# Further studies on the dual-resonance nonlinear filter model of cochlear frequency selectivity: Responses to tones<sup>a)</sup>

## Alberto Lopez-Najerab)

Facultad de Medicina, Universidad de Castilla-La Mancha, C/ Almansa, No. 14, 02006 Albacete, Spain

## Enrique A. Lopez-Poveda

Instituto de Neurociencias de Castilla y León, Universidad de Salamanca, Avda. Alfonso X "El Sabio" s/n, 37007 Salamanca, Spain

#### Ray Meddis

Department of Psychology, University of Essex, Colchester CO4 3SQ, United Kingdom

(Received 23 January 2007; revised 4 July 2007; accepted 12 July 2007)

A number of phenomenological models that simulate the response of the basilar membrane motion can reproduce a range of complex features observed in animal measurements over different sites along its cochlea. The present report shows a detailed analysis of the responses to tones of an improved model based on a dual-resonance nonlinear filter. The improvement consists in adding a third path formed by a linear gain and an all-pass filter. This improvement allows the model to reproduce the gain and phase plateaus observed empirically at frequencies above the best frequency. The middle ear was simulated by using a digital filter based on the empirical impulse response of the chinchilla stapes. The improved algorithm is evaluated against observations of basilar membrane responses to tones at seven different sites along the chinchilla cochlear partition. This is the first time that a whole set of animal observations using the same technique has been available in one species for modeling. The resulting model was able to simulate amplitude and phase responses to tones from basal to apical sites. Linear regression across the optimized parameters for seven different sites was used to generate a complete filterbank. © 2007 Acoustical Society of America.

[DOI: 10.1121/1.2769627]

PACS number(s): 43.64.Bt, 43.66.Ba [WPS]

Pages: 2124-2134

# I. INTRODUCTION

A number of phenomenological models that simulate basilar membrane (BM) responses can reproduce a range of complex features observed in animal measurements over different sites along the cochlea (Giguere and Woodland, 1994; Goldstein, 1990; 1995; Irino and Patterson, 2001; Meddis *et al.*, 2001; Robert and Eriksson, 1999; Zhang *et al.*, 2001; Zilany and Bruce, 2006; Lopez-Poveda, 2005). For example, the dual resonance nonlinear (DRNL) filter of Meddis *et al.* has been shown to be able to simulate a wide range of phenomena characteristic of the vibration of the cochlear partition. These include nonlinear (compressed) responses, changes in effective bandwidth (BW) with signal level, the response to click-stimuli at different levels, two-tone suppression, and the generation of distortion products.

Unfortunately, this model is unable to simulate BM responses to frequencies well above the characteristic frequency (CF), the so-called "plateau response," as measured by Ruggero (1997). The deviation is clearly seen by comparing Figs. 1C and 1D in Meddis *et al.* (2001); the model substantially underestimates the experimental response for 17-kHz stimuli at a site whose CF is 10 kHz. An amendment to the DRNL filter is proposed in the following that addresses this issue and improves the fit at frequencies above CF. These responses may be relatively unimportant at low levels but they substantially change the nature of the mechanical filtering at high signal levels when the filters become extremely wide.

Phenomenological models of the mechanical response have also faced the lack of systematic observations for a wide range of CFs. Difficulties associated with making these measurements have restricted the number of sites along the partition that can be studied. Until recently, model parameters could only be adjusted based on experimental data for three cochlear sites with BFs of 800, 8000, and 18 000 Hz across different species. Any attempt to derive a filterbank representing the whole cochlea necessarily involved a considerable degree of interpolation between these points or a dependence on auditory nerve data to fill the gaps (Sumner et al., 2003). Over time, however, more observations have been made and modelers now have access to experimental BM responses for seven cochlear regions with CFs of approximately 0.8, 5.5, 7.25, 9.75, 10, 12, and 14 kHz (Rhode and Cooper, 1996; Rhode and Recio, 2000; Ruggero et al., 1997) in a single species, the chinchilla. While still far from complete, the new data provide the opportunity to reassess the

<sup>&</sup>lt;sup>a)</sup>Portions of this work were presented in "2aPPb13. A chinchilla nonlinear cochlear filterbank," 143rd Meeting of the Acoustical Society of America [J. Acoust. Soc. Am.**111**, 2357 (2001)], and at the 13th International Symposium on Hearing, Dourdan, France, 2003.

b)Electronic mail: alberto.lopez@uclm.es



FIG. 1. (A) Block diagram of the model. The input to the model is the instantaneous pressure wave form of the pure tone in pascal units. This signal is filtered through a middle-ear stage based on the empirical IR, the output of which is assumed to be stapes velocity (m/s). The output of the model is BM velocity (m/s). (B) Schematic diagram of the TRNL filter. Italic characters under each path inform of the parameters of each stage. The output signals from the three paths are added sample-by-sample to give the output signal from the TRNL filter.

model parameters. More phase data are also now available and this also permits a reexamination of the phase response of the DRNL filter.

