UvA-DARE (Digital Academic Repository)

The mechanical waveform of the basilar membrane. III. Intensity effects

de Boer, E.; Nuttall, A.L.

DOI

[10.1121/1.428436](https://doi.org/10.1121/1.428436)

Publication date

2000

Published in

The Journal of the Acoustical Society of America

[Link to publication](#)

Citation for published version (APA):

de Boer, E., & Nuttall, A. L. (2000). The mechanical waveform of the basilar membrane. III. Intensity effects. *The Journal of the Acoustical Society of America*, 107, 1497-1507. <https://doi.org/10.1121/1.428436>

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

The mechanical waveform of the basilar membrane.

III. Intensity effects^{a)}

Egbert de Boer^{b)}

Room D2-226, Academic Medical Center, University of Amsterdam, Meibergdreef 9, 1105 AZ, Amsterdam, The Netherlands

Alfred L. Nuttall^{c)}

Oregon Hearing Research Center, NRC04, Oregon Health Sciences University, 3181 SW Sam Jackson Park Road, Portland, Oregon 97201-3098 and Kresge Hearing Research Institute, University of Michigan, 1301 E. Ann Street, Ann Arbor, Michigan 48109-0506

(Received 10 May 1999; revised 1 October 1999; accepted 29 November 1999)

Mechanical responses in the basal turn of the guinea-pig cochlea were measured with broad-band noise stimuli and expressed as input–output cross-correlation functions. The experiments were performed over the full range of stimulus intensities in order to try to understand the influence of cochlear nonlinearity on frequency selectivity, tuning, signal compression and the impulse response. The results are interpreted within the framework of a nonlinear, locally active, three-dimensional model of the cochlea. The data have been subjected to inverse analysis in order to recover the basilar-membrane (BM) impedance, a parameter function that, when inserted into the (linearized version of that) model, produces a model response that is similar to the measured response. This paper reports details about intensity effects for noise stimulation, in particular, the way the BM impedance varies with stimulus intensity. In terms of the underlying cochlear model, the decrease of the “activity component” in the BM impedance with increasing stimulus level is attributed to saturation of transduction in the outer hair cells. In the present paper this property is brought into a quantitative form. According to the theory [the EQ-NL theorem, de Boer, *Audit. Neurosci.* **3**, 377–388 (1997)], the BM impedance is composed of two components, both intrinsically independent of stimulus level. One is the passive impedance Z^{pass} and the other one is the “extra” impedance Z^{extra} . The latter impedance is to be multiplied by a real factor γ ($0 \leq \gamma \leq 1$) that depends on stimulus level. This concept about the composition of the BM impedance is termed the “two-component theory of the BM impedance.” In this work both impedances are entirely derived from experimental data. The dependence of the factor γ on stimulus level can be derived by using a unified form of the outer-hair-cell transducer function. From an individual experiment, the two functions Z^{pass} and Z^{extra} are determined, and an approximation ($Z^{\text{pass}} + \gamma Z^{\text{extra}}$) to the BM impedance constructed. Next, the model response (the “resynthesized” response) corresponding to this “artificial” impedance is computed. The same procedure is executed for several stimulus-level values. For all levels, the results show a close correspondence with the original experimental data; this includes correct prediction of the compression of response amplitudes, the reduction of frequency selectivity, the shift in peak frequency and, most importantly, the preservation of timing in the impulse response. All these findings illustrate the predictive power of the underlying model. © 2000 Acoustical Society of America. [S0001-4966(00)02803-4]

PACS numbers: 43.64.Kc, 43.64.Bt [RDF]

INTRODUCTION

It is well known that there exists a close relation between nonlinearity, amplitude compression and frequency selectivity in the cochlea. When stimulus intensity is increased, the degree of nonlinearity in the operation of the cochlea increases, and this affects frequency selectivity, i.e., the way simultaneously presented stimulus components of different frequencies are handled, and it also affects the response amplitude (causing compression). When the stimulus contains one dominant frequency component (or a very nar-

row band of such components), the distribution of nonlinearity over the length of the cochlea differs from that for a wideband noise stimulus. This entails that the relation between responses to wideband stimuli and pure tones is not straightforward. The same is true for the relation between responses to strong clicks and wideband stimuli. In the former case the degree to which the system is driven into nonlinearity will vary greatly in time—starting small, increasing rapidly and decreasing more slowly—and in the latter case the degree of nonlinearity will be fluctuating less but continually. Would it ever be possible to link responses to clicks, pure tones and noise signals to each other, for all levels of stimulation? It is too early to attempt to understand the behavior of the cochlea for stimuli that are *completely* general, and contain rapid variations in level, time and fre-

^{a)}Preliminary results of the subject treated in Sec. V were presented at the ARO 1999 Midwinter meeting (abstract No. 344).

^{b)}Electronic mail: e.deboer@amc.uva.nl

^{c)}Electronic mail: nuttall@ohsu.edu

quency content. In the present paper the first steps of such a most desirable study are undertaken, with the use of simple stimuli. In all our modeling work we firmly base the parameters of the model on the analysis of experimental data on the mechanical response of the basilar membrane (BM).

Experimental and theoretical details of our work are given in two previous publications in this series of papers (de Boer and Nuttall, 1997b, GLIDE, and 2000, DMD) which will be referred to as Part I and Part II, respectively. Briefly, we measured the velocity of the basilar membrane (BM) in the basal part of the guinea-pig cochlea, in a region where the best frequency (BF) is between 15 and 18 kHz. In Part I we described and commented upon the frequency modulation of the impulse response (the “glide”). In Part II we critically analyzed the various types of model that can be used in inverse analysis.

The work in Part II relates directly to a linear system because only low-level stimuli were considered. In the present paper we describe and analyze how the cochlea differentially reacts to *noise stimuli of widely varying levels*. The nonlinear model “ $\mathcal{M}\text{-}\mathcal{NL}$ ” underlying the analysis contains response-enhancing elements (outer hair cells, OHCs) that assist in amplifying the cochlear wave and are nonlinear. In fact, these cells are the only nonlinear elements of the model. For this type of model the data can be interpreted via the EQ-NL theorem. The structure of the model and the meaning of the theorem are briefly reviewed in Appendix A. The proof of the theorem is given in de Boer (1997). A prerequisite is that data have to be acquired in the form of input–output cross-correlation functions (ccf’s) for wideband noise stimuli with constant power density. By using the EQ-NL theorem, we are considering a *nonlinear* model of the cochlea but our conclusions will always refer to a *linear* model, the “comparison model” (defined in the same Appendix), which we will call here model “ $\mathcal{M}\text{-}\mathcal{Lin}$.”

Analysis starts with the inverse solution procedure. The model that will be used is three-dimensional and allows for long, intermediate and short waves to propagate in it. The input to the inverse procedure is the velocity response $v_{\text{BM}}(x, \omega)$ derived from the ccf spectrum data via a frequency-to-place transformation, and the result is the BM impedance $Z_{\text{BM}}(x, \omega)$, both of which are functions of location x and radian frequency ω (see Part II). The computed impedance, then, is the BM impedance of model “ $\mathcal{M}\text{-}\mathcal{Lin}$.” In the present paper responses are treated to strong stimuli that bring the cochlea into a definite state of nonlinearity. At different levels of stimulation the impedance function will be different, and at each stimulus level model “ $\mathcal{M}\text{-}\mathcal{Lin}$ ” has to be equipped with the appropriate impedance in order to simulate the measured response. It is via the variations of $Z_{\text{BM}}(x, \omega)$ with stimulus level that we will interpret nonlinear effects in the real cochlea.

