Basilar membrane nonlinearity and loudness[a)]

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Loudness matching functions for tones for persons with one shifted-threshold ear (hearing loss and noise-shifted thresholds) and one ear within normal limits were used to derive the presumed basilar membrane (BM) input–output (I/O) function in a normal ear. The comparison was made by assuming that the BM I/O function for the ear with the cochlear threshold shift has a slope of one (a linearized cochlea). The function for the normal ear was derived from the loudness matching function based on this assumption. Comparisons were made for archival basilar membrane data [M. A. Ruggero, N. C. Rich, A. Recio, S. S. Narayan, and L. Robles, J. Acoust. Soc. Am. **101**, 2151–2163 (1997)] for chinchilla and archival loudness matches for long-duration tones for persons with various degrees of cochlear hearing loss [F. Miskolczy-Fodor, J. Acoust. Soc. Am. **32**, 486–492 (1960)]. Comparisons were made also between BM I/O functions and ones derived from loudness matches for persons with unilateral hearing loss simulated by broadband noise. The results show a close resemblance between the basilar membrane I/O function and the function derived from loudness matches for long-duration tones, even though the comparison was between human and chinchilla data. As the degree of threshold shift increases from 40 to 80 dB, the derived BM I/O functions become shallower, with slopes for losses of 60 dB or more falling in the range of values reported for physiological data. Additional measures with short-duration tones in noise show that the slope of the loudness function and the slope of the derived basilar membrane I/O function are associated with the behavioral threshold for the tone. The results for long-duration tones suggest a correspondence between BM displacement and loudness perception in cases of recruitment, but the relation between the degree of loss and the amount of BM compression and the relation between signal duration and compression suggests that other factors, such as the neural population response, may play a role. [S0001-4966(98)05104-2]

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INTRODUCTION

The basilar membrane input–output function in a healthy mammal (e.g., chinchilla and guinea pig) is nonlinear and can be described as a compressive function with a slope of 0.13–0.45 for most of its dynamic range when basilar membrane velocity (dB) or displacement (dB) is plotted as a function of sound pressure level (SPL) (Cooper and Yates, 1994; Ruggero *et al.*, 1997).

Yates *et al.* (1990) presented evidence that they argue supports the notion that the basilar membrane determines the form of the loudness function, which is usually described as a compressive function of intensity for persons with normal hearing sensitivity (Stevens, 1970). Yates *et al.* (1990) compared a BM I/O function (derived from single unit data) to loudness magnitude estimation (ME) data for a 1.0-kHz tone from a study by Viemeister and Bacon (1988). Viemeister and Bacon's (1988) loudness slopes (re: sound pressure) for their three subjects were 0.182, 0.192, and 0.11, which bear a striking resemblance to the derived basilar membrane curves with a slope of about 0.2. They concluded that ''loudness perception may be based on a simple coding of basilar membrane displacement at CF'' (characteristic frequency) (Yates *et al.*, 1990; pg. 217).

The striking resemblance between the BM I/O functions in Yates *et al.* (1990) and the loudness ME functions from Viemeister and Bacon's study is interesting, but the generality of this result is debatable when the loudness ME data are considered in the context of other studies. In an analysis of 78 different studies of loudness ME, Hellman (1991) found that the mean value of the slope is 0.6,[1] the same value adopted for an international standard (ISO/R 131-1959). By contrast, the slopes obtained by Viemeister and Bacon (1988) are more than three standard deviations below the average value found in Hellman's retrospective analysis. This discrepancy in the loudness data presents a problem for comparing the *absolute* values of BM I/O measures, a peripheral process, and loudness scaling, a process that is possibly influenced by more central factors (Zeng *et al.*, 1988). This criticism does not imply that such a comparison should not be made, but rather that *relative* measures (loudness matching) might provide a method of examining this idea in greater depth. A good candidate for such a comparison is a cochlear threshold shift, a result known to affect loudness and the BM I/O function. If the loudness function is determined by the BM I/O function, it follows that cochlear hearing loss, which alters the shape of the BM I/O function, should alter the shape of the loudness function in a predictable manner. Recent experiments demonstrate that the basilar membrane I/O function becomes steeper with certain

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types of cochlear hearing losses, chiefly ones that affect the outer hair cells (Ruggero, 1992). It is well known that cochlear hearing loss can cause loudness recruitment, an abnormally rapid growth of loudness. In loudness recruitment, the loudness function (log loudness versus dB SPL) is steeper for much of its range than it is in someone with hearing thresholds within normal limits. This comparison suggests that the form of the BM I/O function and loudness are in qualitative agreement in cochlear hearing loss; that is, both become steeper with cochlear threshold shifts. The intent of our study is to compare these two phenomena quantitatively.

I. GENERAL METHOD

Our method is based on loudness matches between an ear with hearing within normal limits and a threshold-shifted ear. One cannot derive unique functions from matching data if neither function contributing to the matching function is known. However, if one of the functions contributing to the matching function is known, the other function is defined uniquely. For our analysis, we assumed that the slope of the BM I/O function for the threshold shifted ear is 1.0 as is reported when the active process is not operative (Ruggero, 1992). As mentioned above, the BM I/O function is a compressive function of intensity in a healthy ear. When the active process is inoperative, the system shows a loss in gain of between 40 and 80 dB and the I/O function becomes linear (Ruggero *et al.*, 1997). By deriving the BM I/O function for a healthy ear from the loudness-matching function assuming that the BM I/O function for the threshold-shifted ear has a slope of 1.0, we can compare BM I/O functions and loudness functions directly. If the form of the loudness function is determined by BM displacement, our derived functions for normal ears should resemble the BM I/O functions for healthy ears in cases where the hearing loss ear contributing to the loudness matching function had a loss that equals or exceeds the gain of the active process (i.e., in situations presumably yielding a linear cochlear response).