When evaluating models of the response of the cochlear partition, it is important to take into account the frequency response of the outer-middle ear (Cheatham and Dallos, 2001). Fortunately, the experimental impulse response (IR) of the stapes is now available (Rhode and Recio, 2000, private communication). This can be represented as a Finite Impulse Response (FIR) filter so that middle-ear response can be computer-simulated with some confidence. This filter will also be presented and evaluated in the following.

The main improvement to the DRNL filter of Meddis et al. (2001) is the introduction of a third signal processing path, making the filter a triple-path nonlinear (TRNL) model. The third path is a linear, low-gain, all-pass filter. Its gain is low enough so that it is only effective at high signal levels and its frequency response flat to act as an all-pass filter (Robles and Ruggero, 2001). The third filter is addressing the "plateau response" observed at frequencies well above CF (Ruggero et al., 1997). When combined with its low gain, this filter is effective only outside the bandpass of the existing nonlinear and linear bandpass filters. The parameters of the TRNL filter have been adjusted to account for the bulk of BM responses to pure tones that are now available. The most important adjustment, with respect to the original DRNL filter, is an increase in the number of gammatone and low-pass filters required to fit the new data particularly for high frequencies.

## **II. MODEL DESCRIPTION**

The general scheme of the model implementation is illustrated in Fig. 1. A pressure wave form (in units of pascal) is the input to the algorithm. The middle-ear (ME) filter produces stapes velocity (in m/s), which is the input to the TRNL filter. To preserve as many aspects of the experimental stapes response as possible, the ME filter was implemented as a 256-point FIR filter whose coefficients (Oppenheim and Schafer, 1999) were equal<sup>1</sup> to the empirical sensitivity IR of the chinchilla stapes shown in Fig. 2(a) (case CB058 in Rhode and Recio, 2000, private communication). The gain and phase responses of this filter are shown in Fig. 2(b).

The TRNL filter was implemented and evaluated digitally in the time domain. A new parallel path was added to the original DRNL (Meddis *et al.*, 2001) consisting of a linear, zero-phase, all-pass filter. High frequency amplitude and phase plateaus observed in BM tonal responses (Robles and Ruggero, 2001) were not reproduced by the original DRNL filter. The idea by Robles and Ruggero (2001, p. 1313) that the plateaus "[...] reflect, more or less directly [...] stapes motion [...]" suggested the implementation of the new third path as a zero-phase, all-pass filter. Phase responses measured with a sensor placed at 300  $\mu$ m from the BM in the scala vestibuli (Olson, 1998) also support this idea.

Fundamentals for implementing the original DRNL filter can be found in the Appendix of Lopez-Poveda and Meddis, (2001). The zero-phase, all-pass filter in the new third path was implemented digitally by filtering the input signal in both the forward and reverse directions through a secondorder Butterworth low-pass filter with a very high cut-off frequency, almost equal to the Nyquist frequency (Oppenheim and Schafer, 1999). This was achieved using MATLAB's filtfilt function. The output signal from the TRNL filter was the sample-by-sample summation of the output signals from the DRNL filter and the new third path. The gain (scalar) of the third path, k, was free to vary above zero, but was always lower than the gain of the linear path, g, of the DRNL filter. For this reason, the contribution of the third path is promi-



FIG. 2. Transfer characteristics of the ME filter. (A) Experimental impulse of preparation CB058 (Rhode, private communication). This was used as the coefficients for a FIR filter that simulates the ME stage. (B) Sensitivity and phase response of the FIR filter used.

nent only at high levels and for frequencies above the center frequencies of the filters in the linear and the nonlinear path, where the output of the linear and the nonlinear paths are attenuated.

Another difference between the TRNL filter and the DRNL filter is the number of gammatones (GT) and lowpass (LP) filters in cascade. The number of GTs in the linear path was increased to 5, and the number of LP filters was fixed equal to 7. The number of LP filters in the nonlinear path was also increased to 4. A greater number of filters makes the attenuation above CF steeper, where the contribution from the third path is more relevant to the total TRNLfilter output.

