# Inferred basilar-membrane response functions for listeners with mild to moderate sensorineural hearing loss

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Psychophysical estimates of cochlear function suggest that normal-hearing listeners exhibit a compressive basilar-membrane (BM) response. Listeners with moderate to severe sensorineural hearing loss may exhibit a linearized BM response along with reduced gain, suggesting the loss of an active cochlear mechanism. This study investigated how the BM response changes with increasing hearing loss by comparing psychophysical measures of BM compression and gain for normal-hearing listeners with those for listeners who have mild to moderate sensorineural hearing loss. Data were collected from 16 normal-hearing listeners and 12 ears from 9 hearing-impaired listeners. The forward masker level required to mask a fixed low-level, 4000-Hz signal was measured as a function of the masker–signal interval using a masker frequency of either 2200 or 4000 Hz. These plots are known as temporal masking curves (TMCs). BM response functions derived from the TMCs showed a systematic reduction in gain with degree of hearing loss. Contrary to current thinking, however, no clear relationship was found between maximum compression and absolute threshold.  [DOI: 10.1121/1.1675812]

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## I. INTRODUCTION

Cochlear hearing loss is associated with an increase in absolute threshold, an abnormally rapid growth in loudness with level, and a loss of frequency selectivity (see Moore, 1995 for a review). These characteristics may result from dysfunction of the outer hair cells (OHCs) in the organ of Corti. The OHCs are thought to be involved in an "active" mechanism that effectively applies gain to stimulation at frequencies close to the characteristic frequency (CF) of each place on the basilar membrane (BM) (see Yates, 1995 for a review). The gain is greatest at low stimulation levels, and decreases with increasing level. This frequency- and level-dependent gain sharpens BM tuning at low to moderate levels, and also results in a highly *compressive* BM response to mid- and possibly high-level tones close to CF (Robles *et al.*, 1986; Ruggero *et al.*, 1997). Measurements of BM vibration in nonhuman mammals have confirmed that interfering with the function of the OHCs, for example by furosemide injection (Ruggero and Rich, 1991), results in a steeper, more linear response to a tone at CF.

Psychophysical techniques based on forward masking have been used to estimate the growth of response of the human BM. Forward masking is used to avoid simultaneous interactions on the BM (e.g., suppression) that complicate the interpretation of the results (Oxenham and Plack, 1997). Most of these techniques have involved comparisons of the effects of maskers at and below the signal frequency. Since the BM response to a masker well below CF is linear, the off-frequency masking function can be used as a linear reference to derive the BM response to a tone at CF. Oxenham and Plack (1997) measured the forward masker level required to mask a brief signal as a function of the level of the signal (referred to here as the growth of masking, or GOM, technique). When the masker was an octave below the signal frequency of 2000 or 6000 Hz, a given change in signal level required a much smaller change in masker level for the signal to remain at threshold. This is thought to be because the response to the signal is compressive and the response to the masker is linear. Indeed, the shallow off-frequency masking function (masker level plotted against signal level) is an estimate of the BM response function to a tone at CF.

A different technique was developed by Nelson *et al.* (2001). The signal was fixed at a level just above absolute threshold. The masker level required to mask the signal was measured as a function of the masker–signal interval to produce a *temporal masking curve* (TMC). For an *off*-frequency masker, the TMC is assumed to reflect the decay with time of the internal effect of the masker: As the masker–signal interval is increased, the masker level has to increase to compensate for the decay. For an *on*-frequency masker, the TMC reflects the decay of masking, *and* the compression applied to the masker: If the response is compressive, a larger change in physical masker level will be required to produce a given change in BM excitation. It follows that an on-frequency TMC that is steep compared to the off-frequency TMC is indicative of compression. It is also possible to derive response functions from TMC data. It is assumed that, for a given masker–signal interval, the BM excitation level at the signal place in response to the masker is a constant at threshold, regardless of the masker frequency. For a given masker–signal interval, the level of the off-frequency masker re-

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quired is an estimate of the BM excitation required at the signal place (give or take an additive constant on a dB scale). Therefore, a plot of the on-frequency masker level (input level) against the off-frequency masker level (output level) is an estimate of the BM response function for the on-frequency masker.

The results from the GOM and TMC studies for normal-hearing listeners at high frequencies are broadly consistent with the rate of growth of BM velocity at high CFs, as measured in other mammals (Lopez-Poveda *et al.*, 2003; Nelson *et al.*, 2001; Oxenham and Plack, 1997; Plack and Drga, 2003). Most GOM and TMC studies report compression exponents (the slopes of the response functions on dB/dB coordinates) in the range 0.15–0.3. This corresponds to compression ratios (the inverses of the compression exponents) of between 6.7:1 and 3.3:1. Furthermore, the shapes of the estimated response functions, with linear low-level regions and compressive midlevel regions, are also consistent with the physiology, suggesting that both behavioral techniques measure cochlear processes. However, there are two good reasons for favoring the TMC technique. As signal level is increased in the GOM technique, the peak of the traveling wave produced by a high-frequency signal will shift basally on the BM (McFadden, 1986). This means that the GOM technique is probably not measuring the response of a single place on the BM, but rather the growth of the peak of the traveling wave with level. In addition, as signal level is increased excitation will spread to higher CFs. To prevent listeners using information from the high-frequency side of the excitation pattern (where the response growth is much more linear than at the peak), a high-pass noise needs to be added to the stimulus (Oxenham and Plack, 1997). Nelson *et al.* (2001) demonstrated that GOM curves in the absence of a high-pass noise exhibit about half the compression of GOM curves in the presence of the noise. This finding is consistent with the greater compression exponents measured in GOM studies that did not include high-pass noise (Hicks and Bacon, 1999b; Moore *et al.*, 1999; Plack and Oxenham, 2000). Selection of the appropriate noise level is problematic, especially for impaired listeners. The TMC technique avoids both these complications. In the TMC technique the signal is fixed at a low level, and hence presumably causes excitation above detection threshold over a fixed, relatively small, region of the BM. The region of the BM measured does not change with masker level, and since the spread of excitation is limited there is no need for a high-pass noise.

Both the GOM and TMC techniques have been used to estimate the BM response for listeners with cochlear hearing loss. The results suggest that a hearing loss of greater than about 50 dB is associated with an almost linear BM response (Nelson *et al.*, 2001; Oxenham and Plack, 1997): The slopes of the GOM functions and TMCs do not vary with masker frequency in these cases (providing support for the contention that the psychophysical techniques measure cochlear processes). For ears with less severe losses, the results are mixed. Moore *et al.* (1999) used the ratio of the slopes of off- and on-frequency GOM functions as an estimate of compression. They found that the compression exponent only began to increase markedly as hearing loss increased above 35 dB. However, the results may have been compromised by the fact that Moore *et al.* did not use high-pass noise to mask spread of excitation (see above). The compression exponents estimated by Moore *et al.* for normal-hearing listeners were at least twice as great as those from GOM studies that included the high-pass noise (Nelson *et al.*, 2001; Oxenham and Plack, 1997). Hicks and Bacon (1999a), again using the GOM technique without high-pass noise, found that mild temporary hearing loss induced by aspirin was associated with a change in slope, consistent with a reduction in compression. Two listeners with mild permanent sensorineural hearing loss showed similar effects. In a recent study measuring GOM for *simultaneous* notched-noise maskers, Baker and Rosen (2002) reported a reduction in gain and compression for a listener with a hearing loss of only 20 dB. However, compression estimates were generally quite low in this study, possibly because of suppressive interactions between the masker and the signal.

