössbauer measurements of basilar-membrane vibrations at the 3.5-mm site of the chinchilla cochlea suggested, but could not establish unequivocally, that CF input–output functions grow linearly at low stimulus intensities (Robles *et al.*, 1986). Describing responses in one sensitive cochlea, Robles *et al.* stated that, for the CF velocity-intensity function expressed in logarithmic coordinates, ''slope is less than unity even at the lowest velocities we were able to measure with our system.'' Subsequent recalibration of the acoustic-stimulus system has revealed that such apparent compressive growth at low stimulus levels was an artifact caused by incomplete correction of attenuation errors at large nominal attenuations (Pfeiffer, 1974). After fully correcting for this ''feed-through'' artifact, we are now convinced that, at the 8–10 kHz site of the chinchilla cochlea, basilar-membrane responses to CF tones grow linearly at stimulus levels <20 dB SPL (Figs. 2 and 3).

The intensity of CF tones at the transition between linear and compressive basilar-membrane growth (Figs. 2 and 3) nearly coincides with the threshold of chinchilla auditory-nerve fibers (Figs. 11 and 12). Our present estimate of maximal basilar-membrane gain at the 3.5-mm site of the healthy chinchilla cochlea is similar to a previous one that was based on Mössbauer data (Robles *et al.*, 1986). This similarity suggests that the two sets of measurements were carried out in cochleae that were in similar (i.e., near-normal) physiological state, and that the basilar-membrane recording sites were also comparable. [Radial position, which was not measured in these experiments, could cause variations in vibration magnitude as large as 20 dB, depending on distance from the spiral lamina or the spiral ligament (Cooper and Rhode, 1992).] The newly estimated average neural threshold (8 dB SPL), based exclusively on fibers with high-spontaneous activity, differs from a previous value (16 dB) which was based on a different population of auditory-nerve fibers, averaged without regard to spontaneous activity. Thus, our revised estimate of the magnitude of basilar-membrane vibration at neural threshold (39–73 μm/s or 0.62–1.3 nm) is slightly lower than the previous estimate of 100 μm/s or 2 nm (Robles *et al.*, 1986). At the guinea pig basilar-membrane site with CF 18–20 kHz, the transition between linear and nonlinear growth also occurs at intensities close to neural threshold (0–10 dB; Nuttall and Dolan, 1996). However, another study in guinea pig found nearly linear growth for responses to CF (15 kHz) tones at levels as high as 50 dB SPL (Murugasu and Russell, 1995). There is no obvious explanation for the discordant ranges of linear response growth found in these two studies.

D. Nonlinear growth of basilar-membrane responses to supra-threshold CF tones

Mössbauer experiments showed that basilar-membrane responses to CF tones in healthy chinchilla cochleae grow at rates as low as 0.3 dB/dB (Robles *et al.*, 1986) but provided little detail on the range over which such compressive growth occurred. In particular, due to the limited dynamic range of the Lorentzian function, and because of the need to limit the duration of cochlear exposure to intense tones, almost no Mössbauer data were obtained at the chinchilla basilar membrane for responses larger than 1 mm/s or CF tone intensities higher than 90 dB SPL. Taking advantage of the greater linearity and speed of laser velocimetry, the present experiments were able to collect data at more intense stimulus levels, using large off/on time ratios to prevent acoustic trauma (see Sellick *et al.*, 1982 and Patuzzi *et al.*, 1984). It is now clear that basilar-membrane responses to CF tones in normal chinchilla cochleae grow at rates as low as 0.2 dB/dB, and that these highly compressive growth rates may be maintained over a 40–60 dB range of stimulus intensity (Fig.

3), from 40 dB SPL or lower intensities to 90 dB or even higher intensities.