## A. Model parameters

The parameters of the filters, shown in Table I, were optimized by manually fitting the model response to the experimental BM velocity input/output (I/O) functions as in the original DRNL paper (Meddis *et al.*, 2001), but also taking into account the experimental frequency, phase, and IRs (not shown).

The procedure for obtaining the parameters was as described in Meddis *et al.* (2001), that is, we assumed that the output from the nonlinear path dominates the output of the TRNL filter at very low stimulus level near its CF, and the linear-path output dominates the TRNL output at high levels. These two conditions allow obtaining the parameters for the nonlinear and linear paths, respectively. The gain, k, of the new third path was obtained by fitting the output of the TRNL filter to the frequency and phase plateaus observed in the experimental responses for frequencies above CF, for which the output from the linear and the nonlinear paths is negligible.

The number of cascaded filters in each path was obtained by fitting the model phase-shift responses at low and high stimulus levels to the data (Ruggero *et al.*, 1997; Rhode and Recio, 2001).

## B. Evaluation of the model

The model was implemented in MATLAB. Digital sinusoidal tones (sampling frequency of 62 500 Hz) were used as the input, simulating exactly the same stimuli used in the experiments. Input signals had a total duration of 30 ms, including 2-ms rise/fall raised-cosine ramps. Signal levels from 0 to 100 dB SPL were considered. The phase of the model responses was calculated using a sine-wave fitting algorithm (Händel, 2000). The amplitude of model responses were calculated as the peak velocity (m/s) during the last half of the signal. All filters were implemented using the functions available in MATLAB and in its Signal Processing Toolbox.

# **III. RESULTS**

Parameters were optimized for those cochlear sites for which experimental data were available for chinchilla (see Table I). In what follows, model results are compared directly with experimental responses. Only those results and conditions for which experimental observations exist were reproduced with the model: I/O and frequency response functions were reproduced for all CFs; phase versus frequency responses were modeled only for CFs of 0.8, 7.25, and 12 kHz; and level-dependent phase responses were modeled for CFs of 7.25 and 10 kHz.

#### A. Frequency response and input/output curves

Figures 3(a), 3(c), and 3(e) illustrate experimental (left panels) and model (right panels) frequency responses for CFs of 0.8, 5.5, and 7.25 kHz. Figures 3(b), 3(d), and 3(f) show the same data plotted as I/O curves. Similarly, frequency responses for CFs of 9.75, 10, 12, and 14 kHz are plotted in Figs. 4(a), 4(c), 4(e), and 4(g) and the corresponding I/O functions in Figs. 4(b), 4(d), 4(f), and 4(h). By plotting frequency response and I/O functions, the reader can easily visualize filter shapes, linearity, and compression.

## 1. 800-Hz site

Figures 3(a) and 3(b) show sensitivity and I/O curves, respectively, for a cochlear region with a  $CF \sim 800$  Hz [Rhode and Cooper (1996), case CH16]. No ME filter was used to model these data because there were no detailed data available to simulate its response around 800 Hz. Nonlinear responses can be seen only for frequencies of 800, 900, and 1000 Hz around 50 dB SPL as a bend in the I/O functions.

CF	800	5500	7250	9750	10 000	12 000	14 000
case	CH16	CB58	CB61	CB24	L113	CB04	CB21
study	1	2	2	2	3	2	2
Linear							
GT cascade	5	5	5	5	5	5	5
LP cascade	7	7	7	7	7	7	7
CF <sub>lin</sub>	750	5000	7 400	9000	9 000	11 000	13 000
$BW_{lin}$	450	3000	2 500	3000	3 500	5 000	4 000
LP <sub>lin</sub>	750	6000	7 400	9000	8 800	12 000	13 500
Gain, g	500	190	3 000	300	500	500	350
Nonlinear							
GT cascade	3	3	3	3	3	3	3
LP cascade	4	4	4	4	4	4	4
CF <sub>nl</sub>	730	5850	7 800	9800	10 000	12 000	15 000
$BW_{nl}$	350	1800	2 275	1650	1 800	2 000	3 200
LP <sub>nl</sub>	730	5850	7800	9800	10 000	12 000	15 000
Gain, a	850	3000	15 000	9000	15 000	22 500	3 000
Gain, b	0.03	0.04	0.06	0.05	0.06	0.07	0.045
Exponent, c	0.25	0.25	0.25	0.25	0.25	0.25	0.25
Linear all-pass							
Gain, k	10	0.4	20	1	2	20	20

TABLE I. TRNL algorithm parameters used throughout for reproducing the animal observations considered in this report. The top three rows inform of the cochlear site (CF), the preparation number, and the study from which experimental data were taken. Studies: 1: Rhode and Cooper (1996); 2: Rhode and Recio (2000); 3: Ruggero *et al.* (1997).