II. ANALYSIS OF COCHLEAR HEARING LOSS: LONG-DURATION TONES

Figure 1 illustrates loudness matching data for tones from a study by Miskolczy-Fodor (1960) for listeners with unilateral cochlear hearing losses of 40, 50, 60, or 80 dB SPL. These data represent loudness matches from 200 published studies and from 100 subjects from Miskolczy-Fodor's laboratory. The test frequency was not specified, but studies show that the form of the loudness function does not change much for persons with normal hearing at frequencies between 500 and 8000 Hz (Scharf, 1978), the likely range of frequencies selected for these measurements.

Lines were fitted to the group data in Fig. 1 to quantify the slope of the matching function for different degrees of hearing loss.^{2} The lines were anchored at threshold in both ears and the best-fitting line was found using an iterative process that found the intercept and slope that minimized the sum of squared deviations of the data from the predicted line. This procedure was used: (1) for the entire range of tested levels; and (2) for levels between threshold and 30-dB sensation level (SL) in the impaired ear. The second analysis, with the range of levels restricted to 30 dB above threshold, was performed to examine the slope of the matching function for levels below where complete recruitment usually occurs (some authors fit the data in the region of recruitment and the region above this point with separate lines). Our analysis of Miskolczy-Fodor's data, shown in the upper portion of Table I, demonstrates that the same trend holds for both methods; the slope of the loudness-matching function becomes steeper with increased hearing loss. This finding is consistent with

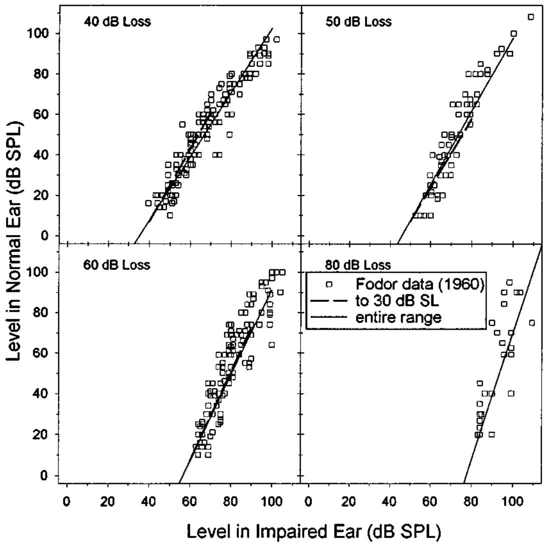

FIG. 1. Loudness matches for persons with unilateral losses from a study by Miskolczy-Fodor (1960) are denoted by squares. The upper-left and upper-right panels show results for persons with 40 dB SPL losses and 50 dB SPL losses, respectively. The lower-left and lower-right panels show results for persons with 60 dB SPL and 80 dB SPL losses, respectively. Regression lines were fitted to the entire data set in each panel (solid lines) and to the data between threshold and 30-dB sensation level (dashed lines). In the lower right panel, the regression lines for both fits are nearly identical. The slope of these regression lines increases with the amount of hearing loss.

TABLE I. The slope of the loudness-matching function categorized by degree of cochlear threshold shift. Data are from a study by Miskolczy-Fodor (1960) for persons with unilateral cochlear hearing loss and from the present study for persons with simulated unilateral hearing loss. Slopes were calculated using two methods. In one method, the entire range of data was used. In the other method, data between threshold and 30-dB sensation level in the poor ear were fitted. For both methods, the line was anchored at threshold in both ears and slope was varied in small steps to minimize the sum of squared deviations of the data from the prediction.

Detection threshold (poor ear, dB SPL)	Slope of the matching function	
	Threshold to 30 dB SL	Entire range of data
Miskolczy-Fodor (1960)		
40	1.79	1.59
50	1.68	1.81
60	2.17	2.10
80	3.12	3.12
Present study		
38 (250 ms)	1.18	1.38
60 (250 ms)	2.17	2.17
62 (2 ms)	1.77	1.82
83 (2 ms)	5.43	5.43

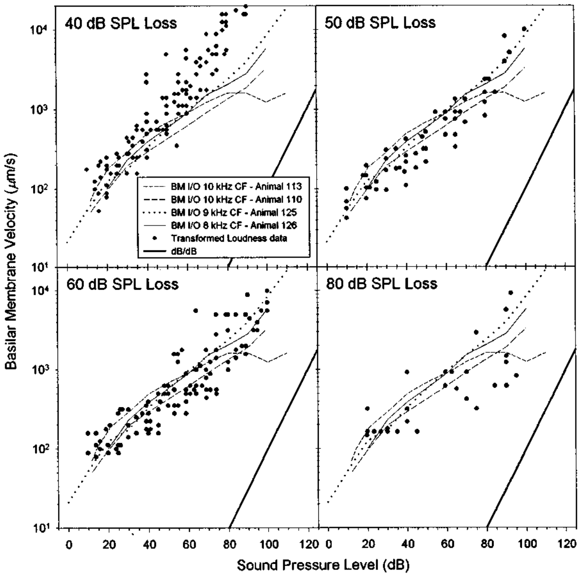

FIG. 2. A comparison of basilar-membrane (BM) input–output (I/O) functions from a study by Ruggero *et al.* (1997) and BM I/O functions derived from Miskolczy-Fodor's (1960) loudness-matching data (Fig. 1). Lines in each panel represent BM I/O functions for the same four chinchillas from the study by Ruggero *et al.* (1997). Filled circles represent BM I/O data for normal ears derived from loudness matching data from the study by Miskolczy-Fodor (1960). As in Fig. 1, Miskolczy-Fodor's (1960) data are categorized by the degree of hearing loss.

studies of loudness matching (Hellman, 1993), magnitude scaling (Hellman and Meiselman, 1990) and cross-modality matching of line length and loudness (Hellman and Meiselman, 1993).

