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Cochlear compression in listeners with moderate sensorineural hearing loss

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Abstract

Psychophysical estimates of basilar membrane (BM) responses suggest that normal-hearing (NH) listeners exhibit constant compression for tones at the characteristic frequency (CF) across the CF range from 250 to 8000 Hz. The frequency region over which compression occurs is broadest for low CFs. This study investigates the extent that these results differ for three hearing-impaired (HI) listeners with sensorineural hearing loss. Temporal masking curves (TMCs) were measured over a wide range of probe (500–8000 Hz) and masker frequencies (0.5–1.2 times the probe frequency). From these, estimated BM response functions were derived and compared with corresponding functions for NH listeners. Compressive responses for tones both *at* and *below* CF occur for the three HI ears across the CF range tested. The maximum amount of compression was uncorrelated with absolute threshold. It was close to normal for two of the three HI ears, but was either slightly (at CFs ⩽ 1000 Hz) or considerably (at CFs ⩾ 4000 Hz) reduced for the third ear. Results are interpreted in terms of the relative damage to inner and outer hair cells affecting each of the HI ears. Alternative interpretations for the results are also discussed, some of which cast doubts on the assumptions of the TMC-based method and other behavioral methods for estimating human BM compression.

Keywords: Basilar membrane; Cochlear compression; Recovery from forward masking; Hearing loss; Inner hair cell; Outer hair cell

1. Introduction

The mammalian basilar membrane (BM) responds compressively to sound level in a frequency-selective manner (Rhode, 1971; Robles and Ruggero, 2001). Low-level sounds elicit a narrowly tuned response that grows nonlinearly with level to become more broadly tuned at high levels (Ruggero et al., 1997; Rhode and Recio, 2000). The degree of compression is less for frequencies well below the characteristic frequency (CF) of the recording site (for a review see Robles and Ruggero, 2001). This response pattern is vulnerable to acoustic trauma, cochlear injury or death (for a review see Ruggero et al., 1996 and Robles and Ruggero, 2001). Direct measurements of BM motion on acoustically or chemically traumatized cochleae show reduced sensitivity near CF and broadly tuned responses that grow more linearly with level than do the responses of healthy BMs. This study investigates how *human* BM compression, as estimated by behavioral methods,

Abbreviations: BM, basilar membrane; CF, characteristic frequency; HI, hearing impaired; IHC, inner hair cell; NH, normal hearing; OHC, outer hair cell; TMC, temporal masking curve; RP, receptor potential; SL, sensation level; SD, standard deviation; SPL, sound pressure level.

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change as a result of moderate sensorineural hearing loss.

Estimates of human BM compression may be inferred from masked thresholds (for reviews see Oxenham and Bacon, 2004; Bacon and Oxenham, 2004). Forward-masking techniques are preferred because they avoid the suppressive effects that can contribute to simultaneous masking. Nelson et al. (2001) proposed one such technique in which BM responses are derived from temporal masking curves (TMCs). A TMC is a plot of the level of a forward masker required to mask a fixed low-level probe as a function of the time interval between the masker and the probe. As the time interval increases, the masker level required increases. However, the rate of increase varies across masker frequencies. For masker frequencies well below the probe frequency, it appears to be constant (at least for high-frequency probes, see Lopez-Poveda et al., 2003; Nelson and Schroder, 2004; Plack and Drga, 2003). On the other hand, for masker frequencies close or equal to the probe frequency, the rate of increase changes as the delay between the masker and the probe increases. In fact, these TMCs show two or three segments with clearly different slopes. Nelson et al. (2001) reasoned that the steeper segments reflect BM compression. Their reasoning requires a number of assumptions. First, it assumes that during the task the listener is always attending to the place on the BM tuned to the probe frequency. Second, it assumes that the internal effect of the masker decays with time in the same way for *all stimulation frequencies* at a given CF. Third, it assumes that the BM is the only source of frequency-specific compression before the effect of the masker interacts with the effect of the probe. If these assumptions hold, BM response functions may be inferred from TMCs by plotting the levels for a masker frequency that elicits a linear BM response (hereafter referred to as the "linear reference TMC") against the levels for any other masker, paired according to time interval.

Lopez-Poveda et al. (2003) used this technique to estimate BM compression in normal-hearing (NH) listeners over a range of CFs from 500 to 8000 Hz, and at a number of stimulation frequencies relative to each CF. They concluded that the degree of cochlear compression for frequencies at CF is approximately constant over the range of CFs they studied. Their compression estimates for tones at CF correspond to BM input/output functions with slopes of 0.2–0.3 dB/dB. They also concluded that the response of the BM is compressive to a wider range of stimulation frequencies (relative to CF) in the apical region of the cochlea. In the basal region, however, the estimated compression was restricted to stimulation frequencies close to CF. Additional studies (Nelson and Schroder, 2004; Oxenham and Dau, 2004; Plack and Drga, 2003; Williams and Bacon, 2005) have confirmed these results with the same or other methods and extended them to other CFs.

The present work extends the study of Lopez-Poveda et al. (2003) to hearing-impaired (HI) listeners. Identical stimuli and methods are used to here to allow a direct comparison between the present results and those previously reported for NH listeners. The aim is to characterize the consequences of this type of hearing impairment with regard to BM compression. A recent study (Plack et al., 2004) on the CF region of 4000 Hz suggests that NH listeners and listeners with mild-to-moderate sensorineural hearing loss may show similar degrees of BM compression. They differ, however, in that compression extends over a narrower range of sound levels in the HI listeners. One aim of the present study was to determine whether this result can be generalized to a wider range of CFs (500–8000 Hz). Furthermore, given that the compression pattern seems to be clearly different at low CFs, another aim was to determine whether at low CFs the compression for tones well below CF changes for HI listeners.

2. Material and methods

2.1. Stimuli

TMCs were measured for probe frequencies (f_p) of 500, 1000, 2000, 4000, and 8000 Hz, and for masker frequencies (f_m) of 0.5, 0.6, 0.7, 0.9, 1.0, 1.05, 1.1, and $1.2 \times f_p$, although some masker frequencies were not tested for all listeners. For any given masker-probe pair (f_m,f_p), masked thresholds were measured for masker-probe intervals ranging from 10 to 100 ms in steps of 10 ms. The time interval was defined as the duration of the silence period between the masker offset and the probe onset. The sinusoidal maskers were gated with 5-ms raised-cosine onset and offset ramps and had a total duration of 110 ms. The sinusoidal probes had a total duration of 10 ms and were gated with 5-ms raised-cosine ramps (no steady-state portion). The level of the probe was kept constant at approximately 14 dB sensation level (SL) for two of the listeners (DHA and ESR), but 10 dB SL for the third listener (ETA).

Because data were collected over a long period of time, different equipment was employed for different listeners. For two of the listeners (DHA and ESR), stimuli were generated digitally on a Silicon Graphics™ O2 workstation at a sampling rate of 32 kHz, with 16-bit resolution. For the third listener (ETA), however, stimuli were generated with a Tucker Davis Technologies™ psychoacoustics workstation (System III) at a sampling rate of 48.8 kHz and 24-bit resolution. All stimuli were played monaurally via the workstations' headphone connections through the same pair of circumaural Sennheiser HD-580 headphones. Listeners sat in a double-walled sound-attenuating room. The sound pressure levels (SPLs) reported below are nominal electrical levels without allowing for the earphone diffuse-field response.

