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DOI

[10.1121/1.418173](https://doi.org/10.1121/1.418173)

Publication date

1997

Published in

The Journal of the Acoustical Society of America

[Link to publication](#)

Citation for published version (APA):

Kanis, L. J., & de Boer, E. (1997). Frequency dependence of acoustic distortion products in a locally active model of the cochlea. *The Journal of the Acoustical Society of America*, 101(3), 1527-1531. <https://doi.org/10.1121/1.418173>

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Frequency dependence of acoustic distortion products in a locally active model of the cochlea^{a)}

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(Received 25 March 1996; revised 19 August 1996; accepted 22 October 1996)

In two-tone experiments it has been shown that acoustic distortion products are “tuned” as a function of primary frequency ratio, that is, at a certain frequency ratio a maximum in emission occurs. Several authors maintain that this “tuning” is caused by band-pass filtering of the distortion products as they are coupled back to the basilar membrane. In this paper one possible other cause for this type of tuning is brought to light. It is shown that the same kind of “tuning” is present in a locally active cochlea model without such a filtering of distortion products. In this view “tuning” becomes evident because, when the frequency ratio is near unity, the primary components tend to suppress one another, and suppress the DP, too. © 1997 Acoustical Society of America. [S0001-4966(97)01203-4]

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

INTRODUCTION

In 1986 Matthews and Molnar showed that in the non-linear cochlea model they used, acoustic distortion products (DPs) were (bandpass) “tuned” as a function of primary frequency ratio. Similar tuning has been observed in experiments where maximal otoacoustic emissions occur at a frequency ratio of about 1.2 (Kim, 1980; Wilson, 1980; Fahey and Allen, 1986; Lonsbury-Martin *et al.*, 1987; Harris *et al.*, 1988; Brown and Gaskill, 1990a, 1990b; Gaskill and Brown, 1990; Whitehead *et al.*, 1992).

In recent papers several authors maintain that the DP “tuning” is the result of an additional filtering mechanism inside the cochlea (Brown and Gaskill, 1990a; Brown and Williams, 1993; Allen and Fahey, 1993). Defining the first filter as the one caused by the resonance mechanism of the BM, the second filter would reside in the micromechanics of the organ of Corti. It is clear why the DP emission decreases when the primary frequency ratio is increased above approximately 1.2. A “second filter” would be necessary to explain why the DP emission also decreases when the primary frequency ratio is lowered from about 1.2 to 1.0.

It should be noted that the “second filter” hypothesis is in contradiction with the findings of Matthews and Molnar because in their model “tuning” was observed while *no* filtering of the DPs was built in. We show in this paper that the same kind of “tuning” is present in a more realistic nonlinear model with local activity in which there is *no* filtering of DPs *after* generation. In other words, we show that one cannot conclude from the available experimental emission data that a DP filtering mechanism is necessarily present in the real cochlea. We also show that the DP “tuning” disappears at levels where the cochlea model operates more in the linear regime, i.e., at input levels of 20 dB SPL and lower. If in experiments DP “tuning” at correspondingly low levels would be shown, this would be strong evidence that the sec-

ond filter exists. In any event, the “tuning” seen at higher levels should not solely result from the second filter.

I. MODEL AND METHOD

In macromechanical models of the cochlea the cochlear partition can be described by an impedance consisting of a mass, a resistance, and a stiffness part. A micromechanical model of the partition may be described by three impedances, for instance Z_{BM} , Z_{RL} , and Z_{OC} ; the first one describing the mechanics of the basilar membrane (BM), and the other two describing the mechanics of the reticular lamina (RL) and the organ of Corti (OC). The situation at one location x is shown schematically in Fig. 1, where $-2p$ denotes the pressure difference across the cochlear partition and v_{BM} , v_{RL} , and v_{OC} stand for BM velocity, RL velocity and velocity of the OC, respectively. Thus, in the case of Fig. 1, the total impedance of the cochlear partition consists of the BM impedance and a parallel combination formed by the impedances of the RL and the OC. In a different model of the same class the parallel combination might be formed by the impedance of the tectorial membrane (TM) and the impedance that describes the stereociliar coupling with the TM.

In a locally active cochlea model the outer hair cells (OHCs) amplify the traveling wave in the peak region by generating an extra pressure difference across the cochlear partition. Since the OHCs are embedded in the organ of Corti, the pressure source is to be added in series with the impedance of the organ of Corti (at the location of the open circle in Fig. 1), so that the OHC pressures are *filtered* as they are coupled back to the BM (details are given in Kanis, 1995, chapter 6). Several recently published locally active cochlea models are of this class (Geisler, 1991; Geisler *et al.*, 1993; Neely, 1993; Neely and Stover, 1993). The model by Neely and Kim (1986) is simpler: the effective action of the OHCs has been put directly across the cochlear partition (at the location of the filled circle in Fig. 1). In their model there is *no* filtering of the OHC-generated pressures.

