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The mechanical waveform of the basilar membrane.

IV. Tone and noise stimuli^{a)}

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Analysis of mechanical cochlear responses to wide bands of random noise clarifies many effects of cochlear nonlinearity. The previous paper [de Boer and Nuttall, *J. Acoust. Soc. Am.* **107**, 1497–1507 (2000)] illustrates how closely results of computations in a nonlinear cochlear model agree with responses from physiological experiments. In the present paper results for tone stimuli are reported. It was found that the measured frequency response for pure tones differs little from the frequency response associated with a noise signal. For strong stimuli, well into the nonlinear region, tones have to be presented at a specific level with respect to the noise for this to be true. In this report the nonlinear cochlear model originally developed for noise analysis was modified to accommodate pure tones. For this purpose the efficiency with which outer hair cells modify the basilar-membrane response was made into a function of cochlear location based on *local* excitation. For each experiment, the modified model is able to account for the experimental findings, within 1 or 2 dB. Therefore, the model explains why the type of filtering that tones undergo in the cochlea is essentially the same as that for noise signals (provided the tones are presented at the appropriate level). © 2002 Acoustical Society of America. [DOI: 10.1121/1.1428548]

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I. INTRODUCTION

In the three preceding papers of the present series (de Boer and Nuttall, 1997, 2000a, 2000b), henceforth to be called Part I, Part II, and Part III, respectively, results of experiments were reported on movements of the basilar membrane (BM) in the cochlea of the guinea pig. Measurements were done with a laser velocimeter, at a cochlear location showing tuning to frequencies in the region of 15 to 18 kHz. Measured responses were compared to the response of a suitably chosen nonlinear bio-mechanical model of the cochlea. In Parts II and III it was demonstrated that via “re-synthesis” this model can be given a response that closely matches the response of the real cochlea. The analysis includes effects of model geometry (Part II) as well as general and subtle effects of nonlinearity in the cochlea due to variations in stimulus level (Part III).

The basic stimulus signal in the experiments described was always wideband noise. This was so because we used a nonlinear cochlear model for which noise signals are optimum stimuli. The mechanical variables and operations acting in a cross section of that model are sketched in Fig. 1. For simplicity only one outer hair cell (OHC) is shown. Each OHC has an input signal, the ciliary deflection $d_{cil}(x, t)$,

which is directly derived from the BM velocity $v_{BM}(x, t)$ by the transformation H_1 . The dynamic variable x denotes position along the length of the model, and t is time; for reasons of clarity these independent variables have been omitted from the figure. The transformation H_1 is assumed to be linear, but will be frequency- and location dependent.¹ The output signal of the OHCs is the local OHC pressure $p_{OHC}(x, t)$. This pressure can be considered to arise from OHC motility, or, alternatively, as resulting from a reaction force produced by the stereocilia; for the functioning of the model these alternatives are equivalent. The pressure $p_{OHC}(x, t)$ gives rise to an *additive* component $p_{add}(x, t)$ of the sound pressure $p(x, t)$ near the BM, again via a linear (and possibly location- and frequency-dependent) transformation, H_2 . In the case where OHC activity occurs via somatic motility, most of the frequency selectivity involved in the feedback loop will be included in H_1 . In the case where active reactions of stereocilia are the main source of feedback, the frequency selectivity will be more or less equally divided between H_1 and H_2 (because of reciprocity). Over a certain range of locations and frequencies the loop shown in Fig. 1 produces positive feedback, whereby the pressure $p_{add}(x, t)$ acts to enhance the response (“local activity”). Transduction in the OHCs, from ciliary deflection $d_{cil}(x, t)$ to local OHC pressure $p_{OHC}(x, t)$, is described as a memoryless compressive nonlinearity. In the model, the nonlinearity of the OHCs is considered to be responsible for all nonlinear mechanical effects that have been observed over the normal

^{a)}Preliminary data on tone versus noise responses were reported at the ARO 2000 Midwinter Meeting (Abstract No. 705).

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FIG. 1. Signal transformations in a cross section of the model. See the text for the meaning of symbols.

operating range of the cochlea. Note that OHCs described as memoryless nonlinearities are present throughout the cochlea, all embedded in structures with different frequency responses. This means that a model with memoryless nonlinearities can exhibit frequency-dependent nonlinearity.

The EQ-NL theorem can be applied to a nonlinear model of this type (de Boer, 1997a). This theorem is formulated in terms of input-output cross-correlation functions (ccfs) for wideband noise signals, and this is where the requirement of using noise stimuli stems from. (A short description of the theorem can be found in Appendix A of Part III.) All conclusions from the analysis relate only to responses to wideband noise signals.

If the model of Fig. 1 is a valid model, it should be equally well applicable to the case where stimuli are sinusoidal signals. This is the subject studied in the present paper. The main characteristic of the model is that the degree of saturation is fully determined by the *total* signal $d_{cil}(x,t)$ acting at the input of the OHCs. For a noise stimulus this signal will contain many components, and will be (nearly) Gaussian, but for sinusoidal stimulation it contains one dominant component and a few weaker ones, and is non-Gaussian. Furthermore, strong pure tones and noise signals have quite different distributions of the degree of OHC saturation over the length of the cochlea. For strong wideband noise signals saturation is evenly distributed, whereas for a strong tone it is more localized to the region of the response peak.

Our hypothesis is that noise components and sinusoidal signals are handled in an identical way when the average degree of saturation they evoke in the OHCs are the same. We will investigate whether the same model, with the same parameters and the same nonlinearity, can predict responses to sinusoidal signals as well as to noise signals. If it does, we can apply that model to the consideration of many more types of signal than wideband flat-spectrum noise, to formants and formant transitions in speech stimuli, for instance. Furthermore, the value of the model for predicting distortion products on the basilar membrane can be studied. In none of these applications should it be necessary to resort to time-domain computations.