2.2. Procedure

Masked thresholds were measured using a two-interval, two-alternative forced-choice paradigm. In one interval, the masker tone was presented alone. In the other interval, the masker was presented followed by the probe. The two intervals were presented to the listeners in random order, who were asked to select the interval containing the probe. Feedback was immediately provided to the listeners after their response.

The initial masker level was approximately 6 dB below the absolute threshold for the probe. A two-up, one-down adaptive rule was used to estimate the 71% correct point on the psychometric function (Levitt, 1971). The level of the masker was increased and decreased by 4 dB for the first four turn points, and by 2 dB thereafter. Sixteen turn points were recorded in each experimental block and the threshold estimate was taken as the mean of the masker levels at the last 12 turn points. The estimate was discarded when the standard deviation (SD) of these 12 turn points exceeded 6 dB. At least three thresholds were obtained in this way for each condition[1], and their mean was taken as the actual threshold. The associated SD was typically less than 3 dB, although on rare occasions it exceeded 6 dB. When the latter happened, a fourth threshold was measured and included in the mean.

For each (f_m,f_p) pair, masker threshold levels were always measured from the shortest (10 ms) to the longest (100 ms) masker-probe interval. An attempt was made to measure a masker threshold for every masker-probe interval. However, clipping occurred for moderate to long intervals whenever the masker level exceeded the maximum SPL output of the system (approximately 100 dB SPL for the Silicon Graphics workstation and 114 dB SPL for the Tucker Davis Technologies workstation). In such instances, the experiment was stopped and the same condition was attempted later. Missing points in the resulting TMCs should be interpreted as indicating that the required masker level exceeded the maximum SPL of the system.

2.3. Listeners

Data were collected for three listeners with sensorineural hearing loss: DHA(l), ETA(l), and ESR(r). Listener DHA (male, 24 years of age) was unilaterally impaired in his left ear. He wore a foam plug in his NH ear during data collection to prevent detection of the probe with his NH ear. Listener ETA (male, 70 years of age) was bilaterally impaired. He reported tinnitus in the ear not used for the TMC measurements. ESR (female, 52 years of age) was bilaterally impaired. They showed no sign of conductive or retrocochlear impairment after standard clinical examination (including tests of the ear's acoustic impedance and auditory-evoked brainstem potentials). None of the listeners had previous experience on psychoacoustic tasks other than those involved in regular clinical tests. They were given several hours of practice in the forward-masking task before data collection began. In return for their services, listeners received free audiologic examinations and an Oticon Adapto™ hearing aid fitted to their personal requirements.

For unilaterally HI listener DHA, TMCs were also measured for his NH ear, DHA(r), for probe frequencies of 500 and 4000 Hz and for masker frequencies equal to f_p and $0.5f_p$. This allowed a within-listener control comparison.

Prior to collecting the TMCs, absolute thresholds were measured with the same equipment using a two-down one-up, two interval, two-alternative forced-choice method. Absolute thresholds were measured for the four ears tested for tones of the same frequencies and durations as the probes and maskers used in the forward-masking experiment. Each threshold was measured at least three times and the results (see Fig. 1) were averaged.

The experiments were approved by the Ethical Committee on Human Experimentation of Albacete University Hospital (Albacete, Spain).

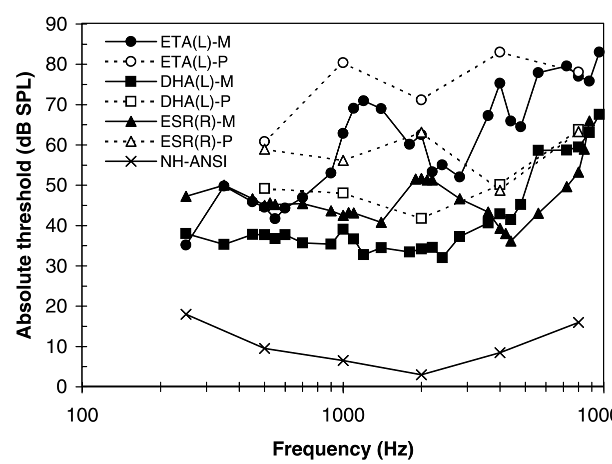

Fig. 1. Absolute thresholds (dB SPL) for the three HI listeners tested. Filled symbols illustrate absolute thresholds for the 110-ms maskers (M) [circles: ETA(l); squares: DHA(l); triangles: ESR(r)]. Open symbols illustrate the absolute thresholds for the 10-ms probes (P). Crosses indicate normal-hearing (NH) absolute thresholds for circumaural headphones according to ANSI 3.6-1996 Specifications for Audiometers.

[1] This did not always apply for listener ESR. Her results for masker levels above approximately 95 dB SPL are sometimes the average of two measurements only. The SD of these two estimates rarely exceeded 3 dB.

3. Results

3.1. Temporal masking curves

Fig. 2 illustrates the resulting TMCs for the three HI listeners. *Average* TMCs for three NH listeners (adapted from Lopez-Poveda et al., 2003) are also shown for comparison (right-most column in Fig. 2). Fig. 3 illustrates the TMCs for the HI (left) and the NH (right) ears of unilaterally HI listener DHA.

The overall rate of increase of masker levels with masker-probe interval is *slower* for the HI ears (Figs. 2