Some of our laboratory's publications noted in passing that velocity-intensity functions of chinchilla basilar-membrane responses to CF tones could approach linearity at high stimulus intensities (Ruggero and Rich, 1991b; Ruggero *et al.*, 1992b; Ruggero *et al.*, 1993). Such tendency toward linearization was rarely observed in Mössbauer experiments in normal cochleae (Sellick *et al.*, 1982; Robles *et al.*, 1986), but some authors argued for its existence on the basis of the effects of acoustic trauma (Patuzzi *et al.*, 1984) and from theoretical considerations (Johnstone *et al.*, 1986; Patuzzi *et al.*, 1989; Yates, 1990; Goldstein, 1995; Nobili and Mammano, 1996). The present investigation shows that within the range of intensities that are physiologically relevant (e.g., up to 100–110 dB) complete linearization does not occur in healthy cochleae. The rate of growth in some sensitive cochleae does become less compressive at the highest intensities than in the mid-intensity range, but it never surpasses 0.7 dB/dB (Fig. 3). On the other hand, responses to high-intensity CF tones do reach growth rates of 0.8–0.9 dB/dB in many insensitive cochleae that nevertheless retain some nonlinearity (not shown), suggesting that the less compressive growth rates at high intensities reflect cochlear damage. Our conclusion is that if responses to CF tones in normal chinchilla cochleae become linear at high stimulus intensities, they must do so at levels higher than 110 dB SPL. In fact, it is possible that in completely normal cochleae responses may approach saturation (i.e., undergo little growth) at levels higher than 70–80 dB SPL (e.g., cochlea L113 in Figs. 2 and 3).

The growth of responses to CF tones at basal sites of the guinea pig basilar membrane is at least as compressive as in chinchilla. Nuttall and Dolan (1996; Table AI) have shown a velocity-intensity function for CF (18-kHz) tones with an average slope of 0.23 dB/dB between 20 and 80 dB and Murugasu and Russell (1995) have measured slopes that average 0.12 dB/dB for CF (16-kHz) tones at stimulus intensities between 50 and 100 dB. Minimal response growth, approaching saturation, has also been deduced from responses of high-CF auditory-nerve fibers in guinea pig (Cooper and Yates, 1994). Similarly, in the hook region of the cat cochlea responses to tones with frequency slightly higher than CF grow at rates as low as 0.3 dB/dB between 65 and 100 dB SPL (Cooper and Rhode, 1992).

E. Nonlinear growth of basilar-membrane responses at frequencies other than CF

Basilar-membrane responses to tones with frequencies somewhat higher than CF grow at highly compressive growth rates (guinea pig: Sellick *et al.*, 1982; Murugasu and Russell, 1995, and Nuttall and Dolan, 1996; cat: Cooper and Rhode, 1992; chinchilla: Robles *et al.*, 1986). At the chinchilla cochlea, for CFs of 9 or 10 kHz, growth rates for tones with frequency 1 kHz higher than CF are at least as compressive as at CF (Figs. 5 and 7). The nonlinearity disappears abruptly at higher frequencies: Growth rates become essentially linear at a frequency about 1/3 octave higher than CF, coinciding with the onset of a magnitude plateau (discussed below; Figs. 8, 9, and 11).

Nonlinear growth disappears progressively at frequencies lower than CF so that, for CFs of 9–10 kHz, responses are linear at all stimulus frequencies lower than 0.4–0.5 octave below CF. At these frequencies, responses are larger than at CF or at any other stimulus frequency at intensities higher than 80–90 dB. The intensity-dependent shift of the response peak toward lower frequencies probably accounts adequately both for equivalent shifts in responses to tones of high-CF auditory-nerve fibers (Geisler *et al.*, 1974; Sachs and Abbas, 1974) and for the fact that temporary threshold shifts induced by intense tones are maximal at frequencies about 0.5 octave higher than the stimulus frequency (Davis *et al.*, 1950; Hood, 1950; Hubbard and Geisler, 1972; Lonsbury-Martin and Meikle, 1978; Cody and Johnstone, 1981).

