Cochlear nonlinearity between 500 and 8000 Hz in listeners with normal hearing

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(Received 20 April 2002; accepted for publication 11 November 2002)

Cochlear nonlinearity was estimated over a wide range of center frequencies and levels in listeners with normal hearing, using a forward-masking method. For a fixed low-level probe, the masker level required to mask the probe was measured as a function of the masker-probe interval, to produce a temporal masking curve (TMC). TMCs were measured for probe frequencies of 500, 1000, 2000, 4000, and 8000 Hz, and for masker frequencies 0.5, 0.7, 0.9, 1.0 (on frequency), 1.1, and 1.6 times the probe frequency. Across the range of probe frequencies, the TMCs for on-frequency maskers showed two or three segments with clearly distinct slopes. If it is assumed that the rate of decay of the internal effect of the masker is constant across level and frequency, the variations in the slopes of the TMCs can be attributed to variations in cochlear compression. Compression-ratio estimates for on-frequency maskers were between 3:1 and 5:1 across the range of probe frequencies. Compression did not decrease at low frequencies. The slopes of the TMCs for the lowest frequency probe (500 Hz) did not change with masker frequency. This suggests that compression extends over a wide range of stimulus frequencies relative to characteristic frequency in the apical region of the cochlea. [DOI: 10.1121/1.1534838]

PACS numbers: 43.66.Dc, 43.66.Mk [MRL]

I. INTRODUCTION

The mammalian cochlear response is nonlinear in healthy animals (Rhode, 1971; Sellick *et al.*, 1982; Robles *et al.*, 1986). An increase in the magnitude of stimulation does not always produce a proportional increase in the velocity or displacement of basilar membrane (BM) vibration. It is generally accepted that for *high* characteristic frequencies[1] (CFs) the response is nonlinear for frequencies close to CF, but linear for frequencies an octave below CF (Robles *et al.*, 1986).

Using physiological techniques, cochlear responses have been measured in *animals* in terms of BM input/output (IO) functions for a wide range of CFs, stimulation frequencies, and levels (e.g., Sellick *et al.*, 1982; Robles *et al.*, 1986; Rhode and Cooper, 1996; Recio and Rhode, 2000; Rhode and Recio, 2000). The aim of the present study was to use psychophysical techniques to estimate the characteristics of the *human* cochlear response over a similar range of parameters.

The nonlinear properties of the human cochlear response can be inferred from threshold measurements of masked probe tones (for a review see Moore, 1997). A number of studies (e.g., Oxenham and Plack, 1997; Rosen *et al.*, 1998; Baker *et al.*, 1998; Glasberg *et al.*, 1999; Hicks and Bacon, 1999; Plack and Oxenham, 2000; Wojtczak *et al.*, 2001; Nelson *et al.*, 2001; Moore *et al.*, 2002) have characterized cochlear nonlinearity in normal-hearing listeners using this approach. In the present study, a revised version of the method of Nelson *et al.* (2001) was used.

The method developed by Nelson *et al.* consists of measuring the level of a pure-tone forward masker required to just mask a pure-tone probe as a function of the masker-probe time interval. The level of the probe is fixed just above absolute threshold. It is thought that the masker level at threshold depends on two variables. First, it depends on the masker-probe interval: the amount of masking decreases as the masker-probe interval increases (Zwislocki *et al.*, 1959; Duifhuis, 1973; Moore and Glasberg, 1983; Nelson and Freyman, 1987). Second, it depends on the relative excitation produced by the masker and the probe at the place on the BM tuned close to the probe frequency (Oxenham and Moore, 1995; Oxenham *et al.*, 1997; Oxenham and Plack, 1997; Nelson *et al.*, 2001). Because the probe level is fixed at all times, the method is assumed to measure the masker level (input) required to generate a fixed level of excitation after decaying during the masker-probe interval. This is the reason that the resulting functions are referred to as *iso-response* temporal masking curves (TMCs).

Obviously, higher masker levels are required as the masker-probe interval increases. However, the slope of the TMC depends on the masker frequency. It has been argued (Nelson *et al.*, 2001) that this is because on-frequency maskers are subject to cochlear compression while others are processed more linearly. Therefore, the slope of the TMCs reflects the amount of compression for a given masker. Nelson *et al.* showed this behavior for a probe frequency of 1 kHz and a wide range of masker frequencies. By assuming that the internal effect of the masker decays at the same rate

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regardless of masker frequency, and that maskers well below the probe frequency yield a *linear* cochlear response, they derived human cochlear IO curves at CF~1000 Hz by plotting the masker levels for the low-frequency masker (a linear reference) as a function of the masker levels for other masker frequencies.

This approach has some advantages over previous methods (e.g., Oxenham and Plack, 1997; Rosen *et al.*, 1998; Baker *et al.*, 1998; Plack and Oxenham, 2000). Fixing the probe level almost guarantees that the region of the cochlea under study is the same for different masker (input) levels. Furthermore, fixing the probe level just above threshold ensures that the CF of the cochlear region under study is close to the probe frequency. In other words, the effects of ''off-frequency listening'' are minimized.[2]

In the present study, TMCs were measured for probe frequencies from 500 to 8000 Hz, and for a range of masker frequencies at each probe frequency. It will be argued that for low probe frequencies, cochlear responses are compressed for maskers well below the probe frequency. This undermines the assumptions of the method developed by Nelson *et al*. for deriving cochlear IO curves from TMCs. An alternative method is suggested based on the more limited assumption that the response to below-CF tones is linear at *high CFs only* (see also Plack and Drga, submitted). It has been suggested by physiological results in the chinchilla (Rhode and Cooper, 1996) and guinea pig (Cooper and Yates, 1994), and by masking studies in humans (Hicks and Bacon, 1999; Plack and Oxenham, 2000), that compression is reduced at low CFs. The new method allowed a test of this hypothesis. Finally, a control experiment is reported that tested the effects of probe and masker ramp durations on the form of the TMCs.