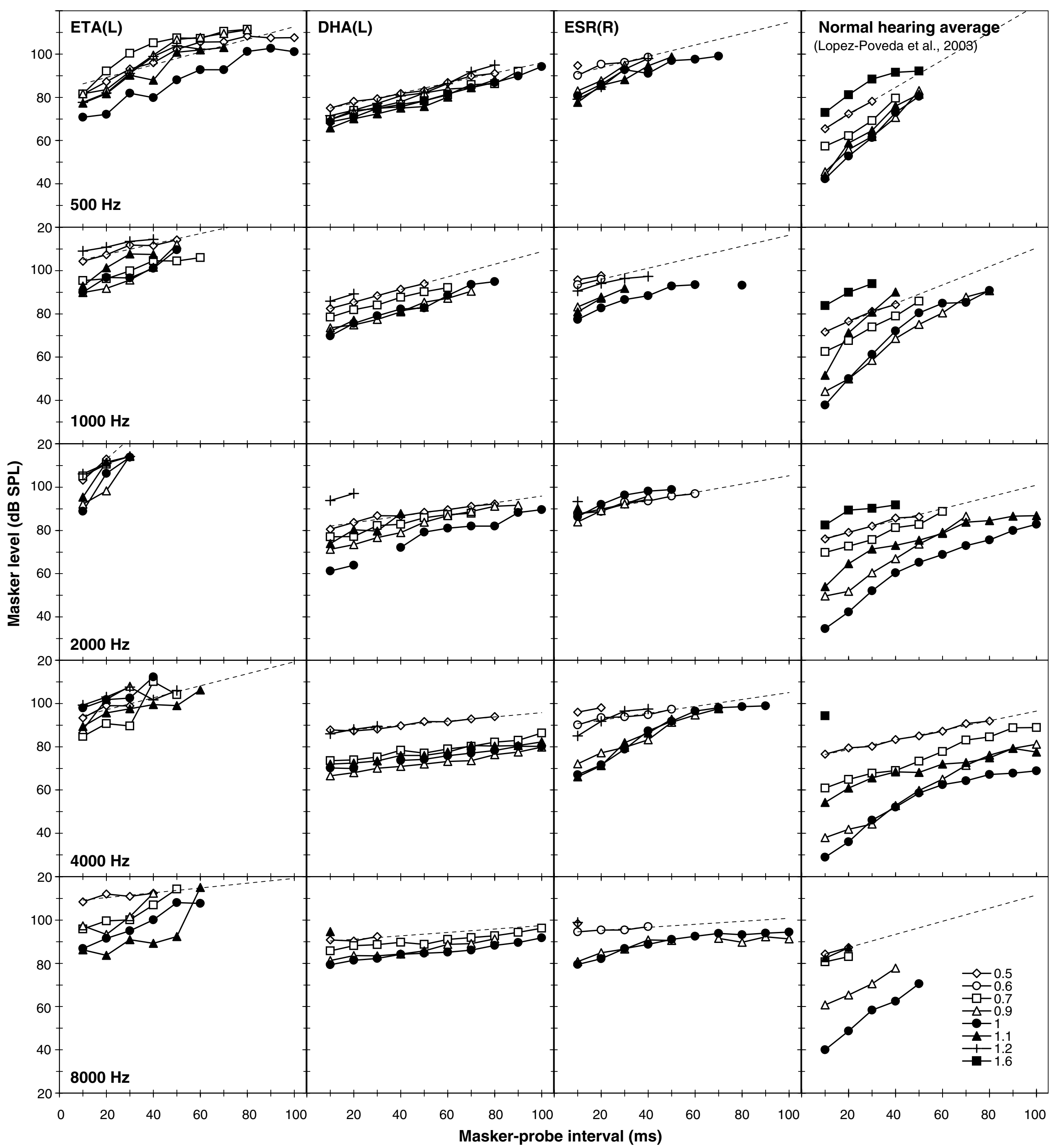

Fig. 2. TMCs for the three HI listeners tested. Each column corresponds to a different ear: ETA(*l*); DHA(*l*); ESR(*r*). The right-most column illustrates average TMCs for three NH individuals (adapted from Lopez-Poveda et al., 2003; Fig. 2). Each row corresponds to a different probe frequency from 500 to 8000 Hz. The inset in the bottom right panel informs of the masker frequencies relative to the probe frequency. Dotted lines illustrate straight lines fit by least squares to the TMCs for off-frequency maskers [$0.5f_p$ for ETA(*l*), DHA(*l*) and normal hearing, but $0.6f_p$ for ESR(*r*)].

and 3). This is most obvious for on-frequency maskers, but occurs for *all* masker frequencies, even for those an octave below the probe frequency (hereafter referred to as "off-frequency" maskers). To illustrate this for off-frequency maskers, straight lines (dotted lines in Fig. 2) were fitted using the least-squares procedure to the TMCs for masker frequencies of $0.5f_p$ for DHA(*l*), ETA(*l*), and DHA(*r*), but $0.6f_p$ for ESR(*r*).[2] The slopes of the fitted lines are plotted in Fig. 4(a) as a function of probe frequency. The slope values are generally smaller for the HI ears (filled symbols) than for the NH ears (open symbols). The only clear exception occurs for ETA(*l*) for the 2000-Hz probe. However, this result should be interpreted with caution because it corresponds to a TMC with two data points only (Fig. 2).

Fig. 4(b) illustrates that the off-frequency TMCs may be up to 3 times steeper for the NH ears than for the HI ears at the lower frequencies, and up to 4.5 times steeper at 8000 Hz. Particularly interesting is that the off-frequency TMCs for the NH ear of listener DHA are approximately 2.5 times as steep as the corresponding TMCs for his HI ear (open squares in Fig. 4), both for 500- and 4000-Hz probes. Possible interpretations of this result and its significance are discussed below (Section 4.2).

On-frequency TMCs are also overall shallower for the HI ears. Despite this, in many of the conditions tested, the on-frequency TMCs of HI ears still show two segments with distinct slopes. This pattern is characteristic of on-frequency TMCs for NH listeners and is commonly interpreted as an indicator of BM compression (Nelson et al., 2001).

3.2. Estimated BM response functions

Approximate BM response functions may be derived from TMCs by plotting the masker levels for a linear reference TMC against the levels of the TMC for the masker frequency of interest, paired according to time interval (see Section 1 and Nelson et al., 2001).

3.2.1. The linear reference TMC

It has been suggested previously (Lopez-Poveda et al., 2003; Plack and Drga, 2003) that the best linear reference is a TMC for a high-frequency probe and a masker frequency an octave or so below probe frequency. The reasons for this choice were: (1) there is evidence that the *apical* portion of the BM responds compressively to tones below CF (Rhode and Cooper, 1996); and (2) existing evidence suggests that the basal portion of the BM responds linearly to frequencies well below CF (evidence reviewed by Robles and Ruggero, 2001). Furthermore, the choice was supported by the

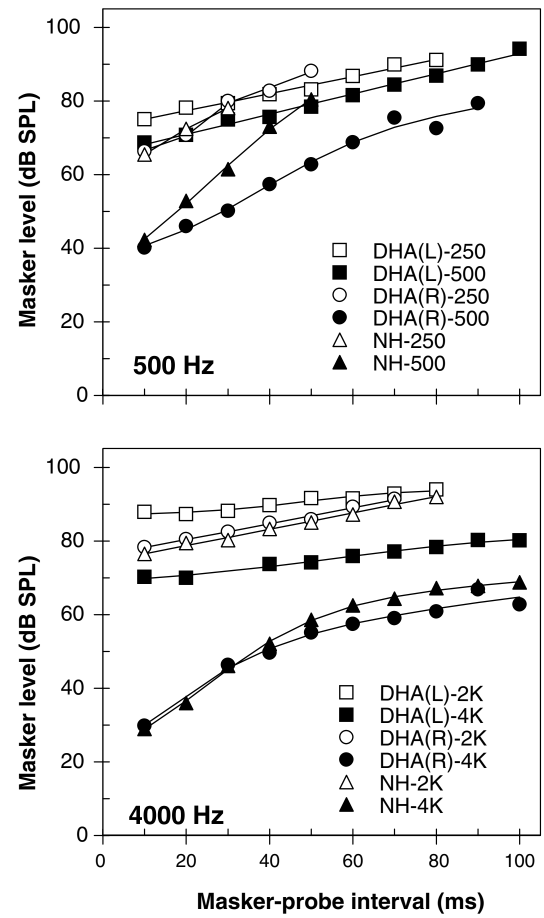

Fig. 3. TMCs for the NH ear, DHA(*r*), and the HI ear, DHA(*l*), of unilaterally HI listener DHA. Average TMCs for three other individuals with NH are also shown (triangles) for comparison (adapted from Lopez-Poveda et al., 2003). Top panel: TMCs for a probe frequency of 500 Hz and masker frequencies of 250 and 500 Hz. Bottom panel: TMCs for a probe frequency of 4000 Hz and masker frequencies of 2000 and 4000 Hz. The numbers in the legend indicate the masker frequency. Note that the TMCs for DHA(*r*) match closely the average NH TMCs for all conditions except for the on-frequency 500-Hz TMC. For this condition, the TMC for DHA(*r*) is shallower than normal. The TMCs for HI ear, DHA(*l*) (squares), are shallower than the TMCs for the NH ears (circles and triangles), both for on (filled symbols) and off-frequency maskers (open symbols) (Fig. 4). The continuous lines illustrate example fits of Eq. (1) to the TMCs. Note that the fits are generally very good.

data of Lopez-Poveda et al. (2003) and Plack and Drga (2003) because their TMCs for off-frequency maskers were shallower for higher probe frequencies. Reasonably, if the slope of the TMCs reflects both the internal rate of decay of the masker effect *and* BM compression, and if it assumed that the slope of the TMC is independent of masker level (see Nelson et al., 2001), the most likely candidate for a linear reference must be the TMC with the *shallowest* slope.