F. The gain of the ''cochlear amplifier''

There is widespread belief that something akin to an amplifier (Davis, 1983; Dallos, 1988, 1992), active in healthy cochleae and presumably residing in the organ of Corti, is responsible for boosting the otherwise insensitive basilar-membrane responses of ''passive'' cochleae. One proposed method for measuring the gain of the cochlear amplifier is based on the presumption that responses to CF tones grow linearly at both low and high levels of stimulation (e.g., Johnstone *et al.*, 1986; Patuzzi *et al.*, 1989; Yates, 1990; Goldstein, 1995). The gain is defined as the difference between the sensitivities of responses to high- and low-level CF tones. However, this method is impractical because basilar-membrane responses to CF tones grow compressively even at the highest of physiologically relevant stimulus intensities (Figs. 2–4, 9). Assuming that linear growth would occur for sufficiently intense stimulation, the data for cochleae L113 and L13 indicate that the amplifier gain must be larger than 69 or 56 dB, respectively (Figs. 4, 9, and 10).

A second definition states that the gain of the amplifier corresponds to the difference between the sensitivity of responses to low-level CF tones in healthy cochleae and in freshly dead cochleae (Nuttall and Dolan, 1996). According to this definition, at the base of the chinchilla cochlea the gain amounts to 60–81 dB (taking into account pre-existing cochlear damage; Fig. 16). At the 18-kHz site of the guinea pig basilar-membrane, the corresponding gain amounts to 65–78 dB (as measured, respectively, by Nuttall and Dolan, 1996 and Sellick *et al.*, 1982, Fig. 15B). All of these values should be viewed with some caution because of the possibility that even the acute effects of death may alter not only ''active'' processes (i.e., requiring expenditure of metabolic energy) but also passive mechanics (e.g., the elasticity of the basilar membrane).

Yet a third definition is possible: The gain of the amplifier corresponds to the difference between the gains of responses to low-level CF tones and of the peak responses to high-intensity tones. According to this definition, the gain of the amplifier at the base of the chinchilla cochlea amounts to 39–60 dB (taking into account surgically induced trauma; Figs. 9 and 10).

G. The variation of response phases with stimulus frequency and intensity

An intensity dependence of near-CF response phases was first described for auditory-nerve fibers (Anderson *et al.*, 1971) and subsequently demonstrated at high-CF basilar-membrane sites in several species (Rhode and Robles, 1974; Geisler and Rhode, 1982; Sellick *et al.*, 1982; Cooper and Rhode, 1992; Ruggero *et al.*, 1992a; Nuttall and Dolan, 1993, 1996). At the chinchilla basilar membrane (Fig. 14), the pattern of the variation of phase with increasing intensity—phase lags for frequencies lower than CF, phase leads for frequencies higher than CF, and little phase variation at CF—strongly resembles that for low-CF auditory-nerve fibers. In the chinchilla, the largest phase leads for frequencies higher than CF are comparable to those measured in basal regions of the cat and guinea pig cochleae (140–230 deg: Cooper and Rhode, 1992; Nuttall and Dolan, 1993, 1996) but the phase lags for frequencies lower than CF (e.g., 100 deg for 8 kHz in the 30–80 dB interval) are larger than those measured in other studies.

The frequency range over which phases are intensity dependent, from about 1/2 octave below CF to 1/3 octave above CF, is similar to the frequency range over which compressive growth occurs at the chinchilla basilar membrane (compare Figs. 9 and 14). Further, the changes of phase are qualitatively appropriate for the concomitant changes of tuning: As intensity increases, the sharpness of tuning decreases (Fig. 9) and group delay (i.e., minus the slope of the phase-versus-frequency curve) also decreases (Fig. 13). It is puzzling that such coupling of tuning and group delays at the basilar membrane, whose responses are nonlinear and non-minimum phase (Recio *et al.*, 1996a, 1996b), are those predictable, at least qualitatively, for linear minimum-phase systems (Geisler and Rhode, 1982).

