Basilar-membrane nonlinearity estimated by pulsation threshold

Christopher J. Plack[a)]
Department of Psychology, University of Essex, Wivenhoe Park, Colchester CO4 3SQ, England

Andrew J. Oxenham
Research Laboratory of Electronics, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139

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The pulsation threshold technique was used to estimate the basilar-membrane (BM) response to a tone at characteristic frequency (CF). A pure-tone signal was alternated with a pure-tone masker. The frequency of the masker was 0.6 times that of the signal. For signal levels from around 20 dB above absolute threshold to 85 dB SPL, the masker level was varied to find the level at which a transition occurred between the signal being perceived as ''pulsed'' or ''continuous'' (the pulsation threshold). The transition is assumed to occur when the masker excitation is somewhat greater than the signal excitation at the place on the BM tuned to the signal. If it is assumed further that the response at this place to the lower-frequency masker is linear, then the shape of the masking function provides an estimate of the BM response to the signal. Signal frequencies of 0.25, 0.5, 1, 2, 4, and 8 kHz were tested. The mean slopes of the masking functions for signal levels between 50 and 80 dB SPL were 0.76, 0.50, 0.34, 0.32, 0.35, and 0.41, respectively. The results suggest that compression on the BM increases between CFs of 0.25 and 1 kHz and is roughly constant for frequencies of 1 kHz and above. Despite requiring a subjective criterion, the pulsation threshold measurements had a reasonably low variability. However, the estimated compression was less than in an earlier study using forward masking. The smaller amount of compression observed here may be due to the effects of off-frequency listening.
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INTRODUCTION

The basilar membrane (BM) in the cochlea has a response function that is highly nonlinear and compressive (Rhode and Robles, 1974; Robles *et al.*, 1986; Murugasu and Russell, 1995; Ruggero *et al.*, 1997; Russell and Nilsen, 1997). Recent results suggest that the BM is the primary source of the nonlinearities observed in psychophysical masking experiments (Oxenham and Moore, 1995; Moore and Oxenham, 1998; Oxenham and Plack, 1998; Plack and Oxenham, 1998). Furthermore, cochlear nonlinearities have a significant influence on a wide range of basic auditory processes, such as frequency selectivity (Hicks and Bacon, 1999; Moore *et al.*, 1999), temporal integration (Oxenham *et al.*, 1997), and loudness growth (Yates, 1990; Moore and Glasberg, 1997; Moore and Oxenham, 1998). It is clear that future models of hearing will need to incorporate a simulation of the characteristics of the BM if they are to provide an accurate account of our perceptions.

While direct physiological measurements of BM vibration have provided a great deal of information about the nature of the nonlinearity, these measurements have been restricted to very high (Ruggero *et al.*, 1997; Russell and Nilsen, 1997) and low (Rhode and Cooper, 1996) characteristic frequencies (CFs): Only the basal and apical turns of the cochlea are readily accessible. In addition, of course, it is not practical to make such measurements in live human beings.

[a)]Electronic mail: cplack@essex.ac.uk

Oxenham and Plack (1997) attempted to estimate the BM response in humans using a psychophysical forward-masking technique. A brief pure-tone signal was presented shortly after a pure-tone masker with a frequency an octave below the signal. A forward-masking design was used so that there could be no interaction between the masker and the signal on the BM (Arthur *et al.*, 1971; Ruggero *et al.*, 1992; Nelson and Schroder, 1997). In this respect the design differed from those that used simultaneous masking to estimate BM compression (Stelmachowicz *et al.*, 1987; Bacon *et al.*, 1999). For a range of signal levels, the masker level was varied to find threshold. The technique relies on the finding that the BM response to a tone well below CF is roughly linear (Murugasu and Russell, 1995; Ruggero *et al.*, 1997; Russell and Nilsen, 1997). In other words, a 10-dB increase in masker level will produce a 10-dB increase in BM vibration (excitation) at the place tuned to the signal frequency. If it is assumed that the signal is detected using the information at this place, and if it is assumed further that the ratio of signal excitation to masker excitation is constant at threshold, then any BM compression applied to the signal will be reflected in the slope of the masking function. For example, if the compression ratio is 5:1, then a 10-dB increase in signal level will produce only a 2-dB increase in BM excitation. Hence, the masker level will only need to be increased by 2 dB for the signal to remain at threshold. In other words, a shallow masking function (masker level plotted against signal level) with a slope less than 1 indicates compression.