Figure 2 illustrates BM I/O functions for normal preparations at CF^3 and BM functions for normal ears derived from Miskolczy-Fodor's (1960) loudness-matching data between impaired ears and a normal ears. The four BM I/O functions from healthy chinchilla ears are from a study by Ruggero *et al.* (1997). Ruggero *et al.* (1997) measured BM responses from 129 chinchillas and obtained useful data from 43 of their preparations. The four shown in our figure represent the four most sensitive BM responses to CF tones for which measurements were made between threshold and at least 90 dB SPL. The slopes of these four functions range from 0.2 to 0.42 (mean = 0.32) for stimulus levels between 50 dB SPL and 90 dB SPL.

The derived BM I/O functions are based on the simple assumption that the hearing loss ear is linear. For this analysis, the slope of the derived function is simply the inverse of the matching function (i.e., the ordinate in Fig. 1 is the abscissa in Fig. 2). To compare quantities for the derived functions (loudness) to the physiological data (velocities), ordinal values on the derived functions in Fig. 2 were scaled so that values for 20 dB SPL were lined up for both data sets. For the 40 dB SPL condition, the transformed loudness data are, on average, steeper than the BM I/O curves, especially for high levels. This finding is consistent with the idea that the hearing loss ear was not linear and the active process was not eliminated completely. The derived BM data for the remaining conditions resemble the physiological data.

III. EXPERIMENT 1. NOISE-SHIFTED THRESHOLDS: SHORT AND LONG DURATION TONES

Thermal noise, either broadband or shaped, is often used to simulate cochlear hearing loss or the effect of a cochlear threshold shift (Steinberg and Gardner, 1937; Schlauch and Wier, 1987; Florentine *et al.*, 1988; Schlauch *et al.*, 1994; De Gennaro and Braida, 1997). The effect of a broadband noise on the response of tones at the level of the basilar membrane has not been investigated; however, studies of two-tone suppression in the basilar membrane show that a suppressor tone decreases the sensitivity of a second tone and linearizes its response [e.g., Fig. 3 in Ruggero *et al.* (1992b), p. 1090]. If broadband noise acts to suppress the response to a tone in noise, the growth of the response of the tone in noise may be linear as it is in the case of two-tone suppression. The idea that either suppression or cochlear damage linearizes cochlear responses to tones is an intriguing one, but it is likely that this presumed linearization of responses as a result of suppression by broadband noise is not identical to linearization due to cochlear damage. For instance, the errors in speech recognition by listeners with simulated, flat hearing losses are only qualitatively similar to those observed in a listener with a flat hearing loss of the same magnitude (De Gennaro and Braida, 1997).

For the loudness of long-duration tones, noise simulated hearing loss using broadband noise produces results nearly identical to those observed for cochlear hearing loss (Hellman, 1988). Given this similarity in results, one would expect that a noise simulated hearing loss greater than 60 dB SPI, would yield loudness results consistent with known changes in the basilar membrane I/O function, as was demonstrated in the previous section for cochlear hearing loss. But what happens when the duration of the tone is only 2 ms? Ruggero *et al.* (1992a) examined basilar membrane responses to clicks and tones and found that the responses were similar. A temporal analysis showed that initial responses to clicks were linear, but later responses grew nonlinearly, as they do for long-duration tones. Cooper and Rhode (1996) showed that two-tone suppression, which is strongly believed to be related to the active process, appears in basilar membrane responses within 1 ms of the stimulus onset. The significance of these findings is that the cochlear amplifier is operative after only a minimal delay.

Assuming that the loudness of a short-duration tone (i.e., duration greater than 1 ms but less than 10 ms) for an ear with thresholds within normal limits grows in a compressive manner, does a 60-dB threshold shift yield results consistent with a linearized cochlea? The detection threshold for a short-duration tone in noise is elevated relative to the threshold for a long duration tone by an amount approximated by differences in energy in the two stimuli (for duration up to 100–300 ms) (Florentine *et al.*, 1988). Thus a lower noise spectrum level is required to shift the threshold of the short-duration tone to 60 dB SPL than is required to shift the threshold for a long-duration tone to the same level. It is unknown whether the system behaves in a linear manner when the detection threshold for a particular stimulus is elevated to a certain point (e.g., 60 dB SPL) or when a fixed

TABLE II. Detection thresholds (dB SPL) for 4.0-kHz tones in quiet and in noise for each subject. The abbreviation ''DNT'' means *did not test*.

	Quiet		Low-level noise		High-level noise	
Subject	2 ms	250 ms	2 ms	250 ms	2 ms	250 ms
S1	25.3	6.0	63.9	37.5	82.4	61.2
S2	26.4	6.8	59.8	DNT	84.1	60.7
S3	25.3	7.6	DNT	DNT	81.7	59.3
S4	29.4	15.3	61.0	38.5	82.0	59.6
Average	26.6	8.9	61.6	38.0	82.6	60.2

noise spectrum level is placed into an ear. To examine this idea, loudness matches between tones in quiet and in noise were made for (1) short-duration tones and (2) long-duration tones.