Most previous investigations of the effects of cochlear insults (such as acoustic trauma or ototoxic drugs) on basilar-membrane responses to sound have found relative phase lags at near-CF frequencies (Cooper and Rhode, 1992; Recio and Ruggero, 1995; Ruggero and Rich, 1991b; Ruggero *et al.*, 1993, 1996a, 1996b; however, see also Patuzzi *et al.*, 1984). The phase effects of death are more controversial. In his pioneering study in squirrel monkey, Rhode (1973) showed post-mortem phase lags at CF, whereas Nuttall and Dolan (1996) found large (270 deg) post-mortem phase leads in guinea pig. Our chinchilla data (Fig. 17; see also Fig. 2 in Ruggero, 1994) also show post-mortem phase leads at frequencies near CF, albeit smaller than in the guinea pig study. The discordance between the phase effects of death and those of other cochlear insults suggests that the former are more complex, probably affecting several sites and processes in a time-varying manner (e.g., the stria vascularis, causing changes of the endocochlear potential, or the concentration of endolymphatic calcium, resulting in mechanical alterations of the tectorial membrane).

H. High-frequency plateau

A high-frequency plateau (a frequency region above CF where response magnitude varies little with stimulus frequency) was first described by Rhode (1971) at the basilar membrane of squirrel monkey cochleae that responded nonlinearly to near-CF tones. Magnitude plateaus were also found at the basilar membrane of cat and guinea pig cochleae (Wilson and Johnstone, 1975; Wilson and Evans, 1983) that responded linearly, presumably as the result of surgically induced damage. The existence of a magnitude plateau in normal cochleae was questioned by Gummer and Johnstone (1984) who, on the bases of the experiments by Sellick *et al.* (1982, 1983b), suggested that the plateau resulted from cochlear damage, including acoustic trauma incurred while testing for the presence of the plateau. Robles *et al.* (1986), however, presented evidence that the plateau is demonstrable in normal chinchilla cochleae using test stimuli that do not impair normal sensitivity (see their Fig. 10). The present results (and those of other investigations using laser interferometry: Cooper and Rhode, 1992, and Nuttall and Dolan, 1996) support the existence of the plateau.

However, we still entertain serious doubts regarding the existence of the plateau, in part because of the possibility that laser velocimetry recordings are contaminated by the aforementioned fluid-depth artifact (Cooper and Rhode, 1992, 1996). Although fluid-meniscus motion probably cannot account for the presence of the plateau in recordings using the Mössbauer method (see Sec. III A), it is possible that the plateau is associated with opening of the otic capsule (Cooper and Rhode, 1996). Furthermore, it is disturbing that recordings from auditory-nerve fibers have never revealed a counterpart of the mechanical plateau, which should appear as a prominent inflection of the frequency-threshold tuning curve (Fig. 11).

ACKNOWLEDGMENTS

We thank Andrei Temchin for processing the neural tuning-curve data. We also thank Mary Ann Cheatham, Laura Dreisbach, John Guinan, and two anonymous reviewers for reading and commenting on previous versions of the manuscript. We were supported by Grants No. 5-P01-DC-00110-21 and 5-R01-DC-00419-09 from the National Institute on Deafness and Other Communication Disorders. L.R. was partially supported by FONDECYT (Chile) Grant No. 92-0976 and DTI, Universidad de Chile Grant No. B-2895.

Anderson, D. J., Rose, J. E., Hind, J. E., and Brugge, J. F. (**1971**). ''Temporal position of discharges in single auditory nerve fibers within the cycle of a sine-wave stimulus: frequency and intensity effects,'' J. Acoust. Soc. Am. **49,** 1131–1139.

Cody, A. R., and Johnstone, B. M. (**1981**). ''Acoustic trauma: Single neuron basis for the 'half-octave' shift,'' J. Acoust. Soc. Am. **70,** 707–711.

Cooper, N. P., and Rhode, W. S. (**1992**). ''Basilar membrane mechanics in the hook region of cat and guinea-pig cochleae: Sharp tuning and nonlinearity in the absence of baseline position shifts,'' Hear. Res. **63,** 163–190.

Cooper, N. P., and Rhode, W. S. (**1996**). ''Fast traveling waves, slow traveling waves, and their interactions in experimental studies of apical cochlear mechanics,'' Aud. Neurosci. **2**, 289–299.