Using the forward-masking technique, Oxenham and Plack (1997) estimated the CF response at 2 and at 6 kHz. They found approximately 5:1 compression for signal levels between about 45 and 80 dB SPL, with a more linear response at low and high levels. The results were consistent with the physiological data (Yates *et al.*, 1990; Ruggero, 1992; Murugasu and Russell, 1995), suggesting that the assumptions of the technique are valid. Furthermore, measurements on hearing-impaired listeners revealed much less compression, consistent with the physiological consequences of cochlear damage (Ruggero and Rich, 1991; Ruggero *et al.*, 1993). Indeed, the experiments of Moore *et al.* (1999), comparing several behavioral measures of BM nonlinearity in normal and impaired listeners, suggest that the forward-masking design may provide a reliable indication of the state of the active mechanism.

Although the results of Oxenham and Plack (1997) are encouraging, there is a serious limitation to their technique. In order to obtain a substantial amount of masking for such a large frequency separation between the masker and the signal, the signal needed to be very brief (4 ms) and presented very shortly after masker offset. The silent interval between the masker and the signal was only 2 ms. At low frequencies it is not advisable to use the same parameters. First, the width of the auditory filter becomes narrow compared to the spectral extent of the signal, so that the effects of ''spectral splatter'' become a serious concern. Second, the longer temporal response of the auditory filters at low frequencies (Kiang *et al.*, 1970) means that the masker and the signal may overlap on the BM, producing nonlinear effects such as suppression that could confound the results (Ruggero *et al.*, 1992; Nelson and Schroder, 1997).

The present article explores an alternative design based on the pulsation threshold technique devised by Houtgast (1972). This technique relies on an auditory illusion whereby an interrupted sound is perceived as being continuous if there is sufficient energy from another sound during the interruption. Consider the situation in which a signal is alternated with a low-frequency masker. If the masker excitation at the place tuned to the signal is greater than the signal excitation, then the signal may be perceived as continuous. As described earlier, for a masker much lower in frequency than the signal, the masker excitation at the signal place is related linearly to the masker level. If threshold is defined as the masker level at which the perception of the signal changes from ''pulsed'' to ''continuous,'' then a plot of masker level at threshold against signal level should provide an estimate of the BM response to the signal, in the same way as in the Oxenham and Plack (1997) forward-masking design.

The advantage of the pulsation threshold technique is that long signals and long maskers can be used, avoiding the frequency limitations inherent in the forward-masking design. Any short-term interactions on the BM at masker and signal transitions are likely to be insignificant with regard to the overall perception of the signal as pulsed or continuous.

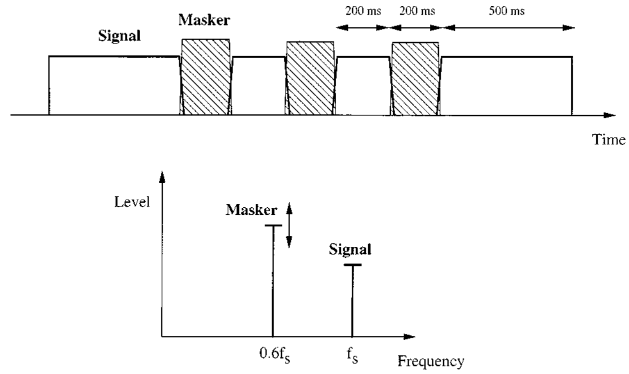

FIG. 1. A schematic illustration of the temporal and spectral characteristics of the stimuli.

I. METHOD

A. Stimuli

The maskers and signals were sinusoids, gated with 20-ms raised-cosine ramps. The masker was presented diotically, and the signal was presented monaurally. This had the effect of spatially separating the two stimuli, such that the masker and signal were lateralized to the center and side, respectively. This made it easier for the listeners to concentrate on the signal, while attempting to ignore the masker. Also, it had the benefit of ruling out the detection of signal pulsation in the contralateral ear, due to acoustic or electric crosstalk. Each interval began with a 540-ms (total duration) signal, followed by an alternating sequence of three maskers and two signals, each with a total duration of 240 ms, and finishing with another 540-ms signal (see Fig. 1). All stimuli began 30 ms before the end of the previous stimulus, so that the ramps of the maskers and signals overlapped and crossed at a point where the envelopes were approximately 1.4 dB below their peak values. This was done to prevent an audible gap between the maskers and the signals being used as a cue for whether the signal was pulsed or continuous.