This effect is reproduced both quantitatively and qualitatively with the model. The model parameters (see Table I, case CH16) were chosen so that the center frequency of the GT filters in the linear path were slightly higher that those of the GT filters in the nonlinear path. The gains for the two paths were also similar. The BWs of the GT filters in the linear and the nonlinear paths were similar. However, the linear-path GT filters were slightly wider than those of the nonlinear path. Compressive responses are visible only around the center frequency of the GT filters in the nonlinear path and between 50 and 70 dB SPL, where the output from the linear path dominates the total filter output. The frequency response of the model with the same model parameters but without the new third path at 90 dB SPL is also shown (thin line, labeled as "No 3rd"). In this case, a plateau does not occur either in the model or in the experimental responses at high frequencies. The value of the gain of the third path (parameter k in Table I) is therefore ambiguous.

#### 2. 5.5-kHz site

Figures 3(c) and 3(d) compare model results and experimental data (Rhode and Recio, 2000, case CB58). In this case, the ME filter used in the model was based on the stapes IR of the same animal. Nonlinear responses occur for all frequencies shown and for levels between 30 and 80 dB SPL, and the model is able to reproduce them. Experimental and model frequency responses are comparable and the plateau is produced only when the third path is used.  $CF_{lin}$  and  $CF_{nl}$  are different, with  $CF_{nl} > CF_{lin}$ . The BWs are also different;  $BW_{lin}$ =3 kHz and  $BW_{nl}$ =1.8 kHz in order to reproduce the level-dependent frequency responses and the shifts of BF between low and high input levels.

#### 3. 7.25-kHz site

Figures 3(e) and 3(f) illustrate experimental (Rhode and Recio, 2000, case CB61) and model responses for a cochlear site with a CF=7.25 kHz. When the new third path is omitted (line labeled "No 3rd") the frequency response does not reach a plateau at frequencies well above 8 kHz. The center frequency of the linear-path GT filters (7.4 kHz) is lower than that of the nonlinear-path filters (7.8 kHz), but the BW of the linear path (2.5 kHz) is larger than that of the nonlinear path (2.275 kHz). These parameters make it possible that the model level-dependent frequency response matches that of the data. Nonlinear responses occur in the model for frequencies between 6.25 and 10 kHz, as occurs in experimental data.

## 4. 9.75-kHz site

Figure 4(a) compares experimental (Rhode and Recio, 2000, case CB24) and model frequency responses. The ME filter used produces a minimum close to 8.5 kHz (line labeled "stapes") and thus affects the model output by producing a nondesirable minimum around that frequency. The model does not reproduce correctly the shape of the experimental filter from low to high levels. This occurs because the center frequency of the linear- and nonlinear-path GT filters are similar (9 and 9.8 kHz, respectively). Corresponding I/O functions are plotted in Fig. 4(b). Nonlinear responses can be seen for all frequencies. Note that the model underestimates the BM velocity at 8 kHz, but this is due to the minimum observed in the ME-filter sensitivity. Because of this, in this case, the fit to experimental data is qualitative rather than quantitative.



FIG. 3. Comparison of model and animal results for cochlear sites with CFs of 800 [data from Rhode and Cooper (1996), animal CH16], 5500, and 7250 Hz [data from Rhode and Recio (2000) animals CB58 and CB61 respectively]. (a), (c), and (e) Experimental and modeled frequency responses for different stimulus levels (as indicated by the insets in dB SPL). Also shown are the frequency response of the model stapes (thick line) and the response of the model without the third path at the highest level (thin line). Left panels: animal observations. Right panels: Model results corresponding to animal observations immediately to the left. (b), (d), and (f) Experimental and model input/output curves. Left panels: animal observations. Right panels: Model results corresponding to animal observations immediately to the left. The insets indicate stimulus frequency in hertz.

#### 5. 10-kHz site

The experimental data for this site is perhaps the most complete set of BM measurements available in literature (Ruggero *et al.*, 1997; Recio *et al.*, 1998). Further details and analysis on modeling these experimental responses to tones and clicks using different ME-filter implementations can be found in Lopez-Najera *et al.* (2005). The model produces filter shapes similar to those observed experimentally [Fig. 4(c)]. Some of the differences possibly reflect the fact that the frequency response of the ME filter used in the model differs from that of the animal from which BM responses were measured [compare the thick continuous lines in the two panels of Fig. 4(c)]. Figure 4(d) compares corresponding I/O functions showing nonlinear responses for frequencies between 9 and 12 kHz in both animal and model responses.