Here, the same convention is applied. The shallowest off-frequency TMCs for the HI ears were used as linear references. For all three HI ears, these correspond to the

[2] The reason that the TMCs for masker frequencies of $0.6f_p$ were used for ESR(*r*) is because they generally have more data points than the TMCs for a masker frequency of $0.5f_p$.

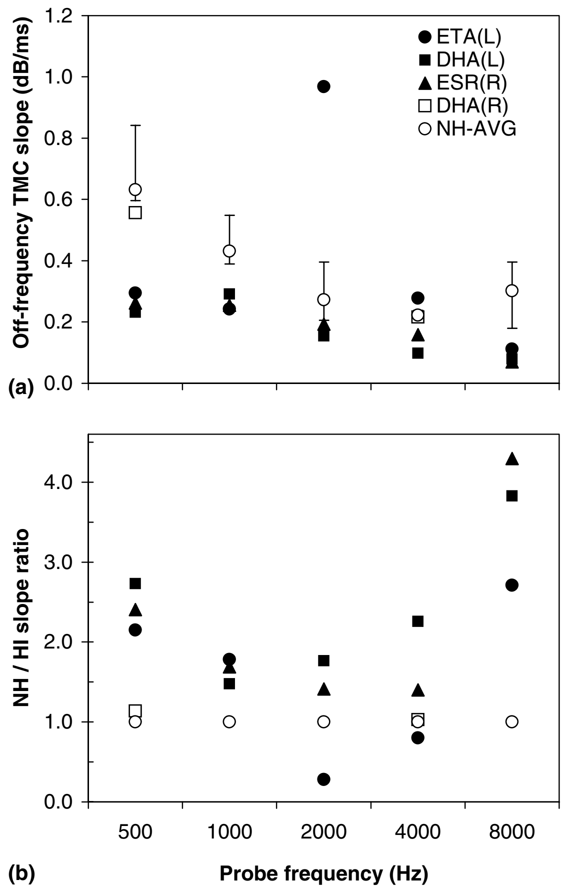

Fig. 4. (a) Slope (dB/ms) of straight lines fitted by least squares to the off-frequency TMCs for the three HI ears (filled symbols) and the NH ear (open squares) tested here. Open circles illustrate the slopes for the average off-frequency TMCs for the three NH listeners in Lopez-Poveda et al. (2003). Error bars are associated to the open symbols and illustrate the range of slope values for the individual TMCs reported in that same study. (b) Ratio of the slopes for the average NH listeners over the slopes for the each of the HI ears (filled symbols) and the NH ear (open squares) tested in the present study. Note that the off-frequency TMCs are almost always steeper for the NH than for the HI ears.

TMCs for an 8000-Hz probe and a 4000-Hz masker [Fig. 4(a)]. Straight lines were fitted to these TMCs by least squares. The resulting straight lines had markedly different ordinate intercept values [108.15, 89.55, and 93.82 dB SPL for ETA(*l*), DHA(*l*) and ESR(*r*), respectively], but similar slopes [0.11, 0.08, and 0.07 dB/ms for ETA(*l*), DHA(*l*) and ESR(*r*), respectively]. Therefore, linear reference TMCs were constructed by reading off new masker levels for each masker-probe interval from straight lines that had the *average* slope (0.086 dB/ms) but individual ordinate intercept values. Linear reference TMCs with the same average-slope from the hearing-*impaired* ears were employed to derive *new* BM response functions for NH listeners from the TMCs in Lopez-Poveda et al. (2003). The validity of the chosen linear reference TMC and its implications are discussed in Section 4.2.

3.2.2. TMC function fits

To obtain smoother BM response functions, an *ad-hoc* function was fitted to the measured TMCs and the fitted masker levels were used instead of the measured masker levels. The following function was employed to fit the TMCs:

$$L_{\mathrm{M}}(\Delta t) = (L_0 + \tau \cdot \Delta t) \times \left(1 + \frac{\beta}{1 + \exp\left(\frac{p - \Delta t}{q}\right)}\right), \qquad (1)$$

where $L_{\mathrm{M}}(\Delta t)$ is the masker level for a given masker-probe interval, Δt; and L_0, τ, β, p, and q are fitting parameters. Optimum parameters to fit each of the TMCs of NH and HI ears were obtained automatically using the Solver Tool of Microsoft® Excel 2000. Parameters τ, β, q were constrained be equal or greater than zero. This guarantees that the fitted TMCs are a monotonically increasing function of the masker-probe interval with a positive growth rate for all intervals. For TMCs with three data points or fewer, parameter β was set to zero so that the fitting function [Eq. (1)] turns into a straight line with two parameters only (L_0 and τ). The R^2 between the original and the fitted masker levels was typically $\geqslant 0.98$. Example fits are illustrated in Fig. 3.

3.2.3. Derived BM response functions

The resulting estimated BM response functions for the three HI ears and for the average NH listeners are illustrated in Fig. 5. Each column illustrates the results for an individual HI listener or for the average NH listeners (right-most column). Each row illustrates the results for a different probe frequency, from 500 Hz (top row) to 8000 Hz (bottom row). Dotted lines illustrate presumed linear responses with zero gain. Fig. 6 shows the BM response functions for the NH and the HI ears of unilaterally HI listener DHA. To facilitate the physiological interpretation, the terms masker frequency and probe frequency are hereinafter referred to as stimulation frequency and CF, respectively [the accuracy of this interpretation is discussed by Nelson et al. (2001) and Lopez-Poveda et al. (2003)].

Most response functions in Figs. 5 and 6 may be described as single- or double-sloped. Single-sloped functions [e.g., ear DHA(*l*), CF = 4000 Hz] appear as straight lines with slopes $\leqslant$1 dB/dB. Double-sloped functions [e.g., ear ESR(*r*), CF = 4000 Hz] are the most common and show two segments with clearly different slopes. Sometimes they show a shallow slope over the lower-level end of the function, and a steeper slope (approximating linearity) over the higher-level end [e.g., ESR(*r*) at *all* CFs]. In other cases, however, [e.g., ETA(*l*), CFs of 4000 and 8000 Hz] they show a steep slope (approximating linearity) over the lower-level end of the function and a shallower slope at higher levels. Unlike what has been previously reported both for some NH listeners (Nelson et al., 2001; Lopez-Poveda