Signal frequencies of 250, 500, 1000, 2000, 4000, and 8000 Hz were tested. The masker frequency was set at 0.6 times the signal frequency. At each frequency, signal levels from about 20 dB above absolute threshold (as measured in each listener individually) to 85 dB SPL were tested.

The maskers and signals were generated digitally and played out separately via a D/A converter (TDT DD1) at a sampling rate of 50 kHz. The stimuli were then low-pass filtered at 20 kHz (TDT FT5) and attenuated (TDT PA4) before being combined (TDT SM3), passed through a headphone buffer (TDT HB6), and presented via a Sony MDR-V6 headset.

B. Procedure

Pulsation thresholds were measured using a one-interval interleaved adaptive procedure, similar to that described by Jesteadt (1980). In a given run, the masker level was varied and the signal level was held constant. Listeners were asked after each trial to decide whether the signal sounded ''pulsed'' or ''continuous'' by pressing the appropriate button. To help them get accustomed to the task, a demonstration program was used before the experiment started, and occasionally before the start of a new session. In this program, the signal level was set at either 55 or 65 dB and the masker level was set 10 dB lower, making any gating of the signal clearly audible. Listeners could then elect to hear either a pulsed or a continuous signal by pushing one of two buttons. In the pulsed case, a stimulus was presented where the gating of the stimuli was identical to that used within the experiment itself. In the continuous case, the signal actually was continuous (and was heard as such), while the masker was gated in the same way as in the experiment. There was no difference in level between the two conditions. This demonstration was found to be very useful in helping naive listeners focus on the temporal characteristics of the signal, while trying to ignore the masker, which was always gated.

Each run consisted of two interleaved tracks, one tracking the point on the psychometric function corresponding to 70.7% of continuous responses (track 1), and the other tracking the point corresponding to 29.3% of continuous responses (or 70.7% of pulsed responses; track 2). The initial levels of tracks 1 and 2 were 95 and 60 dB SPL, respectively. These levels were chosen as they were found in pilot tests to almost always result in continuous and pulsed responses, respectively, in all conditions. For track 1, two consecutive continuous responses resulted in a decrease in masker level, while every pulsed response resulted in an increase in level. For track 2, two consecutive pulsed responses were required to increase the masker level, while one continuous response resulted in a decrease in masker level.

The initial step size of the masker level was 5 dB. For each track independently, the step size decreased to 2 dB after three reversals. Each track was terminated after seven reversals and the mean of the last four reversals was defined as the threshold. The means from both tracks were averaged to estimate the 50% point, at which a pulsed response was as likely as a continuous response. Some difference between the two tracks is expected, given that they were tracking different points on the psychometric function. However, if the difference between the two tracks was 10 dB or more, the run was discarded and rerun at a later time. If more than two of the four runs had to be discarded, that data point was abandoned. This occurred for some listeners at the lowest signal levels tested. The highest allowable masker level was 107 dB SPL at signal frequencies of 250 and 500 Hz, and 100 dB SPL for all other frequencies. If the adaptive procedure called for a level higher than this, the level was set to the maximum allowable level. If the maximum level was used more than five consecutive times in a track, the run was terminated.

Each threshold reported is the mean of at least four threshold estimates (except for listener AO who only completed three repetitions for each condition).

C. Listeners

A total of six listeners participated in the experiment. Their ages ranged from 20 to 45 years (median age 24). All except author AO were college students who were paid for their participation. Absolute thresholds for a 500-ms pure-tone signal, at octave frequencies between 250 and 8000 Hz, were measured using a two interval, forced-choice (2IFC), three-down one-up adaptive procedure. These values are presented in Table I. All listeners had thresholds of 15 dB HL or less over this frequency range.

TABLE I. The absolute thresholds for the six listeners (in dB SPL) at the six frequencies tested in the experiment. The signal was a 500-ms pure tone.

Subject	250 Hz	500 Hz	1 kHz	2 kHz	4 kHz	8 kHz
EF	28	12	8	4	12	18
BT	20	4	−2	2	6	23
KS	28	22	11	19	16	31
EL	18	9	10	13	10	34
YO	25	13	12	10	8	18
AO	26	12	7	10	12	11

All listeners except AO were naive. Between 2 and 4 h practice was needed for performance to stabilize on the pulsation-threshold task.