In more detail, the EQ-NL theorem predicts that the BM impedance $Z_{\text{BM}}(x, \omega)$ is a linear combination of two invariant functions, $Z^{\text{pass}}(x, \omega)$ and $Z^{\text{extra}}(x, \omega)$, whereby the second is multiplied by the (real) coefficient γ , which is between 0 and 1. The term $Z^{\text{pass}}(x, \omega)$ is the impedance of the BM when the OHCs do not function. The function $Z^{\text{extra}}(x, \omega)$ represents the maximal contribution that can be

given to the BM impedance and refers to the condition with the weakest possible stimulation. The coefficient γ reflects the efficiency with which these OHCs operate when they are processing weak ($\gamma \approx 1$) or strong ($\gamma < 1$) signals. This principle is called the “two-component theory of the BM impedance” (more details are given in Sec. III). The two functions $Z^{\text{pass}}(x, \omega)$ and $Z^{\text{extra}}(x, \omega)$ do not depend on stimulus level; γ is the only parameter that depends on stimulus level. It should be noted that the two-component theory results immediately from the EQ-NL theorem. In the development of cochlear mechanics a related principle has been used (see, e.g., Neely and Kim, 1986) but that was simply posed as a hypothesis. In the current work the component impedances are directly derived from experimental data.

The main theme of this paper is to explore the two-component theory. In Sec. III and Appendix B it is shown how the coefficient γ can be calculated when a realistic type of OHC transduction function is assumed. The coefficient γ then becomes a function $\gamma(L)$ of stimulus level L —stimulus level being defined as the sound pressure level (SPL) of one octave of the noise stimulus centered at the best frequency (BF) of the location from where the measurement is made. When the forward solution of the model (resynthesis) is carried out with the two-component impedance using the appropriate value for $\gamma(L)$, the resulting response is found to correspond very closely to the original response used as the input to the inverse procedure, for all values of L . This implies not only that at all levels L the resynthesized response has the same frequency selectivity and tuning as the original response, but also that the amplitude of the resynthesized response shows the same signal compression as the original data (Sec. IV). In the final stage of the work reported in this paper, Sec. V, it is shown that the two-component theory of the BM impedance also accounts for the fact that the timing of the oscillations in the impulse response remains nearly invariant when the stimulus level varies.

I. GENERAL INTENSITY EFFECTS

Data were collected on movements of the basilar membrane (BM) in the basal turn of the guinea-pig cochlea with a laser velocimeter (cf. Nuttall *et al.*, 1990; Nuttall and Dolan, 1996).¹ *Bands of flat-spectrum pseudo-random noise* were used as acoustical stimuli and the velocity of the BM at a location tuned to a frequency between 15 and 18 kHz was measured as a function of time. From stimulus and response signals input–output cross-correlation functions (ccf’s) were computed (see Part I), and the ccf spectrum was derived from the ccf waveform. Furthermore, *composite ccf spectra* were obtained by combining sections of ccf spectra measured with flat-spectrum stimuli of different bandwidths, central frequencies and intensities in the same animal (see de Boer and Nuttall, 1999, INV-3). With this technique the composite ccf spectrum accurately represents the input–output relation over a wide frequency range, from below 1 to over 25 kHz, and over a response range of more than 50 dB (a single wideband noise produces either good accuracy in the peak region or in the low-frequency region, but not in both). In this case the “stimulus level” is the SPL of one octave of the noise signal that has been used for the frequency band

FIG. 1. Upper panel: Composite ccf spectra for various stimulus levels (velocity divided by stapes velocity). Experiment: 7701. *Solid lines*: amplitude; *dashed lines*: phase. Stimulus levels: 20, 60, 70, 80 and 90 dB for live animal, and 100 dB for dead animal (amplitude labeled with “+,” phase with coarser dashing). Maximum ratio of BM to stapes velocity at BF for the 20-dB response: 669, shown as 0 dB. Middle panel: impulse response for 20-dB stimulation. Lower panel: impulse response for the dead animal. Notice that the zero-crossings of the two impulse responses are nearly the same (see the dotted vertical lines).

around the BF (the SPL of the lower bands is higher). The composite ccf spectrum is always derived as the (complex) ratio of BM to stapes velocity. Examples of composite ccf spectra for low- and high-level stimuli will be discussed presently.

The waveform corresponding to the composite ccf spectrum is obtained via the (inverse) Fourier transform. At a very low level of stimulation we can assume that the cochlea is linear, and thus we can interpret the so-obtained ccf waveform (remember that it has been measured with a wideband noise input) as the impulse response of the cochlea. For higher stimulus levels the ccf waveform can be similarly interpreted as an impulse response but this time of model “*M-Lin*.” Typical variations of such impulse-response waveforms with stimulus level have been reported in Part I but will be analyzed more deeply here.

Figure 1, upper panel, shows the composite ccf spectrum, amplitude (solid lines) and phase (dashed lines), for five values of the stimulus level L , from 20 to 90 dB, measured in a normally sensitive animal. In addition, there is a pair of curves for the same animal post-mortem [labeled (+), stimulus level 100 dB, amplitude and phase curves indicated with two arrows]. The response functions are compensated for the stapes response. All curves are superimposed whereby the amplitude curve at the lowest stimulus level is normalized to 0 dB at its peak. See the legend for the maximum BM-to-stapes velocity of this response. The responses have undergone no extra smoothing as in earlier publications (de Boer and Nuttall, 1999, INV-3, Part II). At the lower

frequencies the amplitude curves (solid lines) more or less overlap, implying linear behavior of the cochlea. It is seen that the response peak gradually diminishes in height and moves to lower frequencies with increasing stimulus level. The phase curves (dashed lines) overlap a great deal, but the one corresponding to the post-mortem response (shown with coarser dashes) has the shallowest average slope. The lower two panels of the figure show two impulse responses (inverse Fourier transforms of the ccf spectra), one corresponding to the lowest stimulus level and the other to the post-mortem condition. For these impulse responses the frequency response has been smoothed as detailed in Part II. Note that the low-level impulse response displays six to seven oscillations before it reaches its maximal amplitude and that the frequency of the oscillations increases with time (the “glide” as described in Part I). The post-mortem impulse response dies out through most of its course. It should be noted also that the zero-crossings of these two impulse responses are almost the same, especially the first few (see the vertical dotted lines in the figure). This is an intriguing property of the cochlea to which we will return later in this paper.

For the cochlear model to be used for inverse analysis we can choose among several possibilities (see Part II). A three-dimensional model can be given a uniform shape (the “stylized” model) or its dimensions can be chosen to approximate the real cochlea (the “realistic” model). We have selected the stylized model because our analysis in Part II has shown that there are no major differences in the inverse-analysis results. In the computations we have used the fast and economical approximation method described in de Boer (1998).² In the stylized model the BM moves over its own width εb (a constant fraction ε of the model width b) according to a centered half-period of a sine function over the width εb , as if it were hinged at its inner and outer edges (see de Boer, 1981). The remaining parts of the partition between the two channels in the model remain stationary. These parts represent the bony spiral lamina and the outer section of the spiral ligament. Fluid motion in the model is three-dimensional.