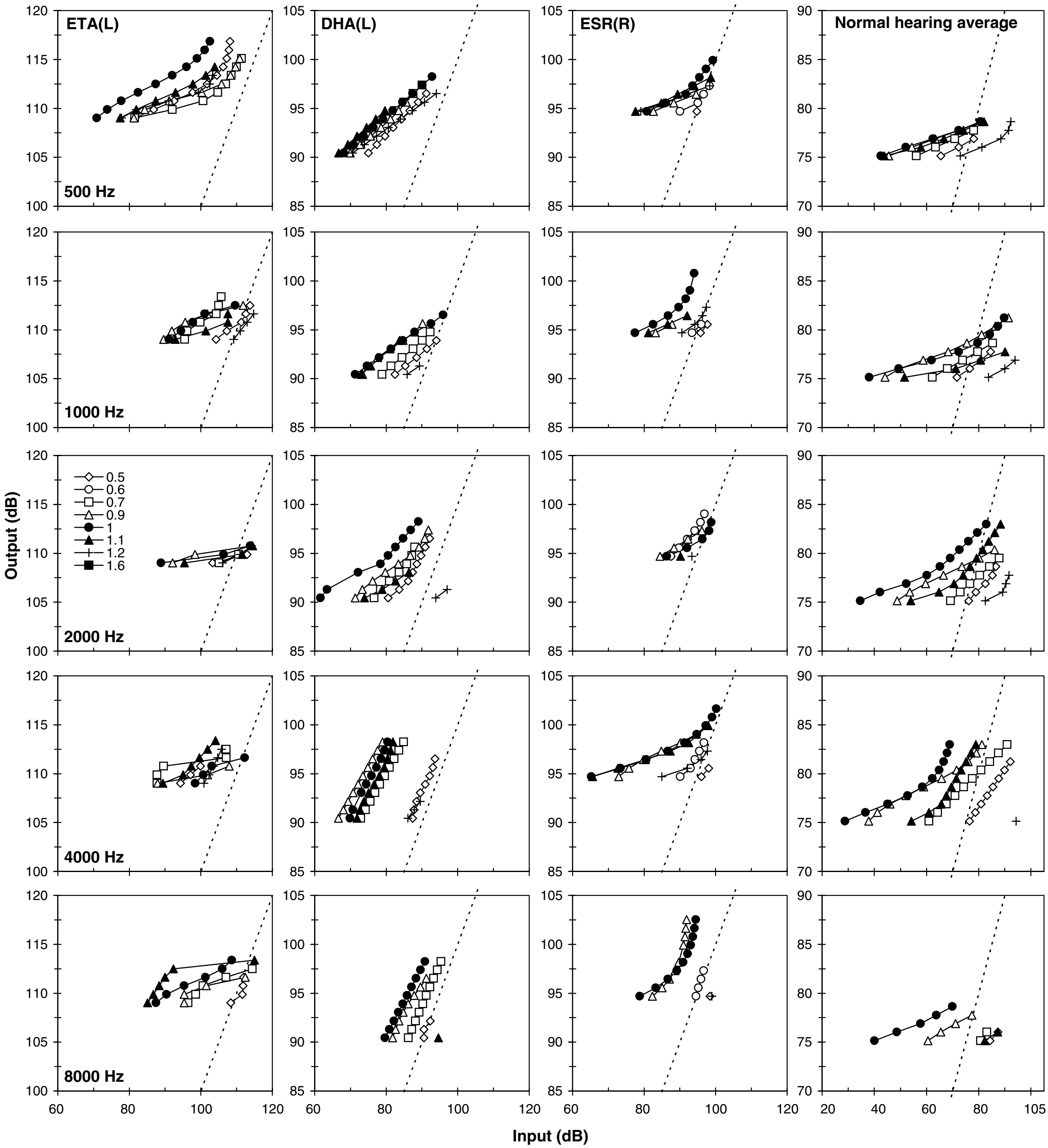

Fig. 5. Inferred BM response functions. Each column illustrates the response functions of a different HI listener or the average of three NH listeners (right-most column). Each row corresponds to a different center frequency from 500 Hz (top row) to 8000 Hz (bottom row). The inset in the mid panel, left column informs of the stimulation frequencies relative to CF. Dotted lines illustrate a perfectly linear response with zero gain.

et al., 2003; Plack and Drga, 2003) and some HI listeners (Plack et al., 2004), the response functions in Fig. 5 rarely show *three* distinct segments with different slopes suggesting a linear response at low levels, a compressive response at moderate levels, and a linear response again at high levels. Such a pattern occurs for ETA(*l*) at 500 Hz only. Possibly, this occurs because the level of the probe was higher here [14 dB SL for ESR(*r*) and DHA(*l*)] than (10 dB SL) in those other studies or for ETA(*l*) of the present study.

3.2.4. Compression at CF

To estimate the degree of compression, the response functions in Fig. 5 were interpreted as curves whose

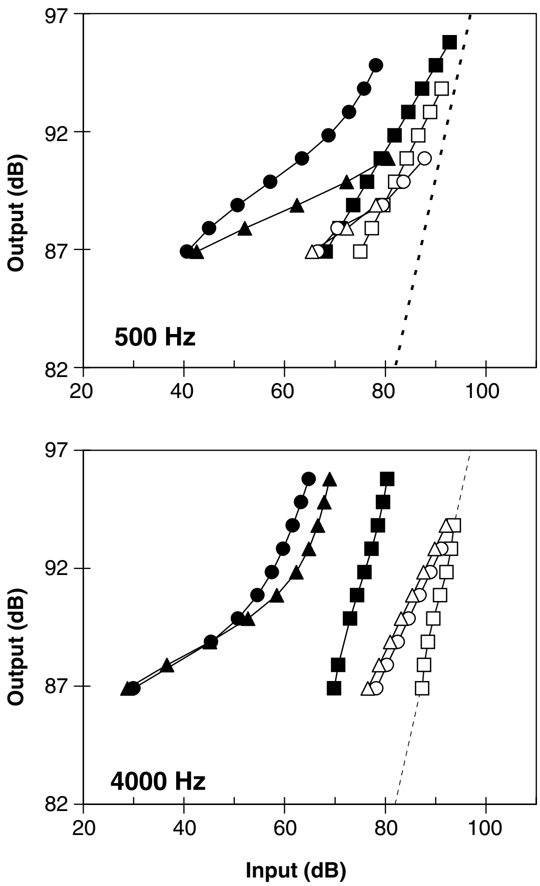

Fig. 6. Inferred BM response functions for the NH [DHA(r), circles] and HI [DHA(l), squares] ears of unilaterally HI listener DHA. Also shown are the response functions for the average of three NH listeners (triangles) (adapted from Lopez-Poveda et al., 2003). Filled symbols: responses for tones at CF; open symbols: responses for tones an octave below CF. Top panel: CF = 500 Hz; Bottom panel: CF = 4000 Hz.

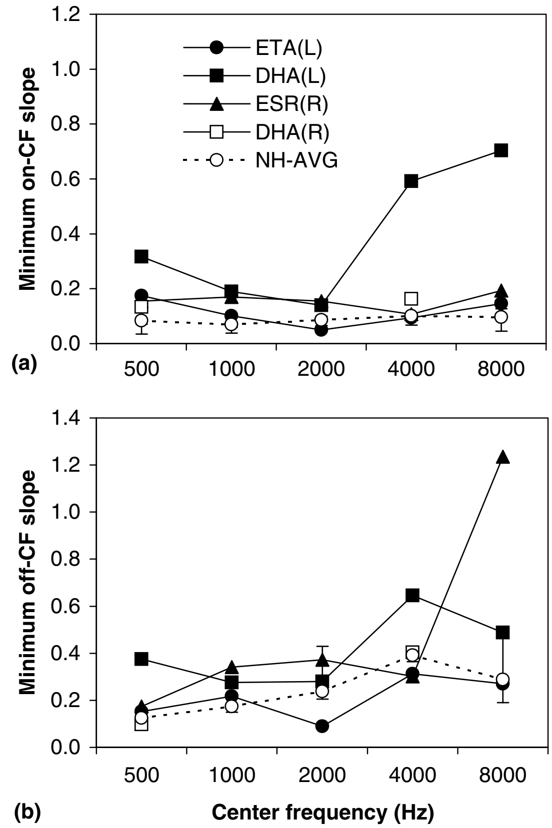

Fig. 7. *Minimum* growth rates (minimum slopes) of the estimated BM response functions for tones at CF (a) and well below CF (b) (measured from the response functions shown in Figs. 5 and 6). Filled symbols: HI ears; open symbols: NH ears. Open circles illustrate corresponding values for the average response functions for three NH listeners. Error bars are associated to the open circles and illustrate the range of individual values for three NH listeners.

slopes vary "smoothly" with level. For any given input/output function, the first derivative (slope) was calculated and plotted as a function of level to obtain a corresponding *growth-rate function* (not shown). Of these, the *minimum* value was noted and regarded as an estimate of the degree of *maximum* compression (Nelson et al., 2001; Nelson and Schroder, 2004). The results are shown in Fig. 7(a).