In the present study, the TMC technique was used to estimate the BM response to a tone at CF for listeners with a range of impairments, from no impairment to mild to moderate. The aim was to determine how the shape of the response function changes with severity of hearing loss, and to test the hypothesis that mild hearing loss is associated with a reduction in compression.

## II. METHOD

### A. Listeners

Sixteen normal-hearing listeners and nine listeners with mild to moderate hearing impairment participated in the study. Normal-hearing listeners (ten females and six males, aged 19–37 years old) were mostly students from the University of Essex. All had normal audiogram thresholds (within 15 dB ANSI, 1996) in octave steps from 250–8000 Hz.

Hearing-impaired listeners (five females and four males), were aged 54–68 years old, except for listener RD, who was 42 years old. Hearing-impaired listeners reported the onset of hearing difficulties between 2 and 15 years ago and had mild-to-moderate amounts of hearing loss. This was most likely sensorineural hearing loss since it came on gradually and was unrelated to any acute trauma or known disease. It was most likely age related, except for listeners PJ, SG, and RD, who reported repeated exposure to noisy environments when younger. RD also had a family history of hearing loss. On average, audiogram levels for the hearing-impaired group were higher than laboratory norms for normal hearing by 20, 30, and 38 dB at 1000, 2000, and 4000 Hz, respectively. Except for ED, the thresholds at lower frequencies were normal or near normal, suggesting that the impairments did not have a substantial conductive component. Although bone-conduction tests were not performed, the close spacing of the on- and off-frequency TMCs for the impaired listeners is also inconsistent with a conductive loss (see Sec. IV A). RD had borderline normal hearing at 4000 Hz, but elevated thresholds (35–42-dB loss) at 6000 and 8000 Hz. His absolute threshold for the brief 4000-Hz signal in the experiment was 5 dB above the highest absolute

TABLE I. Absolute thresholds, stimulus parameters, and estimated BM response parameters for normal-hearing (upper) and hearing-impaired (lower) listeners, ordered according to the absolute threshold for the signal. Listeners were tested in their right ears unless indicated otherwise. Gain estimates are only included when the low-level portion of the response function is defined by at least two points. Compression and gain could not be sensibly estimated for RG and ES due to the variability of their data. Values marked with asterisks are from response functions generated by interpolation of the off-frequency TMCs.

| Listener | Signal absolute threshold (dB SPL) | Audiogram threshold at 4000 Hz (dB SPL) | Noise spectrum level (dB) | Gain (dB) | Compression exponent |
|---|---|---|---|---|---|
| EK | 3.5 | −8.8 | −16.5 | 42.2 | 0.18 |
| VD | 4.9 | −6.2 | −15.1 | 52.8 | 0.13 |
| RG | 5.2 | −5.0 | −14.8 | ⋯ | ⋯ |
| PP | 6.0 | −5.0 | −14.0 | 37.2 | 0.12 |
| RS | 6.2 | −5.7 | −13.8 | 48.9 | 0.38 |
| IG | 6.4 | −8.2 | −13.6 | 46.0 | 0.00 |
| RB | 7.0 | −3.5 | −13.0 | 48.1 | 0.19 |
| TP | 9.2 | 2.2 | −10.8 | 46.5 | 0.29 |
| AC | 9.4 | −4.3 | −10.6 | 39.8 | 0.23 |
| CO | 9.8 | −5.7 | −10.2 | ⋯ | 0.30 |
| ES | 9.9 | 2.2 | −10.1 | ⋯ | ⋯ |
| NB | 10.5 | 2.2 | −9.5 | 40.5 | 0.18 |
| CG | 10.8 | −0.7 | −9.2 | ⋯ | 0.22 |
| JS | 14.3 | 3.7 | −5.7 | 46.2 | 0.14 |
| IY | 15.1 | 8.2 | −4.9 | 35.3 | 0.37 |
| CN | 17.1 | 5.0 | −2.9 | 38.0 | 0.11 |
| RD | 22.7 | 10.0 | 2.7 | 34.2 | 0.29 |
| JC | 25.9 | 24.7 | −4.1 | ⋯ | 0.18/0.26* |
| ED($l$) | 36.2 | 28.2 | −3.8 | 23.3 | 0.15 |
| SG | 40.3 | 37.0 | 0.3 | ⋯ | 0.25/0.29* |
| DJ($r$) | 41.7 | 36.2 | 1.7 | 27.8* | 0.21* |
| RC($r$) | 45.1 | 37.0 | −4.9 | 13.9/13.9* | 0.28/0.28* |
| ED($r$) | 47.4 | 40.0 | −2.6 | 17.4 | 0.37 |
| MB | 52.9 | 44.3 | 2.9 | 17.3* | 0.14* |
| RC($l$) | 54.4 | 48.3 | 4.4 | 6.5* | 0.02* |
| PJ | 56.5 | 51.0 | 6.5 | 18.5* | 0.32* |
| DJ($l$) | 59.3 | 49.2 | −0.7 | 13.0* | 0.46* |
| BH | 60.8 | 52.3 | 10.8 | 10.2* | 0.10/0.33* |

threshold for the normal-hearing group. Audiogram thresholds, and absolute thresholds for the signal used in the experiment, are given in Table I.

All of the listeners were naive except for EK, IY, PP, and VD. The normal-hearing listeners, except for AC, CN, ES, and RB, had 4–8 h practice in pilot studies for the current experiment. AC, CN, ES, and RB, and all of the hearing-impaired listeners received 1–2 h practice in blocks used to determine parameters for them in the main experiment. There were no systematic improvements in thresholds in the experimental sessions. Listeners were paid £5 per hour for their participation.

## B. Stimuli and equipment

The experiment involved forward masking of tonal signals by tonal maskers. The signal had a frequency of $f_s = 4000$ Hz and an absolute duration of 8 ms (4-ms raised-cosine ramps, 0-ms steady state). The masker had a frequency of either $f_m = 2200$ or 4000 Hz and an absolute duration of 104 ms (2-ms raised-cosine ramps, 100-ms steady state). Silent masker–signal intervals (masker envelope offset to signal envelope onset) ranged from 0–100 ms in steps of 5 or 10 ms, with the set of intervals used dependent on each listener's performance. The signal level was set to 10 dB SL, which ranged from 15–27-dB SPL for normal-hearing listeners and from 33–71-dB SPL for hearing-impaired listeners. Masker level was varied trial by trial.

A low-level notched noise was gated on and off with the masker. This was intended as a temporal cue to help reduce possible confusion effects (Neff, 1986) and not as a source of masking. The noise was white except for a notch at the signal frequency (filter cutoffs at $0.883 f_s$ and $1.117 f_s$, with 90-dB/oct filter slope). For normal-hearing listeners and listener RD, the spectrum level in the passband was set 30 dB below the signal level (i.e., 20 dB below signal absolute threshold). For the remaining hearing-impaired listeners the spectrum level was set to either 40, 50, or 60 dB below the signal level so that it fell in the range −5 to 11 dB. For most hearing-impaired listeners, setting the spectrum level to 30 dB below the signal meant having spectrum levels almost up to 40 dB, resulting in masking due to the noise. Setting the spectrum level to a level between −5 and 11 dB was practical in that hearing-impaired listeners could make use of temporal information at lower frequencies without the noise contributing to masking at 4000 Hz. As described above, most of the hearing-impaired listeners had elevated thresholds at 4000 Hz but normal or near-normal absolute thresholds for frequencies below 2000 Hz. Notched-noise levels for each individual are given in Table I.