Animal I/O curves show a notch at 10 kHz and 100 dB SPL that is not produced by the model as it was by Meddis *et al.* (2001). The model produces notches when the outputs from the linear and the nonlinear paths have similar amplitudes but different phases. This condition is not met at 10 kHz with the parameters shown in Table I (case L113). Note that the plateau in the frequency response is only reproduced by the model when the third path is considered.

## 6. 12-kHz site

Figures 4(e) and 4(f) compare experimental and model sensitivity and I/O functions for case CB04 of Rhode and Recio (2000). The model simulates the experimental data



FIG. 4. As for Fig. 3 but for cochlear sites with CFs of 9250, 12 000, 14 000 [data from Rhode and Recio (2000), preparations CB24, CB04, and CB21, respectively], and 10 000 Hz [data from Ruggero *et al.* (1997), animal L113].

qualitatively and quantitatively. The frequency response of the ME filter used in the model exhibits peaks that considerably affect the model frequency response.

## 7. 14-kHz site

The most basal site examined with the model corresponds to case CB21 of Rhode and Recio (2000) and its simulations are shown in the right panels of Figs. 4(g) and 4(h). The model shows a good qualitative and reasonably good quantitative match to the animal data. The experimental I/O curves are significantly compressed for stimulus frequencies above CF; below CF, however, they are almost linear. Model responses to 18- and 19-kHz tones are linear. At 18 kHz, the amplitude of the model response is larger than the experimental one due to the contribution from the third path. At 19 kHz the amplitude of the TRNL-filter response



FIG. 5. Comparison of experimental (A) and modeled (B) normalized amplitude responses for a stimulus level of 50 dB SPL. Experimental data are from Rhode and Recio (2000) for CFs from 6 to 14.7 kHz. Model results are for the CFs shown in Table I, except 800 Hz.

matches that of the experimental data. A notch occurs at 7 kHz in the model frequency response [right panel in Fig. 4(g)] that does not occur in the experimental response. This reflects a notch in the ME-filter frequency response and also possibly a phase cancellation between the output signals from the third path and the linear path.

Model amplitude responses normalized to 1 nm for six cochlear sites with CFs between around 5.5 and 12 kHz are plotted in Fig. 5(b) for a sound level of 50 dB SPL. The experimental data [Fig. 5(a)] were for the same sound level and for sites with CFs of 6, 7, 7.9, 10.7, 12.1, 14.3, and 14.7 (Rhode and Recio, 2000). Overall the model frequency responses are comparable to the experimental ones. They show the characteristic broadening at low CFs (notice that the abscissa is on a logarithmic scale). The model slightly underestimates the BW and shows a steeper slope of frequency responses at stimulation frequencies well above CF than the animal data. This is possibly because the number of GT and LP filters in the linear and nonlinear paths were fixed across CFs. Better fits would have been obtained by allowing the number of filters to vary freely across CFs.

## **B.** Phase responses

Phase responses were analyzed at the same time as amplitude responses during parameter optimization. The number of gammatone and low-pass filters and the relation between the center frequencies and the BWs of the gammatone filters in the linear path and the nonlinear path are crucial to the phase response of the model (Lopez-Najera, 2005).

Model and experimental unwrapped phase-frequency responses are compared in Fig. 6. Results are shown only for CFs of 0.8, 7.25, 10, and 12 kHz because those are the only sites for which both phase and amplitude responses have been reported for the same preparation. Figure 6(a) shows animal observations (Rhode and Cooper, 1996, case CH16) and model responses. The model phase advances over one cycle more than in the animal data. This could be corrected by decreasing the number of filters in the linear and nonlinear path, but to reduce the number of degrees of freedom of the system, the number of filters was fixed across CFs. A phase plateau occurs above 1 kHz in the model but at 800 Hz in the data. The model phase is one cycle shorter than in the data at CF=7.25 kHz [animal data in Fig. 6(b) from Rhode and Recio, 2000], and two cycles shorter at CFs



FIG. 6. Experimental and model phase responses relative to the phase of the middle-ear response for CFs of 800 (Rhode and Cooper, 1996), 7250, 12 000 (Rhode and Recio, 2000), and 10 000 Hz (Ruggero *et al.*, 1997). The insets inform of the stimulus level in dB SPL.

of 10 and 12 kHz [animal data in Figs. 6(c) and 6(d) from Ruggero *et al.* (1997) and Rhode and Recio (2000), respectively].