For NH listeners (open circles), the slope is almost constant across CFs with an average value of 0.09 dB/dB. This value is similar to that of 0.14 dB/dB reported by Nelson and Schroder (2004), but is considerably lower than the 0.26 dB/dB previously reported by Lopez-Poveda et al. (2003) based on the same NH TMC data. The difference with the estimate of Lopez-Poveda et al. (2003) is attributed to two factors. First, and most importantly, Lopez-Poveda et al. used linear reference TMCs from NH listeners. These have been shown to be on average twice as steep as the linear reference TMCs from HI ears employed here (see Fig. 4). Second, Lopez-Poveda et al. (2003) measured the slopes of straight-line segments fitted over a wider range of input levels corresponding to the compression region of the derived BM response functions. Such slopes will certainly be larger than the *minimum* values considered here (or by Nelson and Schroder, 2004).

For HI ears ETA(l) and ESR(r), compressive responses at CF (slopes < 1 dB/dB) are observed across the range of CFs tested [Fig. 7(a)]. The degree of compression is approximately constant across CFs, as is the case for NH listeners. The average slopes [0.11 and 0.16 dB/dB for ETA(l) and ESR(r), respectively] are only slightly larger than normal across CFs. For DHA(l), however, near-normal maximum compression is observed at CF = 2000 Hz only (slope = 0.14 dB/dB). For CFs < 2000 Hz, compression is three to four times less than for the average NH listeners. For CFs > 2000 Hz, on-CF response functions are much less compressive (slopes of 0.6 and 0.7 dB/dB, respectively, see also Fig. 5). In summary, for two of the three HI ears, maximum on-CF compression is close to normal. For the third one, however, the degree of compression varies depending on the CF.

It is noteworthy that at 4000 Hz, the response functions of HI ears DHA(l) and ESR(r) are very different [compression is considerably greater for ESR(r)] despite the fact the two ears have almost identical absolute thresholds for this frequency (Fig. 1). Possible interpretations of this result are discussed below (Section 4.1.2).

3.2.5. Compression below CF

The degree of *maximum* compression for tones below CF was estimated by calculating the *minimum* slope of the response functions for frequencies of 0.5CF for ETA(l) and DHA(l,r), and of 0.6CF for ESR(r)[2]. The results are shown in Fig. 7(b). For NH ears (open circles), compressive responses (slope < 1 dB/dB) are observed across CFs, with slopes that increase gradually from 0.15 dB/dB at 500 Hz to ~0.4 dB/dB at 4000 Hz. This result is qualitatively consistent with that reported previously for NH listeners (Lopez-Poveda et al., 2003; Plack and Drga, 2003). Quantitatively, however, the present slopes are approximately half of those previously reported by Lopez-Poveda et al. (2003) based on the same NH TMC data. Again, the differences may be attributed to the fact that in the present study the linear reference TMCs were taken from HI listeners, and that *minimum* growth rates are considered (see Section 3.2.4).

The results for the HI ears vary. Nearly normal off-CF compression across CFs is observed for ETA(l) only. For DHA(l) and ESR(r), however, off-CF compression appears less than normal, with minimum slopes being from 1.5 to 4.5 times steeper. It is noteworthy that the off-CF slopes of the HI ears do not reach unity at 8000 Hz. One would reasonably expect this to happen given that the off-frequency TMCs for an 8000 Hz probe were regarded as the linear reference TMCs. Indeed, this is the reason that in Fig. 5 the derived off-CF BM response functions appear almost linear at 8000 Hz. However, careful inspection of the off-CF response functions reveals segments that suggest compressive responses over a very narrow range of input levels. Fig. 7(b) illustrates the slopes (<1 dB/dB) of these segments.

4. Discussion

The general aim of the present experiment was to investigate the consequences of sensorineural hearing loss on BM compression over a wide range of CFs (500–8000 Hz) and levels. For three HI listeners, TMCs were measured for probe frequencies equal to the CFs of interest and for a number of masker frequencies around each probe frequency. Then, approximated BM response functions were derived from the TMCs. Estimates of maximum compression for tones at and below CF were obtained.

4.1. Compression in HI listeners

Results suggest that for the HI ears compression for tones *at* CF may occur *across* a CF range from 500 to 8000 Hz [Figs. 5–7(a)]. For two of the three HI ears [ETA(l) and ESR(r)], *maximum* compression is approximately constant *across CFs* and comparable to that of NH ears [Fig. 7(a)]. For the third HI ear [DHA(l)], however, near-to-normal on-CF compression occurs for a CF of 2000 Hz only. Elsewhere, compression is either slightly (CF < 2000 Hz) or considerably reduced (CF > 2000 Hz). Furthermore, the pattern of BM responses for off-frequency tones is similar for NH and HI ears: compression is greatest at a CF of 500 Hz and decreases progressively as the CF increases [Fig. 7(b)]. Nevertheless, there are hints of residual off-CF compression at high CFs in *both* normal and HI ears.

4.1.1. Interpretations

There are two possible interpretations (not mutually exclusive) of the fact that maximum compression for tones at CF is generally comparable for NH and HI listeners. First, it is possible that the HI ears suffer from hearing loss related to inner hair cell (IHC) damage. This type of damage is believed to affect the transduction mechanism but not the properties of the BM response (gain or compression), which are thought to depend mostly on the physiological condition of outer hair cells (OHCs) (evidence reviewed by Patuzzi, 1996). Therefore, people with IHC damage would show normal compression.

This interpretation agrees with the conclusions of Heinz and Young (2004), who suggested that acoustic trauma causes as much (if not more) IHC loss than OHC loss. They compared the growth of total auditory nerve response in fibers from NH cats and cats with noise-induced hearing loss. They found that the slopes of rate-level functions were on average shallower for the HI fibers. Heinz and Young reasoned that this is inconsistent with OHC damage, because this type of noise-induced damage produces BM input/output functions which appear to be more linear, hence steeper, overall (Ruggero et al., 1996; Patuzzi, 1996). Instead, their results are consistent with IHC damage. Absolute thresholds would occur at higher levels of BM excitation in ears suffering from IHC damage than in NH ears or in ears suffering from OHC damage. Such a degree of excitation may fall within the compressive region of the BM response, leading to auditory-nerve rate-level functions that are shallower than normal.

The second possible interpretation of the fact that maximum compression for tones at CF is comparable for NH and HI ears has been recently suggested by Plack et al. (2004). They measured TMCs for a probe frequency of 4000 Hz and masker frequencies of 2200 and 4000 Hz, for 16 NH and 12 HI ears. They found that maximum compression at a CF of 4000 Hz is uncorrelated with absolute threshold, but reported a strong negative correlation between the gain at low levels and absolute threshold. This led them to suggest that OHC-related 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 BM active mechanism [see their Fig. 7(c)]. The present results support the conclusion of Plack et al. (2004) regarding the absence of correlation between maximum on-CF compression and absolute threshold and extend it to a wider range of CFs (500–8000 Hz).