II. METHOD

A. 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, 0.7, 0.9, 1.0, 1.1, and $1.6\times f_p$. For any given pair (f_m, f_p), masked thresholds were measured for masker-probe intervals (Δt) ranging from 10 to 100 ms in steps of 10 ms. Δt was defined as the duration of zero-amplitude points between the masker offset and the probe onset. The sinusoidal maskers were gated with 4-ms raised-cosine onset and offset ramps and had a total duration of 108 ms. The sinusoidal probes had a total duration of 8 ms and were gated with 4-ms raised-cosine ramps (no steady-state portion). For each f_p, the level of the probe was kept constant at 14 dB above the listener's absolute threshold for the probe.

Stimuli were generated digitally on a Silicon Graphics O2 workstation at a sampling rate of 32 kHz, with 16-bit resolution. They were played monaurally via the workstation headphone connection through a pair of circumaural Sennheiser HD-580 headphones. Listeners sat in an EYMASA CI-40 single-walled sound-attenuating booth. The booth was placed in a quiet environment to further reduce background noise. The sound pressure levels (SPLs) reported below are nominal electrical levels without allowing for the earphone diffuse-field response.

B. Procedure

The procedure was similar to that used by Plack and Oxenham (1998). 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 listener in random order, but each of them coincided in time with the highlighting of a window on the workstation monitor. Listeners were asked to select the interval containing the probe by pressing ''1'' or ''2'' on the numerical keyboard of the workstation, depending on whether the probe was judged to accompany the first or the second light, respectively. Visual feedback was immediately provided to the listener by means of a green or red highlighted window on the monitor, indicating correct and incorrect answers, respectively.

The initial masker level was 35 dB SPL. 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 turnpoints, and by 2 dB thereafter. Sixteen turnpoints were recorded in each experimental block and the threshold estimate was taken as the mean of the masker levels at the last 12 turnpoints. For masker levels below approximately 90 dB SPL at least three estimates were made for each condition, and the results were averaged. In some cases, it was difficult to make three measurements for masker levels above 90 dB SPL because clipping often occurred during the adaptive procedure and listeners were instructed to stop the experiment at the first sign of clipping. When this occurred with one of the estimates, the two remaining estimates were averaged. It follows that the reported masker levels above 90 dB SPL are likely to be underestimates of the true threshold.

C. Listeners

Data were collected for the left ear of three listeners (CMR, ALN, and ELP, aged 22, 26, and 31, respectively) with normal hearing.[3] Listener ELP was one of the authors, but, like the other two listeners, had no previous experience on the task. Absolute thresholds were measured 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. Listeners were given at least 10 h of practice on the forward-masking task before data collection began.

III. RESULTS

A. Temporal masking curves

Results are shown in Fig. 2. Each column corresponds to a different listener (or the mean). Each row corresponds to a different probe frequency (from 500 Hz in the top row to 8000 Hz in the bottom row). As explained above, data points

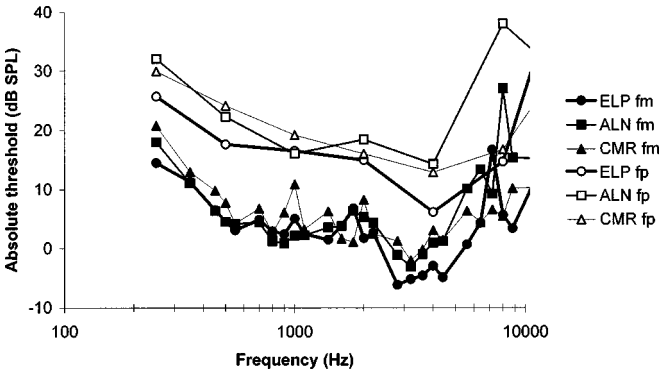

FIG. 1. Absolute hearing thresholds for the three listeners (ELP, CMR, and ALN). Open symbols show the thresholds for the 8-ms probe tones (f_p). Filled symbols represent the thresholds for the 108-ms masker tones (f_m). Data points represent the mean of three measurements. Note the high thresholds of ELP for the 7200-Hz masker and of ALN for the 8000-Hz probe and masker. These coincide with deep notches in the listeners' headphone-related frequency responses[3] (not shown).

below around 90 dB SPL are based on the average of three measurements, whereas those above 90 dB SPL are sometimes based on the average of two measurements only. Standard deviations across measurements are not shown in order to avoid clutter. These were variable across conditions and listeners, ranging from 0.0 dB (listener ELP, $f_p=500$ Hz, $f_m=800$ Hz, $\Delta t=10$ ms) to 23.0 dB (listener ELP, $f_p=8000$ Hz, $f_m=8000$, $\Delta t=50$ ms), with a mean and a standard deviation across listeners and conditions of 3.1 and 2.3 dB, respectively. The right-most column in Fig. 2 shows average TMCs across the three listeners.

Masker levels increase as Δt increases. This is reasonable since the recovery from masking is greater for longer masker-probe intervals (Zwislocki *et al.*, 1959; Duifhuis, 1973; Moore and Glasberg, 1983; Nelson and Freyman, 1987). However, for *high* probe frequencies, the rate of increase is markedly different for maskers an octave below the probe frequency (unfilled diamonds) than for masker frequencies equal to the probe frequency (filled circles). For $f_m=0.5f_p$, the TMC shows a single slope. As f_m approaches f_p, however, the TMC can be described in most cases as a two-sloped function, with a steeper slope at short to moderate Δt, and a shallower slope at long Δt. In some cases (e.g., ELP, $f_m=f_p=8000$ Hz), the TMC shows a *three*-slope pattern with a shallow slope at short Δt, followed by a steeper slope at moderate Δt, followed by a shallow slope again at longer Δt.