Figure 7 illustrates the level dependence of model and animal phase responses for CFs of 10 [Fig. 7(a), animal data from Ruggero *et al.* (1997)] and 7.25 kHz [Fig. 7(c), animal data from Rhode and Recio (2000)]. At 10 kHz, the model simulates qualitative and quantitative aspects of the phase response relative to 80 dB SPL [compare Figs. 7(a) and 7(c)], but only for frequencies below the CF. At CF



FIG. 7. Experimental and model level-dependent phase responses for cochlear sites with CFs of 10 [(A) and (B)] and 7.25 kHz [(C) and (D)]. The experimental data for 7.25 and 10 kHz are from Rhode and Recio (2000) and Ruggero *et al.*, (1997), respectively. Insets inform of the stimulus level in dB SPL.

=7.25 kHz, the model reproduces qualitatively and (reasonable well) quantitatively the behavior of phase at different level referred to 30 dB SPL. The relation between the center frequency, the BWs, and the number of filters in cascade in the linear and nonlinear paths are critical to reproducing this behavior (Lopez-Najera, 2005).

The longitudinal spatial distribution of BM motion for individual stimulus frequencies has received little attention because the required measurements are difficult. However, measurements exist for the spatial distribution of the excitation produced by a 15-kHz pure tone in the guinea pig cochlea (Russell and Nilsen, 1997) and a complete set of phase responses for several locations along the basal region of the chinchilla cochlea (Rhode and Recio, 2000). Model phase responses are compared with the latter in Fig. 8. Experimental responses are for CFs of 6, 7, 7.9, 10.7, 12.1, and 14.7 kHz, while model responses are for CFs of 5.5, 7.25, 10, 12, and 14 kHz. Model and experimental responses differ



FIG. 8. Experimental and model phase responses at 70 dB SPL for different cochlear sites. Experimental data are from Rhode and Recio (2000). Inset information of the CF in hertz.



FIG. 9. (A) Values of the optimum model parameters used to model the animal data presented in this report. The actual numerical values are given in Table I. (B) Parameter values as calculated by linear regression of the optimum parameters [Eq. (1)]. Note that some symbols and lines overlap.

slightly, but the main characteristics of the experimental phase responses are simulated reasonably well by the model for CFs from 800 Hz to 14 kHz.

TABLE II. Linear regression coefficients  $p_0$  and m for creating the filterbank assuming a relationship of the form:  $\log_{10}$  (parameter)= $p_0$ + $m \log_{10}$ (CF), with CF in Hz.

	$p_0$	т
DRNL filter parameter		
CF <sub>lin</sub>	-0.01	0.9947
$BW_{lin}$	0.373	0.7949
$LP_{lin}$	-0.0187	1.0016
Gain, g	2.7781	-0.0214
CF <sub>nl</sub>	-0.1545	1.0424
$BW_{nl}$	0.59	0.6851
LP <sub>nl</sub>	-0.1545	1.0424
Gain, a	0.3717	0.896
Gain, b	-2.1953	0.2321
k	0.6937	-0.0019

#### **IV. THE FILTERBANK**

Having assembled a whole set of parameters for seven different sites along the chinchilla cochlea, the next step was to build a filterbank that allows estimating parameters for intermediate sites. The method used is based on the assumption that the parameters have a linear dependence with CF in a log-log scale [Fig. 9(a)] (cf. Lopez-Poveda and Meddis, 2001). In other words by assuming the following relationship:

$$\log_{10}(\text{parameter}) = p_0 + m \log_{10}(\text{CF}). \tag{1}$$

The coefficients  $p_0$  and *m* calculated for the linear regression are shown in Table II. Figure 9(b) shows the new parameters calculated using the filterbank. To be consistent in the analysis, linear regression for all parameters was used, even with *k*, the gain of the third path, despite the fact that it is less clear that its value depends similarly on CF [Fig. 9(a)].

Figure 10 compares the experimental I/O functions for CF pure tones, for the seven different CFs considered earlier with model simulations using the approximate filterbank parameters. The model captures the fundamental characteristics of the experimental responses. The differences are attributable mainly to the gain values used rather than to the BWs or the filters' center frequencies. It is noteworthy, however, that experimental responses vary more across CF than do model



FIG. 10. Comparison of experimental and model I/O curves for stimuli at CF and for the seven sites considered in this report (see CFs in Table I). Model responses were obtained with the filterbank parameters [see Eq. (1) and Table II] rather than with the optimum parameters.

responses. For instance, the experimental I/O function at 7 kHz is more linear than the I/O curves at any other CFs. These across-CF differences are not captured by the model, but their physiological relevance is uncertain. They might reflect different degrees of cochlear injury across preparations.