A. Subjects

Four young adults (age 22–24) with hearing sensitivity within normal limits participated. Subjects were selected based on the following criteria. First, thresholds were 10 dB HL or better (less) at audiometric frequencies (octave intervals between 250 and 8000 Hz). Second, bilateral thresholds for a 4.0-kHz, 250-ms tone differed by 5 dB or less. These thresholds at the test frequency (4.0 kHz) were measured using an adaptive procedure that targeted 79% correct detections and were based on four 50-trial blocks.

B. Stimuli

A stimulus frequency of 4.0 kHz was selected to minimize the effect of splatter on judgments of loudness. At this frequency, the critical bandwidth is 700 Hz (Scharf, 1970), which would encompass nearly all of the energy of a 2-ms tone with a gradual rise and fall time.

Pure tones at 4.0 kHz were digitally generated at a sampling rate of 20 kHz by a custom-designed, 16-bit digital-to-analog converter. Tones were either 2 ms or 250 ms with $\cos^2$ rise and fall times of 1 ms. Two channels were employed. One channel-generated the standard tone. The other channel generated the comparison tone. The level in each channel was adjusted by separate, computer controlled attenuators.

One of the pure-tone channels was mixed with broadband noise that was low-pass filtered at 10 kHz (Kemo model VBF/25). The noise was produced by a custom-designed generator. The spectrum level of the noise, which was left on continuously during a block of trials, was either 18 dB/Hz or 38 dB/Hz. Noise levels were selected based on pilot data which showed that detection thresholds for a 250-ms tone were shifted to 40 dB SPL (18 dB/Hz) or 60 dB SPL (38 dB/Hz). In subsequent sections of the paper the 18- and 38-dB/Hz conditions will be referred to as the low-level and high-level noise conditions, respectively.

C. Procedure

Prior to data collection, tonal thresholds were measured in continuous broadband noise and in quiet. Thresholds were measured using a 2IFC adaptive procedure that targeted 79% correct detections (Levitt, 1971). Correct answer feedback was provided after each trial. The results for 2-ms and 250-ms tones are shown in Table II. As expected based on temporal integration (Watson and Gengel, 1969; Florentine *et al.*, 1988), thresholds for the 2-ms condition are elevated by roughly 20 dB more than are the thresholds for the 250-ms tone in quiet or in conditions with the same level of noise.

Loudness matches were measured using a 2IFC adaptive procedure for subjective judgments (Jesteadt, 1980). Each trial contained two observation intervals marked by lights and separated by 500 ms. The standard tone was presented to one ear and the comparison tone to the other. Two performance levels were tracked concurrently by interleaving trials controlled by separate decision rules. One track converged on the stimulus level judged louder 21% of the time; the other track converged on the stimulus level judged louder 79% of the time (Levitt, 1971). The subject's task was to indicate which interval contained the louder tone by depressing a response button. Listeners were not given feedback regarding performance because loudness is a subjective measure.

Starting levels for each track were begun 10 dB above (79% track) or 10 dB below (21% track) the expected equal loudness level. If the initial starting levels were not close to the final stopping point of the run, that initial track was discarded and subsequent runs were based on a revised starting level that allowed subjects to bracket the point of subjective equality. The step size was 3 dB at the beginning of a block of trials and was reduced to 1.5 dB after two reversals in level. Thresholds for each track were calculated based on the mean of reversals in stimulus level direction excluding the first two reversals, which were discarded. Data points plotted for each subject represent the mean thresholds of between four and eight 100-trial blocks.

To control for potential biases, measurements were made for conditions with the standard tone in the quiet ear and for the standard tone in the noise-shifted ear. For both noise conditions (high and low level) and a 2-ms tone, standard levels in quiet ranged from 30 dB SPL to 90 dB SPL in 10-dB steps. Standard levels for the 2-ms tone in the low-level noise condition (comparison tone in quiet) ranged from 65 to 90 in 5-dB steps whereas standard levels for the 2-ms tone in the high-level noise condition ranged from 85 dB SPL to 103 dB SPL in 3-dB steps. For the 250-ms tone, standard levels in quiet were 15, 25, 35, 45, 55, 65, and 80 dB SPL. For the high-level noise condition, standard levels