B. Interpretation of the TMCs

The interpretation of the TMCs depends upon two assumptions: (1) that the internal representation of the masker decays with time at the same rate for all masker frequencies and (2) that the residual excitation at the time of the probe at masked threshold is the same for all maskers. Similar assumptions were made by Nelson *et al.* (2001).

The first assumption (uniform rates of decay across masker frequency) makes it possible to identify nonlinear increases of excitation strength with masker level. To understand how this is possible, it helps to consider that the decay is exponential. An exponential decay is consistent with previous studies of recovery from forward masking (e.g., Duifhuis, 1973; Widin and Viemeister, 1979) and is also supported by the present data. The *y*-axis in Fig. 2 is logarithmic and, therefore, a straight-line is consistent with a simple exponential decay. Some straight lines are, indeed, evident. For example, the combination of a 2000-Hz masker and a 4000-Hz probe produces a straight line. Other examples can also be seen, particularly for high probe frequencies paired with low masker frequencies. In these cases, it is assumed that the masker excitation increases as a simple linear function of masker level. These instances can be used as linear reference functions (see below). Therefore, when the slope of the TMC becomes steeper than the linear reference function, this is an indication that the masker is subject to compression. For example, at high frequencies the on-frequency TMC slopes are generally steeper than the TMC slope for a masker an octave below the probe. This suggests that the on-frequency masker is being compressed.

The second assumption allows the reconstruction of the shape of the cochlear IO functions from the TMCs. The method consists of plotting the masker level of a linear-reference masker against the level for the masker of interest (Nelson *et al.*, 2001; Plack and Drga, submitted), where each pair of levels has the same masker-probe interval. The resulting curve reveals the cochlear IO function by compensating for the decay of internal masker excitation. Note that the function describing the decay of internal masker excitation cancels out in this process if it is the same for all masker frequencies. Hence, its actual form (whether exponential or otherwise) is irrelevant.

C. The choice of the best linear reference

The choice of a linear reference is critical if valid estimates of cochlear compression are to be made from the derived cochlear IO functions. A careful examination of Fig. 2 shows that the slope of TMCs for $f_m=0.5f_p$ is steeper for $f_p=500$ Hz than for $f_p=8000$ Hz. Furthermore, the former is closer to the steeper portion of the TMC for maskers at the probe frequency. To make this observation clearer, straight lines (dashed lines in Fig. 2) were fit by a method of least squares to the TMCs for $f_m=0.5f_p$, and their slopes were plotted as a function of f_p. The results are shown in Fig. 3. The slopes of the TMCs for $f_m=0.5f_p$ are much higher for lower f_p's, decrease with increasing f_p up to 2000 Hz, and then remain relatively constant.

Given that the shape of the TMC may be influenced both by the decay of the internal masker effect with time *and* by cochlear compression, this observation may be interpreted in two ways. It may mean that the rate of decay of the masker effect is *faster* for lower probe frequencies (that is, the first assumption would be incorrect). This explanation, however, is unlikely. It would imply that the temporal resolution of the auditory system improves at low frequencies. Shailer and Moore (1987) have shown that this is not the case (see also Moore *et al.*, 1993). They studied the detection of gaps in sinusoids and concluded that it varies little for frequencies between 200 and 2000 Hz and, if anything, becomes poorer