As in Part II we will use the following model parameters:

$$\begin{aligned} \varepsilon &= 0.2, \quad b = 1 \text{ (mm)}, \quad h = 1 \text{ (mm)}, \\ \rho &= 10^{-3} \text{ (g mm}^{-3}\text{)}, \quad L = 6 \text{ (mm)}, \end{aligned} \quad (1)$$

and the following parameters in the frequency-to-place transformation (cf. de Boer and Nuttall, 1999, INV-3):

$$\alpha = 0.5 \text{ (mm}^{-1}\text{)}, \quad \omega_{\max} = 2\pi 45 \text{ (kHz)}. \quad (2)$$

The meanings of the symbols are given in the cited papers. A model length of 6 mm is sufficient to accommodate the high frequencies that we are considering here. We made N , the number of sections in the longitudinal direction, equal to 700 and occasionally used values up to 1400.

Figure 2 shows, for the same experiment as Fig. 1, the response functions $v_{\text{BM}}(x, \omega)$, i.e., the ccf spectra converted from the frequency to the x domain, panel (a) the amplitude and panel (b) the phase (*dashed* curves in both panels). Of the abscissa x only the most interesting part (from 2 to 5

FIG. 2. Response and BM impedance. Experiment: 7701. *Dashed curves*: original responses in the x domain, amplitude and phase (ordinate scales on the sides). See Eq. (2) for the parameters used in the f -to- x transformation. Stimulus levels: 20, 60, 70, 80, and 90 dB for live animal, 100 dB for dead animal (shown with coarser dashes). The constant ω is made equal to 2π times the best frequency, 16.6 kHz, at the 20-dB stimulus level. *Solid curves*: BM impedance $Z_{BM}(x, \omega)$ recovered by inverse solution, real [panel (a), left] and imaginary parts [panel (b), right]. The “stylized” three-dimensional model is used, see text. Number of sections (N): 700. “Unit” of impedance (see thick vertical bars along sides of panels): $2 \text{ (g mm}^{-2} \text{ s}^{-1}) = 2000 \text{ (kg m}^{-2} \text{ s}^{-1})$. Smaller impedance values are plotted linearly, larger ones are logarithmically compressed.

mm) is shown. The constant ω is made equal to 2π times the best frequency (BF) at the lowest stimulus level. The maximum response amplitude at the lowest stimulus level is normalized to 0 dB. Data smoothing is as described in Part II. Dashes are longer for the post-mortem curves.

The *solid curves* in Fig. 2 show the *BM impedance* $Z_{BM}(x, \omega)$ computed with the inverse method, panel (a) the real and panel (b) the imaginary part. The ordinate scales for the impedance are nonlinear (compressed for large values), as was the case for the impedance figures in Part II. The reference value for the impedance is given in the legend. In both panels the zero point for the impedance is in the center of the ordinate scale. It is stressed that, by their very nature, impedance functions show large variations near the left margin of the figure; these variations are mostly due to data errors (see Part II).

Where the *real part* of $Z_{BM}(x, \omega)$ is negative, the wave in the model is amplified (its power is increased), and because the region of “activity” is limited in length we call the model “locally active.” In the region just to the left of the response peak, the real part of the impedance has the largest excursion into the domain of negative values at the lowest stimulus level, and this negative excursion is observed to decrease as stimulus level increases. For the post-mortem case, the real part is positive. The solid curves in panel (b), showing the *imaginary part* of the impedance, overlap very much in the “active” region. They are all in the logarithmic region of the ordinate scale; apparently, relative variations of the imaginary part with stimulus level are much smaller than those of the real part. In the absolute sense, the variations are of similar magnitude as those of the real part. It is noted that,

FIG. 3. Response and BM impedance. Experiment: 7611. *Dashed curves*: original responses. *Solid curves*: BM impedance $Z_{BM}(x, \omega)$ recovered by inverse solution. Layout as Fig. 2. Stimulus levels: 50, 60, 70, 80, and 90 dB for live animal, 100 dB for dead animal.

at the right side of the peak, the *imaginary part* does not show a clear tendency to move toward or to cross the zero line. For low stimulus levels the place of the response peak is not primarily defined by “resonance” of mass and stiffness of the BM (a zero-crossing of the imaginary part) but is closely related to the place where the *real part* crosses the zero line, from negative to positive (cf. de Boer, 1983).

Figures 3 and 4 show results from two other experiments. These figures confirm what is concluded from Fig. 2. The three figures together illustrate the large variability in input data and impedance functions. [These figures should be complemented with the findings reported in de Boer and Nuttall (1997a, DAM).] We infer that, with increasing stimulus level, the BM impedance function is more and more “deprived” of a special component. We will call this variable component the “extra” component. For low stimulation levels this component causes the model to become “active,”

FIG. 4. Response and BM impedance. Experiment: 7619. *Dashed curves*: original responses. *Solid curves*: BM impedance $Z_{BM}(x, \omega)$ recovered by inverse solution. Layout as Fig. 2. Stimulus levels: 50, 60, 70, 80, and 90 dB for live animal, 100 dB for dead animal.

i.e., to produce wave amplification. For stronger stimuli this component still tends to diminish power dissipation in the model. In our figures the variations are the most conspicuous in the real part. We found the same trends in 17 other experiments. This idea will be worked out in later sections of this paper.

Resynthesized response curves in the x domain overlap the original ones so well that there is no need to illustrate them. One important consequence is that *amplitude compression* is the same in original and resynthesized responses. This entails that model “ $\mathcal{M}\text{-Lin}$ ” is capable of demonstrating the correct input–output amplitude function of the cochlea. The proviso is that at each stimulus level the appropriate BM impedance function is used. The variations of the impedance are obviously of the right type to explain amplitude compression.

In de Boer and Nuttall (1999, INV-3) it has been reported that resynthesis of the *impulse response* is virtually perfect. We found the same feature in this study, for various values of the stimulus level L . Therefore, there is no need for a figure. We want to stress one particular feature of these results: *The timing of individual cycles of the ccf waveform is nearly the same for all stimulus levels*, and this is true for original as well as for resynthesized responses. Therefore, model “ $\mathcal{M}\text{-Lin}$ ” with its level-dependent BM impedance is also capable of reproducing the near-invariance of timing. The earliest report about this near-invariance property in *mechanical* impulse responses of the cochlea appears to be Robles *et al.* (1976), while more specific data are given in Ruggero *et al.* (1992) and, more recently, in Recio *et al.* (1998). For responses of primary auditory-nerve fibers a similar property has been found in PSTH histograms (Kiang *et al.*, 1965) and in revcor functions, see, e.g., Carney and Yin (1988), Carney (1993) and Carney *et al.* (1999). We confirmed this property for mechanical data in Part I (the end of Sec. II C). In particular, we found that the course of the “instantaneous frequency,” evaluated for a low stimulus level, neatly lines up with that at higher levels (the relation between instantaneous frequency and timing of zero-crossings should be obvious). One conclusion to be drawn is that near-invariance of timing is not specifically linked with nonlinearity (cf. Sec. II B in Recio *et al.*, 1998). In a way quite the opposite can be stated: near-invariance persists despite nonlinearity (all our resynthesized responses are obtained with a linear model). In Part I it was proposed that the “glide” (the general rise in instantaneous frequency with time in the impulse response) should be one of the marks by which the validity of a cochlear model is to be judged. We can now go one step further and propose that the near-invariance of the timing of oscillations in the resynthesized impulse response should also be considered in judging the validity of a cochlear model. Our model “ $\mathcal{M}\text{-Lin}$,” at each stimulus level provided with the appropriate BM impedance function, passes the test of acceptance. This is not too impressive a result, however, so we will try to analyze this intriguing near-invariance property more deeply.