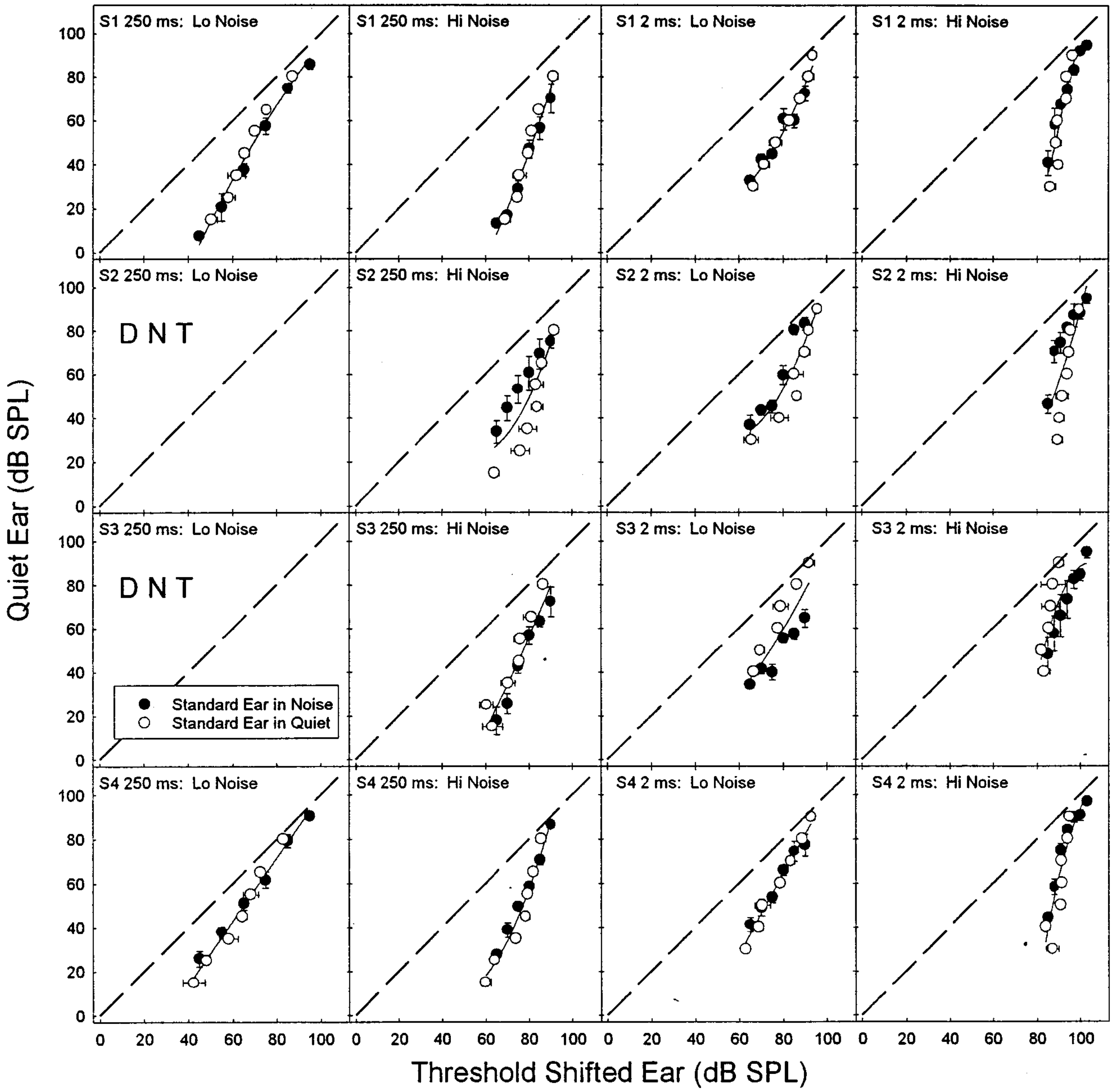

FIG. 3. Loudness matches for individual subjects for 2-ms tones and 250-ms tones for high and low noise levels. Open symbols represent conditions where the standard tone was in the quiet ear. Filled symbols represent conditions where the standard tone was presented in noise. The lines fitted to each data set are best-fitting second-order polynomial regressions. Error bars represent plus and minus one standard deviation. Error bars are omitted for levels with a standard deviation less than 1 dB.

for the 250-ms tone in noise ranged from 65 dB SPL to 90 dB SPL in 5-dB steps. Due to attrition, only two of the four subjects completed the low-level noise condition for the 250-ms tone. Standard levels for the low-level noise condition ranged from 45 dB SPL to 95 dB SPL in 10-dB steps.

Data for the 2-ms tone for both noise levels and for the 250-ms tone in the high-level noise condition were collected in semi-random order. Data for the 250-ms low-level noise condition were collected at the end of the study. Subjects were run in 1- or 2-h blocks until data collection was completed.

D. Results

Figure 3 illustrates loudness matches for four listeners in two levels of noise. The matching functions are very similar across listeners for identical conditions. Group-mean data for each of the conditions are shown in Fig. 4. As reported in other studies, the slope of the loudness function is steeper in a high-level noise condition than it is in a low-level noise condition (Stevens and Guirao, 1967). We also found that short-duration tones can produce a steeper matching function than long-duration tones in the same level of background noise. Richards (1977) reported a minor increase (a few degrees) in the slope of the matching function with a decrease in signal duration, but comparisons are difficult with his study because the stimuli were different. Richard’s (1977) shortest-duration tone was 10 ms and the tones being matched were of different durations.

The lower portion of Table I shows an analysis of matching-function slopes for each condition for the average

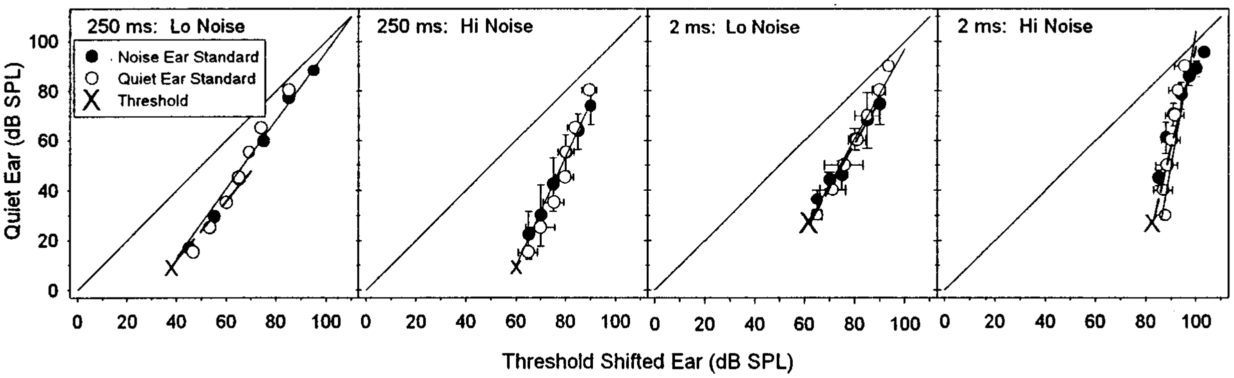

FIG. 4. Group-mean loudness matches for 2-ms tones and for 250-ms tones for high and low noise levels. The symbols are identical to those of Fig. 3. Regression lines were fitted to the entire data set in each panel (solid lines) and to the data between threshold and 30-dB sensation level (dashed lines), as in Fig. 1. Standard deviations were not calculated for the 250-ms, low-noise condition given that only two subjects participated.