II. RESULTS

The individual and mean results are shown in Fig. 2. The average standard deviation across listeners and conditions was 3.2 dB. The missing data points are for conditions in which the signal was too close to absolute threshold for a reliable masked threshold to be found, or where the masker exceeded the highest allowable level. While listener YO shows lower thresholds than the others (note that lower thresholds suggest *less* frequency selectivity), overall the form of the data is consistent between the six listeners. The thick lines show the mean results for conditions where thresholds were available from all six listeners. As explained in the Introduction, the masking function is an estimate of the BM response function for the place with CF equal to the signal frequency. The dotted lines in Fig. 2 show a slope of 1 (linear growth) for comparison. Slopes shallower than unity indicate compression. It is clear that the masking functions for the two lower frequencies (250 and 500 Hz) are steeper than those for the higher frequencies. Indeed, the slopes at 250 Hz do not differ greatly from unity.

Table II shows the slopes of the masking functions for the six listeners together with the mean slopes. These values were obtained by straight-line fits to the data for signal levels from 50 to 80 dB SPL inclusive. (The earlier data of Oxenham and Plack, 1997, suggest that compression is maximal between 50 and 80 dB SPL.) A within-subjects analysis of variance (ANOVA) conducted on these values found a highly significant main effect of frequency [$F(5,25)=18.095$, $p<0.000\,05$]. Pairwise comparisons (Tukey) revealed that the slopes at 250 Hz differed from the slopes for all the other frequencies, and that in addition the slopes at 500 Hz differed from the slopes at 2 kHz. No other comparisons were significant. Table II also shows the compression ratios for each frequency. These values are simply the inverse of the mean slopes.

III. DISCUSSION

A. Comparison with previous results

The masking function slopes for high signal frequencies from the present study are about twice those reported by

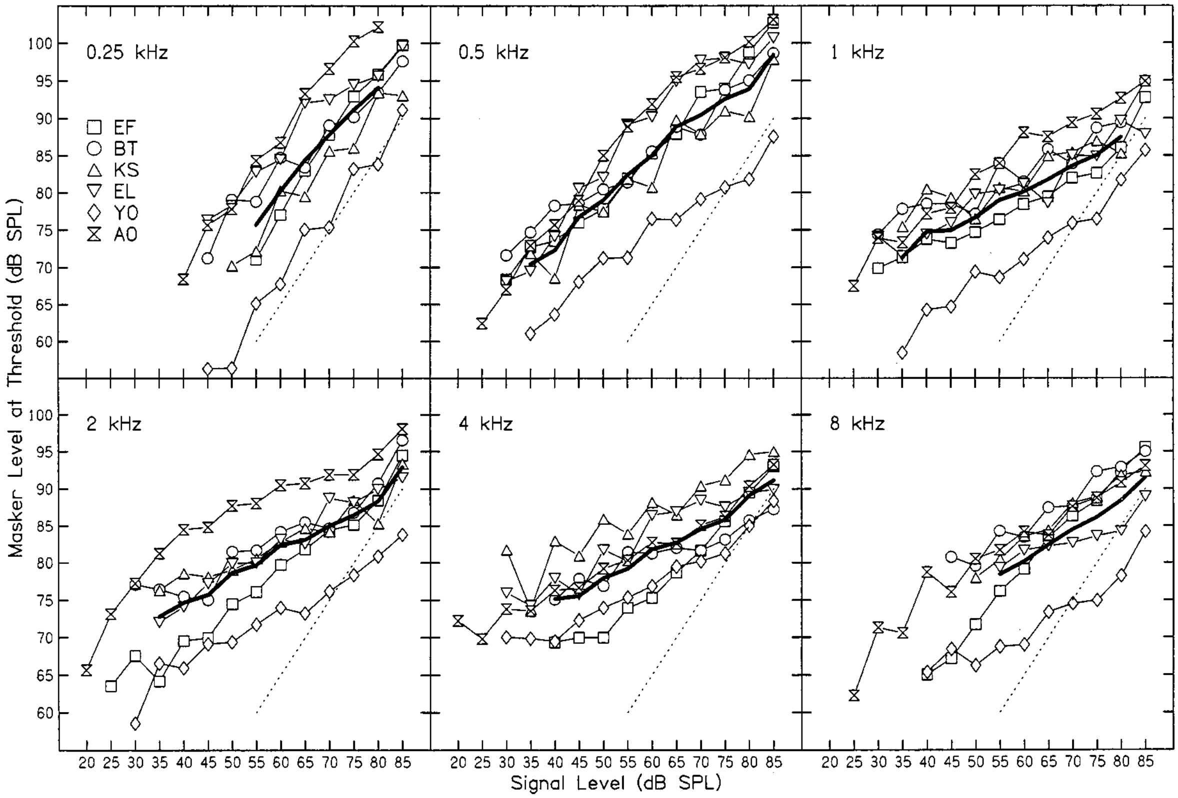

FIG. 2. The results from the main experiment, showing the masker level at pulsation threshold as a function of signal level. The thick lines show the mean results. The dashed lines show a slope of 1 (linear response) for comparison.