The experiment was run using custom-made software on a PC workstation located outside a double-walled soundattenuating booth. Stimuli were digitally generated and were produced using an RME Digi96/8 PAD 24-bit soundcard set at a clocking rate of 48 000 Hz. The soundcard includes an antialiasing filter. The headphone output of the soundcard was fed via a patch panel in the sound-booth wall, without filtering or amplification, to Sennheiser HD 580 circumaural headphones. Each listener sat in the booth and decisions were recorded via a computer keyboard. Listeners viewed a computer monitor through a window in the sound booth. Lights on the monitor display flashed on and off concurrently with each stimulus presentation and provided feedback at the end of each trial.

### C. Procedure

All stimuli were presented monaurally. Normal-hearing listeners were tested in their right ear. Hearing-impaired listeners were tested in their right ear, or in both left and right ears if their audiogram thresholds at 4000 Hz differed across ears by more than 10 dB. Those tested in both ears wore an earplug in their contralateral ear to prevent the possibility of airborne sound aiding performance.

The experiment used a two-interval, forced-choice adaptive tracking procedure with the interstimulus interval set to 500 ms. The signal level was fixed at 10 dB SL and the masker level was varied adaptively using a two-up, one-down rule to obtain the masker level needed to achieve 70.7 percent correct (Levitt, 1971). The masker frequency and masker–signal interval were fixed in any given block of trials. For normal-hearing listeners, the initial masker level was set to 0 dB SPL. The step size of the adaptive track was 8 dB for the first four turnpoints and 2 dB for 12 subsequent turnpoints. Data for listeners RD and BH were collected using these settings, but we found it was desirable to slightly modify the procedure for the rest of the hearing-impaired listeners, due to limitations in the equipment's maximum output (102-dB SPL rms). The modifications were that the initial masker level was set to 20–40 dB below estimated threshold, and the step size was 4 dB for the first four turnpoints and 2 dB for the 12 subsequent turnpoints. For all listeners, the mean of the last 12 turnpoints was taken as the threshold estimate for each block of trials. If the standard deviation of the turnpoints was greater than 6 dB the estimate was discarded and the block was later repeated. Data were also discarded and repeated if possible for any blocks in which the masker clipped more than twice at levels above 102 dB SPL.

Listeners ran blocks of trials lasting 2–4 min per block and spent 15–60 min in the sound booth at any one time, taking breaks as needed. A replication consisted of a complete run of 10–20 blocks per listener, depending on the range of the masker–signal interval at each $f_m$, which was determined during each listener's practice trials. The order of blocks was randomized across masker–signal interval and $f_m$ until all blocks in a replication had been completed. Unless otherwise indicated, the mean threshold across four replications was taken as the threshold estimate for each combination of masker–signal interval and $f_m$. Absolute thresholds for the signal were measured using the same basic procedure, except that signal level was varied using a two-down, one-up adaptive rule.

## III. RESULTS AND ANALYSES

### A. Temporal masking curves

Individual TMCs are presented in Fig. 1 for normal-hearing listeners and in Fig. 2 for hearing-impaired listeners. In general, on-frequency TMCs (triangles) are steeper, in part or in whole, than the accompanying off-frequency TMCs. Assuming the BM response to off-frequency maskers is linear at the signal place, then steeper portions of the on-frequency TMC indicate a compressive response to the on-frequency masker. Such results were found for both the normal-hearing and the hearing-impaired groups.

For three impaired ears, RC($l$), MB, and PJ, it was not possible to reliably measure on-frequency thresholds at the longest masker–signal interval. In two successive runs, they *consistently* detected the signal when the 4000-Hz masker was at 100 dB SPL. The equipment clipped at the next higher level in the adaptive track (102 dB SPL), so the data point for the longest masker–signal interval presented in Fig. 2 for these three listeners was set at 100 dB SPL, and in each case this value was used (when required) in the analyses described below. Limiting the level in this way resulted in *underestimates* of their thresholds and consequently, based on linear extrapolation of their off-frequency TMCs, underestimates of the amount of compression (overestimates of the compression exponents). For several impaired ears, the off-frequency masker levels at the longer intervals also clipped at some stage during the adaptive track on every replication, and these measurements were aborted [see MB, PJ, DJ($l$), and BH in Fig. 2]. However, unlike the on-frequency measurements for the three ears described above, the signal was only *occasionally* detected with the masker at the clipping threshold (the adaptive track touched the clipping point before retreating). It may be assumed that the "true" off-frequency masker level for these missing points lies somewhat below the clipping threshold.

A surprising aspect of the data is that the slopes of the *off*-frequency TMCs appear to be different for the normal-hearing and hearing-impaired listeners. Two analyses were conducted to illustrate and quantify this difference. First, the slopes of the straight lines connecting consecutive points on the off-frequency TMCs were calculated for each listener. The slope values for all the listeners were then combined and ordered by masker–signal interval or by masker level. The upper panels of Fig. 3 show running averages of these values, plotted against running averages of masker–signal interval (upper left) and masker level (upper right). The running averages were calculated separately for the normal-hearing and hearing-impaired groups. The graphs indicate that there are some trends in the data. First, the off-frequency TMC slopes for the normal-hearing group show a tendency to decrease with increasing masker–signal interval. The correlation between masker–signal interval and slope is significant for the normal-hearing group ($r=-0.231$, $n=106$, $p=0.017$). On the other hand, there is little variation in slope with masker–signal interval for the hearing-impaired group,