## V. DISCUSSION

The model presented in this report is able to simulate BM amplitude and phase responses to tones reasonably well. The new TRNL filter improves the match between model and experimental amplitude and phase responses with respect to the DRNL filter of Meddis *et al.* (2001) for frequencies above the CF, in the plateau region. Parameters for seven different sites along the chinchilla cochlea have been reported. A filterbank using seven sets of parameters from 0.8 Hz to 14 kHz has been developed and tested.

An important feature of the present model is its capability of reproducing BM amplitude and phase plateaus that occur for frequencies well above CF. This has been achieved following a suggestion of Robles and Ruggero (2001) that the plateaus reflect more or less directly stapes motion. At one time, consensus was lacking on whether these plateaus were a general feature of BM responses, particularly because they have been hardly reported in corresponding auditory nerve responses. However, plateaus have been widely reported in BM responses of several mammalian species measured using different experimental techniques and in healthy preparations [a comprehensive review of the evidence is provided in pp. 1312–1313 of Robles and Ruggero (2001) and will not be repeated here]. Therefore, they are now accepted as a physiological characteristic of BM responses (Robles and Ruggero, 2001).

The main aim of this study was to test if the DRNL filter was able to simulate BM mechanics from the basal partition of the cochlea to the apical region, and how it was possible, if it was, to improve it. The model responses shown in Figs. 3, 4, and 6 indicate that parameters can be found to reproduce empirical data for different sites over the chinchilla cochlea, even when the number of filters in cascade is previously fixed. The TRNL filter produces gain and phase plateaus for frequencies above BF in each case.

Parameters were optimized by attending not only to I/O functions, but also to amplitude and phase frequency responses, and IRs (not shown). In some instances, the model appears not to capture the experimental phase response in the plateau region. Better fits to the experimental phase responses can be found by changing the number of filters in cascade, but this would introduce another degree of freedom into the system that should be analyzed in further studies (Lopez-Najera, 2005). On the other hand, the experimental phase jumps by more than a cycle between two successive frequencies [e.g., Figs. 6(b)-6(d)] and this casts doubts on the reported experimental phases.

The method for modeling the ME response has improved the model IR (not shown) but it does it at the expense of affecting the frequency response of the model. A simple Butterworth bandpass filter could have been used instead to model the ME transfer characteristics, but it would be unlikely to produce an appropriate phase and IR for the whole system. Some of the discrepancies between the experimental and model results occur because the same ME filter implementation has been used throughout to reproduce BM responses for seven different cochlear sites of seven different animals measured in three different laboratories with different degrees of cochlear injury.

Another weakness of the model [already reported by Meddis *et al.* (2001) and Lopez-Poveda and Meddis (2001)] is that the BF does not change gradually with signal level. Instead, a rather abrupt shift occurs between the BFs of the linear and the nonlinear paths. The main advantage of this model is its simplicity and adding more resonances could improve its responses but it would complicate its simple structure. It is important to remember that the model is a phenomenological model and does not represent cochlear mechanics at a physical level but it is useful to preprocess the input to higher-level auditory models. An approximated transfer function was developed (Lopez-Poveda, 2003) that further simplifies the understanding of the DRNL filter.

#### ACKNOWLEDGMENTS

The simulation of the experimental data would have been impossible without the generous and helpful cooperation of Alberto Recio and Mario Ruggero. Work supported by FIS (PI020343 and G03/203), MEC (BFU2006-07536/ BFI), PROFIT (CIT-390000-2005-4), and IMSERSO (131/ 06).

<sup>1</sup>The experimental IR of the chinchilla stapes consisted of 1024 samples recorded at sampling rate of 250 kHz (hence the total duration was 0.4096 ms). Since the model was evaluated at a sampling rate of 62.5 kHz, the ME FIR filter coefficients were obtained by downsampling the experimental IR keeping every fourth sample starting with the first one. Hence, the final FIR filter had 256 coefficients.