Oxenham and Plack (1997). Consequently, the estimated compression (around 2.8:1) is half as great as that derived from the earlier study. Part of the discrepancy may be attributed to a difference in the stimuli. Oxenham and Plack used a high-pass noise to restrict off-frequency listening on the high-frequency side of the excitation pattern. No such noise was used in the present study.

Off-frequency listening may have a strong influence on thresholds in the presence of a low-frequency masker (Johnson-Davies and Patterson, 1979; O'Loughlin and Moore, 1981). As signal level is increased, excitation spreads to the higher CFs. The resulting ''expansive'' improvement in detectability as more channels become available may counteract the on-frequency compression to some extent, reducing the effect of BM nonlinearity on the slope of the masking function. Furthermore, if listeners use auditory filters with CFs greater than the signal frequency, the amount of compression will be less (compression decreases as the input frequency is moved away from CF, see for example Ruggero *et al.*, 1997). When Oxenham and Plack (1997) ran a control condition without the high-pass noise, the slope they found was much less than for the noise conditions, and was in fact very similar to the slopes reported in Table II. Moore *et al.* (1999) found slopes similar to those reported here for their normal listeners using forward masking in the absence of a high-pass noise.

B. BM nonlinearity as a function of frequency

The results suggest that the amount of compression on the BM increases from 250 Hz to 1 kHz and is roughly constant for frequencies of 1 kHz and above. In this respect,

TABLE II. The slopes of the masking functions (for signal levels from 50 to 80 dB SPL) for the six listeners in the experiment. Also shown are the compression ratios (the inverse of the mean slopes).

Subject	250 Hz	500 Hz	1 kHz	2 kHz	4 kHz	8 kHz
EF	1.007	0.681	0.357	0.461	0.629	0.668
BT	0.501	0.507	0.349	0.275	0.216	0.430
KS	0.732	0.457	0.317	0.258	0.306	0.450
EL	0.596	0.503	0.306	0.371	0.285	0.177
YO	0.900	0.379	0.410	0.357	0.343	0.385
AO	0.819	0.489	0.324	0.213	0.339	0.347
Mean slope:	0.759	0.502	0.344	0.323	0.353	0.410
Compression ratio (dB/dB):	1.318	1.992	2.908	3.101	2.833	2.442

the results are consistent with those of Oxenham and Plack (1997), who found no difference between the slopes of the masking functions at 2 and 6 kHz. Hicks and Bacon (1999) examined the effect of frequency on three different psychophysical measures of auditory nonlinearity: frequency selectivity as a function of level; two-tone suppression; and growth of forward masking with masker frequency lower than the signal frequency. All the measures showed a progressive increase in nonlinearity from 750 Hz to 3 kHz with no evidence of nonlinear processing at 375 Hz. The results of Hicks and Bacon, particularly those for the growth-of-masking experiment, are broadly consistent with the results reported here. Similarly, Bacon *et al.* (1999), using the upward spread of simultaneous masking to estimate BM nonlinearity, found evidence for less compression at 400 to 750 Hz than at 1944 to 5000 Hz.

The conclusions based on psychophysical data do depend on an important assumption, however. In the design of Oxenham and Plack (1997), and in the present design, the masking-function slopes will only differ from unity if there is *differential* compression between the signal and the masker. If both the masker and the signal are compressed equally, then the two effects should cancel out and the slope of the masking function will be unity. In other words, the present results are consistent with the possibility that the BM response function is just as compressive at low frequencies as at high frequencies. If this is the case, however, the region of compression at low frequencies must extend over a wider range of frequencies relative to CF.

The two additional techniques used by Hicks and Bacon (1999) may also depend on this assumption. Frequency selectivity will change as a function of level only if the growth of excitation differs between frequency regions relative to CF. In other words, the compression must be frequency selective. Psychophysical two-tone suppression, the other frequency-dependent measure of compression reported by Hicks and Bacon, is more complex. However, it is possible to imagine situations in which there is a great deal of compression without any suppression. For example, if compression is applied after filtering, then the (nominal) suppressor can only add to the overall output of the channel, not reduce it. Incidentally, this is also a situation in which the compression would not be frequency selective.