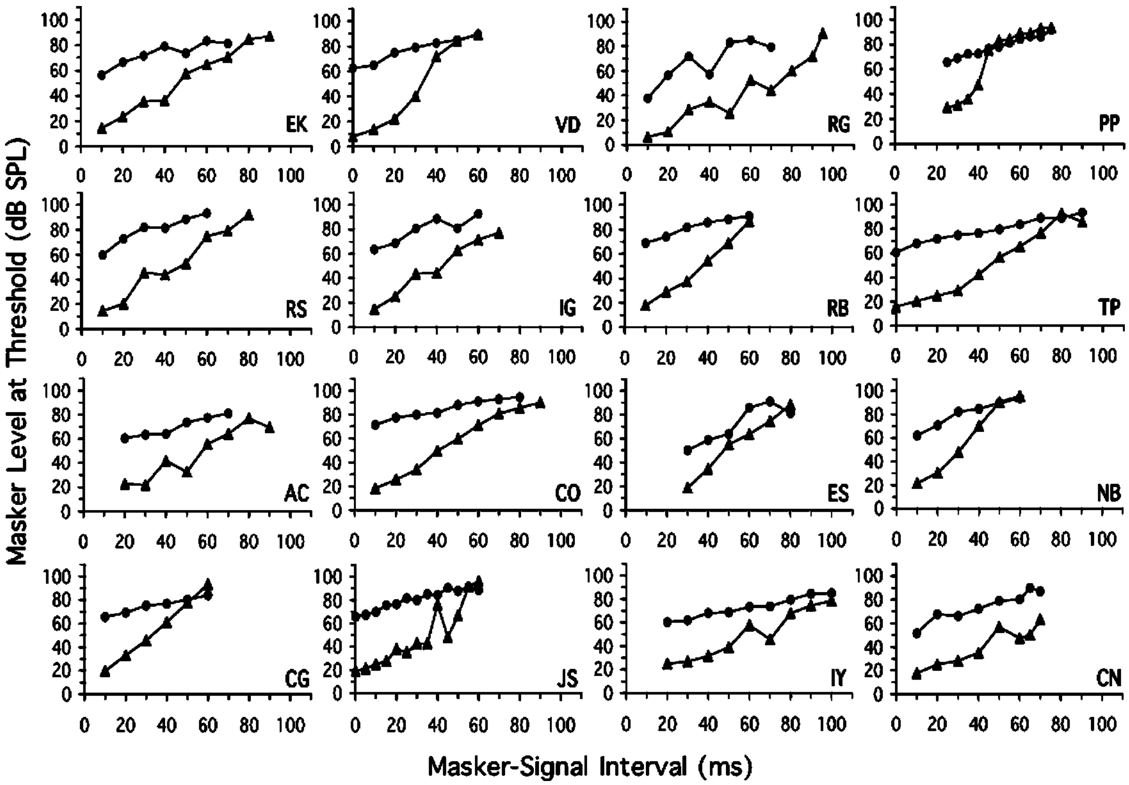


FIG. 1. TMCs for normal-hearing listeners, showing mean masker level at threshold as a function of masker–signal interval for on-frequency (4000-Hz) maskers (triangles) and off-frequency (2200-Hz) maskers (circles).

and the correlation is not significant ($r=-0.155$, $n=48$, $p=0.293$). Second, the off-frequency TMC slopes for the normal-hearing group show a tendency to decrease with increasing masker level, and the correlation between level and slope is significant ($r=-0.271$, $n=106$, $p=0.005$). The correlation between level and slope is not significant for the hearing-impaired group ($r=-0.159$, $n=48$, $p=0.282$), although the range of levels for this group is much less than for the normal-hearing group.

A second analysis investigated the relationship between absolute threshold and off-frequency TMC slope at a specific masker–signal interval and at a specific masker level. Second-order polynomials were fit to the off-frequency TMCs for each listener, and the slopes of the functions calculated (analytically) at a masker–signal interval of 30 ms and, separately, at a masker level of 85 dB SPL. A slope value was only included when the masker–signal interval (either 30 ms, or the calculated masker–signal interval for an 85-dB SPL masker) fell within the range of intervals tested for that listener. The calculated slopes are shown in the lower

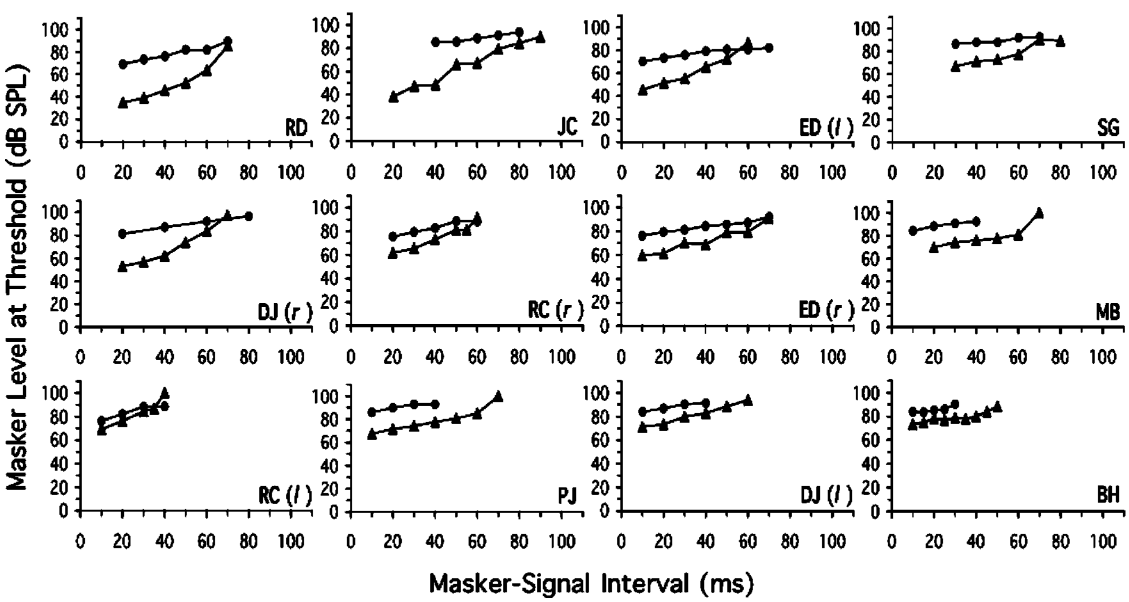


FIG. 2. As Fig. 1, except showing TMCs for hearing-impaired listeners.

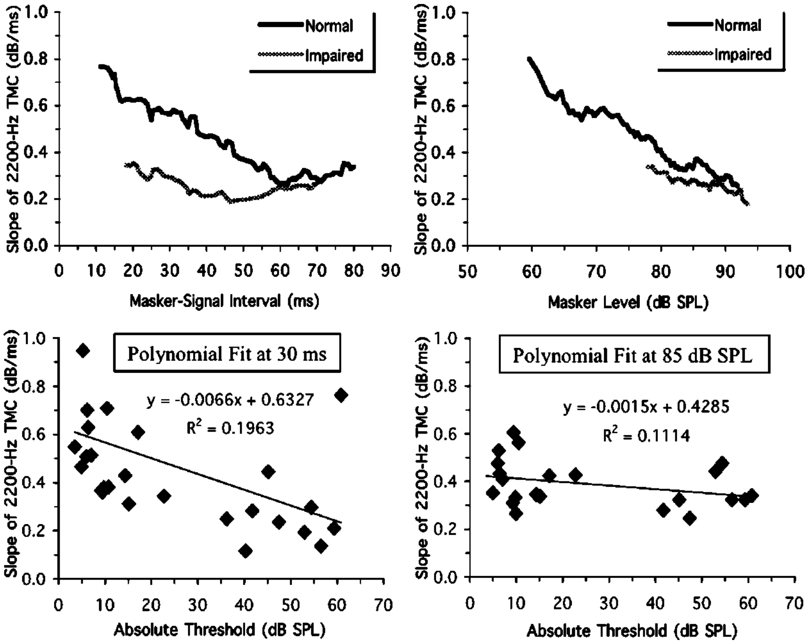


FIG. 3. The upper panels show the slopes of the 2200-Hz TMCs, collapsed across listeners and plotted as running averages over 20 consecutive points. The slopes are shown as a function of masker–signal interval (upper left) and masker level (upper right). The lower panels show scatterplots of 2200-Hz TMC slope against signal absolute threshold. The slopes were derived by fitting second-order polynomials to the TMC data for each listener. The slopes at a masker–signal interval of 30 ms (lower left) and at a masker level of 85 dB SPL (lower right) were calculated from the fitted functions. The lines show linear regression fits, with equations and $R^2$ values displayed on the figure.

two panels of Fig. 3, plotted against the absolute thresholds for the signal. There is a significant negative correlation between absolute threshold and slope at a 30-ms masker–signal interval ($r=-0.443$, $n=27$, $p=0.021$), but no significant correlation between absolute threshold and slope at an 85-dB SPL masker level ($r=-0.334$, $n=22$, $p=0.129$). In summary, the results show that at short masker–signal intervals the off-frequency TMC slopes are shallower for the hearing-impaired listeners than for the normal-hearing listeners. However, the difference may be related to the fact that the masker thresholds were at a higher level for the hearing-impaired listeners. There appears to be little difference in slope between the normal-hearing and hearing-impaired groups when the TMCs are matched for masker level.