FIG. 2. Propagation of a single component of a noise stimulus (16.8 kHz) in a cochlear model. Amplitude of the response, corrected for the stapes response (see the text). On the ordinate the ratio 1 corresponds to 0 dB. Abscissa: distance from stapes/round-window location. Two stimulus levels, 60 dB apart. For the lower one, (solid line) propagation is a linear process. For the higher one (dashed line) partial saturation causes nonlinearity.

II. GENERAL CONSIDERATIONS: A STRATEGY

Let us first consider what happens to a single-frequency component of a noise signal inside the cochlea. The noise response has been measured at one location x , and has been analyzed into its frequency components.² The lower curve in Fig. 2 (solid line) illustrates the amplitude of the wave produced by one of the frequency components—as we imagine it to propagate in the cochlea. In this case the stimulus had a low intensity (20 dB per octave). The measured response has been transformed to a function of location x by assuming that the cochlea “scales,” i.e., that different frequencies (f) project to different locations (x) along the length of the cochlea. In particular, we assume that the log of the frequency f transforms linearly to location x [for more details see de Boer and Nuttall (1999)]. The abscissa in Fig. 2 denotes location x starting at the stapes. The figure shows the amplitude of the noise component at 16.7 kHz. Because this is a high frequency, and does not travel far, it is not necessary to make the model longer than 6 mm. The phase is omitted from the figure and is not considered in this report.³

For the solid line the noise signal was presented at 20 dB (SPL) per octave. For each frequency the spectral component is normalized with respect to the stapes velocity as if the stapes response were measured at the same frequency and *at the same spectral level*. If the cochlea operates linearly, the solid line of Fig. 2 will also show the response pattern of a 16.7-kHz *pure tone*, at least when it is plotted normalized to the stapes response *for the same stimulus*.

The BM velocity is seen to rise gradually with increasing x from the stapes location ($x=0$). In a spatial region that is specific to the frequency, the BM velocity rises more rap-

idly to reach a maximum. In that region the cochlear wave is amplified by the BM and its associated cell structures—positive feedback resulting from the loop shown in Fig. 1. After having passed that region the wave extinguishes rapidly. In the peak region, size and form of the response are controlled by the feedback loop; outside the peak region the influence of the feedback is small. As stated above, the pattern is shown for the frequency 16.7 kHz. For a component or a tone with a higher frequency the response maximum will lie more to the left, nearer to the stapes; for a lower frequency it will lie more to the right. Frequency- and place-dependent properties of the BM and the feedback loop are responsible for this type of scaling.

With stronger stimulation the cochlea will react in a nonlinear way. While the *solid* line in Fig. 2 shows the propagation of the 16.7-kHz component of a noise signal presented at 20 dB per octave, the *dashed* line shows the response to a signal at 80 dB (SPL) per octave, transformed by the same frequency-to-place (f -to- x) transformation. The response is normalized with respect to the same stapes noise response at 20 dB (SPL) per octave so that the leftmost part of the dashed curve lies 60 dB higher than the solid line. Clearly, the peak of the high-level response is depressed in size, the bandwidth is increased, and the location of the maximum has moved to the left. All three effects are well-known properties of cochlear nonlinearity. In terms of the model, the nonlinear effects are attributed to *partial saturation* of the outer hair cells (OHCs).

For a strong wide band of *noise*, the average amplitude of vibration of the BM will be about the same for all locations along the length of the cochlea. Consequently, all OHCs will be excited to about the same extent, and will be saturated to about the same degree. The 80-dB response pattern shown by the dashed line in Fig. 2 is associated with such an even distribution of saturation. For stimulation by a strong *tone* the situation is entirely different. In the initial part of the wave, near the stapes, there will be only little saturation because the wave amplitude is small. When the wave is nearing the peak, saturation becomes more and more pronounced until it reaches a maximum at the response peak. After the wave has passed the peak, saturation rapidly vanishes. The tone response should show a peak of the same general shape as a noise component when the degrees of saturation are the same. It should be clear, now, that we have to modify the formalism that we used to explain noise responses in order to accommodate tones. To explain noise responses by our nonlinear model, we used a coefficient γ , signifying the degree of saturation, $\gamma=1$ for no saturation and $\gamma=0$ for complete saturation (or absence of OHCs). See Part III of this series. The parameter γ is independent of x . In the case of tone stimulation, we have to replace this by a function $\gamma(x)$ of x . The local value of $\gamma(x)$ reflects the *local* excitation.

The principal questions we are asking and trying to answer in this paper are: (a) What is the frequency response of the cochlea measured for tones compared to that for noise? and (b) Can the nonlinear model that we used to explain noise responses be extended (in the way we just indicated) to account for the data? Finally, there probably will be differ-

ences between the responses to tones and noise. Can we explain these by the same mechanism?

III. DATA ACQUISITION AND PROCESSING

We collected data on movements of the basilar membrane (BM) in the basal turn of the guinea-pig cochlea with a laser velocimeter (see Nuttall *et al.*, 1991 and Part I).⁴ In the earlier described experiments *bands of flat-spectrum pseudorandom 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. One period of the noise signal contains 4096 samples, presented at the rate of 208 kHz. As a consequence, the frequency components are spaced by 50.78 Hz. Noise-response data were collected in the form of input–output cross-correlation functions (ccfs). For greater accuracy we collected “composite ccf spectra” responses; we this did by combining sections of ccf spectra measured with flat-spectrum stimuli of different bandwidths, central frequencies, and intensities in the same animal. The high-frequency part was measured with a noise signal 1 octave wide, presented at stimulus level L . In the lower frequency ranges the cochlea is (nearly) linear, and filtered noise bands at higher stimulus levels could be used. See de Boer and Nuttall (1999) for details. The resulting composite ccf spectrum represents the response to a noise signal that covers more than 5 octaves, from below 1 kHz to well over 40 kHz. The spectral level (in dB SPL per octave) associated with the response is the level L employed in measuring the highest frequency band.