The apical BM displacement measurements of Rhode and Cooper (1996) suggest that the compression may indeed be less frequency selective at low frequencies than at high, with a broad band of frequencies affected relative to CF. Although the overall compression they measured was less than that found basally, consistent with the psychophysical results, it could be argued that the techniques used to investigate the apex of the cochlea are more disruptive to the physiology than those used in the basal region. Specifically, Reissner's membrane is opened in the apical procedure, which may disrupt the ionic balance of the scala media, thereby damaging the active mechanism.

Another concern with the present data is that the masker frequency was always a constant fraction of the signal frequency. Estimates of the equivalent rectangular bandwidth (ERB) of the auditory filter show that, when expressed as a proportion of CF, the ERB increases with decreasing frequency (Moore and Glasberg, 1983; Glasberg and Moore, 1990). Considered together with the findings of Rhode and Cooper, it could be argued that for low signal frequencies the masker frequency was too close to CF to be within the linear response region. To test this idea, additional masking functions were measured for a 250-Hz signal with a masker frequency of only 100 Hz. Three listeners were tested; the results are shown in Fig. 3. The slopes of the masking functions (for signal levels from 50 to 80 dB SPL) were 0.583, 0.803, and 1.107 for listeners EL, YO, and AO, respectively. These values are similar to those for the equivalent conditions from the main experiment, and there is certainly no evidence that the slope of the masking function decreases as the masker is moved away from the signal frequency. This conclusion is similar to that drawn by Bacon *et al.* (1999) using simultaneous masking. They found little difference between using a masker that was a fixed fraction of the signal frequency (about 0.69), or a masker that was a fixed number of ERBs (3) below the signal frequency. The data lend support to the hypothesis that BM compression decreases at low CFs in humans, although it is still conceivable that the compressive range reported by Rhode and Cooper would encompass both masker and signal, even for the wide frequency separation in the final experiment. At least it can be argued that there is strong psychophysical and physiological evidence for a larger frequency-selective component of nonlinearity at high CFs than at low.

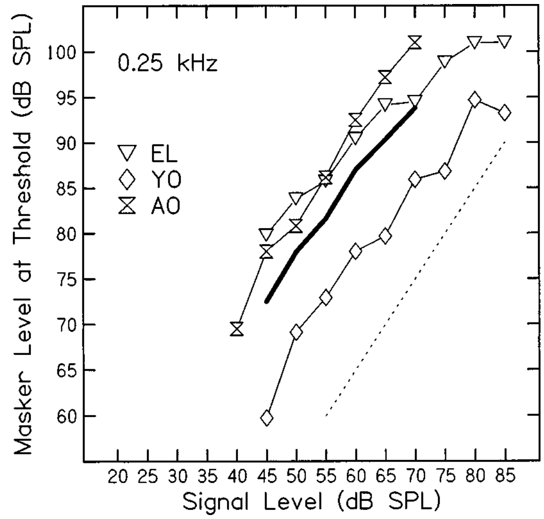

FIG. 3. The results from the experiment described in Sec. III B, showing the masker level at pulsation threshold as a function of signal level, for a 100-Hz masker and a 250-Hz signal. The thick line shows the mean results.

C. An evaluation of the pulsation-threshold technique

As described in Sec. III A, the estimates of compression at high frequencies from the present experiment are less than those reported by Oxenham and Plack (1997), and less than those predicted by the physiology (Murugasu and Russell, 1995; Ruggero *et al.*, 1997; Russell and Nilsen, 1997). It was suggested that the difference could be explained by off-frequency listening. Oxenham and Plack (1997) argued that the effects of off-frequency listening could be minimized by using the ratio of slopes for an off-frequency masker and an on-frequency masker as the estimate of compression. The reasoning is that the expansive effects of off-frequency listening on the two masking functions should cancel out to some extent. The pilot data of Oxenham and Plack (1997) using one listener supported this argument. Moore *et al.* (1999) also used the ratio-of-slopes technique to estimate compression in their study. The argument is correct if one assumes that off-frequency listening increases detectability by increasing the number of channels that can contribute to detection, as this would be the same for both on- and off-frequency maskers. However, the argument may not be sound for situations in which the signal is detected through a channel with a much higher CF than the signal frequency. In this case, the excitation due to both the signal and the masker will grow roughly linearly (the BM response to a tone well below CF is linear). When the masker and the signal have the same frequency and a similar level, the form of the BM response function has little effect on threshold (since the masker and signal are either both compressed or both passed linearly). In other words, the slope of the masking function for the on-frequency condition should not be affected greatly by listening at a higher CF. However, for the case where the masker frequency is less than the signal frequency (the crucial condition), the use of a channel with a CF higher than the signal frequency may produce a more *linear* masking function. Thus, the ratio of slopes for the on- and off-frequency maskers may not provide an accurate estimate of BM compression, if off-frequency listening is not accounted for. With respect to the present design, Houtgast (1972) and Duifhuis (1980) used on-frequency pulsation maskers and found that signal thresholds were about 3 dB lower than the masker level and generally increased linearly with masker level. In other words, with respect to the present data it is unlikely that the ratio-of-slopes estimate would predict any more compression than that reported in Table II.