It is conceivable that the results for the shorter masker–signal intervals were influenced by the notched noise that was presented as a cue to the offset of the masker. The noise level was generally higher relative to the signal level for the normal-hearing group compared to the hearing-impaired group (see Table I). Although in all conditions the signal was clearly above threshold in the presence of the noise alone, if the noise had contributed to the masking of the signal at the short masker–signal intervals, then the masker level at threshold may have been artificially lowered for the normal-hearing group at the short intervals (both on and off frequency) leading to an increase in TMC slope. One way to test this hypothesis is to examine the masker levels at threshold for the on-frequency masker. It is assumed that, for a given masker–signal interval at threshold, the ratio of BM velocity in response to the signal to BM velocity in response to the masker is constant. Furthermore, the BM response to a low-level on-frequency masker should have been affected in a similar way as the response to the 10-dB SL signal by any attenuation (or loss of gain) resulting from the hearing impairment: If the hearing impairment resulted in the response to the signal being attenuated by $x$ dB, then the response to the masker should also have been attenuated by $x$ dB. It follows that the difference between the *physical* levels of the signal and the masker at threshold should have been unaffected by the hearing loss, *if* there was no additional source of masking for the normal-hearing listeners.

At a masker–signal interval of 10 ms, the mean difference between signal level and on-frequency masker level is $-1.7$ dB for the normal-hearing group and 2.0 dB for the hearing-impaired group. At an interval of 20 ms, the values are 6.1 and 5.5 dB, respectively. So, although there is a suggestion that the noise may have contributed to masking at the 10-ms gap, there appears to have been no effect at a 20-ms gap, for which there is a clear difference in off-frequency TMC slope between the two groups.

### B. Response functions

Following the approach of Nelson *et al.* (2001), TMCs for each listener were converted into BM response functions by plotting the off-frequency masker threshold against on-frequency masker threshold, paired according to masker–signal interval. For several hearing-impaired ears, off-frequency masker levels were not available at all the masker–signal intervals for which on-frequency masker levels were measured. For these ears, it was assumed that the slopes of the off-frequency TMCs do not change significantly with masker–signal interval. Given that there was no significant correlation between masker–signal interval and slope for the hearing-impaired listeners (see Sec. III A), this was felt to be a reasonable assumption. For those masker–signal intervals missing a measured off-frequency masker level, an off-frequency masker level was generated by interpolation, using a linear fit to the off-frequency data.

The response functions for normal-hearing listeners and for hearing-impaired listeners are plotted in Figs. 4 and 5, respectively. These show the growth of level with masker–signal interval for the off-frequency masker relative to the growth for the on-frequency masker. Open symbols indicate those points that were generated by interpolating the off-frequency TMCs. The positive diagonal ($y=x$) is included

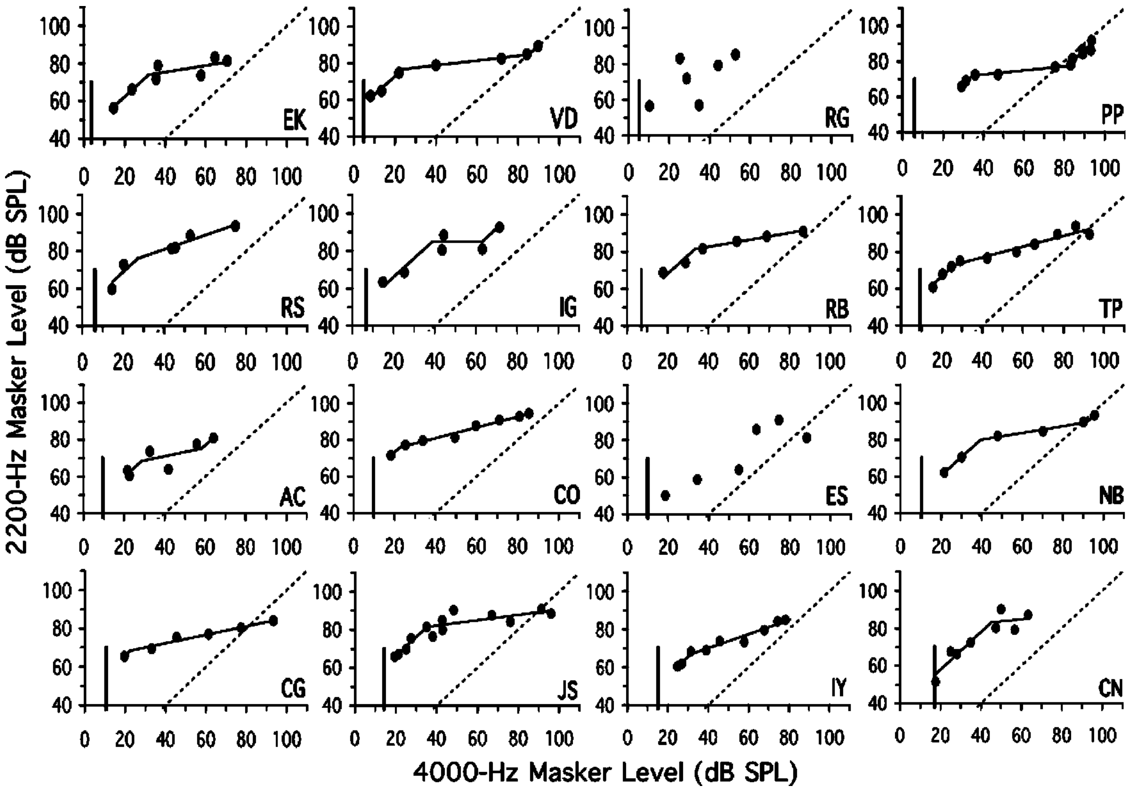


FIG. 4. Estimated response functions for normal-hearing listeners, showing the 2200-Hz masker level at threshold plotted against the 4000-Hz masker level at threshold, paired according to masker–signal interval. The positive diagonal (straight line) indicates the expected response of a passive, linear system. The vertical line indicates signal absolute threshold (*re*: the *x* axis). The kinked line shows the piecewise linear fit (see the text for details).

in Figs. 4 and 5 to indicate the expected response of a linear system with 0-dB gain (see below). Masker–signal intervals over which the on-frequency TMC is parallel to the off-frequency TMC translate to portions of the response functions with slope unity, implying a linear BM response. Masker–signal intervals over which the on-frequency TMC is steeper than the off-frequency TMC translate to portions of the response functions with slope less than unity (compression).