Responses to *tones* were gathered with sinusoidal stimuli. Tone bursts were 380 ms in duration, and had by default an abrupt onset. Except for extremely strong stimuli well above the best frequency (BF) the abrupt onset had no effect on amplitude and phase of the averaged response. We verified that this was the case. All data, for noise and tone stimuli, are corrected for the stapes response.⁵ Tones were presented in steps of 5 dB. In the processing of responses data could be interpolated in steps of 1 dB.

As regards inverse solution and resynthesis, the “stylized” three-dimensional model of Part III was used, with the same parameters. The model equations were solved by the efficient solution method described by de Boer (1998). The inverse solution produces the BM impedance, to be denoted by $Z_{BM}(x, \omega)$, where the independent variable x is the longitudinal coordinate of the model and ω is constant (made equal to 2π times the best frequency for low-level signals).

IV. RESULTS I: THE MEASURED FREQUENCY RESPONSE

Figure 3 shows a typical result, response amplitudes for tones and noise, plotted together as functions of frequency, for experiment 9924. All noise response data are normalized by the stapes response measured with wideband noise presented at 50 dB (SPL) per octave. Upper and lower parts of the figure refer to two values for the noise stimulus level, 50 and 80 dB (SPL) per octave, respectively. Recall that the

FIG. 3. Comparison of measured responses to tones (circles) and noise signal components (solid line). Experiment 9924 (amplitudes shown only). Data are corrected for the stapes response (see the text). Two stimulus levels for the noise signal, 50 and 80 dB SPL per octave. The response to the stronger noise stimulus is compared with responses to tones presented at three levels, 60, 70, and 80 dB SPL. The 70-dB response gives the best fit.

responses have been measured at a cochlear location that has 16.7 kHz as its best frequency for low stimulus levels.

Consider first the lowermost part of the figure; it represents weak-signal stimulation. The *solid line* shows the amplitude of the frequency response for a wideband noise signal presented at 50 dB (SPL) per octave. Each spectral component, when presented alone, would be equivalent to a tone of approx. 17 dB (SPL). The data shown are derived from a “composite-spectrum” file as described in Sec. III. For the solid line the amplitude plotted corresponds to the ratio of BM velocity to stapes velocity. The *small circles* show the response to single pure tones presented at 40 dB (SPL)—weak enough to render the cochlea linear. Forty-one frequencies distributed over two octaves were selected, and presented one by one. The tone responses are shown scaled as if each tone were presented at the same level (17 dB SPL) as one component of the noise stimulus. Outside the peak region some circles are drawn smaller, denoting that in the tone measurements the signal-to-noise ratio decreased to below 30 dB. Over the entire frequency range the circles practically lie on the solid curve, indicating that the cochlea is indeed reacting in a linear way. For all stimulus levels in the linear range we can expect the same type of relation between tone and noise responses. Hence, if we were to plot responses to 20- or 30-dB tones, *with appropriate scaling*, the circles would again nearly lie on the continuous line.

The upper sets of curves in Fig. 3 illustrate noise (solid line) and tone results (circles) for a higher level of the noise stimulus (80 dB SPL per octave). The scaling of the noise response is the same as before so that in the low-frequency region the solid curve (noise response) lies 30 dB above the

FIG. 4. Comparison of measured responses to tones (circles) and noise signal components (solid line). Experiment 9922. High-, medium-, and low-level responses superimposed (amplitudes shown only). Levels as indicated. For amplitude scaling see the text.

curve for 50 dB per octave. Three sets of tone-response data are shown, measured at three stimulus levels, 60, 70, and 80 dB (SPL). For each set the tone response is scaled with respect to the stapes response at its own level minus 30 dB so that the low-frequency part of the graph nearly coincides with the noise response. This is not so in the peak region, where the sharpness depends on level. The tone response measured at 70 dB (SPL) produces the best agreement with the noise-response curve. Tones at 80 dB (SPL) produce a response that is too flat, tones at 60 dB (SPL) a response that is too sharp. For the optimum stimulus level (70 dB SPL) the frequency selectivity of the cochlea for tones is virtually the same as for noise. In other words, for that level the effect of nonlinearity is the same for single pure tones as for components of a noise signal.

Other examples of tone-to-noise comparison are shown by Figs. 4, 5, and 6. The solid lines show the noise responses, the sets of circles the tone responses. For all figures the reference level is taken from the noise record with the lowest level (for this record the amplitude is plotted as the ratio of BM to stapes velocity). In these figures three levels of stimulation are illustrated, one in the linear range and two high enough to cause appreciable nonlinearity. At the two higher levels the tone response that produces the best agreement with the noise response has been selected. For optimal agreement the stimulus level of the higher-level tones has to be 5 to 10 dB lower than that of the noise per octave. The four figures also illustrate the variability between experiments.