4.1.2. Differences between hearing-impaired ears with similar absolute thresholds

The present results show that the estimated BM responses may be very different for different HI ears, even when they have almost identical absolute thresholds. For instance, Fig. 1 shows that the two HI ears DHA(*l*) and ESR(*r*) have almost identical thresholds (~50 dB SPL) at 4000 Hz. However, at 4000 Hz the inferred BM response for tones at CF is highly compressed for ESR(*r*) but less so for DHA(*l*) [Figs. 5 and 7(a)].

This result may be understood, again, in terms of the relative amounts of damage to inner and outer hair cells: while DHA(*l*)'s responses are consistent with the type of impairment associated with OHC damage, those of ESR(*r*) are more consistent with mostly IHC damage. Further evidence in support of this interpretation is as follows. Damage to basal OHCs is known to reduce the so-called "active mechanism" of the BM (reviewed by Patuzzi, 1996), leading to broader BM threshold tuning curves with reduced sensitivity near the CF but normal sensitivity in the low-frequency tail (Fig. 15 in Sellick et al., 1982; Fig. 6 in Nuttall and Dolan, 1996). Analogous studies of auditory nerve threshold tuning curves show that IHC damage reduces sensitivity not only at CF but also in the low-frequency tail (reviewed by Liberman et al., 1986). In Fig. 2, the vertical distance at the shortest masker-probe interval (10 ms) between the off-frequency TMCs for the normal and the HI ears may be regarded as a measure of the loss of sensitivity in the low-frequency tail of a near threshold psychophysical tuning curve (Small, 1959). Such a distance is greater for ESR(*r*) (19.5 dB) than for DHA(*l*) (11.3 dB). Furthermore, for any given listener, the vertical distance between his/her on- and off-frequency TMCs at the shortest masker-probe interval may be taken as a measure of their degree of frequency selectivity near threshold (Small, 1959). That distance is greater for ESR(*r*) (29.0 dB) than for DHA(*l*) (17.6 dB). In summary, DHA(*l*) shows greater sensitivity to low frequency sounds (relative to CF) and less frequency selectivity than ESR(*r*). For the reasons explained above, these results are consistent with the idea that, at 4000 Hz, the hearing impairment of DHA(*l*) relates mostly to OHC dysfunction whereas that of ESR(*r*) is mostly related to IHC damage.

4.2. Off-frequency TMCs

It has been shown [Fig. 4(b)] that, with some exceptions, the slopes of the TMCs for masker frequencies an octave below the probe frequency are shallower for the HI ears than for the NH ears *across* the probe frequencies tested (500–8000 Hz). This result is *not* peculiar to the present data. For instance, Rosengard et al. (2003) have also reported shallower off-frequency TMCs for HI listeners for a 1000-Hz probe. Drga and Plack (2003) and Plack et al. (2004) also reported a negative correlation between the slope of the TMCs for the off-frequency maskers and absolute threshold for a probe frequency of 4000 Hz. The slope of their off-frequency TMCs decreased by approximately a factor of 0.5 across the range of absolute thresholds tested.

Given that the slope of the TMCs is assumed to depend on the decay of the internal effect of the masker *and* on cochlear compression, the result has several possible interpretations (see also Plack et al., 2004). It could be that for HI listeners the internal effect of the masker decays more slowly with time, possibly as a result of masker levels being higher for HI listeners. Indeed, Plack et al. (2004) showed that when the same range of masker levels is considered, the slopes of off-frequency TMCs for NH listeners are comparable to those for HI listeners. It is conceivable that very high masker levels produce some long-term adaptation that does not vary much over the masker-probe time intervals used here, and hence approximately the same masker level was needed for threshold at different masker-probe time intervals.

Another interpretation for the result could be that compression for tones well below CF occurs not only at CFs < 4000 Hz, as has been previously suggested (Lopez-Poveda et al., 2003; Nelson and Schroder, 2004; Plack and Drga, 2003; Oxenham and Dau, 2004), but also at higher CFs. Indeed, careful inspection of published IHC data reveals that in guinea pig, the receptor potential (RP) of basal units grows compressively with level even for tones as far below CF as an octave. For instance, Fig. 1(c) in Patuzzi and Sellick (1983, case 1020) shows that for a CF of 18000 Hz and a stimulation frequency of 0.39 × CF, the dc component of the RP grows nonlinearly with level above approximately 80 dB SPL, with a slope of 0.5 dB/dB. Similarly, Fig. 2 in Cheatham and Dallos (2001) shows a compressive growth of the average IHC RP for levels above 40 dB SPL for a CF of 4000 Hz and a stimulation frequency of 2000 Hz. Again, the slope is approximately 0.5 dB/dB. Another example can be found in the report of Russell et al. (1986). Their Fig. 6 illustrates that the dc component of the RP of an IHC with a CF of 16,000 Hz grows compressively with level for a stimulation frequency of 10,000 Hz with a slope of 0.53 dB/dB. On the other hand, while compressive BM responses to tones an octave (or so) below CF have been reported for sites in the apex of the BM (Rhode and Cooper, 1996), no evidence exists of similar observations for more basal sites (Robles and Ruggero, 2001). Hence, it is unclear whether the compression observed in those IHC studies originates at the BM or the IHC. However, it is noteworthy that the value of 0.5 dB/dB for the slope of IHC RP very closely approximates to the inverse ratio of the slopes of off-frequency TMCs for NH and HI ears [Fig. 4(b); see also Fig. 3 in Plack et al., 2004]. It is, therefore, tempting to speculate that the off-frequency TMCs, even those for high-frequency probes, are steeper for NH ears because they reflect either BM or IHC-related compression that is reduced (or absent) in ears with sensorineural hearing loss.

4.3. Concerns on the use of behavioral techniques for estimating BM response functions and compression

The fact that the slopes of off-frequency TMCs are shallower for the HI ears than for the NH ears, even for high-frequency probes [Fig. 4(b) and Plack et al., 2004], complicates the selection of the linear reference TMC, hence the application of the method of Nelson et al. (2001) for estimating BM compression from TMCs. A crucial assumption of the method is that "...the decay of the internal effect of a masker is the same (for all masker and probe frequencies) regardless of the magnitude of the internal effect, i.e., the recovery process is well defined by (...) a level-independent time constant" (Nelson et al., 2001, p. 2049). If the shallower off-frequency TMCs reflect a slow decay of the internal effect of the masker for HI listeners simply as a result of masker levels being higher (Plack et al., 2004), then the above assumption would be false, hence the method should be fully revised.

Alternatively, if the shallower off-frequency TMCs reflect less off-frequency compression for HI listeners, then the interpretation of results differ depending on whether such compression is eventually confirmed to originate at the BM or the IHC. If it originates at the BM, as has been assumed in the present work, that would mean that the linear reference TMCs that have been used previously for NH listeners (Lopez-Poveda et al., 2003; Nelson and Schroder, 2004; Plack and Drga, 2003; Plack et al., 2004) may actually be compressed by approximately 2:1. Consequently, previous reports will have underestimated the degree of human BM compression by approximately a factor of two. It is noteworthy that this applies to compression estimates obtained not only with the TMC-based technique but also with other behavioral methods that are based on comparing on-and off-CF BM responses (e.g., the growth of masking method of Oxenham and Plack, 1997; or the pulsation threshold method of Plack and Oxenham, 2000).