It may be necessary instead to modify the pulsation threshold stimuli to include a high-pass noise to mask the spread of excitation. Some pilot experiments were run with a background noise, but listeners found the task much harder under these conditions and produced much more variable results, leading to the attempt being abandoned. It remains to be seen whether additional manipulations will prove more successful.

With respect to the reliability of the design, the results are quite encouraging. Despite the fact that threshold depends on a subjective criterion (whether or not the signal sounds pulsed), the standard deviation between replications was quite low, with an average of 3.2 dB. The average standard deviation between replications for the Oxenham and Plack (1997) forward-masking study was 2.1 dB, so the ''subjective'' tracking procedure is by no means disgraced by the conventional 2AFC adaptive technique. The finding of reasonably consistent results supports a similar conclusion drawn by Duifhuis (1980). Using on-frequency maskers in conjunction with a suppressor, he found that the within- and across-session standard deviations were very similar for forward masking and pulsation threshold.

The amount of time taken to reach stable performance on the present task varied between listeners. Some were stable right away while others took a few hours' practice to stabilize. Again, the pulsation-threshold technique did not differ from the forward-masking technique in this regard.

IV. CONCLUSIONS

(i) Masking functions generated by the pulsation-threshold technique showed a strong dependence on signal frequency. The slopes were roughly constant for frequencies of 1 kHz and above but became more linear as the signal frequency decreased from 1 kHz to 250 Hz. The estimated BM compression varied from 1.3:1 at 250 Hz to around 2.8:1 at the higher frequencies.

(ii) The pulsation-threshold technique for estimating BM compression yields thresholds with a reasonably low variability, and allows a wide range of frequency regions to be explored. However, the technique may underestimate the amount of compression, possibly because listeners use information on the high-frequency side of the excitation pattern which was not masked in the present study.

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Arthur, R. M., Pfeiffer, R. R., and Suga, N. (**1971**). ''Properties of 'two tone inhibition' in primary auditory neurones,'' J. Physiol. (London) **212**, 593–609.

Bacon, S. P., Boden, L. N., Lee, J., and Repovsch, J. L. (**1999**). ''Growth of simultaneous masking for $fm<fs$: Effects of overall frequency and level,'' J. Acoust. Soc. Am. **106**, 341–350.

Duifhuis, H. (**1980**). ''Level effects in psychophysical two-tone suppression,'' J. Acoust. Soc. Am. **67**, 914–927.

Glasberg, B. R., and Moore, B. C. J. (**1990**). ''Derivation of auditory filter shapes from notched-noise data,'' Hear. Res. **47**, 103–138.

Hicks, M. L., and Bacon, S. P. (**1999**). ''Psychophysical measures of auditory nonlinearities as a function of frequency in individuals with normal hearing,'' J. Acoust. Soc. Am. **105**, 326–338.

Houtgast, T. (**1972**). ''Psychophysical evidence for lateral inhibition in hearing,'' J. Acoust. Soc. Am. **51**, 1885–1894.

Jesteadt, W. (**1980**). ''An adaptive procedure for subjective judgements,'' Percept. Psychophys. **28**, 85–88.

Johnson-Davies, D. B., and Patterson, R. D. (**1979**). ''Psychophysical tuning curves: Restricting the listening band to the signal region,'' J. Acoust. Soc. Am. **65**, 765–770.

Kiang, N. Y.-S., Moxon, E. C., and Levine, R. A. (**1970**). ''Auditory-nerve activity in cats with normal and abnormal cochleas,'' in *Sensorineural Hearing Loss*, edited by G. E. W. Wolstenholme and J. Knight (Churchill, London), pp. 241–268.

Moore, B. C. J., and Glasberg, B. R. (**1983**). ''Suggested formulae for calculating auditory-filter bandwidths and excitation patterns,'' J. Acoust. Soc. Am. **74**, 750–753.