Most of the normal-hearing listeners show evidence of compression, having shallow portions in their response functions in Fig. 4, although this is not so clear for listeners RG and ES, whose data are variable. Most of the hearing-impaired listeners also show evidence of compression, as

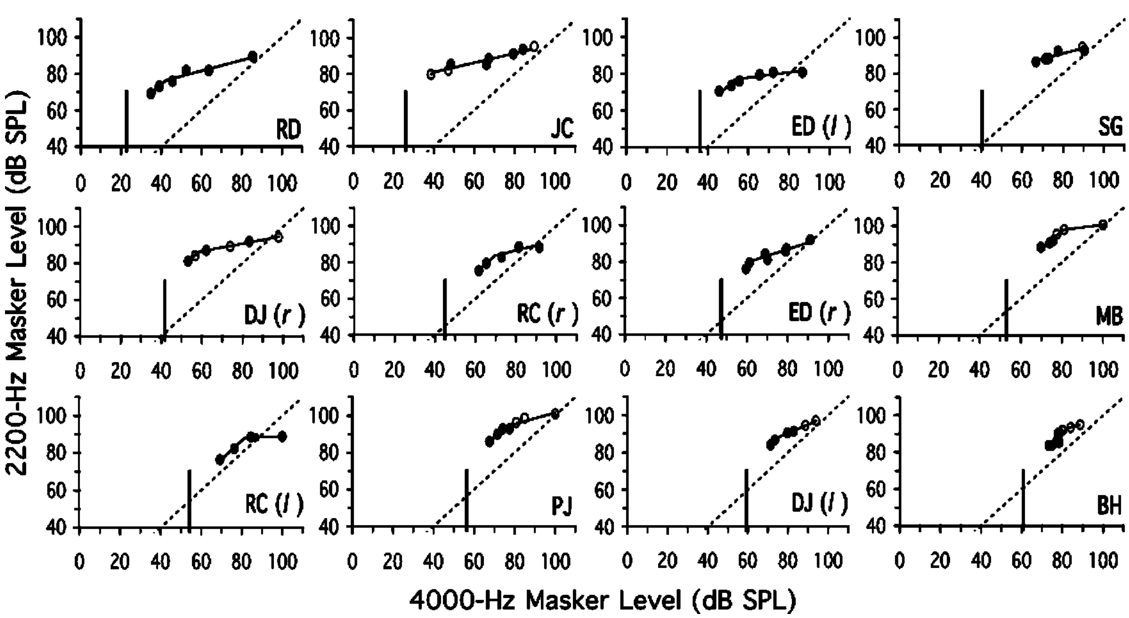


FIG. 5. As Fig. 4, except for hearing-impaired listeners. Open circles show points on the response functions that were estimated by interpolation of the off-frequency data, using straight-line fits to the off-frequency TMCs. Left and right ears are indicated by (*l*) and (*r*), respectively.

seen in the shallow portions of their response functions in Fig. 5. Indeed, many of the hearing-impaired response functions appear at least as compressive as those seen for normal-hearing listeners, although the compression extends over a smaller range of levels for the former. This suggests that BM compression is present even when sensitivity is much reduced compared to normal-hearing listeners. Some normal-hearing listeners (VD,PP,IG,NB) show evidence of a return to linearity at the highest masker levels, with on-frequency TMCs becoming shallow at long masker-signal intervals, and hence the response functions becoming steeper at high levels. This is not the case in general for hearing-impaired listeners. If such a pattern is to be found with hearing-impaired listeners, it must occur at very high levels (>100 dB SPL).

### C. Estimates of gain and compression

The maximum gain of the active mechanism can be estimated using the horizontal distance between the left-most, linear portion of a response function and the positive diagonal. This is an estimate of the difference between the levels of a 4000-Hz masker and a 2200-Hz masker required to produce the same BM response. If it is assumed that no gain is applied to the off-frequency masker (so that the positive diagonal approximates the off-frequency response even at low input levels), then this estimate is equivalent to the difference in the BM response between a low-level masker at 4000 Hz and a low-level masker at 2200 Hz. This measure of gain is similar to that used by others, e.g., Ruggero *et al.* (1997), in that it estimates the difference between the active BM response and the maximum passive response at signal place. The data of Ruggero *et al.* suggest that the off-frequency response to a tone at 0.55×CF is slightly less (by 2–4 dB) than that of the maximum passive response. Since the passive response has broad tuning, it is assumed that any discrepancy between the off-frequency response and the maximum passive response is approximately constant across individuals. If so, this should not affect any correlation of gain with absolute threshold in our analyses below.

To help quantify gain and compression, a three-section fit was applied to each listener's BM response function (Lopez-Poveda *et al.*, 2003; Yasin and Plack, 2003). The function comprised a linear low-level region [Eq. (1)], a compressive mid-level region [Eq. (2)], and a linear high-level region [Eq. (3)]. The three sections were joined by two breakpoints, a lower breakpoint ($BP_1$) joining sections 1 and 2, and an upper breakpoint ($BP_2$) joining sections 2 and 3. The equations for the three sections are given by

$$L_{out}=L_{in}+G \quad (L_{in}\leqslant BP_1), \tag{1}$$

$$L_{out}=cL_{in}+k_1+G \quad (BP_1<L_{in}\leqslant BP_2), \tag{2}$$

$$L_{out}=L_{in}+k_2+G \quad (L_{in}>BP_2), \tag{3}$$

where $G$ is the gain (dB), $c$ is the slope of the compressive region (dB/dB) or the compression exponent, $k_1=BP_1(1-c)$, $k_2=BP_2(c-1)+k_1$. $L_{in}$ (input level, level of 4000-Hz masker) and $L_{out}$ (level of BM response, level of 2200-Hz masker) are both expressed in dB. The function was fit to the data using the *fminsearch* function in MATLAB to satisfy a least-squares regression criterion. The slopes of the lower and upper sections were fixed at unity (linear response), while the slope of the middle section ($c$) and the breakpoints ($BP_1$ and $BP_2$) were varied by the fitting procedure. The only constraint on the fitting procedure was that the compression exponent $c$ was not allowed to be negative; otherwise, the parameters were allowed to vary freely. In some cases either the lower breakpoint or the upper breakpoint estimated by the fitting procedure was beyond the range of the data, so that effectively the data were fit using a reduced number of parameters. The fits were first made to the response function data without any off-frequency interpolation (just the filled symbols in Figs. 4 and 5), and then separately including the interpolated data (i.e., filled *and* open symbols). Fits were not included when there were less than five points on the response function [i.e., for DJ($r$), MB, RC($l$), PJ, and DJ($l$), without interpolated data]. The lines fit to the response functions including the interpolated data are shown in Figs. 4 and 5. The fits for listeners RG and ES had high rms errors (9 and 7 dB, respectively) and are not included in the figures or in subsequent analyses. For the other listeners, however, the fits generally provide a good description of the data (rms errors less than 4 dB).

Scatterplots of maximum gain against signal absolute threshold and compression against signal absolute threshold are shown in Fig. 6. Gain and compression estimates were taken from the three-section fits. A gain estimate was included only if there were at least two points on the response function that were below $BP_1$. The results are shown separately for fits to the response-function data without interpolation (left-hand panels) and for fits to the data including the interpolated off-frequency values (right-hand panels). The fits that involved interpolated values are shown as open symbols. Data from both normal-hearing and hearing-impaired listeners are presented together in each graph. A straight-line fit to the scatterplot data, and the squared correlation coefficient, are also displayed. Individual gain and compression estimates are given in Table I.