The results of Figs. 4–6 confirm the conclusion from Fig. 3: for a specific stimulus level the frequency response for tones is almost the same as for noise. We do observe deviations, however, that seem systematic. On the high-

FIG. 5. Comparison of measured responses to tones (circles) and noise signal components (solid line). Experiment 9923. Layout as Fig. 4.

frequency side, the tone responses have a tendency to be a few dB higher than the noise response. In the way of the reasoning presented in Sec. II, some systematic deviations would be expected. When a sinusoidal wave starts to approach the region of the response peak, it will find a region with less saturation than with a noise stimulus. The pure tone may here be amplified somewhat more than a noise component of the same frequency and level. Let us call this effect “ α .” When the tone-evoked wave has passed the peak, it again encounters a region where OHC saturation is less for a

FIG. 6. Comparison of measured responses to tones (circles) and noise signal components (solid line). Experiment 9920. Layout as Fig. 4.

tone than for noise. In that region we may again expect the tone response to be slightly stronger than a noise component response, and we will call this effect “ β .” Apparently, in Figs. 3–6 evidence of effect “ β ” is small but visible, but effect “ α ” cannot be seen. Why does this near-equivalence in frequency response between tones and noise exist? And why are the expected effects “ α ” and “ β ” so small? To explain these results it is necessary to go into modeling of the cochlea in more detail.

V. PROPAGATION OF SINUSOIDAL WAVES IN A NONLINEAR MODEL

We will apply the same “locally active” model (see Fig. 1) as used in preceding papers of the present series to the case of tonal stimulation. As stated in the Introduction, the OHCs are assumed to be nonlinear for strong stimuli as a result of (partial) saturation. In contrast, the two transformations H_1 and H_2 are linear. Both transformations may well be frequency- and place dependent and thus act as filters. In Appendix A a number of relevant relations are derived which will be used in what follows.

In order to develop a method to compute the propagation of a sinusoidal signal in this nonlinear model, two basic principles will be needed. The first one is that in the major part of the model the degree of distortion will be small so that some form of approximation method (or variational analysis) can be applied. For noise stimulation—as studied earlier—combination tones formed by the multitude of frequency components are neglected (shown as justified in de Boer, 1997a). For tone stimulation second- and higher-order harmonics can be neglected so that for the first harmonic the model acts as a *linear* model (see for further justification Kanis and de Boer, 1993, 1997). The second principle is that the *local* propagation of a cochlear wave is mainly determined by the *local* BM impedance $Z_{BM}(x, \omega)$ and its variation with x . The “classical” LG or WKB⁶ solution utilizes that notion in the computation of waves in complicated cochlear models [key papers: Steele and Taber (1979, 1981), generalized analyses of two- and three-dimensional models: de Boer and Viergever (1982, 1984)].

It is easy to understand that the pressure component $p_{add}(x, \omega)$, when divided by the BM velocity $v_{BM}(x, \omega)$, produces an *additive* contribution to the basilar-membrane (BM) impedance $Z_{BM}(x, \omega)$. In other words, the BM impedance is intrinsically built up from two components, the second of which being generated by OHCs, is subject to saturation. In Part III the effect of saturation was expressed by the efficiency coefficient γ that is equal to 1 for weak stimuli and a viable cochlea, and approaches zero for stronger stimuli or in the case of cochlear pathology. The two-component concept of the BM impedance is expressed by Eq. (A8b) of Appendix A. Application of the two principles of the preceding paragraph leads to the assumption that, at every location x , the BM impedance is composed of two terms but that *for tone stimulation* the efficiency coefficient γ depends on *local* stimulation and thus is a function $\gamma(x)$ of x . This is expressed by the following modification of the aforementioned equation:

$$Z_{\text{BM}}(x, \omega) = Z^{\text{pass}}(x, \omega) + \gamma(x)Z^{\text{mact}}(x, \omega). \quad (1)$$

The function $Z^{\text{pass}}(x, \omega)$ is derived from the postmortem response. The function $Z^{\text{mact}}(x, \omega)$ is found as the difference of the BM impedances corresponding to (a) a low-level response from a viable cochlea and (b) the postmortem response. It is repeated that the additivity of the terms in Eq. (1) stems from the fact that the pressure $p_{\text{add}}(x, t)$ in Fig. 1 is to be *added* to the local pressure $p(x, t)$. Once we know $\gamma(x)$ as a function of x , and thus the form of $Z_{\text{BM}}(x, \omega)$, propagation of a pure tone in the (nonlinear) model can be computed from a linear model.

Let us now briefly recapitulate how the two-component theory was used in Part III to account for the effect of stimulus level and how individual experiments were handled. That information is needed in order to develop the method to compare responses to tones and noise in the present paper. The stimulus signal in the earlier work was a wide band of noise. The OHC input signal (deflection of the stereocilia) was assumed to be proportional to v_{rms} , a “synthetic” rms value, which served as a kind of normalized BM velocity amplitude. In the first instance v_{rms} was made proportional to the stimulus amplitude A_1 , but a correction factor C_1 was included to express amplitude compression

$$v_{\text{rms}} = A_1 C_1. \quad (2)$$

Both factors depend on stimulus level L . For 0-dB stimulation level A_1 equals 1, for 20 dB 10, for 40 dB 100, and so on. The compression factor C_1 gradually decreases from 1 to zero for increasing stimulus level, and is around 0.5 for levels of 80 to 90 dB (Part III, Figs. 7 and 8). Neither of the two factors depends on x because for wideband noise the rms BM velocity is (approximately) the same at all locations. Each experiment was characterized by an individual normalization factor v_1 by which v_{rms} was scaled. According to the EQ-NL theorem (de Boer, 1997a), the efficiency γ of OHC transduction is proportional to the average slope of the transducer’s transfer function, averaged over the OHC input signal’s excursions, i.e., averaged over a Gaussian noise signal with v_{rms}/v_1 as its rms value. The nonlinear OHC transduction function is assumed to be the same for all experiments. Taken together, these steps were sufficient to compute γ as a function of stimulus level L for each individual experiment. It was shown in Part III that for noise responses the model response resynthesized from the two-component BM impedance agrees well with experimental data, over the entire range of stimulus levels (L) explored. For different experiments v_1 had to be different, and this was the only parameter to distinguish one experiment from another.