FIG. 5. Amplitude of response as a function of stimulus level L . See text. Dashed line shows linear relation. Thick line follows Eq. (3).

II. SIGNAL COMPRESSION IN THE DATA

For better understanding intensity effects we must embark upon more detailed theoretical considerations. In particular, we need to know *how the average transduction of the OHCs in the model depends on stimulus level*. The result will be applied to the computation of model responses. As the first step, we will formalize how the amplitude of the response to noise stimuli depends on stimulus level. Figure 5 illustrates measured response amplitude versus stimulus level L . The curves connecting small circles show the total power (in arbitrary units) over the ccf spectrum for 11 experiments as functions of stimulus level. The thick continuous curve depicts an average function matched to the data. We used the following expression for this curve:

$$v_{\text{rms}} = \exp\left[\left\{2/(1 + (L/80)^4) - 2 + (L/20)\right\} \ln(10)\right], \quad (3)$$

where v_{rms} is the response amplitude and L is in dB. The particular function in Eq. (3) is not based on any physiological reasoning; it is chosen as a convenient expression involving a maximal compression of 40 dB. For $L=0$ (dB) v_{rms} is normalized to 1. Note that the curves of Fig. 5 refer to stimulation by bands of noise. The amplitude compression shown reflects mainly the compression in the frequency region around the best frequency (BF), but this is of the same order as the compression of single pure tones in that range. Equation (3) will be used in Sec. III to describe the amplitude of the input to OHCs in the model.

III. THEORY: TWO COMPONENTS OF THE BM IMPEDANCE

We have reported on the effect of stimulus intensity on the BM impedance earlier (de Boer and Nuttall, 1997a, DAM). In the stimulus-level range from 10 to 40 dB the *real part* of the BM impedance $Z_{\text{BM}}(x, \omega)$ in the “active” region was found to vary little, but from 50 dB on it gradually became less negative to become positive at the highest levels (90–100 dB). The *imaginary part* of the impedance did not vary much (in the relative sense). Our present results show

the same properties but in greater detail. With model “ $\mathcal{M}\text{-}\mathcal{NL}$ ” these results can be explained in a qualitative way. With the stimulus level increasing, the signal at the input to the OHCs makes larger and larger excursions and there will be more and more saturation in the (nonlinear) transfer function of these cells. As a result the average transduction of individual components of the noise signal decreases and “activity” decreases likewise.

Let us make this reasoning more precise. In the nonlinear model “ $\mathcal{M}\text{-}\mathcal{NL}$ ” we assume that OHCs give rise to an additional component $p_{\text{add}}(x, t)$ of the sound pressure $p(x, t)$ in the fluid near the BM (see Appendix A). In the linear model “ $\mathcal{M}\text{-}\mathcal{Lin}$ ” this component is written as $p_{\text{add}}(x, \omega)$, which is no longer a real function of location x and time t but a complex function of x and ω . The pressure component $p_{\text{add}}(x, \omega)$ will be proportional to the efficiency of OHC transduction $\gamma(L)$ (for wideband noise stimuli γ is a function of L , and not of x or ω , see Appendix A). The additional pressure component $p_{\text{add}}(x, \omega)$, when divided by the (complex) BM velocity $v_{\text{BM}}(x, \omega)$, will produce an *additive* contribution to the BM impedance $Z_{\text{BM}}(x, \omega)$, and this contribution will also be proportional to $\gamma(L)$. Hence, the BM impedance $Z_{\text{BM}}(x, \omega)$ can be written as the sum of a “passive” term $Z^{\text{pass}}(x, \omega)$ that represents the “dead” or “passive” cochlea (with no functioning of OHCs at all), and an additional term $\gamma(L)Z^{\text{extra}}(x, \omega)$ that is solely due to OHC transduction:

$$Z_{\text{BM}}(x, \omega) = Z^{\text{pass}}(x, \omega) + \gamma(L)Z^{\text{extra}}(x, \omega). \quad (4)$$

The parameter $Z^{\text{extra}}(x, \omega)$ represents the *maximum* contribution that can be given to the BM impedance. All x -dependent quantities in this relation are complex functions, but the coefficient $\gamma(L)$ is real. Note that the parameters $Z^{\text{pass}}(x, \omega)$ and $Z^{\text{extra}}(x, \omega)$ do not depend on L , whereas $\gamma(L)$ goes down from 1 to 0 with increasing L . We will call this concept the two-component theory of the BM impedance. It is valid for all models to which the EQ-NL theorem applies. We can rewrite relation (4) in terms of the impedance $Z^{\text{weak}}(x, \omega)$ which is the BM impedance for the intact cochlea with a very low level of stimulation [$\gamma(L) = 1$], as follows:

$$Z_{\text{BM}}(x, \omega) = Z^{\text{pass}}(x, \omega) + \gamma(L)[Z^{\text{weak}}(x, \omega) - Z^{\text{pass}}(x, \omega)]. \quad (5)$$

This expression is “closer to experiments” than Eq. (4) since its constituents can directly be derived from data. It is stressed that *only the coefficient $\gamma(L)$ depends on the stimulus level L* ; the other parameters in the equations are invariant functions of x and do not depend on L .

We can now ask three principal questions:

(A) Does the BM impedance vary with stimulus level L as predicted?

(B) If that is the case, does the two-component theory predict the correct dependence of amplitude and phase of the response upon L , for each individual experiment?

(C) Can the two-component theory simulate the near-invariance of timing of the impulse response?

Note that all three questions are concerned with the *predictive* power of the model; we are no longer in the *descrip-*

tive state. For all values of L , Eq. (4) or (5) should provide a good approximation to the actual BM impedance. It should be remembered, though, that the constituent impedances $Z^{\text{weak}}(x, \omega)$ and $Z^{\text{pass}}(x, \omega)$ in Eq. (5) have considerable intrinsic errors, especially $Z^{\text{weak}}(x, \omega)$.

In the present section question (A) will be treated, and in the next two sections questions (B) and (C). According to the reasoning underlying the EQ-NL theorem, OHC transduction should be proportional to the average slope of the transducer’s transfer function, averaged over the OHC input signal’s excursions (de Boer, 1997). In Appendix A this is expressed by Eq. (A1). The OHC input signal is proportional to v_{rms} as expressed by Eq. (3) of Sec. II. Thus, given an acceptable OHC transfer function $F(\cdot)$, the average slope, i.e., the transducer efficiency γ , can be calculated for every value of v_{rms} . In Appendix B it is shown how the calculation is done, with a transfer function $F(\cdot)$ firmly based on experimental data. The calculation contains the response amplitude v_{rms} normalized by the factor v_1 . The function γ gradually decreases from 1 to 0 with increasing v_{rms} . For the chosen function $F(\cdot)$, making v_{rms} equal to v_1 makes γ equal to 0.513.