Cooper, N. P., and Yates, G. K. (**1994**). ''Nonlinear input–output functions derived from the responses of guinea-pig cochlear nerve fibres: Variations with characteristic frequency,'' Hear. Res. **78,** 221–234.

Dallos, P. (**1988**). ''Cochlear neurobiology: Some key experiments and concepts of the past two decades,'' in *Auditory Function-Neurobiological Bases of Hearing*, edited by G. M. Edelman, W. E. Gall, and W. M. Cowan (Wiley, New York), pp. 153–188.

Dallos, P. (**1992**). ''The active cochlea,'' J. Neurosci. **12,** 4575–4585.
Davis, H. (**1983**). ''An active process in cochlear mechanics,'' Hear. Res. **9,** 79–90.
Davis, H., Morgan, C. T., Hawkins, Jr., J. E., Galambos, R., and Smith, F. W. (**1950**). ''Temporary deafness following exposure to loud tones and noise,'' Acta Oto-Laryngol. Suppl. **88,** 1–56.
Geisler, C. D., and Rhode, W. S. (**1982**). ''The phases of basilar-membrane vibrations,'' J. Acoust. Soc. Am. **71,** 1201–1203.
Geisler, C. D., Rhode, W. S., and Kennedy, D. T. (**1974**). ''Responses to tonal stimuli of single auditory nerve fibers and their relationship to basilar membrane motion in the squirrel monkey,'' J. Neurophysiol. **37,** 1156–1172.
Goldstein, J. L. (**1995**). ''Relations among compression, suppression, and combination tones in mechanical responses of the basilar membrane: Data and MBPNL model,'' Hear. Res. **89,** 52–68.
Gummer, A. W., and Johnstone, B. M. (**1984**). ''Group delay measurements from spiral ganglion cells in the basal turn of the guinea pig cochlea,'' J. Acoust. Soc. Am. **76,** 1388–1400.
Hood, J. D. (**1950**). ''Studies in auditory fatigue and adaptation,'' Acta Oto-Laryngol. **92,** 1–57.
Hubbard, A. E., and Geisler, C. D. (**1972**). ''A hybrid-computer model of the cochlear partition,'' J. Acoust. Soc. Am. **51,** 1895–1903.
Johnstone, B. M., Patuzzi, R., and Yates, G. (**1986**). ''Basilar membrane measurements and the travelling wave,'' Hear. Res. **22,** 147–154.
Khanna, S. M. (**1984**). ''Inner ear function based on the mechanical tuning of the hair cells,'' in *Hearing Science: Recent Advances*, edited by C. I. Berlin (College Hill Press, San Diego), pp. 213–240.
Kliauga, P., and Khanna, S. M. (**1983**). ''Dose rate to the inner ear during Mössbauer experiments,'' Phys. Med. Biol. **28,** 359–366.
Lonsbury-Martin, B. L., and Meikle, M. B. (**1978**). ''Neural correlates of auditory fatigue: Frequency-dependent changes in activity of single cochlear nerve fibers,'' J. Neurophysiol. **41,** 987–1006.
Murugasu, E., and Russell, I. J. (**1995**). ''Salicylate ototoxicity: The effects on basilar membrane displacement, cochlear microphonics, and neural responses in the basal turn of the guinea pig cochlea,'' Aud. Neurosci. **1**, 139–150.
Nobili, R., and Mammano, F. (**1996**). ''Biophysics of the cochlea. II: Stationary nonlinear phenomenology,'' J. Acoust. Soc. Am. **99,** 2244–2255.
Nuttall, A. L., and Dolan, D. F. (**1993**). ''Two-tone suppression of inner hair cell and basilar membrane responses in the guinea pig,'' J. Acoust. Soc. Am. **93,** 390–400.
Nuttall, A. L., and Dolan, D. F. (**1996**). ''Steady-state sinusoidal velocity responses of the basilar membrane in guinea pig,'' J. Acoust. Soc. Am. **99,** 1556–1565.