All this applies to (broadband) noise stimuli. The procedure now needs to be adapted to tones. Instead of v_{rms} (valid for uniformly exciting noise) we will define a synthetic rms value $v_{\text{tone}}(x)$ for tone stimulation, but this is no longer a constant. It has become a function of location x . In lieu of Eq. (2) we write

$$v_{\text{tone}}(x) = A_1 C_2(x), \quad (3)$$

where the factor A_1 is proportional to the signal amplitude, but now that of the stimulating tone. The factor $C_2(x)$ is

normalized in such a way that, when it would be evaluated for noise stimulation (at the appropriate stimulus level), and summed over all contributing frequency components, $C_2(x)$ would be equal to C_1 . The method for this summation is detailed in Appendix A. The quotient $v_{\text{tone}}(x)/v_1$ is used to find the effective degree of saturation, in other words, the value of $\gamma(x)$. Appendix B gives details of this transformation (the result of which is slightly different for tones and noise signals).

The *variations* of $C_2(x)$ for tones with x should parallel the *variations* of the ciliary excitation signal $d_{\text{cil}}(x, \omega)$. Appendix A describes how the signal $d_{\text{cil}}(x, \omega)$ depends on the BM velocity $v_{\text{BM}}(x, \omega)$. We repeat Eq. (A9)

$$d_{\text{cil}}(x, \omega) = -\frac{Z^{\text{mact}}(x, \omega)}{2S_0(x)}v_{\text{BM}}(x, \omega), \quad (4)$$

where $S_0(x)$ is a parameter with the character of stiffness. To conform with response scaling (frequency versus location), the parameter $S_0(x)$ should be proportional to the square of the local frequency associated with x . However, in the summation over frequency components $S_0(x)$ in Eq. (4) remains constant. Relation (4) holds true when the transformation H_2 from $p_{\text{OHC}}(x, t)$ to $p_{\text{add}}(x, t)$ is taken to be unity. It will be shown further on that in the context of the present paper elaborations on other choices for H_2 are not strictly necessary.

The procedure is now as follows. Start by assuming that the local tone response $v_{\text{BM}}(x, \omega)$ —as a function of x —is like that for the corresponding component of a noise signal, presented at an appropriate stimulus level. Compute $v_{\text{tone}}(x)$ from $v_{\text{BM}}(x, \omega)$ using Eqs. (4) and (3), and derive $\gamma(x)$ for all locations x . Finally, generate the BM impedance $Z_{\text{BM}}(x, \omega)$ from Eq. (1), and compute the response of the model to the tone (do “resynthesis”). The result, again a function $v_{\text{BM}}(x, \omega)$ of x , will differ somewhat from the initially assumed response. Compute $v_{\text{tone}}(x)$ and $\gamma(x)$ again, and perform a few iterations (as is characteristic of the work of Kanis and de Boer) until sufficient convergence is obtained. As long as $\gamma(x)$ faithfully represents how the first harmonic of the signal is compressed, the implied approximation is accurate. When indeed noise and tone responses are comparable, using the appropriately chosen noise-derived function $v_{\text{BM}}(x, \omega)$ in the first step already produces an acceptable result. For experiments 9920, 9922, 9923, and 9924 that first step produces a tone-response result that is not more than 5 dB different from the ultimate result.

We found that three steps of iteration are sufficient to reduce variations to less than 2 dB. We interpret this rapid convergence as confirming the validity of the model used. We do not believe that a different “division of labor” between the two transformations H_1 and H_2 would lead to a materially different result. Therefore, in view of the present findings there is no need to investigate other choices for the transformation H_2 .

FIG. 7. Propagation of a pure tone (16.6 kHz) in a cochlear model (amplitude shown only). Noise-response data from experiment 9922. Dashed line: resynthesized response with uniform gamma ($\gamma=0.67$), representative for a single component of a noise signal. Solid line: computed for pure tone. Dash-dot line: the location-dependent OHC efficiency $\gamma(x)$, scale (0 to 1) on the right.

VI. RESULTS II. COCHLEAR PATTERNS FOR TONE AND NOISE

Figure 7 shows as an example of a result, the amplitude of the model response to a sinusoidal stimulus compared to that for a wideband noise signal, both plotted as functions of location x . The dashed line shows (as in Fig. 2) the propagation of a component of the noise signal (80 dB per octave), for experiment 9922 (the same experiment as was used for Fig. 4). The solid line illustrates the solution of the model equation for a sinusoidal stimulus (presented at 70 dB). From the figure it is apparent that the computed tone response is very close in amplitude to the noise response. A similar agreement will exist in the frequency domain. A third curve is present: the dash-dot line, which shows the local effective OHC efficiency $\gamma(x)$. This curve has its ordinate scale, going from zero to 1, on the right. It is seen that $\gamma(x)$ starts on the left near 1 (corresponding to weak excitation) and decreases to appreciably lower values in the region of the response peak.

For the preceding figures the “high” noise levels were selected as 70 and 90 dB per octave. For the present and later figures we used 80 dB per octave because that yields a value for the average γ between 0.6 and 0.8. As can be seen from Fig. 11 (Appendix B), in this region γ is the most sensitive to variations in excitation. Hence, this is the best region for exploring deviations between noise and tone responses. See the legends to this and the following figures for the values of γ applying to the noise responses.

Figures 8, 9, and 10 show results derived from basic data for three other experiments. Compare these figures with Figs. 5, 6, and 3, respectively. Note that for both Figs. 6 (experiment) and 9 (theory) a smaller level difference between tone and noise was used than in the other figures. From all four figures we can draw the same conclusion, but we also observe that there is a wide variation in the course of

FIG. 8. Propagation of a pure tone (16.9 kHz) in a cochlear model (amplitude shown only). Noise-response data from experiment 9923. Dashed line: resynthesized response with uniform gamma ($\gamma=0.61$), representative for a single component of a noise signal. Solid line: computed for pure tone. Dash-dot line: the location-dependent OHC efficiency $\gamma(x)$, scale (0 to 1) on the right.