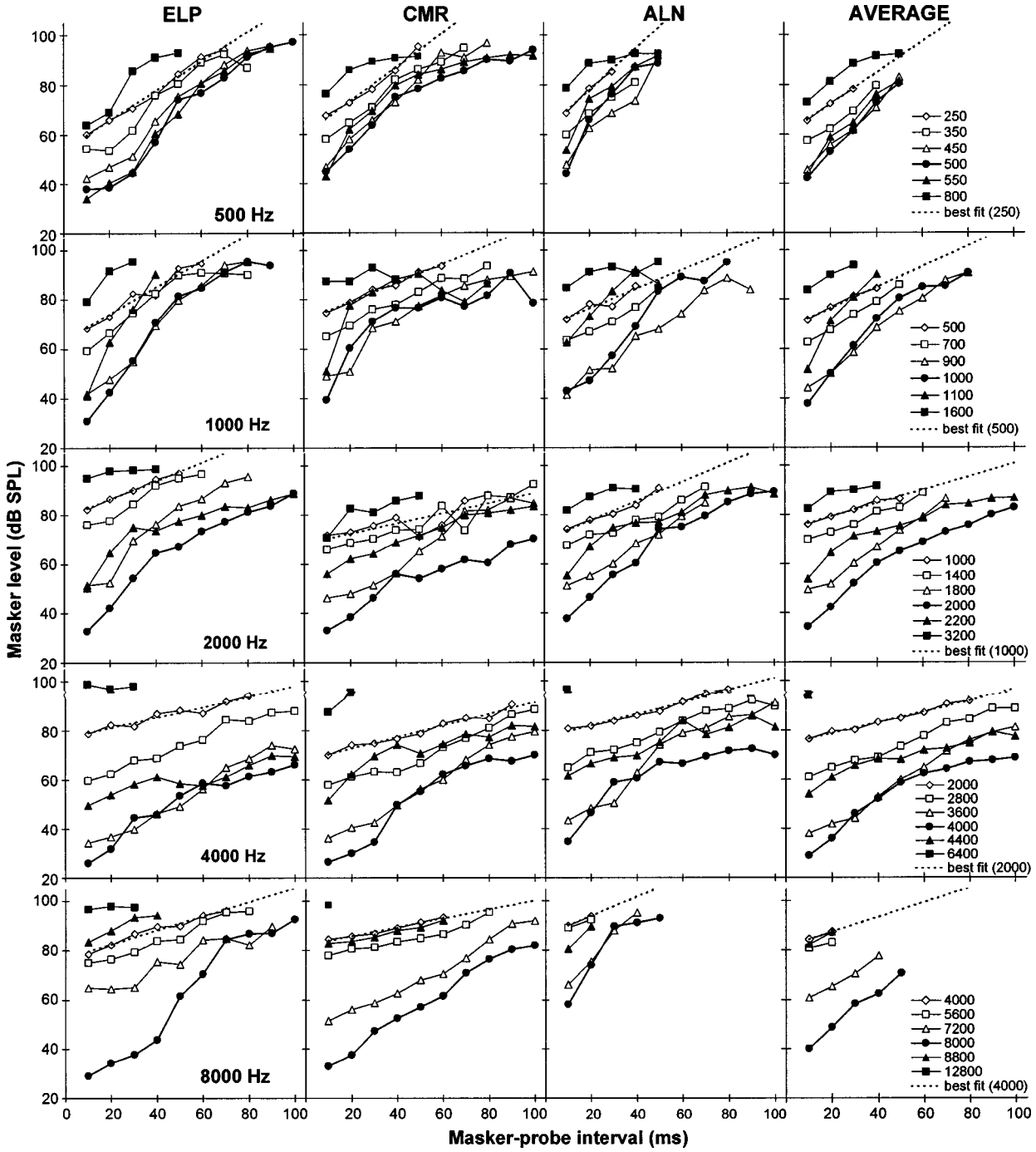

FIG. 2. Iso-response temporal masking curves for each listener (columns) at the five probe frequencies (f_p) tested (rows). The right-most column shows the results averaged across the three listeners. Insets in the panels of the right column show the masker frequencies (f_m). Open symbols represent conditions where $f_m < f_p$. Filled symbols represent conditions where $f_m \geq f_p$. The dotted lines represent the best-fit (by least squares) straight lines for the condition $f_m = 0.5 f_p$, the slopes of which are plotted in Fig. 3.

at low frequencies. Therefore the second, and most likely, interpretation of the data in Fig. 3 is that the human cochlear response for low probe frequencies is *still compressive* as the stimulus frequency is moved *below CF*. In other words, not only do the present data provide evidence for substantial compression at low CFs, but they also support the physiological finding that compression is not frequency dependent at low CFs (Rhode and Cooper, 1996).

As a result of this analysis, the individual (or average) TMCs for $f_p = 4000$ Hz, $f_m = 2000$ Hz, were chosen as the optimum linear references to derive the cochlear IO curves for each listener (or for the average). Furthermore, these linear references were *fixed* across probe frequencies. There are several reasons for this choice: First, the TMCs in question appear as shallow straight lines, suggesting no deviation from linearity across level; second, the slope of the TMC for this condition is the least variable across listeners (see Fig. 3); third, a large number of data points are available for every listener; and finally, the available physiological data (Rhode and Recio, 2000) at reasonably close CFs (5500 Hz)

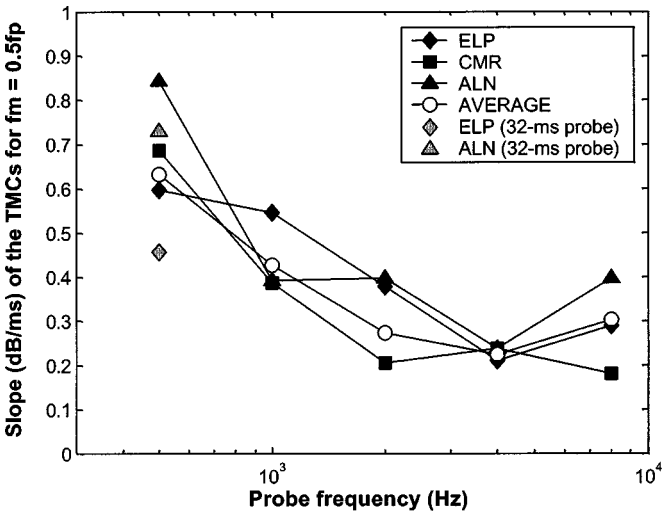

FIG. 3. Slopes of straight-line best fits to the TMCs (Fig. 2, dotted lines) for masker frequencies an octave below the probe frequency. Note that the slope decreases with increasing probe frequency up to 2000 Hz, and then remains approximately constant. This suggests that the cochlear response to low-frequency tones may be compressed at low CFs (see text for details). Filled and open symbols represent the slopes of below-f_p TMCs for a short, 8-ms probe with 4-ms onset/offset ramps. Gray symbols (at 500 Hz only) represent the slopes of below-f_p TMCs for a longer, 32-ms probe with 16-ms ramps (see Fig. 5 and main text in Sec. III E).

suggest that a 2000-Hz stimulus frequency will produce a linear response at the 4000-Hz place.

For convenience, instead of using the original data as the linear reference, a smoothed version was used. This was obtained by reading off a new masker level for each Δt from the regression lines fit (dashed lines in Fig. 2) to the TMCs in question. Therefore, for each listener, cochlear IO functions were derived by plotting their individual, smoothed, linear reference against the masker levels for any other TMC.

D. Derived cochlear IO curves

Figure 4 shows the resulting cochlear IO curves (note that the *y*-axis scale is different for different panels). To ease the physiological interpretation, f_p and f_m have been equated to CF and stimulus frequency, respectively, in the discussion below.[4]

1. Compression at CF

All of the IO curves for tones at CF show shallow slopes (<1 dB/dB) for a range of input levels. This suggests that compression at CF occurs *across the range* of CFs tested. To facilitate a quantitative analysis, the curves at CF are considered as two- or three-stage functions showing two or three segments, L1, L2, and L3, with markedly different slopes at low, moderate, and high input levels, respectively. The limits of these segments are depicted (after visual inspection) by the vertical thin line in each panel of Fig. 4 (note that L1 and/or L3 might not be present in some curves). Table I shows the slopes in every segment for each CF, for each listener, and for the average data across listeners.