^{a)}Preliminary results were presented during the 1995 Midwinter Meeting of the Association for Research in Otolaryngology, St. Petersburg, FL.

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FIG. 1. Electrical circuit for a cochlear section. The velocity of the BM is denoted by v_{BM} , the velocity of the reticular lamina (RL) by v_{RL} , and the velocity associated with compression and expansion of the organ of Corti by v_{OC} . The impedance Z_{BM} is the BM impedance, the impedance Z_{RL} describes how the cilia are attached to the modiolus via the tectorial membrane, and Z_{OC} represents the internal mechanics of the organ of Corti. The pressure p_{OHC} is the pressure generated by the outer hair cells, and $-2p$ is the pressure difference over the cochlear partition.

To sharpen our arguments we will use in this paper a (long-wave) model of the cochlea that is similar to that of Neely and Kim. For details of the model and the method that we used to solve for the response (called the *quasilinear* solution method) we refer to Kanis and de Boer (1993). It is to be remembered that the only nonlinear elements in the model are the OHCs, and that OHC transduction is assumed to be instantaneous.

When two primary components are present in the input stimulus, two peaks will occur in the velocity response of the cochlear partition. In a nonlinear model they will give rise to various DP components in the locally generated OHC pressure. In our model the locally generated DP pressure is applied to the BM directly without being filtered. In what follows DP will denote only the component with frequency $2f_1 - f_2$. This DP pressure (at one location) is shown in Fig. 1 by the filled circle. From the assembly of such DP pressure sources along the x axis, a traveling wave is set up which during its travel towards the place of resonance will be amplified by the OHCs. As a result, the total input to the OHCs consists of the two primary components and the DP components. The DP pressure component with radian frequency ω_{DP} generated by the OHCs will be called $P_{OHC}(x; \omega_{DP})$.

In this paper the response of the nonlinear model is solved in the frequency domain by considering only the relevant Fourier components in the pressures generated by the OHCs. Thus, we first compute the responses to the two primaries as described in Kanis and de Boer (1994), then we proceed with the computation of the DP responses without bothering about the primaries; this is done in a number of

FIG. 2. DP emissions as a function of primary frequency ratio displayed for three different primary input levels (50 dB SPL: thin solid line; 60 dB SPL: dashed line; 70 dB SPL: thick solid line). We have monitored the pressure at the location of the stapes with a reference level of $1 \times 10^{-5} \text{ N m}^{-2}$. The experimental curve with the squares is taken from Gaskill and Brown (1990, Fig. 2d, dashed line). The reference level of the experimental curve is $3.16 \times 10^{-8} \text{ N m}^{-2}$.

iteration steps. The whole procedure is justified because the influence of higher-order components on primary components is negligible (see Kanis and de Boer, 1993, Appendix B). With the two primary responses we compute $P_{OHC}^{(1)}(x; \omega_{DP})$, an initial guess to the ultimate pressure distribution $P_{OHC}(x; \omega_{DP})$, and $Z_{OHC}^{(1)}(x; \omega_{DP})$, an initial guess to the quasilinear OHC transfer impedance at the DP frequency $Z_{OHC}^{ql}(x; \omega_{DP})$. These two functions lead to a first estimate $v_{BM}^{(1)}(x; \omega_{DP})$ of the DP component of the velocity response $v_{BM}(x; \omega_{DP})$ [see Kanis and de Boer, 1993, Eq. (B7)]. In the second iteration step we compute $P_{OHC}^{(2)}(x; \omega_{DP})$ which is the pressure generated by a local OHC if both primaries *and* the estimate $v_{BM}^{(1)}(x; \omega_{DP})$ are used as input. In fact, $P_{OHC}^{(1)}(x; \omega_{DP})$ includes amplification effects at the DP frequency, and provides a better approximation to the ultimate pressure distribution $P_{OHC}(x; \omega_{DP})$. The estimate for the effective OHC impedance function in the k th iteration step is

$$Z_{OHC}^{(k)}(x; \omega_{DP}) = \frac{P_{OHC}^{(k)}(x; \omega_{DP}) - P_{OHC}^{(1)}(x; \omega_{DP})}{v_{BM}^{(k-1)}(x; \omega_{DP})}. \quad (1)$$

In theory the iteration sequence can be carried on indefinitely. In practice two iteration steps suffice to get a good estimate of $P_{OHC}(x; \omega_{DP})$, $Z_{OHC}^{ql}(x; \omega_{DP})$, and $v_{BM}(x; \omega_{DP})$, i.e., an estimate that differs by less than 1 dB from the result after 20 more iterations. It should be noted that in all iteration steps we use $P_{OHC}^{(1)}(x; \omega_{DP})$ as the “distributed excitation” to the cochlea. Details of the computational method are given by Kanis and de Boer (1993, 1994, Appendix A).