A rough estimate of the normalization factor v_1 can be obtained with the data from Fig. 4 in de Boer and Nuttall (1997a, DAM), which figure shows the BM impedance averaged over a fixed region of x (in fact, the “active” region for the lowest stimulus level) as a function of L , for seven experiments. We averaged these results over the seven experiments, and found the real part of the BM impedance to reduce its negative-going excursion to one-half its maximal value around the stimulus level of 73 dB. When we choose v_1 equal to 1100, the function $\gamma(L)$ reduces to 0.5 for L equal to 73. We further verified that *on the average* the negative-going excursion of the real part of the BM impedance indeed varies with L in approximately the same way as our calculated function $\gamma(L)$. In this way question (A) posed above has been answered in the affirmative. We may conclude that the concepts inherent in our nonlinear model are realistic. Therefore, let us go ahead and try to make the prediction more refined. This will be done by including resynthesis, and going from the average over experiments to individual experiments.

IV. APPLICATION TO INDIVIDUAL EXPERIMENTS I: BM RESPONSE

In this section we will address question (B) of Sec. III. We will use $\gamma(L)$ calculated according to Appendix B to predict $Z_{\text{BM}}(x, \omega)$ for every value of stimulus level L , and compute model response curves for this choice. Instead of averaged impedance values we will now handle *full functions of x obtained in a single experiment*. The procedure is as follows.

- (i) Take, from the collection of responses (ccf’s) in one animal, two responses, one for the “live” animal, with a weak stimulus, and one post-mortem. Choose a value for v_1 .
- (ii) Derive from the two responses the two impedance functions $Z^{\text{weak}}(x, \omega)$ and $Z^{\text{pass}}(x, \omega)$, for all x over the entire range.

FIG. 6. Resynthesis of response when BM impedance is composed of two components as in Eqs. (4) and (5). Experiment: 7701. *Dashed curves*: original responses (the 20-dB and the post-mortem responses included). *Solid curves*: resynthesized responses with predicted impedance function. Stimulus levels: 60, 70, 80, and 90 dB. Normalization constant v_1 : 2440.

- (iii) Calculate, for a given stimulus level L , the value of $\gamma(L)$ according to Appendix B.
- (iv) Find the “predicted” BM impedance function from Eq. (5).
- (v) Perform resynthesis in model “ $\mathcal{M}\text{-}\mathcal{L}in$ ” with this impedance.
- (vi) Compare the model response $v_{BM}(x, \omega)$ with the actual response data for the same value of L .
- (vii) Do steps (iii) through (vi) for every stimulus level L , keeping the normalizing factor v_1 the same.

It turns out that for every experiment v_1 has to be given its “own” value to obtain the best-fitting result over the entire range of L .

We illustrate the outcome with a figure that applies to experiment 7701 (the one used for Figs. 1 and 2). The function $Z^{\text{weak}}(x, \omega)$ refers to the stimulus level of 20 dB, and we choose $Z^{\text{pass}}(x, \omega)$ from the post-mortem case. Then, for stimulus levels from 50 to 90 dB, the “predicted” BM impedance is computed from Eq. (5) and the response is resynthesized for that impedance.

Figure 6 shows the resulting responses in the x domain. The original responses are shown by dashed lines [the responses on which $Z^{\text{weak}}(x, \omega)$ and $Z^{\text{pass}}(x, \omega)$ are based are included], and the resynthesized responses by solid lines. Recall that in this resynthesis the BM impedance function is simply a linear combination of two fixed x -dependent components, and it is only one of the coefficients, $\gamma(L)$, that varies with stimulus level L . The value of the normalization factor v_1 giving the best fit for this experiment is 2440. The efficiency $\gamma(L)$ then reduces to 0.5 for L equal to 86 dB. The resynthesized response functions are seen to resemble the original ones and to follow their variations with stimulus level. It is evident that the two-component theory predicts not only the correct frequency selectivity and tuning but also the correct amplitude compression in the input–output function.³ Moreover, it produces the correct response phase. Thus, question (B) of Sec. III has been answered.

There is one aspect of this result that seems, at first sight, unsatisfactory. To calculate the efficiency coefficient

FIG. 7. Resynthesis of impulse response when BM impedance is composed of two components as in Eqs. (4) and (5). Experiment: 7701. Stimulus levels as indicated. *Dashed lines*: original impulse responses. *Solid lines*: resynthesized impulse responses with predicted impedance function. Note how well the timing of the zero-crossings is preserved (see vertical dotted lines).

$\gamma(L)$ we started from Eq. (3) as expressing the signal amplitude value as a function of L . We then used this to calculate $\gamma(L)$, substituted $\gamma(L)$ in the BM impedance expression Eq. (5) and found the resynthesized response to show the “correct” amplitude compression. This seems like circular reasoning, we started from and ended with the same “compression.” We could have followed a different path, namely, starting with uncompressed BM velocity values, calculating $\gamma(L)$, and using that in resynthesis. We would then find too much compression, and we could use the newly computed BM velocity (which is too small) to recalculate $\gamma(L)$, and to do another resynthesis (producing too large an amplitude). After a number of iterations we would end up by finding that the “correct” type of compression in the measured velocity values corresponds with the “correct” compression of resynthesized amplitude values. And this is just what we did in a straightforward way.

V. APPLICATION TO INDIVIDUAL EXPERIMENTS II: IMPULSE RESPONSE

A most critical test forms the impulse response [question (C) of Sec. III]. Figure 7 shows the impulse responses corresponding to the curves in Fig. 6; the one corresponding to the 20-dB condition is included. The original impulse responses are the dashed lines. The impulse responses computed with the “two-component theory” are shown by solid lines. For different conditions the curves have been normalized to show the same maximum amplitude but *original and resynthesized impulse responses have always been normalized by the same factor*. At many places the solid lines completely cover the dashed lines. At the lowest levels the cor-

FIG. 8. Resynthesis of impulse responses in two more experiments. Left, experiment 7611. Right, experiment 7619. Normalization constants: 2200 and 1830, respectively. Vertical dotted lines assist in judging near-invariance of timing.

response is seen to be almost perfect, as expected because $\gamma(L)$ is close to 1. At higher levels the resynthesized waveforms are very similar to the original ones, but there appear small deviations, in the course of the envelope waveform as well as in the phase of the oscillations. Four vertical dotted lines are added to the figure to illustrate that the zero-crossings are nearly invariant with stimulus level.

Figure 8 shows results for the experiments used for Fig. 3 [panels (a)–(e)] and Fig. 4 [panels (f)–(j)]. For all three experiments illustrated by Figs. 7 and 8 the correspondence between original and resynthesized impulse responses is outstanding, the more so when we take into account how the BM impedance is represented by Eq. (5) as the sum of two terms both having considerable inherent errors. We found corresponding results in 11 other experiments, envelope variations were similar to those shown in Figs. 7 and 8, and the zero-crossings were never more than 0.1 period different between original and resynthesized responses. As implied earlier, v_1 had to be adjusted to each individual experiment but one value then served for all stimulus levels. The largest variations of v_1 with respect to the earlier mentioned value of 1100 amounted to a factor of 3, mostly upward. What is important here is that *the model's impulse response displays almost the same near-invariance of timing as the original impulse response*. In this way, question (C) posed in Sec. III has also been answered in the affirmative. For different values of L the BM impedance functions in the model differ only in the second term of Eq. (5). Apparently, this is one condition to leave the phase of the impulse-response oscillations nearly the same. We have not been able to prove that this condition is necessary (in the mathematical sense).