The slope of segment L2, where compression is most obvious, is approximately constant at 0.2–0.3 dB/dB across CF. Although larger variability must be acknowledged when looking at the values for individual listeners (varying from 0.15 dB/dB at 8000 Hz for ALN to 0.38 dB/dB at 8000 Hz for CMR), the most common value is also within the range 0.2–0.3 dB/dB. This suggests compression ratio (inverse of the slope) estimates of 3:1 to 5:1 across the CF range tested. Remarkably, compression does *not* decrease for lower CFs, as has been suggested previously (Hicks and Bacon, 1999; Plack and Oxenham, 2000).

The slopes of L1 and L3 are less than one in most cases, suggesting that the cochlear response may be compressive also for low and high input levels. However, the values are always larger than the slope of L2. This is consistent with other studies that have reported less compression, approaching linearity, for very low (e.g., Nelson *et al.*, 2001, p. 2054) and very high signal levels (e.g., Plack and Oxenham, 1998; Nelson *et al.*, 2001). Indeed, the slope of L3 is close to unity for CFs of 4000 and 8000 Hz. For one case only, its value exceeds unity considerably (1.46 dB/dB), but this corresponds to a condition (ALN at 8000 Hz) for which only two data points are available (see Fig. 4).

2. Compression below CF

Figure 4 shows *compressive* IO curves for *tones below CF at low CFs*. The slopes of straight lines fit to the IO curves for 0.5CF tones are <1.0 for CFs$\leqslant$2000 Hz (see Table I). Overall, there is a trend for the below-CF slopes to increase with CF until they approach unity at 4000 Hz, suggesting that the response to below-CF tones becomes linear for high CFs. The slopes of the IO curves for stimulus frequencies of 0.5CF at CF$=$4000 Hz are necessarily very close[5] to unity because these curves were used as the basis for the linear reference for deriving all other IO curves.

However, it is noteworthy that the slopes of the 0.5CF curves at CF$=$8000 Hz differ from unity. They are lower for two listeners (ELP and ALN) and for the average, but higher for listener CMR. The deviation from unity, and the observed variability, may be the result of slope estimates that are based on considerably fewer points[6] than at 4000 Hz, particularly for ALN and the average data sets.

E. Detection mediated by spectral splatter

The spectral splatter produced by a short probe may improve the detectability of the probe in some circumstances. For a given probe duration, the effects would be expected to be greatest at low frequencies, where cochlear frequency selectivity is greatest (i.e., absolute filter bandwidths are narrower), and hence where the spread of excitation produced by the splatter would be most detectable. The probe used in the current experiments was relatively short (8 ms). It could be argued, therefore, that the detection of spectral splatter may have had an influence on the masker levels at threshold at low frequencies.

Furthermore, the detection of the probe may be also affected by the spectral splatter caused by an abrupt masker offset. A remote-frequency masker may be more effective with a short decay ramp because the spectral splatter caused by its abrupt offset may reach the place on the BM tuned to the probe frequency. In the current experiments, the masker decay ramps were relatively short (4 ms). Therefore, it could