II. RESULTS

To monitor the emission of the DP, we have considered the DP pressure at the location of the stapes. In Fig. 2, two tones with frequencies and f_1 and f_2 ($f_2 > f_1$) and equal amplitudes have been used as primary tones. The amplitude of the $2f_1 - f_2$ DP emission computed with the model is shown

FIG. 3. DP emissions as a function of primary frequency ratio. Same as Fig. 2 but for lower input levels (20 dB SPL: thin solid line; 30 dB SPL: dashed line; 40 dB SPL: thick solid line). We see that the DP “tuning” disappears completely at the level of 20 dB SPL.

as a function of primary frequency ratio (f_2/f_1) with the DP frequency held constant at 6 kHz. The curves were obtained for input levels of 50, 60 and 70 dB SPL. In this figure we see that “tuning” of the DP is clearly present. Keeping the lower primary frequency f_1 or the higher frequency f_2 constant (instead of the DP frequency) does not change the nature of this result. One experimental curve by Gaskill and Brown (1990, Fig. 2d, dashed line, shown here as squares) is added for comparison.¹

Since in the model the DPs are not filtered after generation, the “tuning” shown by Fig. 2 cannot be produced by a second filter. One possible explanation is that the “tuning” near $f_2/f_1=1$ is a principal byproduct of nonlinear “overloading” in the system. To check whether this is true, we computed the DP emission at lower levels than in Fig. 2. The result is shown in Fig. 3 for which we have used primary levels of 20, 30, and 40 dB SPL. We see that, at the lowest level, the emission increases monotonically as the frequency ratio decreases to 1.0, or, in other words, DP “tuning” disappears completely at that level. Therefore, in our model DP “tuning” is a direct result of overloading.

To examine whether suppression of the active mechanism at the DP frequency by the primary components might be the cause of the DP “tuning” we have artificially removed this suppression; that is, we have taken the impedance $Z_{\text{OHC}}^{(k)}(x; \omega_{\text{DP}})$ of Eq. (1) as fully active [see Eq. (9) in Kanis and de Boer (1993)]. (Note that such an action is only possible with the quasilinear method and not with time-domain methods.) We have plotted the resulting DP emission as a function of primary frequency ratio in Fig. 4. The solid line is the 50 dB SPL curve from Fig. 2, and the dashed line the corresponding unsuppressed curve. We observe that the “tuning” has not fully disappeared. This indicates that suppression of the DP by the primary components is a partial, but not the full explanation of the “tuning”. The “tuning” is also caused by complex interaction of waves originating from many different locations.

Several authors have stated that for DPs of different or-

FIG. 4. Effect of removal of nonlinearity on DP emissions. The solid curve has been obtained as a function of primary frequency ratio and is the same as the 50 dB SPL curve from Fig. 2. The dashed curve has been obtained with the same parameters but the suppressive effect of the primaries on the amplification of the DP has artificially been removed. We see that although the “tuning” of the dashed curve is much less than for the solid curve, it has not fully disappeared.

der the DP emission curves (as a function of DP frequency) peak at the same primary frequency ratio (e.g., Allen and Fahey, 1993). This is not universally true, however, as can be seen from Fig. 4 from Brown and Gaskill (1990a). In that figure the primary frequency ratio at which a DP response curve peak shifts to a lower value for higher order of the DP. In our modeling we found the same property.

III. DISCUSSION

In our model filtering is involved in the *input* path to the OHCs. However, such a filtering cannot produce the observed type of “tuning” of the DPs. This is seen as follows. Consider one OHC, its input (stereociliary displacement) being a filtered version of the BM response. The nonlinear effects in that OHC will be largest when the overlap between the input signals produced by the two primary tones is largest. Irrespective of how the BM response is filtered before it arrives at the OHC, the overlap between these two excitations is largest when the two frequencies are equal (i.e., for $f_2/f_1=1$), and this is true for all OHCs.

In this paper we have demonstrated that in order to explain the “tuning” of DP emissions one does not absolutely need a filtering mechanism in the *output* path of OHCs (as hypothesized by Brown and Gaskill, 1990a; Brown and Williams, 1993; Allen and Fahey, 1993; Neely and Stover, 1993). We have replicated “tuning” of acoustic DPs in a cochlea model in which OHC-generated pressures are *not* filtered as they are coupled back to the BM. In our model, DP “tuning” results from *overloading* of the active process. Therefore, our model does not show DP “tuning” at low levels. Because entirely comparable stimulus conditions have not yet been exploited in experiments, we have to await future experiments to decide whether DP “tuning” exists at low levels. In any event, the “tuning” seen at higher levels should not solely result from the second filter.