If, on the contrary, the off-frequency compression originates at the IHC, the previous interpretations would remain valid (unless the degree of IHC compression varies across CFs), and the BM compression reported here would be an overestimate. In the latter case, if the NH off-frequency TMCs were taken as the linear reference TMCs, the off-CF response functions of the HI ears would appear *expansive* (slope > 1 dB/dB), possibly (but not necessarily) as a result of reduced (or absent) IHC compression.

5. Conclusions

1. For listeners with moderate cochlear hearing loss, residual BM compression for tones at CF may occur across a range of CFs from 500 to 8000 Hz. In two out of three listeners tested, maximum compression is approximately the same as for normal-hearing listeners.
2. Residual BM compression for tones well below CF may occur for listeners with moderate sensorineural hearing loss. The degree of compression may be similar to or less than that for NH listeners. Results in this respect are mixed.
3. Different HI listeners with similar absolute thresholds may show clearly different degrees of BM compression. This may be explained in terms of relative damage to IHCs and OHCs. An absence of compression is consistent with total OHC dysfunction.
4. TMCs for maskers an octave below the probe frequency are steeper for ears with normal hearing, even for probe frequencies of 4000 Hz and higher. This difference in slope may reflect a slower decay of the internal effect of the masker for HI listeners. Alternatively, it may reflect residual BM or IHC compression for tones an octave below CF. Discerning between these possibilities is critical for the TMC-based method and other behavioral methods of estimating human BM compression.

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References

Bacon, S.P., Oxenham, A.J., 2004. Psychophysical manifestations of compression: hearing-impaired listeners. In: Bacon, S.P., Fay, R.R., Popper, A.N. (Eds.), Compression: From Cochlea to Cochlear Implants. Springer, New York, pp. 107–152.

Cheatham, M.A., Dallos, P., 2001. Inner hair cell response patterns: implications for low-frequency hearing. J. Acoust. Soc. Am. 110, 2034–2044.

Drga, V., Plack, C.J., 2003. Psychophysical estimates of basilar membrane compression at 4 kHz in normal-hearing and hearing-impaired listeners, presented at 26th Annual Midwinter Research Meeting of the Ass. Res. Otolaryngol., Daytona Beach, FL.

Heinz, M.G., Young, E.D., 2004. Response growth with sound level in auditory-nerve fibers after noise-induced hearing loss. J. Neurophysiol. 91, 784–795.

Levitt, H., 1971. Transformed up-down methods in psychoacoustics. J. Acoust. Soc. Am. 49, 466–477.

Liberman, M.C., Dodds, L.W., Learson, D.A., 1986. Structure–function correlation in noise-damaged ears: a light and electron-microscopic study. In: Salvi, R.J., Henderson, D., Hamernik, R.P., Colletti, V. (Eds.), Basic and Applied Aspects of Noised-Induced Hearing Loss. Plenum Publishing Corporation, pp. 163–177.

Lopez-Poveda, E.A., Plack, C.J., Meddis, R., 2003. Cochlear nonlinearity between 500 and 8000 Hz in listeners with normal hearing. J. Acoust. Soc. Am. 113, 951–960.

Nelson, D.A., Schroder, A.C., 2004. Peripheral compression as a function of stimulus level and frequency region in normal-hearing listeners. J. Acoust. Soc. Am. 115, 2221–2233.

Nelson, D.A., Schroder, A.C., Wojtczak, M., 2001. A new procedure for measuring peripheral compression in normal-hearing and hearing-impaired listeners. J. Acoust. Soc. Am. 110, 2045–2064.

Nuttall, A.L., Dolan, D.F., 1996. Steady-state sinusoidal velocity responses of the basilar membrane in guinea pig. J. Acoust. Soc. Am. 99, 1556–1565.

Oxenham, A.J., Bacon, S.P., 2004. Psychophysical manifestations of compression: normal-hearing listeners. In: Bacon, S.P., Fay, R.R., Popper, A.N. (Eds.), Compression: From Cochlea to Cochlear Implants. Springer, New York, pp. 62–106.

Oxenham, A.J., 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., Dau, T., 2004. Masker phase effects in normal-hearing and hearing-impaired listeners: evidence for peripheral compression at low signal frequencies. J. Acoust. Soc. Am. 116, 2248–2257.

Patuzzi, R., 1996. Cochlear micromechanics and macromechanics. In: Dallos, P., Popper, A.N., Fay, R.R. (Eds.), The Cochlea. Springer, New York, pp. 186–257.

Patuzzi, R., Sellick, P.M., 1983. A comparison between basilar membrane and inner hair cell receptor potential input-output functions in the guinea pig cochlea. J. Acoust. Soc. Am. 74, 1734–1741.

Plack, C.J., Drga, V., 2003. Psychophysical evidence for auditory compression at low characteristic frequencies. J. Acoust. Soc. Am. 113, 1574–1586.

Plack, C.J., Drga, V., Lopez-Poveda, E.A., 2004. Inferred basilar-membrane response functions for listeners with mild to moderate sensorineural hearing loss. J. Acoust. Soc. Am. 115, 1684–1695.

Plack, C.J., Oxenham, A.J., 2000. Basilar-membrane nonlinearity estimated by pulsation threshold. J. Acoust. Soc. Am. 107, 501–517.

Rhode, W.S., 1971. Observations of the vibration of the basilar membrane in squirrel monkeys using the Mössbauer technique. J. Acoust. Soc. Am. 49 (Suppl.2), 1218.

Rhode, W.S., Cooper, N.P., 1996. Nonlinear mechanics in the apical turn of the chinchilla cochlea in vivo. Audit. Neurosci. 3, 101–121.

Rhode, W.S., Recio, A., 2000. Study of mechanical motions in the basal region of the chinchilla cochlea. J. Acoust. Soc. Am. 107, 3317–3332.

Robles, L., Ruggero, M.A., 2001. Mechanics of the mammalian cochlea. Physiol. Rev. 81, 1305–1352.

Rosengard, P.S., Oxenham, A.J., Braida, L.D., 2003. Estimates of basilar-membrane compression in listeners with normal hearing derived from growth-of-masking functions and temporal masking curves, presented at 26th Annual Midwinter Research Meeting of the Ass. Res. Otolaryngol., Daytona Beach, FL.

Ruggero, M.A., Rich, N.C., Recio, A., Narayan, S.S., 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., Rich, N.C., Robles, L., Recio, A., 1996. The effects of acoustic trauma, other cochlear injury, and death on basilar-membrane responses to sound. In: Axelsson, A., Borchgrevink, H., Hellström, P.-A., Henderson, D., Hamernik, R.P., Salvi, R.J. (Eds.), Scientific Basis of Noised-Induced Hearingpp. Thieme Medical, New York, pp. 23–35.

Russell, I.J., Cody, A.R., Richardson, G.P., 1986. The responses of inner and outer hair cells in the basal turn of the guinea-pig cochlea and the in the mouse cochlea grown in vitro. Hearing Res. 22, 199–216.

Sellick, P.M., Patuzzi, R., Johnstone, B.M., 1982. Measurement of basilar membrane motion in the guinea pig using the Mössbauer technique. J. Acoust. Soc. Am. 72, 131–141.

Small, A.M., 1959. Pure-tone masking. J. Acoust. Soc. Am. 31, 1619–1625.

Williams, E.J., Bacon, S.P., 2005. Compression estimates using behavioral and otoacoustic emission measures. Hearing Res. 201, 44–54.