- Cheatham, M. A. and Dallos, P. (2001). "Inner hair cell response patterns: Implications for low-frequency hearing," J. Acoust. Soc. Am. 110, 2034– 2044.
- Giguere, C., and Woodland, P. C. (1994). "A computational model of the auditory periphery for speech and hearing research. I. Ascending path," J. Acoust. Soc. Am. 95, 331–342.
- Goldstein, J. L. (1990). "Modeling rapid waveform compression on the basilar membrane as multiple-bandpass-nonlinearity filtering," Hear. Res. 49, 39–60.
- Goldstein, J. L. (1995). "Relations among compression, suppression, and combination tones in mechanical responses of the basilar membrane: Data and MBPNL model," Hear. Res. 89, 52–68.
- Händel, P. (2000). "Properties of the IEEE-STD-1057 four parameter sine wave fit algorithm," IEEE Trans. Microwave Theory Tech. 49, 1189–1193.
- Irino, T., and Patterson, R. D. (2001). "A compressive gammachirp auditory filter for both physiological and psychophysical data," J. Acoust. Soc. Am. 109, 2008–2022.
- Lopez-Najera, A. (2005). "Simulación computacional de la membrana basilar" (Computational simulation of the basilar membrane), Ph.D. thesis. Departamento de Biología Celular y Patología. Universidad de Salamanca, Salamanca, Spain.
- Lopez-Najera, A., Meddis, R., and Lopez-Poveda, E. A. (2005). "A computational algorithm for computing cochlear frequency selectivity: Further studies," in *Auditory signal processing: Physiology, Psychoacoustics and Models*, edited by D. Pressnitzer, A. de Cheveigné, S. McAdams, and L. Collet (Springer, New York), pp. 14–20.
- Lopez-Poveda, E. A. (2003). "An approximate transfer function for the dual-resonance nonlinear algorithm of auditory frequency selectivity," J.

Acoust. Soc. Am. 114, 2112–2117.

- Lopez-Poveda, E. A. (2005). "Spectral processing by the peripheral auditory system: Facts and models," Int. Rev. Neurobiol. 70, 7–48.
- Lopez-Poveda, E. A., and Meddis, R. (2001). "A human nonlinear cochlear filterbank," J. Acoust. Soc. Am. 110, 3107–3118.
- Meddis, R., O'Mard, L. P., and Lopez-Poveda, E. A. (2001). "A computational algorithm for computing nonlinear auditory frequency selectivity," J. Acoust. Soc. Am. 109, 2852–2861.
- Olson, E. S. (1998). "Observing middle and inner ear mechanics with novel intracochlear pressure sensors," J. Acoust. Soc. Am. 103, 3445–3463.
- Oppenheim, A. V., and Schafer, R. W. (1999). *Discrete-Time Signal Processing* (Prentice-Hall International, Englewood Cliffs, NJ).
- Recio, A., Rich, N. C., Narayan, S. S., and Ruggero, M. A. (1998). "Basilarmembrane responses to clicks at the base of the chinchilla cochlea," J. Acoust. Soc. Am. 103, 1972–1989.
- Rhode, W. S., and Cooper, N. P. (1996). "Nonlinear mechanics in the apical turn of the chinchilla cochlea in vivo," Aud. Neurosci. 3, 101–121.
- Rhode, W. S., and Recio, A. (2000). "Study of mechanical motions in the basal region of the chinchilla cochlea," J. Acoust. Soc. Am. 107, 3317– 3332.
- Robert, A., and Eriksson, J. L. (1999). "A composite model of the auditory

periphery for simulating responses to complex sounds," J. Acoust. Soc. Am. 106, 1852–1864.

- Robles, L., and Ruggero, M. A. (2001). "Mechanics of the mammalian cochlea," Physiol. Rev. 81, 1305–1352.
- Ruggero, M. A., Rich, N. C., Recio, A., Narayan, S. S., and Robles, L. (1997). "Basilar-membrane responses to tones at the base of the chinchilla cochlea," J. Acoust. Soc. Am. 101, 2151–2163.
- Russell, I. J., and Nilsen, K. E. (1997). "The location of the cochlear amplifier: Spatial representation of a single tone on the guinea pig basilar membrane," Proc. Natl. Acad. Sci. U.S.A. 94, 2660–2664.
- Sumner, C. J., O'Mard, L. P., Lopez-Poveda, E. A., and Meddis, R. (2003). "A nonlinear filter-bank model of the guinea-pig cochlear nerve: Rate responses," J. Acoust. Soc. Am. 113, 3264–3274.
- Zhang, X., Heinz, M. G., Bruce, I. C., and Carney, L. H. (2001). "A phenomenological model for the responses of auditory-nerve fibers. I. Nonlinear tuning with compression and suppression," J. Acoust. Soc. Am. 109, 648–670.
- Zilany, M. S., and Bruce, I. C. (2006). "Modeling auditory-nerve responses for high sound pressure levels in the normal and impaired auditory periphery," J. Acoust. Soc. Am. 120, 1446–1466.