In the cochlea model by Neely and Stover (1993) the evidence about DP “tuning” at low input levels is meager (Neely, personal communication). In their model DP components in the OHC pressures are filtered before they are coupled back to the BM. However, this DP filtering cannot give rise to DP “tuning” because the maximum of the filter $F(x; \omega)$ in Eq. (A6) lies at the same location as the peak of the velocity response (at least for low levels). Therefore, the DP filtering cannot give rise to DP “tuning” in their model. The situation is different for the locally active model by Geisler (1991). In that model the filter peak lies at a more basal location than the DP’s resonance place. Thus, in Geisler’s model DP “tuning” at low levels would be possible.

With a future experiment performed at low levels it might be possible to discriminate between a class of models in which DP filtering is reflected in the acoustic distortion data and a class of models in which that is not the case. It is a fact that the OHCs are embedded in the organ of Corti, and it is therefore likely that the DPs are filtered before they are coupled back on the BM. The question is what the nature of this filter is. If a future experiment shows DP “tuning” at sufficiently low levels (equal primary levels of 20 dB SPL), the class of models to which Neely and Stover’s model belongs is not of the right type. Such a finding would be in favor of models like that of Geisler (1991) in which a filter is present.

APPENDIX: FILTERING OF THE OHC PRESSURE

In the frequency domain one longitudinal section of the cochlear models by Neely and Stover (1993) and Geisler *et al.* (1993) can be represented by a similar network as the one shown in Fig. 1 with the active pressure source at the location of the open circle. We will show in this appendix that in that case the pressure generated by the OHCs is filtered as it is coupled back to the BM.

The network is described by three equations:

$$Z_{BM}(x; \omega)v_{BM}(x; \omega) + Z_{RL}(x; \omega)v_{RL}(x; \omega) = -2p(x; \omega), \quad (A1)$$

$$v_{OC}(x; \omega) = v_{BM}(x; \omega) - v_{RL}(x; \omega), \quad (A2)$$

and

$$Z_{OC}(x; \omega)v_{OC}(x; \omega) - Z_{RL}(x; \omega)v_{RL}(x; \omega) = P_{OHC}(x; \omega). \quad (A3)$$

Here all variables and impedances are complex functions of location x and radian frequency ω ; $Z_{RL}(x; \omega)$ is the impedance with which the reticular lamina (RL) are attached to the modiolus via the tectorial membrane, $Z_{OC}(x; \omega)$ the impedance of the organ of Corti, and $Z_{BM}(x; \omega)$ the BM impedance. Furthermore, $v_{BM}(x; \omega)$ and $v_{RL}(x; \omega)$ are the BM velocity and the velocity of the RL, respectively. The difference between these two velocities is $v_{OC}(x; \omega)$, the measure of amplitude changes of the organ of Corti.

For the distortion products the pressure $P_{OHC}(x; \omega_{DP})$, generated by the OHCs, consists of a term $P_{OHC}^{(1)}(x; \omega_{DP})$ that is produced by the primaries, and a term that is produced by the DP itself:

$$P_{OHC}(x; \omega_{DP}) = P_{OHC}^{(1)}(x; \omega_{DP}) + Z_0^{ql}(x; \omega_{DP})v_{RL}(x; \omega_{DP}) \quad (A4)$$

with $Z_0^{ql}(x; \omega_{DP})$ the (quasilinear) transduction impedance of the OHCs at the frequency of the DP. The impedance $Z_0^{ql}(x; \omega_{DP})$ is influenced by the primaries and by self-suppression. Solving Eq. (A1) for $v_{RL}(x; \omega_{DP})$ leads to

$$[Z_{BM}(x; \omega_{DP}) + Z_{OC}(x; \omega_{DP})F(x; \omega_{DP})]v_{BM}(x; \omega_{DP}) = -2p(x; \omega_{DP}) + F(x; \omega_{DP})P_{OHC}^{(1)}(x; \omega_{DP}), \quad (A5)$$

where $F(x; \omega)$ is given by

$$F(x; \omega) = \frac{Z_{RL}(x; \omega)}{Z_{OC}(x; \omega) + Z_{RL}(x; \omega) + Z_0^{ql}(x; \omega)}. \quad (A6)$$

On the right-hand side of Eq. (A5), $F(x; \omega)$ is to be interpreted as *the* filtering of the DPs before they are added to the pressure difference over the BM. Whether, at very low input levels, “tuning” is detected in the DP emissions or not depends on where the maximum of the filter $F(x; \omega)$ lies. If it lies at the same location as the velocity peak of the DP, there will be no tuning of the DP emissions.

¹With the time-domain model described in Kanis and de Boer (1996) DP “tuning” becomes somewhat less than in Fig. 2 due to differences between the quasilinear and the time-domain method at some combinations of input parameters. The main conclusions of this paper, however, remain the same.

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