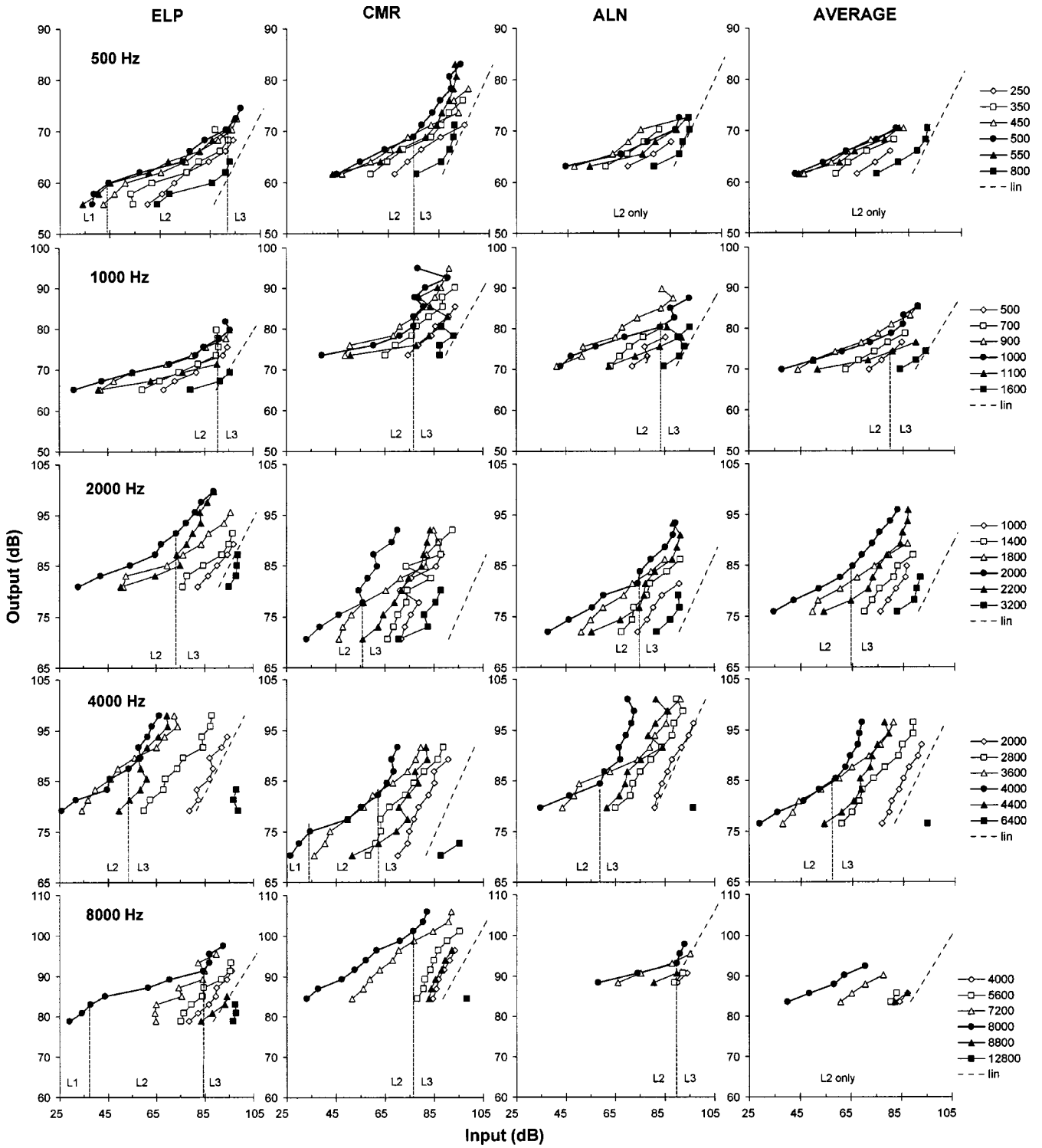

FIG. 4. Cochlear input/output curves derived from the TMCs in Fig. 2. Each row corresponds to a different CF or probe frequency in Fig. 2 (in bold on the left column panels). Legends on the right show the stimulus frequencies (f), corresponding to the masker frequencies in Fig. 2. Open symbols represent conditions where $f<$CF. Filled symbols represent conditions where $f\geqslant$CF. Dashed lines illustrate linear growth. The thin vertical lines only apply to the on-CF curves, and delimit segments (L1, L2, and L3) with clearly different slopes after visual inspection. The curves were derived assuming that the TMC for $f_p=4000$ Hz, and $f_m=2000$ Hz reflects a cochlear linear response (see text for details). Under this assumption, responses at CF are compressed over the whole range of CFs. Moreover, the degree of compression over segment L2 varies little across CFs (see Table I). At low CFs, compression extends to tones an octave below CF.

be argued that the reported levels for *remote* maskers are lower than would have been obtained if longer ramps had been used. The effect would not occur for on-frequency maskers, and would be less important for off-frequency maskers at high probe frequencies, where the frequency differences between the masker and the probe were large.

To investigate these possibilities, TMCs were measured for two listeners (ELP and ALN), for $f_p=500$ Hz, and for two masker frequencies (f_p, and $0.5f_p$). This time, however, the total duration of the probe was 32 ms (16-ms ramps, no

TABLE I. Slopes (dB/dB) of the cochlear IO curves of Fig. 4. Slopes are given for IO curves corresponding to stimulus frequencies (f) of CF and 0.5CF. For the IO curves at CF, two or three slopes are given (CF/L1, CF/L2, CF/L3) corresponding to each of the characteristic segments depicted in Fig. 4. N/A: segment not observed, or insufficient data points for a good slope estimate.

	CF (Hz)				
f (Hz)	500	1000	2000	4000	8000
			Listener ELP		
CF/L1	0.54	N/A	N/A	N/A	0.47
CF/L2	0.22	0.19	0.24	0.29	0.17
CF/L3	0.69	0.54	0.56	0.85	0.72
0.5CF	0.35	0.37	0.55	0.93	0.71
			Listener CMR		
CF/L1	N/A	N/A	N/A	0.57	N/A
CF/L2	0.24	0.22	0.30	0.25	0.38
CF/L3	0.75	0.38	0.81	1.15	0.80
0.5CF	0.34	0.61	0.71	0.97	1.29
			Listener ALN		
CF/L1	N/A	N/A	N/A	N/A	N/A
CF/L2	0.20	0.22	0.27	0.20	0.15
CF/L3	N/A	0.56	0.60	1.05	1.46
0.5CF	0.28	0.51	0.58	0.98	0.60
			Average responses		
CF/L1	N/A	N/A	N/A	N/A	N/A
CF/L2	0.23	0.21	0.28	0.29	0.29
CF/L3	N/A	0.52	0.62	1.04	N/A
0.5CF	0.35	0.47	0.79	0.99	0.74

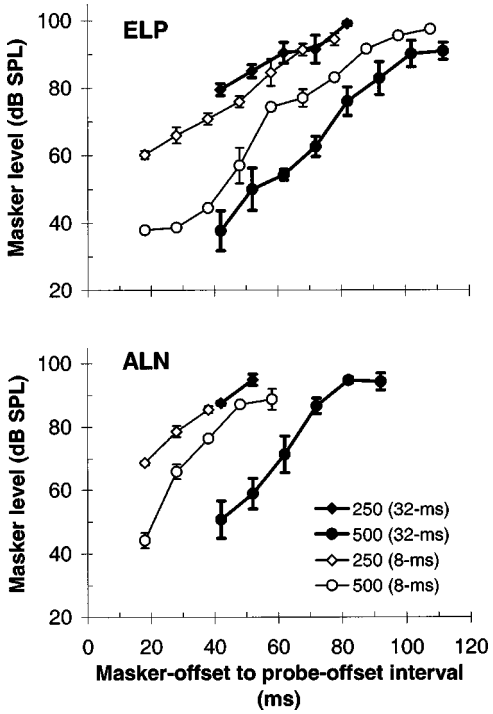

FIG. 5. TMCs for $f_p = 500$ Hz and two masker frequencies (250 and 500 Hz), for different probe durations, and different ramp durations on the masker. Each panel corresponds to a different listener (ELP and ALN). The legend informs about the masker frequency (Hz), and the total duration of the probe (ms). Open symbols represent TMCs (replotted from Fig. 2) for 8-ms probes and 108-ms maskers, both gated with 4-ms onset and offset ramps. Filled symbols represent TMCs for 32-ms probes and 132-ms maskers both gated with 16-ms onset and offset ramps. Every black datapoint is the average of at least four measurements. Error bars represent one standard deviation across trials.

steady-state portion). The masker had a total duration of 132 ms and was gated with 16-ms rise/decay ramps. The probe level was fixed at 14 dB above absolute threshold for the 32-ms probe. At least four measurements were made per condition (even for masker levels above 90 dB SPL). The average results are shown in Fig. 5. The results from the main experiment (with 8-ms probe, 4-ms ramps on the masker) are replotted from Fig. 2 for comparison. This time, however, masker level is plotted against the time interval between the masker offset and the probe offset (at the half-amplitude points). For a given value of the offset-onset interval, the duration of the offset-offset interval is different for both experiments.