The condition is not sufficient either. From Part I we recall that one locally active model of the cochlea, Geisler and Sang (1995), qualitatively shows the correct “glide” property while another one, Neely and Kim (1986), does not.

If we vary the feedback factor in these models—to mimic variations of stimulus level—we find that the Geisler–Sang model approximately shows the near-invariance property while the Neely–Kim model does not. It is important to note that *both* models obey the conditions for the EQ-NL theorem, and their BM impedances thus should obey Eqs. (4) and (5). Therefore, the model property that corresponds to near-invariance of timing in the impulse response is a subtle one. Further study is needed to work out the exact connection.

VI. SUMMARY AND CONCLUSIONS

For stimulation by weak signals it is generally agreed that the cochlea operates as a linear system. In Part II of this series it has been shown that in that case the stimulus–response relation of the cochlea can be simulated by that of a well-chosen model. Characteristically, that model is locally active. In the present paper the procedure is extrapolated to the case where the cochlea is nonlinear. By invoking the EQ-NL theorem the result can be interpreted in terms of a linear model (“ $\mathcal{M}\text{-}\mathcal{L}in$ ”). When stimulus level increases, the degree of activity in model “ $\mathcal{M}\text{-}\mathcal{L}in$ ” is found to decrease (Figs. 2–4).

In this paper one further step is taken: from *analysis* to *prediction*. First, the EQ-NL theorem predicts that the BM impedance is a linear combination of two components, the “two-component theory of the BM impedance.” This is expressed by Eq. (4). Second, the same theorem provides the way to *calculate* the reduction of activity as a function of stimulus level. Given the functional form of OHC transduction, only one parameter, the scaling factor v_1 , is involved. The result is the (real) transduction efficiency coefficient $\gamma(L)$ which goes from 1 to 0 with increasing L . With this theory the variations in the BM impedance function with stimulus level can be explained quite well. For the best fit to the average of an earlier data set, $\gamma(L)$ should reduce to 0.5 when the stimulus level is 73 dB. However, for each of the experiments illustrated by Figs. 6–8 the stimulus level L at which $\gamma(L)$ reduces to 0.5 is larger than 80 dB. That level is indeed found to be higher than 73 dB in the majority of the 14 experiments in which we tested the “two-component theory of the BM impedance.”

These findings can be compared to published data for the guinea pig. In Yates *et al.* (1989) the local cochlear microphonic (CM) potential is reduced to 50% of its maximum value by a tone of 83 dB SPL (see Fig. 4 of that paper); see also Geisler *et al.* (1990). Patuzzi *et al.* (1989) report [see their Fig. 1(c)] that the CM reduces to 50% at slightly over 80 dB SPL. Measuring the CM potential can be seen as estimating the efficiency of the OHCs. Given the enormous differences in experimental technique, the agreement with our estimates is satisfactory.

The same two-component theory of the BM impedance has been applied to *individual experiments*. For each experiment the appropriate value of the scaling factor v_1 has to be selected. With the two-component impedance the model is capable of reproducing all aspects of the processing that noise signals undergo in the cochlea, for all stimulus levels. In the frequency domain this property includes correct reproduction of

- (i) variation of frequency selectivity,
- (ii) the downward shift of the peak frequency, and
- (iii) compression of the response amplitude with varying stimulus level (see Fig. 6).

In the time domain typical characteristics of the impulse response are simulated:

- (i) the shape of the envelope of the impulse response, and
- (ii) the glide.

In the measured time-domain responses a long-known property is confirmed:

- (iii) With increasing stimulus level the timing of the individual oscillations remains approximately constant; this near-invariance is also accurately simulated by the model's impulse response (see Figs. 7 and 8).

Characteristic is the fundamental property that the BM impedance is a linear combination of two fixed impedance functions [Eq. (4)] and that only the coefficient $\gamma(L)$ of one of these varies with stimulus level L . It follows that *one* model now explains *all* manifestations of nonlinearity due to variations in the noise stimulus level L . Only one parameter, v_1 , needs to be adapted to an individual experiment but one value serves for all levels L . This illustrates the far-reaching potential of the two-component theory. In Sec. V we explained that the two-component theory for the BM impedance is not a necessary-and-sufficient condition for near-invariance.

In Sec. I we proposed that the near-invariance of the timing of oscillations in the (resynthesized) impulse response should be taken into account in judging the validity of a cochlear model. We have found in Sec. V that a model that is provided with a BM impedance that consists of two components of which only the coefficient of one of the components varies with stimulus level [as in Eq. (4)] is indeed capable of explaining near-invariance of timing in the impulse response. Therefore, with the two-component theory of the BM impedance, we can quantitatively understand the way in which cochlear nonlinearity, frequency selectivity, peak frequency, signal amplitude and impulse-response (waveform *and* timing) vary with stimulus level. All this applies only to the case of stimulation by wideband noise, and under the assumption that the real cochlea operates as the model we have been using, of course.

ACKNOWLEDGMENTS

The work for this paper was carried out in two countries. The authors are indebted to (in alphabetical order) Gary Dootz, Anders Fridberger, Meng He Guo, Bob Masta, Darren Miller, Irina Omelchenko, Edward Porsov and Jiefu Zheng, for their help in setting up and performing the experiments. Fruitful discussions with Laurel Carney on the relation between neural timing and stimulus intensity are gratefully acknowledged. Two anonymous JASA reviewers provided useful suggestions for improving the text. The USA part of this work has been supported by NIH, under Grant No. NIDCD-DC-00141, and VA Rehabilitation Research &

Development Center (Grant No. RCTR-597-0160, Portland, VAMC); the part carried out in The Netherlands is the continuation of project No. SLW 01.011 of the Netherlands Foundation for Scientific Research (NWO).

APPENDIX A: THE EQ-NL THEOREM—BASIS AND MEANING

For the purpose of this paper it is necessary to review the basic premises of the cochlear model in somewhat greater detail than has been done in previous papers. This has specifically to do with the elements of the model that are assumed responsible for amplifying the cochlear fluid wave and are also assumed to be the sources of nonlinearity. Consider a model “ $\mathcal{M}\text{-}\mathcal{NL}$ ” of the cochlea consisting of two elongated fluid-filled channels separated by the “cochlear partition” containing the organ of Corti. Along the entire length of the model, a part of the width of the partition is occupied by a flexible membrane, the basilar membrane (BM). It is assumed that outer hair cells (OHCs) of the organ of Corti are able to cause a local sound pressure $p_{\text{OHC}}(x, t)$ (an oscillating pressure, on a cycle-to-cycle basis) which gives rise to an additional component $p_{\text{add}}(x, t)$ of the sound pressure $p(x, t)$ near the BM in the fluid. By way of this extra pressure the OHCs may enhance and sharpen the frequency response of the system via amplification of the cochlear wave. Transduction in the OHCs is assumed to be nonlinear (saturating) and instantaneous which makes the model *nonlinear*. All other signal transformations in the model are linear (but are place and frequency dependent).