data. The simulated thresholds show the same trend as the cochlear losses in the upper portion of the table; the matching-function slope increases with the amount of threshold shift in the poorer ear.

The variability of data obtained with the standard tone in the noise-shifted ear is greater than the variability of data obtained with the standard tone in quiet. This finding has been reported by others (Hellman and Zwislocki, 1964; Hellman *et al.*, 1987; Rankovic *et al.*, 1988). Average within subject standard deviations are 3.5 dB and 2.2 dB for conditions with the standard tone in the noise-shifted ear and the quiet ear, respectively. Average standard deviations are nearly identical for 2-ms tones (s.d.=2.8 dB) and for the 250-ms tones (s.d.=2.9 dB).

Figure 5 shows a comparison of Ruggero *et al.*'s (1997) BM I/O functions and BM I/O functions derived from loudness matches for group-mean data. The method for this comparison is identical to that used to transform loudness data shown in Fig. 2. The group-mean data are shown for conditions with the standard tone in noise (filled symbols) and for the standard tone in quiet (open symbols). The derived functions are similar in appearance to the BM I/O functions of Ruggero *et al.* (1997).

Figure 6 shows the quantitative relation between the derived basilar membrane slope (50–90 dB SPL) and detection threshold in the continuous noise for the various conditions for each subject. These values are shown for conditions with

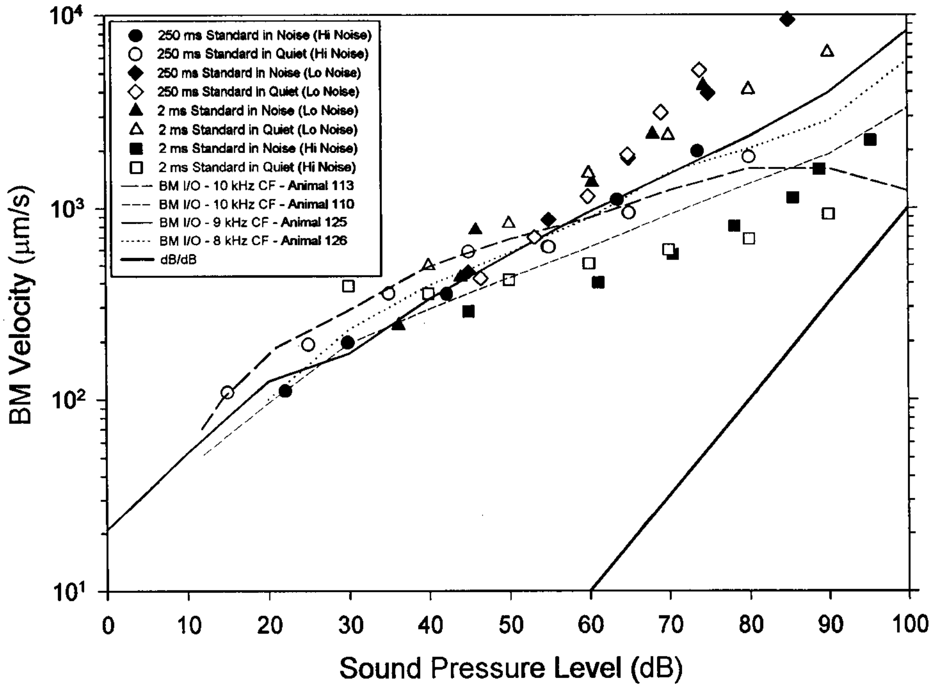

FIG. 5. A comparison of basilar-membrane (BM) input–output (I/O) functions from a study by Ruggero *et al.* (1997) and BM I/O functions derived from group-mean loudness-matching data for conditions of simulated unilateral hearing loss (Fig. 4). Lines represent BM I/O functions for four chinchillas from the study by Ruggero *et al.* (1997). Filled circles represent data derived from conditions with the standard presented in the threshold-shifted ear. Open symbols represent conditions with the standard in presented in quiet. The lowest levels of the derived functions for standards in quiet and in noise were scaled so that the midpoint of those two measures matched the BM velocities for Ruggero *et al.*'s (1997) functions for those levels.