Patuzzi, R., Johnstone, B. M., and Sellick, P. M. (**1984**). ''The alteration of the vibration of the basilar membrane produced by loud sound,'' Hear. Res. **13,** 99–100.
Patuzzi, R. B., Yates, G. K., and Johnstone, B. M. (**1989**). ''Outer hair cell receptor current and sensorineural hearing loss,'' Hear. Res. **42,** 47–72.
Pfeiffer, R. R. (**1974**). ''Consideration of the acoustic stimulus,'' in *Handbook of Sensory Physiology, Vol. V/1: Auditory System*, edited by W. Keidel and W. Neff (Springer-Verlag, Berlin), pp. 9–38.
Recio, A., Narayan, S. S., and Ruggero, M. A. (**1996a**). ''Wiener-kernel analysis of basilar-membrane responses to white noise,'' Assoc. Res. Otolaryngol., Midwinter Meet., Abstracts, 19, 55.
Recio, A., Narayan, S. S., and Ruggero, M. A. (**1996b**). ''Wiener-kernel analysis of basilar-membrane responses to white noise,'' in *Diversity in Auditory Mechanics*, edited by E. R. Lewis, G. R. Long, P. A. Leake, P. M. Narins, and C. R. Steele (World Scientific Publishing, Singapore) (in press).
Recio, A., Rich, N. C., Narayan, S. S., and Ruggero, M. A. (**1997**). ''Basilar-membrane responses to clicks at the base of the chinchilla cochlea'' (submitted).
Recio, A., and Ruggero, M. A. (**1995**). ''Effects of quinine on basilar-membrane responses to sound,'' Assoc. Res. Otolaryngol., Midwinter Meet., Abstracts, 18, 200.
Rhode, W. S. (**1971**). ''Observations of the vibration of the basilar membrane in squirrel monkeys using the Mössbauer technique,'' J. Acoust. Soc. Am. **49,** 1218–1231.
Rhode, W. S. (**1973**). ''An investigation of post-mortem cochlear mechanics,'' in *Basic Mechanisms in Hearing*, edited by A. R. Møller (Academic, New York), pp. 49–63.
Rhode, W. S. (**1978**). ''Some observations on cochlear mechanics,'' J. Acoust. Soc. Am. **64,** 158–176.
Rhode, W. S., and Cooper, N. P. (**1993**). ''Two-tone suppression and distortion production on the basilar membrane in the hook region of cat and guinea pig cochleae,'' Hear. Res. **66,** 31–45.
Rhode, W. S., and Robles, L. (**1974**). ''Evidence from Mössbauer experiments for nonlinear vibration in the cochlea,'' J. Acoust. Soc. Am. **55,** 588–596.
Robles, L., Ruggero, M. A., and Rich, N. C. (**1986**). ''Basilar membrane mechanics at the base of the chinchilla cochlea. I. Input–output functions, tuning curves, and response phases,'' J. Acoust. Soc. Am. **80,** 1364–1374.
Ruggero, M. A. (**1994**) ''Cochlear delays and traveling waves: comments on 'Experimental look at cochlear mechanics' [A. Dancer, Audiology **31**, 301–312 (1992)],'' Audiology **33**, 131–142.
Ruggero, M. A., and Rich, N. C. (**1983**). ''Chinchilla auditory nerve responses to low-frequency tones,'' J. Acoust. Soc. Am. **73,** 2096–2108.
Ruggero, M. A., and Rich, N. C. (**1991a**). ''Application of a commercially manufactured Doppler-shift laser velocimeter to the measurement of basilar-membrane vibrations,'' Hear. Res. **51,** 215–230.
Ruggero, M. A., and Rich, N. C. (**1991b**). ''Furosemide alters organ of Corti mechanics: Evidence for feedback of outer hair cells upon the basilar membrane,'' J. Neurosci. **11,** 1057–1067.
Ruggero, M. A., Robles, L., and Rich, N. C. (**1986**). ''Basilar membrane mechanics at the base of the chinchilla cochlea. II. Responses to low-frequency tones and relationship to microphonics and spike initiation in the VIII-Nerve,'' J. Acoust. Soc. Am. **80,** 1375–1383.