Previous work (Zwislocki *et al.*, 1959) suggests that poststimulatory thresholds depend mainly on the time interval between the masker-offset and the probe-offset, rather than on the duration of the zero-amplitude gap or of the probe. Therefore, when plotted against the offset-offset interval (as in Fig. 5), the masker levels for both experiments should overlap (unless other effects, such as those described above, mediate probe detection). This is the case for the off-frequency masker, but not for the on-frequency masker. For the latter, masker levels are considerably lower for the long-ramp/long-probe condition, particularly for short to moderate offset-offset intervals.

A possible interpretation of these results is that detection of the short probe is *not* facilitated by splatter. Otherwise, masker levels for the short probe would be consistently higher both for on- and off-frequency maskers. This explanation seems reasonable, as the level of the probe was too low to cause significant splatter (Moore, 1981). If this were true, the lower masker levels for the on-frequency masker in the long-ramp/long-probe condition could be the result of ''confusion'' (Terry and Moore, 1977; Moore and Glasberg, 1982). That is, probe detection would be harder because it would be harder to distinguish the probe from a continuation of the masker as a result of using longer ramps (Moore, 1981). This confusion would not occur for the off-frequency masker because its frequency differs considerably from the probe frequency.

An alternative explanation for the results is that spectral splatter caused by the short probe *does* facilitate detection, both for on- and off-frequency maskers. The reason that it does not affect threshold for the off-frequency masker may be that the effect is cancelled out by the additional masking produced by the short *masker* ramps, as suggested above.

In any case, the most important feature of the data in Fig. 5 is, perhaps, that the shapes of the TMCs from both experiments are similar. The slopes of the TMCs for the 250-Hz masker are *slightly* shallower for the 32-ms probe than for the 8-ms probe (see Fig. 3). This suggests that the steepness of the $0.5f_p$ TMCs at 500 Hz may be attributed in part to using short probes and/or short ramps. However, Fig. 3 also shows that the slopes of the TMCs for the longer probe are still considerably greater than the slopes for the $0.5f_p$ TMCs at 4000-Hz, which are assumed to reflect a linear cochlear response. Therefore, it can be reasonably con-

cluded that compression of below-CF tones occurs at low CFs, although the slopes for the 0.5CF tones at 500 Hz given in Table I may be slight overestimates of the amount of compression.

IV. DISCUSSION

The aim of this paper was to compare the characteristics of the human cochlear response with measurements made physiologically in other mammals. In particular, the aim was to study compression as a function of CF, over the range of CFs from 500 to 8000 Hz.

A. Cochlear compression across CFs

The results presented here suggest that the response of the human cochlea to tones at CF is compressed over the studied frequency range (Fig. 4, right-most column), and that, on average, the amount of compression at moderate levels varies between 3:1 and 5:1 across CFs (see slopes CF/L2 in Table I). Compression at CF does not decrease for lower CFs. Additionally, the results suggest that compression spans a wider frequency range relative to CF at the low CFs (see slopes 0.5CF in Table I).

B. Assumptions and interpretations

These conclusions are based on the assumption that the response to a 2000-Hz tone is linear at a CF of 4000 Hz, but allows for the possibility that the off-frequency response may be compressive for lower CFs. Support in favor of this assumption comes from the data in Figs. 2 and 3, and from recent data on TMCs and forward-masking growth with level (Plack and Drga, submitted). The present assumption is also supported by BM responses to tones well below CF in chinchilla, which appear to be compressive for CFs around 400–800 Hz (Rhode and Cooper, 1996, Fig. 7), but linear from 5500 to 14000 Hz (Rhode and Recio, 2000).

The choice of the linear reference is critical when cochlear compression at CF is estimated by comparison of *on*-CF, and *below*-CF responses. Different assumptions lead to different conclusions. For instance, Plack and Oxenham (2000) suggested that, in contrast to the present results, compression on the human BM increases from 1.3:1 at 500 Hz, to 2.8:1 at 4000 Hz, or 2.4:1 at 8000 Hz. However, they assumed that linear responses to below-CF tones occur for *any* CF. Plack and Oxenham acknowledged that their results, and those of Hicks and Bacon (1999), are consistent with high compression at low CFs, *if* the compression does not vary with frequency in the apical region of the cochlea. The present results suggest that their estimates of compression for tones at CF should be regarded as *relative* to the compression for the below-CF tones. Estimates of relative compression from the present data can be derived from the values in Table I as the ratio of the slopes of derived IO curves for 0.5CF and CF/L2. The resulting values (based on the average responses) range from 1.5:1 at 500 Hz, to 3.4:1 at 4000 Hz or 2.55:1 at 8000 Hz. These estimates closely match those reported by Plack and Oxenham (2000).