Moore, B. C. J., and Glasberg, B. R. (**1997**). ''A model of loudness perception applied to cochlear hearing loss,'' Aud. Neurosci. **3**, 289–311.

Moore, B. C. J., and Oxenham, A. J. (**1998**). ''Psychoacoustic consequences of compression in the peripheral auditory system,'' Psychol. Rev. **105**, 108–124.

Moore, B. C. J., Vickers, D. A., Plack, C. J., and Oxenham, A. J. (**1999**). ''Inter-relationship between different psychoacoustic measures assumed to be related to the cochlear active mechanism,'' J. Acoust. Soc. Am. (in press).

Murugasu, E., and Russell, I. J. (**1995**). ''Salicylate ototoxicity: The effects on basilar membrane displacement, cochlear microphonics, and neural responses in the basal turn of the guinea pig cochlea,'' Aud. Neurosci. **1**, 139–150.

Nelson, D. A., and Schroder, A. C. (**1997**). ''Linearized response growth inferred from growth-of-masking slopes in ears with cochlear hearing loss,'' J. Acoust. Soc. Am. **101**, 2186–2201.

O'Loughlin, B. J., and Moore, B. C. J. (**1981**). ''Improving psychoacoustical tuning curves,'' Hear. Res. **5**, 343–346.

Oxenham, A. J., and Moore, B. C. J. (**1995**). ''Additivity of masking in normally hearing and hearing-impaired subjects,'' J. Acoust. Soc. Am. **98**, 1921–1934.

Oxenham, A. J., Moore, B. C. J., and Vickers, D. A. (**1997**). ''Short-term temporal integration: Evidence for the influence of peripheral compression,'' J. Acoust. Soc. Am. **101**, 3678–3687.

Oxenham, A. J., and Plack, C. J. (**1997**). ''A behavioral measure of basilar-membrane nonlinearity in listeners with normal and impaired hearing,'' J. Acoust. Soc. Am. **101**, 3666–3675.

Oxenham, A. J., and Plack, C. J. (**1998**). ''Suppression and the upward spread of masking,'' J. Acoust. Soc. Am. **104**, 3500–3510.

Plack, C. J., and Oxenham, A. J. (**1998**). ''Basilar membrane nonlinearity and the growth of forward masking,'' J. Acoust. Soc. Am. **103**, 1598–1608.

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 Robles, L. (**1974**). ''Evidence from Mossbauer experiments for nonlinear vibration in the cochlea,'' J. Acoust. Soc. Am. **55**, 588–596.

Robles, L., Ruggero, M. A., and Rich, N. C. (**1986**). ''Basilar membrane mechanics at the base of the chinchilla cochlea. I. Input–output functions, tuning curves, and response phases,'' J. Acoust. Soc. Am. **80**, 1364–1374.

Ruggero, M. A. (**1992**). ''Responses to sound of the basilar membrane of the mammalian cochlea,'' Curr. Opin. Neurobiol. **2**, 449–456.

Ruggero, M. A., and Rich, N. C. (**1991**). ''Furosemide alters organ of Corti mechanics: Evidence for feedback of outer hair cells upon the basilar membrane,'' J. Neurosci. **11**, 1057–1067.

Ruggero, M. A., Rich, N. C., and Recio, A. (**1993**). ''Alteration of basilar membrane responses to sound by acoustic overstimulation,'' in *Biophysics of Hair Cell Sensory Systems*, edited by H. Duifhuis, J. W. Horst, P. v. Dijk, and S. M. v. Netten (World Scientific, Singapore), pp. 258–264.

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.

Ruggero, M. A., Robles, L., Rich, N. C., and Recio, A. (**1992**). ''Basilar membrane response to two-tone and broadband stimuli,'' Philos. Trans. R. Soc. London, Ser. B **336**, 307–315.

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. USA **94**, 2660–2664.

Stelmachowicz, P. G., Lewis, D. E., Larson, L. L., and Jesteadt, W. (**1987**). ''Growth of masking as a measure of response growth in hearing-impaired listeners,'' J. Acoust. Soc. Am. **81**, 1881–1887.

Yates, G. K. (**1990**). ''Basilar membrane nonlinearity and its influence on auditory nerve rate-intensity functions,'' Hear. Res. **50**, 145–162.

Yates, G. K., Winter, I. M., and Robertson, D. (**1990**). ''Basilar membrane nonlinearity determines auditory nerve rate-intensity functions and cochlear dynamic range,'' Hear. Res. **45**, 203–220.