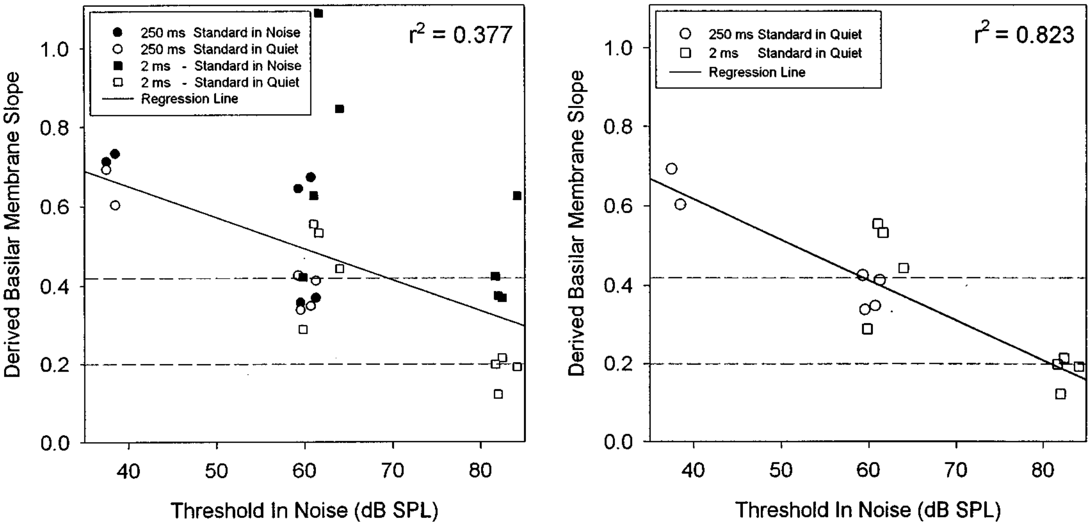

FIG. 6. The relation between detection threshold in noise (dB SPL) and the slope of the derived BM I/O function between 50 and 90 dB SPL. Squares represent conditions with 2-ms tones. Circles represent conditions with 250-ms tones. Open symbols are for conditions with the standard tone in the quiet ear. Filled symbols are for conditions with the standard tone in the threshold-shifted ear. The solid line represents a regression line fitted to data for all of the conditions (left-hand panel) or for conditions with the standard tone presented to the ear in quiet (right-hand panel). Dotted and dashed horizontal lines represent the range of BM I/O slopes for four healthy chinchilla cochleas from Ruggero *et al.* (1997).

the standard tone in quiet (open symbols) and the standard tone in noise (filled symbols). Both methods show the same general trend; the slope of the derived BM I/O function becomes shallower as threshold increases. The standard tone in the noise-shifted ear produced more variable data, as noted earlier, and for all but one condition for one subject (13 out of 14 comparisons), the slope of the derived BM I/O function was steeper when the standard tone was presented in noise than when the standard tone was presented in quiet. When all of the data are evaluated (standard tone in quiet and standard tone in noise), the regression line relating derived basilar membrane slope and detection threshold in noise shows a functional relation. The regression line for this analysis, shown in the left-hand panel of Fig. 6, accounts for 38% of the variance ($r=0.615$; $df=24$; $p=0.001$).[4] The right-hand panel of Fig. 6 shows that when only the less variable conditions with the standard tone presented to the ear in quiet are evaluated, the fit improves. The regression line in the right-hand panel accounts for 82% of the variance ($r=0.91$; $df=11$; $p<0.001$). By comparison, when threshold was shifted to 60 dB SPL (2-ms low-level noise and 250-ms high-level noise), the slope of the derived BM I/O function showed no apparent difference due to changes in spectrum level. The regression line fitted to derived BM I/O function slope and spectrum level for conditions with threshold shifted to roughly 60 dB SPL accounted for 7% of the variance for conditions with the standard presented to either ear (all data with threshold shifted to 60 dB SPL) ($r=0.269$; $df=12$; $p=0.35$). When only the conditions with the standard tone presented to the quiet ear are fitted, the regression line accounts for only 9% of the variance ($r=0.295$; $df=7$; $p=0.52$).

Horizontal dotted lines in Fig. 6 delimit the range of slopes for BM I/O functions for the four functions selected from Ruggero *et al.* (1997). All of the data for our derived slopes for the low-level noise and long-duration tone fall outside this range. By contrast, for conditions with threshold shifted to 60 dB SPL many of the derived slopes are within the range of BM I/O slopes. For threshold shifts of 80 dB SPL, the slopes for the derived functions and actual functions are more nearly comparable.

IV. GENERAL DISCUSSION

The nonlinear BM I/O function is presumably produced by an active process or ''cochlear amplifier'' that is physiologically vulnerable (Ruggero, 1992). The cochlear amplifier is described well by a compressive function with a shallow slope. When the active process is removed temporarily by a drug, such as furosemide, the BM I/O function steepens until the system becomes linear and there is a corresponding loss in sensitivity (Ruggero, 1992). Our BM I/O functions derived from loudness matching data between shifted threshold ears and ears with normal hearing sensitivity resemble actual BM I/O functions, but the correspondence between loudness and BM I/O functions is not perfect. The notable differences are related to the degree of hearing loss and the effect of tonal duration.

Physiological data show that elimination of the active process results in a roughly 40–80 dB loss in gain and that this loss is closely related to the health of the preparation (Ruggero, 1992; Ruggero *et al.*, 1997). The reason for the large range in estimates of the gain of the cochlear amplifier results from differences in methods commonly used to specify the gain. One method compares the difference in sensitivity to tones at CF in a healthy specimen and in the same animal shortly after death (Ruggero *et al.*, 1997). This method yields gain estimates of between 60 and 81 dB (Ruggero *et al.*, 1997). Another method compares the difference in gain between low-level tones at CF and high-level tones at the place yielding the largest response. This second method yields gains of between 39 and 60 dB (Ruggero *et al.*, 1997).

Moore and Glasberg (1997) modeled loudness growth in cochlear hearing loss and assumed that the gain of the cochlear amplifier has an upper limit consistent with estimates made using this second approach (55 dB–65 dB).