We also consider a “comparison model,” called “ $\mathcal{M}\text{-}\mathcal{Lin}$ ” in this paper, which is *linear* and identical in structure and functioning to the nonlinear model when that works with extremely weak signals. Responses and variables in this model are expressed in the frequency or ω domain. In model “ $\mathcal{M}\text{-}\mathcal{Lin}$,” $p_{\text{OHC}}(x, \omega)$ and $p_{\text{add}}(x, t)$ both have to be multiplied by the (real) factor γ that is called the *transduction efficiency coefficient*. Let γ be 1 for optimal operation of the model, corresponding to stimulation with very weak signals. The coefficient γ will be smaller in a model that represents a strongly stimulated or deteriorated cochlea and zero in a “dead” cochlea. Saturation of the OHCs in the nonlinear model “ $\mathcal{M}\text{-}\mathcal{NL}$ ” thus corresponds to a decrease of γ in the linear model “ $\mathcal{M}\text{-}\mathcal{Lin}$.” The EQ-NL theorem states the following correspondence between the two models, the nonlinear model under study and the linear model:

The input–output cross-correlation function (ccf) for the nonlinear model “ $\mathcal{M}\text{-}\mathcal{NL}$ ”, determined with a wideband random-noise input signal with a given stimulus level, is equal to the ccf for model “ $\mathcal{M}\text{-}\mathcal{Lin}$ ” that has exactly the same structure and the same parameters, but in which all OHCs are linear and operate with a reduced efficiency coefficient γ .

Further properties are described by the following:

With wideband flat-spectrum random-noise stimuli the efficiency coefficient γ is the same for all OHCs and for all frequencies. With stronger stimuli γ will be reduced more and more.

The acronym EQ-NL has been chosen to emphasize the aspects of “equivalence” and “nonlinearity.” For the proof of the theorem, see de Boer (1997). The main argument in this proof is that at the input to each nonlinear OHC transducer a composite noise signal is present (with a near-Gaussian distribution and a large number of components) which causes each component of that signal to be *compressed* (in the average) to exactly the same degree (the factor γ). Note that for one OHC this compression is *the same for all frequencies* because the nonlinearity involved is memoryless and the component amplitudes are small. The latter condition requires that all signals have a large number of degrees of freedom.⁴ In its concentration upon the handling of small-amplitude components, the EQ-NL theorem forms an extension to the pseudo-linear solution method advocated by Kanis and de Boer (1993), which has proven useful in the study of two-tone suppression and distortion-product generation (Kanis and de Boer, 1994, 1997).

For a no-memory transducer with transducer characteristic $F(\cdot)$ and input signal u the average transduction coefficient γ is given by

$$\gamma = \int_{-\infty}^{\infty} F'(u)P(u)du, \quad (\text{A1})$$

where $P(u)$ is the probability density of the signal u , $F'(\cdot)$ is the derivative of $F(\cdot)$ which should be a monotonically decreasing function of the magnitude of its argument, and $F'(0)$ is assumed to be equal to 1. Then, for very small signals the coefficient γ is equal to 1. For stronger signals γ expresses, by its reduction from 1, the *average state of saturation* in the system. How γ can actually be calculated is detailed in Appendix B.

If we assume that the functioning of the actual cochlea can be described by the nonlinear model under consideration, the signals involved in the theory can be replaced by the ones used and obtained in the experiment, and conclusions about the cochlea can be formulated in terms of properties of the linear “comparison model,” model “ $\mathcal{M}\text{-}\mathcal{L}in$.” In order to carry out the entire procedure on recorded data, stimulation has to occur with wideband flat-spectrum noise signals and “responses” are to be acquired in the form of input–output cross-correlation functions (ccfs).

APPENDIX B: THE EFFICIENCY OF TRANSDUCTION

Let the input to one outer hair cell (OHC) be the deflection $d_{cil}(x,t)$ of the OHC stereocilia. The output is the local pressure $p_{OHC}(x,t)$ mentioned in Appendix A. Express the nonlinear instantaneous transduction function of the OHC by

$$p_{OHC}(x,t) = S_0 d_1 F[d_{cil}(x,t)/d_1], \quad (\text{B1})$$

where $F(\cdot)$ is a saturating no-memory nonlinear real function that is equal to its argument for very small values of the argument and remains finite for extreme values of the argument, d_1 is a scaling factor for $d_{cil}(x,t)$, and S_0 is a constant. Assume the signal $d_{cil}(x,t)$ to be narrow-band noise with a large number of degrees of freedom. Transduction of each of the many (small) components of $d_{cil}(x,t)$ will be determined by the average slope $F'(\cdot)$ of the function $F(\cdot)$, averaged

over all values of the signal $d_{cil}(x,t)$ [see Eq. (A1)]. Because $d_{cil}(x,t)$ is a linear transform of BM displacement $d_{BM}(x,t)$, the function $F'(\cdot)$ can also be averaged over the distribution of $d_{BM}(x,t)$ provided a different normalization constant is introduced instead of d_1 . Similarly, we can work with the normalized BM *velocity* $v_{BM}(x,t)$ instead of the normalized BM *displacement*. This leads to the alternative formulation

$$p_{OHC}(x,t) = Z_0 v_1 F[v_{BM}(x,t)/v_1], \quad (\text{B2})$$

where we have introduced another constant Z_0 instead of S_0 and a new scaling factor, v_1 . We will take care of the filtering between BM velocity and ciliary deflection, and the associated phase difference, later. Because this filtering is assumed to be linear, the ratio of the coefficients v_1 and d_1 does not depend on stimulus level.

In model “ $\mathcal{M}\text{-}\mathcal{L}in$ ” (see Appendix A), OHC transduction is written as

$$p_{OHC}(x,\omega) = \gamma Z_1(x,\omega) v_{BM}(x,\omega). \quad (\text{B3})$$

This pressure can be represented by a complex number, and its amplitude will be proportional to the real coefficient γ . There will also be a phase shift that is part of the transformation between BM velocity and ciliary displacement. This phase shift does not vary with stimulus level and the transformation can thus adequately be represented by the complex coefficient $Z_1(x,\omega)$. Another phase shift is relevant: that between the local OHC-generated $p_{OHC}(x,\omega)$ and the corresponding component $p_{add}(x,t)$ of the pressure $p(x,\omega)$ near the BM. This phase shift does not vary with stimulus level either. Equation (B3) has the following counterpart for the pressure component $p_{add}(x,t)$:

$$p_{add}(x,\omega) = \gamma Z_2(x,\omega) v_{BM}(x,\omega). \quad (\text{B4})$$

The entire space- and frequency-dependent filtering in the feedback path—from the BM via $p_{OHC}(x,\omega)$ and $p_{add}(x,t)$ back to the BM—and both phase shifts involved are included in the (complex) coefficient $Z_2(x,\omega)$. By using complex functions we thus have incorporated the phase shifts and filtering that we formerly omitted. A more detailed formulation is found in Kanis and de Boer (1993).

In good approximation the probability distribution of $d_{cil}(x,t)$ as well as $v_{BM}(x,t)$ will be Gaussian. We then find the efficiency coefficient γ of OHC transduction as the average slope $F'(u)$ of $F(u)$ over the values of $[v_{BM}(x,t)/v_1]$ for a Gaussian distribution [see Eq. (A1)]:

$$\gamma = \int_{-\infty}^{\infty} F'(av_{rms}/v_1)P_G(a)da, \quad (\text{B5})$$

where v_{rms} is the rms value of $v_{BM}(x,t)$ and $P_G(\cdot)$ stands for the Gaussian probability density function with unity variance. When we know the form of $F(u)$ and the value of v_1 , we can calculate γ as a function $\gamma(L)$ of stimulus level L because v_{rms} is assumed to depend on L in the way expressed by Eq. (3) of the main text.