$\gamma(x)$ as a function of x . In the final section of this paper we return to this finding.

VII. INTERPRETATION AND CONCLUSION

In this report we have demonstrated that the response of the cochlea to tones is, to a good approximation, equivalent to that of components of a noise signal. As a matter of fact, stimuli of the appropriate levels have to be compared; see Fig. 3. We found that equivalence in the data and have corroborated it by theory. Briefly: insofar as frequency filtering (the differential treatment of frequencies) is concerned, the cochlea is not “more nonlinear” or “less nonlinear” for tones than for noise. For tone stimulation the signal at the input of the OHCs is (nearly) sinusoidal. For a noise stimulus

FIG. 9. Propagation of a pure tone (17.1 kHz) in a cochlear model (amplitude shown only). Noise-response data from experiment 9920. Dashed line: resynthesized response with uniform gamma ($\gamma=0.82$), representative for a single component of a noise signal. Solid line: computed for pure tone. Dash-dot line: the location-dependent OHC efficiency $\gamma(x)$, scale (0 to 1) on the right.

Experiment: 9924 noise level: 80 dB per oct.
tone level: 70 dB

FIG. 10. Propagation of a pure tone (16.7 kHz) in a cochlear model (amplitude shown only). Noise-response data from experiment 9924. Dashed line: resynthesized response with uniform gamma ($\gamma=0.69$), representative for a single component of a noise signal. Solid line: computed for pure tone. Dash-dot line: the location-dependent OHC efficiency $\gamma(x)$, scale (0 to 1) on the right.

it is a multicomponent signal. In both cases the degree of saturation is determined by the (average) rms amplitude of the *total* signal at the input to the OHCs. Here lies the root of the comparison between tone and noise responses. Note that with the model that we use—in which the efficiency coefficient $\gamma(x)$ is a function of location x —the full extent of the variations of the response with stimulus level L can now be explained. This holds for noise as well as for tones. With respect to frequency filtering of stationary signals, the cochlea acts almost as an intensity-dependent linear filter.

As described in Sec. IV, we may have expected small differences in level between noise and tone responses, effects “ α ” and “ β .” Effect α is not found in the experimental data, and appears only as very small in the model results. The explanation why effect α is so small can be found from the course of the local efficiency function $\gamma(x)$. This function is not only well below 1 in the peak region but also more basally. Apparently, the domain over which a pure tone causes saturation (nonlinearity) extends sufficiently far to the left of the peak region to make the difference between excitation by tones and by noise minimal. In this respect, it may be expected that variations in $\gamma(x)$ would cause corresponding variations in suppression of high-frequency by low-frequency tones, upward suppression. Note that in the field of psychophysics, upward suppression would contribute to upward spread of masking (increased nonlinearity above a suppressing tone’s frequency). It is worthwhile to delve deeper into this topic.

As regards effect β , we found evidence of it in the data but detected it also in the low-level data.⁷ It is not present in the model results; on the contrary, the theoretical tone responses seem to have a small negative effect β , even at low levels. This may indicate an inadequacy of the model. We should realize that our computation method has been chosen as the one that corresponds most closely to our insight. It is a hybrid method, based on one of the principles of the LG or WKB method, but it does not utilize the concept of the wave

number $k(x)$ at all. In fact, the actual model computation is performed not as in the WKB or LG approximation but in the “exact” way, via solution of a matrix equation. In view of this we should not pay particular attention to deviations of 1 to 2 dB.

A single, very strong sinusoid will be distorted heavily (by the OHCs) but the harmonics cannot propagate (their frequencies are above the local best frequency). That has been the main reason why, in computing wave propagation, we could concentrate on the first harmonic. When *two tones* are presented, there will arise a host of distortion products (DPs) and many of them (intermodulation products) can and will propagate. With the experience gained by the present work, the propagation of these DPs can be computed according to the same modeling concept. It is in this area where we might need to investigate the possible influence of the transformation H_2 , namely, whether or not DPs undergo a second filtering (cf. Allen and Fahey, 1993 versus Kanis and de Boer, 1997).

In one respect tones, signals consisting of a finite number of fixed frequency components, and random-noise signals are similar: all are stationary signals. Our understanding of how the cochlea processes stationary signals is fairly complete now. It is for *non-stationary* (rapidly varying) signals that we have to extend our repertoire of mathematical operations in order to formulate and verify a satisfactory theory.

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APPENDIX A: THE INPUT SIGNAL OF OUTER HAIR CELLS

In this Appendix the effective strength of excitation of OHCs is computed. The model on which this is based is briefly described in the Introduction, and illustrated by Fig. 1. Input to the OHCs is the signal $d_{cil}(x,t)$, the deflection of the OHC stereocilia, and output the pressure $p_{OHC}(x,t)$ developed in the immediate surroundings of these cells. The instantaneous nonlinear transduction function of the OHCs is expressed by

$$p_{OHC}(x,t) = S_0 d_1 F[d_{cil}(x,t)/d_1], \quad (A1)$$

where d_1 is a scaling factor for $d_{cil}(x,t)$, $F(\cdot)$ is a saturating, no-memory, nonlinear real function, and S_0 is a constant. The function $F(\cdot)$ is assumed to be equal to its argument for very small values of the argument and to remain finite for extreme values of the argument. Equation (A1) is identical to Eq. (B1) of Appendix B in Part III. For very small signals Eq. (A1) reads