As shown by Fig. 6, the estimated gain of the cochlear amplifier decreases systematically with increasing hearing loss. The correlation is statistically significant both for the data without interpolation ($r=-0.930$, $n=16$, $p<0.0005$; slope$=-0.736$ dB/dB) and for the data with interpolation ($r=-0.951$, $n=22$, $p<0.0005$; slope$=-0.647$ dB/dB). Figure 6 also shows that, although there is a range of compression values for both normal-hearing listeners (left half of the data) and hearing-impaired listeners (right half of the data), there is little correlation between compression and absolute threshold. The correlations are not significant either for the data without interpolation ($r=0.101$, $n=21$, $p=0.662$) or for the data with interpolation ($r=0.284$, $n=26$, $p=0.159$). For some of the more impaired ears the compressive region is defined by only a couple of points (often interpolated). However, the ears with milder impairments [RD, JC, ED($l$), SG, DJ($r$), RC($r$), and ED($r$)] have well-defined shallow sections in their response functions and compression exponents within the normal range (0.29, 0.26,

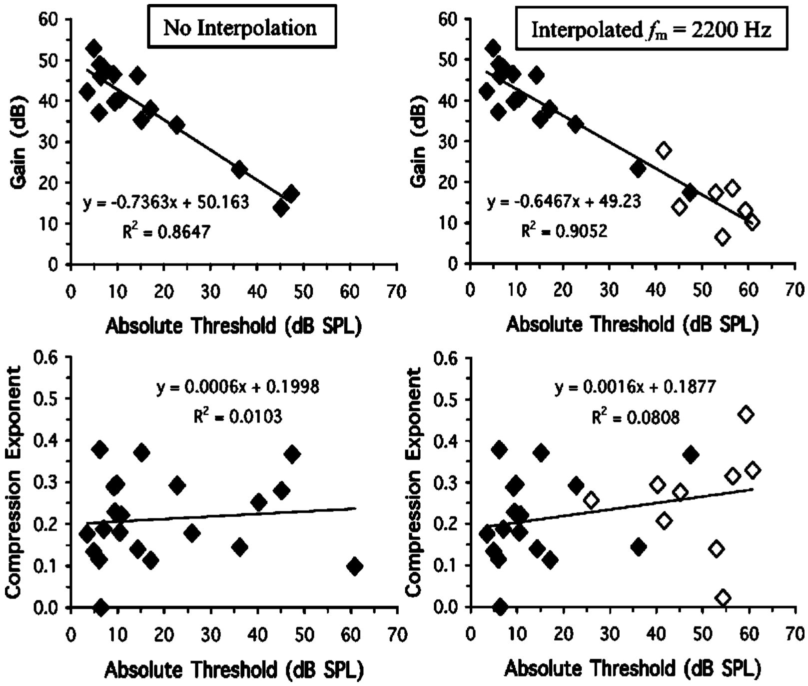


FIG. 6. Scatterplots of maximum gain against signal absolute threshold (upper panels), and response-function slope against signal absolute threshold (lower panels), at 4000 Hz. The left-hand panels show the results for response functions generated without interpolation. The right-hand panels include the results for response functions that were generated using interpolated off-frequency masker levels (indicated by the open symbols). Gain estimates are only included when the low-level portion of the response function is defined by at least two points (see Table I).

0.15, 0.29, 0.21, 0.28, and 0.37, respectively, for the interpolated data). The mean compression exponent for the interpolated data is 0.20 for the normal-hearing listeners and 0.26 for the hearing-impaired listeners.

There is an issue regarding whether the three-section straight-line fits provide an accurate characterization of the response functions. Third-order polynomials have been used previously to fit response functions (Nelson *et al.*, 2001; Plack and Drga, 2003). Such fits were attempted on the present data but gave very inconsistent results, with negative slopes in some cases. It was felt that the three-section fits, although not ideal, do capture the main features of the response functions for the normal-hearing and hearing-impaired listeners: The reduction in gain with hearing loss (also reflected in the vertical spacing between the on- and off-frequency TMCs), and the preservation of a shallow slope in the response function (compression), even for ears showing the largest hearing loss.

## IV. DISCUSSION

### A. Consequences of inner and outer hair cell dysfunction

An elevation in absolute threshold may result from a dysfunction of the inner hair cells (IHCs) or of the OHCs (see Moore, 1995). IHC dysfunction reduces the efficiency of transduction of BM vibration (hence reducing sensitivity) but is not thought to affect the mechanical properties of the BM itself (Liberman *et al.*, 1986). OHC dysfunction affects the response of the BM, but not the transduction process *per se*. Now, imagine a situation in which a cochlea has damage to the IHCs only. For a given input level, the response properties of the BM should be *identical* to that for a healthy ear. According to the measures described earlier, the maximum gain of the active mechanism, the input level at the first breakpoint in the response function, and the compression exponent, should all be unaffected by the hearing loss, and hence independent of the degree of hearing loss. For an ear with purely OHC dysfunction, however, the maximum gain should be strongly related to the absolute threshold. Specifically, a plot of gain (in dB) against absolute threshold (in dB) should be a straight line with a slope of $-1$. Turning down the gain by 10 dB should result in an increase in absolute threshold by 10 dB.

If the hearing loss experienced by our listeners were simply a matter of non-frequency-specific attenuation *prior* to the BM, as might result from conductive hearing loss, then both on- and off-frequency TMCs would increase by the same amount and, consequently, the estimated maximum gain would remain unchanged as a function of hearing loss. Similarly, pure IHC loss (post-BM attenuation) should result in no change in the estimated maximum gain (although it is only possible to measure the lower breakpoint on the response function if it is above absolute threshold). These predictions do not seem to describe the present data. The strong relation between maximum gain and absolute threshold (Fig. 6) suggests that the hearing loss in the impaired listeners tested here was mainly the result of OHC dysfunction. Off-frequency TMCs were somewhat higher in level for the hearing-impaired compared to the normal-hearing group, but it was the general increase in level for the on-frequency TMCs relative to the off-frequency TMCs that characterized the impaired group, again consistent with OHC damage. Including the interpolated data, the plot of gain against absolute threshold has a slope of $-0.65$, which suggests that most of the threshold elevation can be attributed to a reduction in gain. The fact that the slope was not $-1$ suggests that there may have been some IHC dysfunction among the listeners (contributing to perhaps 35% of the threshold elevation for those ears for which the gain was measurable). Indeed, from the results of other studies examining the relative proportions of IHC and OHC hearing loss, it would be surprising if there