The exact form of the nonlinear transfer function $F(u)$ is not critical. As the basis for $F(u)$ the hyperbolic tangent function as used in the work of Kanis and de Boer (1993) is taken. A weighted sum of two such functions has a two-stage

variation of the slope which corresponds better to the non-linear odd-order character of hair-cell transfer functions (cf. Geisler, 1998, Figs. 8.3 and 8.5):

$$F(u) = [\tanh w + c \tanh(w/c)] / (1 + c), \quad (\text{B6})$$

where

$$w = (1 + c)u/2. \quad (\text{B7})$$

The parameter c is a constant which must be nonzero. For every value of c the function $F(u)$ has unity slope at $u=0$ and it reaches $+1$ for $u \rightarrow \infty$ and -1 for $u \rightarrow -\infty$. For $c = 1$, $F(u)$ reduces to a single tanh function. The parameter c is taken equal to 0.2. For $u=1$, $F(u)$ is equal to 0.613. Substitution of Eq. (B6) into Eq. (B5) yields the efficiency coefficient γ as a function of v_{rms}/v_1 . For v_{rms} equal to v_1 , γ becomes equal to 0.513. Application of Eq. (3) of the main text gives γ as a function $\gamma(L)$ of stimulus level L .

¹This study was consistent with NIH guidelines for humane treatment of animals and was reviewed and approved by the University of Michigan Committee on Use and Care of Animals and the Oregon Health Sciences Committee on the Use and Care of Animals.

²MATLAB[®] programs for inverse and forward model solutions using sparse matrices can be requested from the first author (preferably via e-mail).

³The slight flattening of the curves to the right is due to smoothing of the BM impedance function.

⁴The number of degrees of freedom is $2WT$, where W is the bandwidth and T is the period of the pseudo-random noise. In our experiments $2WT$ is minimally of the order of 40. For the strongest stimuli it is of the order of 180. These values are large enough for the formalism described to be applicable.

Carney, L. H. (1993). "A model for the responses of low-frequency auditory-nerve fibers in cat," *J. Acoust. Soc. Am.* **93**, 401–417.

Carney, L. H., and Yin, T. C. T. (1988). "Temporal coding of resonances by low-frequency auditory nerve fibers: Single fiber responses and a population model," *J. Neurophysiol.* **60**, 1653–1677.

Carney, L. H., McDuffy, M. J., and Shekhter, I. (1999). "Frequency glides in the impulse response of low-frequency auditory-nerve fibers," *J. Acoust. Soc. Am.* **105**, 2384–2391.

de Boer, E. (1981). "Short waves in three-dimensional cochlea models: Solution for a 'block' model," *Hear. Res.* **4**, 53–77.

de Boer, E. (1983). "No sharpening? A challenge for cochlear mechanics," *J. Acoust. Soc. Am.* **73**, 567–573.

de Boer, E. (1997). "Connecting frequency selectivity and nonlinearity for models of the cochlea," *Aud. Neurosci.* **3**, 377–388.

de Boer, E. (1998). "A method for forward and inverse solutions of a three-dimensional model of the cochlea," *J. Acoust. Soc. Am.* **103**, 3725–3728.

de Boer, E., and Nuttall, A. L. (1997a-DAM). "On cochlear cross-correlation functions: connecting nonlinearity and 'activity'," in *Diversity in Auditory Mechanisms*, edited by E. R. Lewis, G. R. Long, R. F. Lyon,

P. M. Narins, C. R. Steele, and E. Hecht-Poinar (World Scientific, Singapore), pp. 291–297.

de Boer, E., and Nuttall, A. L. (1997b-GLIDE). "The mechanical waveform of the basilar membrane. I. Frequency modulations ('glides') in impulse responses and cross-correlation functions," *J. Acoust. Soc. Am.* **101**, 3583–3592.

de Boer, E., and Nuttall, A. L. (1999-INV-3). "The 'inverse problem' solved for a three-dimensional model of the cochlea. III. Brushing-up the solution method," *J. Acoust. Soc. Am.* **105**, 3410–3420.

de Boer, E., and Nuttall, A. L. (2000-DMD). "The mechanical waveform of the basilar membrane. II. From data to models—and back," *J. Acoust. Soc. Am.* **107**, 1487–1496.

Geisler, C. D. (1998). *From Sound to Synapse* (Oxford U.P., Oxford).

Geisler, C. D., and Sang, C. (1995). "A cochlear model using feed-forward outer-hair-cell forces," *Hear. Res.* **86**, 132–146.

Geisler, C. D., Yates, G. K., Patuzzi, R. B., and Johnstone, B. M. (1990). "Saturation of outer hair cell receptor currents causes two-tone suppression," *Hear. Res.* **44**, 241–256.

Kanis, L. J., and de Boer, E. (1993). "Self-suppression in a locally active nonlinear model of the cochlea: A quasi-linear approach," *J. Acoust. Soc. Am.* **94**, 3199–3206.

Kanis, L. J., and de Boer, E. (1994). "Two-tone suppression in a locally active nonlinear model of the cochlea," *J. Acoust. Soc. Am.* **96**, 2156–2165.

Kanis, L. J., and de Boer, E. (1997). "Frequency dependence of acoustic distortion products in a locally active model of the cochlea," *J. Acoust. Soc. Am.* **101**, 1527–1531.

Kiang, N. Y.-S., Watanabe, T., Thomas, E. C., and Clark, L. F. (1965). *Discharge Patterns of Single Fibers in the Cat's Auditory Nerve* (MIT, Cambridge, MA).

Neely, S. T., and Kim, D. O. (1986). "A model for active elements in cochlear biomechanics," *J. Acoust. Soc. Am.* **79**, 1472–1480.

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.

Nuttall, A. L., Dolan, D. F., and Avinash, G. (1990). "Measurements of basilar membrane tuning and distortion with laser Doppler velocimetry," 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. 288–295.

Patuzzi, R. B., Yates, G. K., and Johnstone, B. M. (1989). "Outer hair cell receptor current and its effect on cochlear mechanics," in *Cochlear Mechanisms: Structure, Function and Models*, edited by J. P. Wilson and D. T. Kemp (Plenum, New York), pp. 169–176.

Recio, A., Rich, N. C., Narayan, S. S., and Ruggero, M. A. (1998). "Basilar-membrane responses to clicks at the base of the chinchilla cochlea," *J. Acoust. Soc. Am.* **103**, 1872–1889.

Robles, L., Rhode, W. S., and Geisler, C. D. (1976). "Transient response of the basilar membrane measured in squirrel monkeys using the Mössbauer effect," *J. Acoust. Soc. Am.* **59**, 926–939.

Ruggero, M. A., Rich, N. C., and Recio, A. (1992). "Basilar membrane responses to clicks," in *Auditory Physiology and Perception*, edited by Y. Cazals, L. Demany, and K. Horner (Pergamon, London), pp. 85–91.

Yates, G. K., Geisler, C. D., Patuzzi, R. B., and Johnstone, B. M. (1989). "Saturation of receptor currents accounts for two-tone suppression," in *Cochlear Mechanisms: Structure, Function and Models*, edited by J. P. Wilson and D. T. Kemp (Plenum, New York), pp. 177–187.