$$p_{OHC}(x,t) = S_0 d_{cil}(x,t) \quad \text{when } |d_{cil}(x,t)| \ll d_1, \quad (A2)$$

where S_0 is the only factor relating $p_{\text{OHC}}(x, t)$ to $d_{\text{cil}}(x, t)$. It is assumed that $d_{\text{cil}}(x, t)$ is a *linear* transform of the BM velocity $v_{\text{BM}}(x, t)$

$$d_{\text{cil}}(x, t) = [H_1^{(\text{op})}] v_{\text{BM}}(x, t), \quad (\text{A3})$$

where $H_1^{(\text{op})}$ is a linear operator (it includes the integration operator transforming velocity into displacement) corresponding to the transformation H_1 in Fig. 1. The filtering in $H_1^{(\text{op})}$ will be frequency- and place dependent. In a more general setting, $H_1^{(\text{op})}$ may operate over a certain range of x values—such as in a “non-classical” model (Steele *et al.*, 1993; Geisler and Sang, 1995; Fukazawa, 1997; de Boer, 1997b), but we restrict ourselves here to the simpler case of a “classical” model where $H_1^{(\text{op})}$ operates on the *local* velocity. We will use symbols with time t replaced by radian frequency ω to denote the corresponding variables in the frequency domain and tacitly imply that a Fourier transformation has taken place. In the frequency domain, Eq. (A3) is then written as

$$d_{\text{cil}}(x, \omega) = H_1(x, \omega) v_{\text{BM}}(x, \omega), \quad (\text{A4})$$

where $H_1(x, \omega)$ is the transfer function corresponding to $H_1^{(\text{op})}$. Notice that $H_1^{(\text{op})}$ and $H_1(x, \omega)$ do not depend on stimulus level since the transformation H_1 is linear. The relation between $p_{\text{OHC}}(x, t)$ and the pressure $p_{\text{add}}(x, t)$ near the BM is expressed in a similar way by

$$p_{\text{add}}(x, t) = [H_2^{(\text{op})}] p_{\text{OHC}}(x, t), \quad (\text{A5})$$

with its frequency-domain counterpart

$$p_{\text{add}}(x, \omega) = H_2(x, \omega) p_{\text{OHC}}(x, \omega). \quad (\text{A6})$$

$H_2^{(\text{op})}$ and $H_2(x, \omega)$ represent the filtering from $p_{\text{OHC}}(x, t)$ to $p_{\text{act}}(x, t)$ which, again, is linear. For reasons of simplicity we assume that $H_2^{(\text{op})}$ is the unity operator so that $H_2(x, \omega)$ is identically equal to 1. This choice means that we consider all frequency- and place dependence of the feedback loop in Fig. 1 as concentrated in the transformation $H_1(x, \omega)$. Possible effects of this restriction would only be expected in the treatment of distortion products, which is outside the scope of this paper.

All parameters and variables that are functions of both x and ω are assumed to “scale,” i.e., any change in ω can be offset by a change in x . This transformation implies a “cochlear map” which, again for reasons of simplicity, is assumed to be linear from x to the logarithm of ω . The factor S_0 in Eq. (A1) has the dimension and the character of stiffness, and S_0 is assumed to vary (exponentially) with x but not to depend on ω . Therefore, in what follows it is written as $S_0(x)$.

The pressure component $p_{\text{add}}(x, \omega)$, when divided by the BM velocity $v_{\text{BM}}(x, \omega)$, produces an *additive* contribution to the basilar-membrane (BM) impedance $Z_{\text{BM}}(x, \omega)$ that we call $Z^{\text{add}}(x, \omega)$; it is defined by

$$Z^{\text{add}}(x, \omega) = \frac{-2p_{\text{add}}(x, \omega)}{v_{\text{BM}}(x, \omega)}. \quad (\text{A7})$$

The concept of an impedance is relevant in a linear system, i.e., in the weak-signal case. If we introduce $Z^{\text{mact}}(x, \omega)$ for the maximum value of $Z^{\text{add}}(x, \omega)$ (associated with the weak-

est stimuli), and call the BM impedance without the contribution of the OHCs $Z^{\text{pass}}(x, \omega)$, the total BM impedance $Z_{\text{BM}}(x, \omega)$ in the weak-signal case is equal to the sum of two components

$$Z_{\text{BM}}(x, \omega) = Z^{\text{pass}}(x, \omega) + Z^{\text{mact}}(x, \omega). \quad (\text{A8a})$$

In the more general case, where the OHCs partly saturate, the concept of impedance can be retained for wideband noise stimulation [the EQ-NL theorem (de Boer, 1997a)]. The term $Z^{\text{add}}(x, \omega)$ will then include the real coefficient γ so that Eq. (A8a) changes into

$$Z_{\text{BM}}(x, \omega) = Z^{\text{pass}}(x, \omega) + \gamma Z^{\text{mact}}(x, \omega). \quad (\text{A8b})$$

For very weak signals γ equals 1, and with increasing signal strength it decreases towards zero; see Part III where this “two-component theory of the BM impedance” is worked out in detail. The parameter γ is the only factor that varies with stimulus level; the basic parameter functions $Z^{\text{pass}}(x, \omega)$ and $Z^{\text{mact}}(x, \omega)$ do *not* depend on stimulus level. Furthermore, for wideband, flat-spectrum noise signals γ does not depend on ω or x .