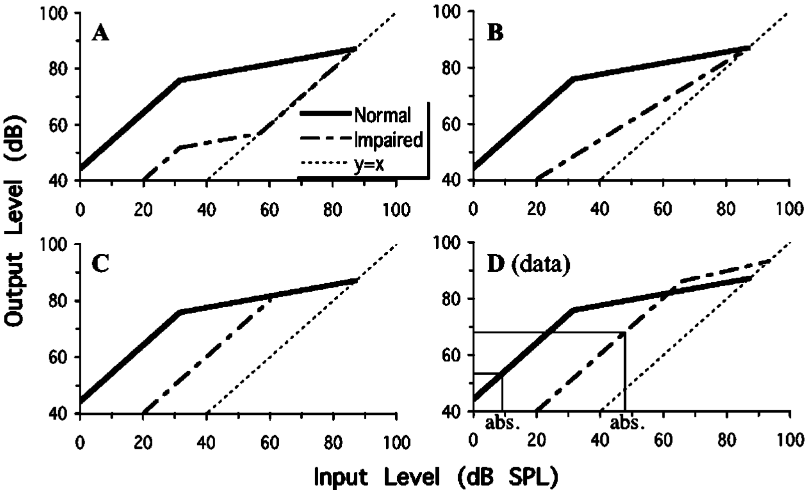


FIG. 7. BM response functions for normal-hearing and hearing-impaired listeners. The normal response function is an average function generated from the present data (see the text for details). In panels (A) to (C) the response functions for the hearing-impaired listeners are hypothetical. In panel (A), the gain for hearing-impaired listeners is reduced equally at all input levels up to the passive response. In panel (B), the reduction in gain is greatest at low input levels, with a diminishing reduction as level is increased. In panel (C), the gain is reduced at low input levels, but unaffected at high input levels. Panel (D) shows average response functions, for both normal-hearing and hearing-impaired listeners, generated from the present data (see the text for details). In panel (D), the thin vertical lines show the average absolute thresholds for the signal, and the thin horizontal lines the associated response levels, for the normal-hearing and hearing-impaired listeners used to generate the response functions.

were not some evidence of IHC dysfunction (Lopez-Poveda *et al.*, 2004; Moore and Glasberg, 1997; Moore *et al.*, 1999). IHC dysfunction will raise the output level on the BM response function that corresponds to absolute threshold, and may explain why the low-level linear segment on the response function is generally shorter for the hearing-impaired listeners than for the normal-hearing listeners (see Figs. 4 and 5, and Sec. IV B). However, given that OHC dysfunction was probably the main cause of the reduction in sensitivity, what do the present results tell us about the effects of OHC dysfunction on the response of the BM?

### B. Effects of outer hair cell dysfunction on the BM response

To aid the discussion of the effects of OHC dysfunction on the shape of the BM response function, three different hypothetical scenarios are illustrated in Fig. 7. Each panel of the figure shows the normal response function (continuous black line, generated from the present data as described below), the passive response function with no active mechanism (thin dotted line), and a hypothetical response for a listener with mild hearing loss (alternate dashes and dots). In the upper left panel (A) the gain is reduced equally at all input levels up to the passive response. In the upper right panel (B) the reduction in gain is greatest at low input levels, with a diminishing reduction as level is increased. In the lower-left panel (C) the gain is reduced at low input levels, but unaffected at high input levels. The lower-right panel (D) shows average response functions generated from the present data. These functions were obtained by averaging the $x$ and $y$ values of the lower breakpoints and the compression exponents derived from the fitting procedure, across the normal-hearing listeners and across the hearing-impaired listeners. Upper breakpoints were omitted because they often could not be specified (the values from the fitting procedure were above the highest points on the response functions), and (as for the gain estimates) the results for ears with less than two points on the response function below the lower breakpoint were also omitted. For those ears that remained, it seems clear that the data are best summarized by option C. Although there are individual differences in the response functions, overall it appears that mild cochlear hearing loss is associated with a reduction in the gain at the *lower input levels only*, and not across the whole range of input levels that are affected by the active mechanism. This is why the slope of the compressive part of the response function did not vary significantly with absolute threshold (see Fig. 6).

In this respect, the present data do not appear to be consistent with some physiological models of hearing loss. The BM response function of a chinchilla injected 40 min previously with furosemide showed a reduction in gain at all levels (Ruggero and Rich, 1991), more similar to option (A) in Fig. 7. As with the present data, however, BM compression was relatively unaffected by this mild hearing loss. Murugasu and Russell (1995) report guinea pig displacement measurements during salicylate perfusion. Some of their response functions show a reduction in gain at all levels, but some show an effect only at low levels, similar to the functions reported here. Recent auditory-nerve recordings from cats with noise-induced hearing loss also seem consistent with the present data (Heinz *et al.*, in press). For mild hearing loss, a measure of the total auditory-nerve activity showed a reduction in response at low levels but not at high levels, consistent with a reduction in gain at low levels only.

The thin vertical and horizontal lines in panel (D) of Fig. 7 show the average absolute threshold for the signal, and the associated response level, for those normal-hearing and hearing-impaired listeners used to generate the average response functions. Notice that the BM response level at threshold is higher for the hearing-impaired group. This may be interpreted as a reduction in sensitivity resulting from IHC dysfunction. These lines also illustrate the point made in Sec. IV A that the linear segment of the response function measurable in the experiment (threshold to first breakpoint) is shorter for the hearing-impaired listeners.

### C. Off-frequency temporal masking curves

A surprising incidental finding of the experiment was that the slopes of the off-frequency TMCs were *shallower* for hearing-impaired listeners than for normal-hearing listeners when compared at short masker–signal intervals. Recently, Rosengard *et al.* (2003) have also reported shallow off-frequency TMCs in hearing-impaired listeners compared to normals. The analysis described in Sec. III A suggests that the difference may be related to the higher off-frequency masker levels for the hearing-impaired listeners. When the off-frequency TMC slopes were compared at the same masker level (or at long masker–signal intervals) there was little difference between the groups.

According to the interpretation of TMCs outlined in the Introduction, the shape of the off-frequency TMC should depend only on the internal decay of forward masking, a measure of temporal resolution. There is little evidence to suggest that hearing-impaired listeners in general have a deficit in temporal resolution, at least as measured by tasks such as gap detection with sinusoidal markers (Moore and Glasberg, 1988) and modulation detection (Bacon and Gleitman, 1992; Moore *et al.*, 1992). However, it is the case that the hearing-impaired listeners in the present study were older and received less training than the normal-hearing listeners, and this may have influenced temporal processing. If the effects of hearing impairment on the off-frequency TMCs were *not* a consequence of a general temporal resolution deficit, two possibilities remain. The first is that the aspect of temporal resolution measured by forward masking is unconnected with the aspect (or aspects) measured in other tasks, and that hearing-impaired listeners have a specific deficit in forward masking. This might be possible if forward masking is a consequence of adaptation at the IHC/auditory nerve synapse (Furukawa and Matsuura, 1978; but see Oxenham, 2001; Smith, 1979), and that IHC dysfunction affects this in some way. The second possibility is that the auditory system responds nonlinearly to an off-frequency masker, either at the level of the BM or more centrally. To account for the difference between the normal and impaired ears, the off-frequency compression exponent may be invariant with level but increased in impaired ears (leading to a shallow TMC slope in impaired ears), or the compression exponent may be increased at high levels (leading to a shallow TMC slope at high levels). The finding that the TMC slopes were similar for normal and impaired ears at long masker–signal intervals favors the latter explanation.

## V. CONCLUSIONS

(i) BM response functions derived from on- and off-frequency TMCs generally show a linear low-level region and a compressive midlevel region. With hearing loss the low-level region shifts to the right, reflecting the reduction in sensitivity, but there is little evidence for a change in the slope of the compressive region with losses up to 50 dB or so.

(ii) The results suggest that mild to moderate sensorineural hearing loss is associated with a reduction in the gain for low-level CF tones, but little change in the gain for higher-level tones, and consequently little change in the maximum compression.

(iii) Hearing-impaired listeners show shallower off-frequency TMCs than normal-hearing listeners when measured at short time intervals. However, there is little effect of impairment on TMC slope at long time intervals, or if the TMCs are matched for off-frequency masker level.


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