C. Comparison with other studies of auditory nonlinearity

The present results are consistent with other psychophysical studies where no specific assumptions were made about the linearity of the response for tones below CF. For instance, Duifhuis (1980) reported slightly larger amounts of two-tone suppression for a 200-Hz suppressor and a 500-Hz suppressee than for an 800-Hz suppressor and 2000-Hz suppressee (see Fig. 12 in Duifhuis, 1980). Suppression is likely to be evidence of compression (Rhode and Cooper, 1993). The fact that low-frequency suppressor tones produce similar amounts of suppression on probe tones of 500 and 2000 Hz suggests similar amounts of compression at CFs of 500 and 2000 Hz. Plack and Drga (submitted) reported similar TMCs to those presented here at probe frequencies of 250, 500, and 4000 Hz and reached the same conclusions. In addition, they showed that the growth of forward masking with masker level, another estimate of compression, does not vary between 250 and 4000 Hz. Oxenham and Dau (2001) reported large effects of the relative phase of harmonics on the amount of masking produced by a complex tone. If a system is compressive, then the response to peaky waveforms is less than that to flat waveforms, for the same input rms level. An effect on masking of harmonic phase, which alters the envelope of the waveform, is taken as evidence for auditory compression. Oxenham and Dau found large phase effects for signal frequencies as low as 125 Hz. A final result in support of the present findings is that loudness growth with level, which may be related to cochlear compression (Schlauch *et al.*, 1998), hardly varies across the range of CFs studied here (see Moore, 1997 for a review; see also Plack and Drga, submitted).

In contrast to the results in humans, compression may decrease for low CFs in other mammals. In *chinchilla*, BM responses for tones at CF appear more linear at CFs $\sim$400–800 Hz (Rhode and Cooper, 1996) than at CFs between 4000 and 14000 Hz (Rhode and Recio, 2000). As for *guinea pig*, Cooper and Yates (1994) derived cochlear IO functions over a wide range of CFs from auditory-nerve fiber responses. For each fiber, they plotted the response rate for a tone well below CF against the response rate for a tone of the same level but at CF. Their results show a distinct variation in the degree of compression along the length of the guinea pig cochlea. Their compression ratio estimates vary from 2:1 for CFs$<$4000 Hz to as much as 7:1 for CFs$>$4000 Hz. Again, they assumed linear cochlear responses to tones well below CF for *all* fibers. This assumption may be justified in their case (guinea pig), because of ''...the relative stability of the below-CF (auditory-nerve fiber) rate-level slopes with CF'' (Cooper and Yates, 1994, p. 230), as shown in their Fig. 5A. However, the TMC data in Fig. 2 suggests that the same is not true for humans, as the slopes of the TMCs for maskers well below CF do vary across CFs (Fig. 3). Therefore, while it may be justified to conclude that compression is reduced for low CFs in guinea pigs, the same may not be true for humans.

D. The source of compression

Despite the focus on cochlear processing in the current discussion, it could well be argued that the compression at low CFs inferred from Fig. 2 does not originate in the cochlea. It could reflect, instead, other nonlinear processes in the auditory receptor, such as the saturation of the receptor potential of inner-hair cells, or of auditory-nerve fiber discharge rates, which need not be frequency-specific relative to CF. If these nonlinear processes are different for different CFs, they might account for the observed decrease in the slope of the TMCs for $0.5f_p$ maskers with increasing f_p illustrated in Fig. 3. The issue may be resolved by studies on listeners with sensorineural hearing loss at low frequencies. For example, if the TMCs for these listeners were shallower than those for normal-hearing listeners, then that would be good evidence that the compression is cochlear in origin.

V. CONCLUSIONS

The main conclusions of the present study can be summarized as follows:

(i) Human cochlear responses to tones at CF are compressed over the CF range from 500 to 8000 Hz. On average, the estimated compression for moderate input levels ranged from 3:1 to 5:1. Compression does *not* decrease for lower CFs, as has previously been suggested.

(ii) Compression extends over a wider range of stimulus frequencies at low CFs than at high CFs. The estimated compression to tones *an octave below* CF decreased with increasing CF, from 2.8:1 at CF $=500$ Hz to approximately 1:1 at CF$=4000$ Hz.

ACKNOWLEDGMENTS

This work was supported by the Consejería de Sanidad of the Junta de Comunidades de Castilla-La Mancha (ref. 01044), and by EPSRC Project Grant No. GR/R65794/01. We thank Consuelo Martínez Redondo and Alberto López-Nájera for gathering some of the data presented in this report. We also thank José Luis Blanco and Almudena Eustaquio-Martin for technical support. We are indebted to Brian C. J. Moore and an anonymous reviewer for their excellent and helpful reviews of earlier versions of this paper.

[1]It is a physiological property of the mammalian cochlea (at least in nonhuman mammals) that the frequency of a pure-tone stimulus required to yield a maximal response at a given BM site changes with stimulation level (Johnstone *et al.*, 1986; Sellick *et al.*, 1982). In the present report, the term ''characteristic frequency'' (CF) refers to the frequency of a pure-tone stimulus that yields a maximum response at stimulation levels close to absolute hearing threshold.

[2]The use of a fixed, low-level probe confines the spread of the probe's excitation pattern and, hence, reduces off-frequency listening. However, off-frequency listening is not fully eliminated (Johnson-Davis and Patterson, 1979; O'Loughlin and Moore, 1981). For this reason, care is taken to distinguish between f_p and CF in the text. f_p is used when describing the psychophysical data, whereas the term CF is used when discussing the data in terms of the physiological behavior; for instance, when commenting on the cochlear IO functions derived from TMCs.

[3]The threshold of listener ALN at 8000 Hz was 27 dB SPL; that is, 11 dB above the normal audibility threshold for a circumaural headphone according to ANSI 3.6-1996. Hence, this listener could be argued to be at the limit of normal hearing at this frequency. However, this high threshold corresponded to a sharp notch in the listener's headphone frequency response (not shown). Therefore, the threshold is possibly the result of sound cancellation in the external ear (Lopez-Poveda and Meddis, 1996) and not of cochlear damage.

[4]Equating CF to f_p is not strictly correct because, as explained in footnote 2, off-frequency listening may occur.

[5]IO curves were actually derived by plotting a *smoothed* version of the low-frequency data at CF$=4000$ Hz (the linear reference) as a function of the original data. The linear reference was obtained by linear regression of the original data. Therefore, the abscissa and ordinate values are not identical. That is the reason that the slopes differ slightly from unity.

[6]Data points for longer Δt were not collected because of clipping problems.

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