Returning to the weak-signal case, we can combine Eq. (A2) with Eqs. (A6) and (A7) and arrive at the following expression for the signal $d_{\text{cil}}(x, \omega)$ at the input to the OHCs:

$$d_{\text{cil}}(x, \omega) = - \frac{Z^{\text{mact}}(x, \omega)}{2S_0(x)} v_{\text{BM}}(x, \omega). \quad (\text{A9})$$

Although this relation is derived for weak signals it remains valid for any stimulus level and any stimulus type because the transformation H_1 is linear. The impedance $Z^{\text{mact}}(x, \omega)$ can be estimated from an experiment with a weak *noise* stimulus and an experiment postmortem [Eq. (A8a)]. We would only need an estimate of $S_0(x)$ to know the transformation (A9) completely.

For stimulation with a *noise* signal all frequency components of the noise have to be taken into account. When the noise signal has components at radian frequencies ω_j ($-\infty < j < \infty$), Eq. (A9) must be summed over all frequency components of the noise and Fourier transformed to find the time function $d_{\text{cil}}(x, t)$. The variance of $d_{\text{cil}}(x, t)$ is found as the sum of the intensities of all the components, Eq. (A9) with ω_j substituted for ω . In the summation $S_0(x)$ remains the same. For this operation we need to scale the impedance $Z^{\text{mact}}(x, \omega)$ (which has been determined as a function of x for constant ω to become a function of ω for constant x . Location x is scaled to radian frequency ω according to the inverse of the transformation from ω to x ; for the impedance a factor ω has to be included.

APPENDIX B: OHC TRANSDUCTION FUNCTION

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

$$\gamma = \int_{-\infty}^{\infty} F'(u) P(u) du, \quad (\text{B1})$$

where $P(u)$ is the probability density of the signal u , $F'(\cdot)$ is the derivative of $F(\cdot)$, which should be a monotonically

FIG. 11. Gamma (γ_G for Gaussian noise and γ_S for tones) as a function of $|d_{cil}/d_1|$ (abscissa in dB). *Solid line*: γ_G (for Gaussian noise), *dotted line*: γ_S (for a tone) but in this case $|d_{cil}|/d_1$ is taken as 1.78 times the value on the abscissa. In the text this factor is rounded off to 2.

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.

For stimulation with noise the probability distribution of $d_{cil}(x,t)$ will be nearly Gaussian. The efficiency coefficient γ_G is the average slope $F'(u)$ of $F(u)$ over the values of $[d_{cil}(x,t)/d_1]$ for a Gaussian distribution

$$\gamma_G = \int_{-\infty}^{\infty} F'(ad_{cil}/d_1) P_g(a) da, \quad (B2)$$

where $P_g(\cdot)$ stands for the Gaussian probability density function with unity variance. The normalizing factor d_1 plays the same role as in Part III. In Sec. V of the present paper $[d_{cil}(x,t)/d_1]$ is expressed in the “synthetic” forms $[v_{rms}/v_1]$ and $[v_{tone}(x)/v_1]$, for noise and tone, respectively, and by way of the factor v_1 it is adapted to an individual experiment.

For sinusoidal stimulation the corresponding efficiency coefficient γ_S will be equal to the first Fourier component of the distorted signal $F[d_{cil}(x,t)/d_1]$ divided by the original signal’s amplitude

$$\gamma_S(x) = (2/\pi) \int_0^\pi F[|d_{cil}(x)/d_1| \cdot \sin \varphi] \times \sin \varphi d\varphi / (d_{cil}(x)/d_1). \quad (B3)$$

In Sec. V it is explained how the quotient $[d_{cil}(x,t)/d_1]$ is estimated in the form of $[v_{tone}(x)/v_1]$, again adapted to an individual experiment.

Our function $F(u)$ is based on the hyperbolic tangent function used by Kanis and de Boer (1993). A weighted sum of two such functions has a two-stage variation of the slope which corresponds better to the nonlinear odd-order character of measured hair-cell transfer functions (cf. Geisler, 1998, Figs. 8.3 and 8.5)

$$F(u) = [\tanh w + c \tanh(w/c)] / (1 + c), \quad (B4)$$

where

$$w = (1 + c)u/2. \quad (B5)$$

The parameter c is a constant which must be nonzero. For every (nonzero) 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.

It is illuminating to compare γ_G for Gaussian noise with γ_S for tones. In Fig. 11 the *solid line* shows γ_G from Eq. (B2) (for Gaussian noise) as a function of $|d_{cil}|/d_1$ (on a log scale). The *dashed line* illustrates γ_S from Eq. (B3) (for a tone) but $|d_{cil}|/d_1$ is taken as 1.78 times the value on the abscissa. The two curves are nearly coincident; the differences are of the order of 2%. Apparently, the two functions demonstrate very similar behavior of the efficiency coefficient as a result of OHC saturation. The sinusoidal signal is about half as effective in reducing the efficiency γ as a noise signal of the same rms value. This is easily understood from the shape of the signal distribution function: the waveform of the sine signal never exceeds the maximum value, whereas signal values for a noise signal cover a large range outside the rms value. The ratio of 1.78 and 2.0 amounts to approx. 1 dB and will be neglected.

¹In this paper we assume that the transformation H_1 is a local one. Equivalently, we assume a classical model (cf. Appendix A and de Boer, 1997b).

²We have presented pseudorandom noise which has a periodic waveform and, therefore, analyzes into discrete components. In our case the components were separated by 50.78 Hz.

³In comparing responses to tones and noise the effective stimulus levels are similar, therefore, phase differences will be minimal.

⁴The present study was consistent with NIH guidelines for humane treatment of animals and was reviewed and approved by the Oregon Health Sciences Committee on the Use and Care of Animals.

⁵The stapes response was measured postmortem. We acquired the stapes response in the form of a cross-correlation function (ccf) for wideband noise. This stapes ccf can serve to normalize noise as well as tone responses.

⁶LG stands for Liouville–Green, WKB for Wentzel, Kramers, and Brillouin.

⁷One possible influence in the data could be due to efferent effects.

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