Ruggero, M. A., Rich, N. C., Robles, L., and Shivapuja, B. G. (**1990**). ''Middle ear response in the chinchilla and its relationship to mechanics at the base of the cochlea,'' J. Acoust. Soc. Am. **87,** 1612–1629.
Ruggero, M. A., Rich, N. C., and Recio, A. (**1992a**). ''Basilar membrane responses to clicks,'' in *Auditory Physiology and Perception*, edited by Y. Cazals, L. Demany, and K. Horner (Pergamon, London), pp. 85–91.
Ruggero, M. A., Robles, L., and Rich, N. C. (**1992b**). ''Two-tone suppression in the basilar membrane of the cochlea: Mechanical basis of auditory-nerve rate suppression,'' J. Neurophysiol. **68,** 1087–1099.
Ruggero, M. A., Rich, N. C., and Recio, A. (**1993**). ''Alteration of basilar membrane responses to sound by acoustic overstimulation,'' in *Biophysics of Hair Cell Sensory Systems*, edited by H. Duifhuis, J. W. Horst, P. van Dijk, and S. M. van Netten (World Scientific Publishing, Singapore), pp. 258–264.
Ruggero, M. A., Rich, N. C., and Recio, A. (**1996a**). ''The effect of intense acoustic stimulation on basilar-membrane vibrations,'' Aud. Neurosci. **2**, 329–345.
Ruggero, M. A., Rich, N. C., Robles, L., and Recio, A. (**1996b**). ''The effects of acoustic trauma, other cochlear injury, and death on basilar-membrane responses to sound,'' in *Scientific Basis of Noise-Induced Hearing Loss*, edited by A. Axelsson, H. Borchgrevink, R. P. Hamernik, P.-A. Hellstrom, D. Henderson, and R. Salvi (Thieme Medical Publishers, New York), pp. 23–35.
Ruggero, M. A., Rich, N. C., Robles, L., Recio, A., and Narayan, S. S. (**1996c**). ''Laser velocimetry measurements of basilar-membrane responses to tones at the base of the chinchilla cochlea,'' Assoc. Res. Otolaryngol., Midwinter Meet., Abstracts, 19, 101.
Sachs, M. B., and Abbas, P. J. (**1974**). ''Rate versus level functions for auditory-nerve fibers in cats: Tone-burst stimuli,'' J. Acoust. Soc. Am. **56,** 1835–1847.
Sellick, P. M., Patuzzi, R., and Johnstone, B. M. (**1982**). ''Measurement of basilar membrane motion in the guinea pig using the Mössbauer technique,'' J. Acoust. Soc. Am. **72,** 131–141.
Sellick, P. M., Patuzzi, R., and Johnstone, B. M. (**1983b**). ''The influence of Mössbauer source size and position on phase and amplitude measurements of the guinea pig basilar membrane,'' Hear. Res. **10,** 101–108.
Temchin, A. N., Rich, N. C., and Ruggero, M. A. (**1997**). ''Frequency-threshold curves of chinchilla auditory-nerve fibers,'' Assoc. Res. Otolaryngol., Midwinter Meet., Abstracts, 20, 152.
Wilson, J. P., and Evans, E. F. (**1983**). ''Some observations on the 'passive' mechanics of the cat basilar membrane,'' in *Mechanisms of Hearing*, edited by W. R. Webster and L. M. Aitkin (Monash University Press, Clayton, Victoria, Australia), pp. 30–35.
Wilson, J. P., and Johnstone, J. R. (**1975**). ''Basilar membrane and middle-ear vibration in guinea pig measured by capacitive probe,'' J. Acoust. Soc. Am. **57,** 705–723.
Yates, G. K. (**1990**). ''The basilar membrane nonlinear input–output function,'' in *The Mechanics and Biophysics of Hearing*, edited by P. Dallos, C. D. Geisler, J. W. Matthews, M. A. Ruggero, and C. R. Steele (Springer-Verlag, Berlin), pp. 106–113.