In their model of loudness in cochlear hearing loss, Moore and Glasberg (1997) assume that the loss of inner hair cells (IHC) results in a simple attenuation of gain whereas the loss of outer hair cells (OHC), which are linked with the active process, results in a steepening of the loudness function as well as a loss of gain. Moore and Glasberg (1997) assumed that complete damage to OHC would result in a loss of 55 dB for frequencies below 2.0 kHz; this assumption implies that the loudness function reaches its maximum slope for complete OHC loss. Moore and Glasberg (1997) compared the predictions of their model to Miskolczy-Fodor's (1960) data and found close agreement with this idea for losses between 40 and 60 dB SPL. For Miskolczy-Fodor's group with 80 dB SPL losses, however, many data points fell outside the range of slopes predicted by their model.[5] This result is probably due to the loudness function steepening for losses greater than 60 dB. Although Miskolczy-Fodor's (1960) data for 80 dB SPL losses are somewhat variable and not as extensive as his data for losses of 40, 50, and 60 dB SPL, Hellman and Meiselman (1993) found that, on average, the slope of the loudness function continues to steepen for hearing losses greater than 60 dB SPL. Our data for conditions of noise-simulated hearing losses support this idea as well.

There are several possible explanations for the loudness function steepening for losses as great as 80 dB SPL. First, the effective gain of the cochlear amplifier could be as great as 80 dB, as estimated by the technique that compares sensitivity in healthy, live preparations to that of fresh, dead ones. Another possibility is that cochlear gain is more than simply ''active'' gain. Ruggero *et al.* (1997) found 66 dB–76 dB of gain between the BM and the stapes. This estimate includes passive and active gain, both of which may be relevant for loudness coding in shifted thresholds. Finally, the neural population response that contributes to loudness may differ in an important way from BM I/O functions. BM I/O functions represent the velocity (or displacement) at a single place whereas the neural response to an intense sound represents excitation along a major extent of the BM. Although loudness measures in cochlear hearing loss (Hellman, 1994; Moore *et al.*, 1985) and in noise simulated hearing loss (Schlauch, 1994) are influenced to a small extent by spreading excitation, the effect may be large enough to result in slope changes across conditions as noted in our study.

The results from our study for conditions with noise-simulated hearing loss and short-duration tones are also difficult to explain based on known properties of the BM. In our study, the loudness function steepened and the derived BM I/O function became more compressive as tonal duration was reduced from 250 ms to 2 ms. This result suggests that the slope of the loudness function in noise is coupled tightly with threshold, which changes with tonal duration, and not the spectrum level of the noise.[6] Given that the active process is believed to be operative within about 1 ms of stimulation (Ruggero *et al.*, 1992a; Cooper and Rhode, 1996), elimination of the active process by cochlear hearing loss should result in a parallel shift of the BM I/O function with changes in tonal duration. That is, the slope of the BM I/O function is predicted to remain the same for changes in tonal duration. Oxenham and Plack (1997), who examined the relation between BM I/O functions and psychophysical forward masking in persons with cochlear hearing loss, report such a finding, but their range of durations was much smaller (4 ms–14 ms) than ours (2 ms–250 ms).

A possible explanation for the finding that the slope of the derived BM I/O function follows threshold rather than the spectrum level of the noise is that noise-shifted thresholds do not mimic cochlear hearing loss in every way. Although broadband noise and cochlear hearing loss result in nearly identical loudness functions for long-duration tones (Hellman, 1988), the same may not be true for short-duration tones and this difference may be related to changes in temporal integration for detection. The amount of temporal integration for detection thresholds for tones in noise follows signal energy (Florentine *et al.*, 1988) as it does in quiet (Plomp and Bouman, 1959; Watson and Gengel, 1969), but in cochlear hearing loss the amount of integration is reduced significantly (Florentine *et al.*, 1988). Why is the amount of temporal integration different in noise-shifted ears than it is in ears with cochlear hearing loss? It is possible that noise and cochlear hearing loss both linearize the cochlea but the cochlear hearing loss damages the system in an additional manner not simulated by the noise. Indirect evidence for this finding is seen in the slope of the psychometric functions for detection. In noise shifted thresholds, the psychometric function slopes are identical to those obtained in quiet from persons with hearing thresholds within normal limits (comparison between results in Green and Swets, 1966, p. 192, and those of Watson, 1972).[7] In cochlear hearing loss, the slope of the psychometric function for detection is sometimes steeper than the slope for persons with normal hearing (Arehart *et al.*, 1990; Carlyon *et al.*, 1990).

The possibility that mechanisms responsible for loudness perception may be different in cochlear hearing loss and noise-shifted thresholds has implications for modeling loudness. Many investigators assume that loudness can be modeled as a power function of intensity and that hearing loss represents a subtractive component (Steinberg and Gardner, 1937; Zwislocki, 1965, 1970; Humes *et al.*, 1992), perhaps due to a reduction in the number of neurons (Steinberg and Gardner, 1937) or a reduction in the overall firing rate of neurons that are able to convey information about signal intensity. For this class of models, the exponent relating intensity to loudness does not change with the degree of hearing loss. For this genre of models, the equation formulated by Zwislocki (1965) provides an excellent description of loudness functions for tones for persons with sensorineural hearing loss (Hellman and Meiselman, 1990) and hearing loss simulated by broadband noise (Schlauch *et al.*, 1995). An alternative method would be to describe loudness based on a power function in which the exponent varies to reflect a steepening of the loudness function with cochlear hearing loss (e.g., Stevens, 1966; Launer, 1995). To model changes in BM function, the exponent would be a low value (less

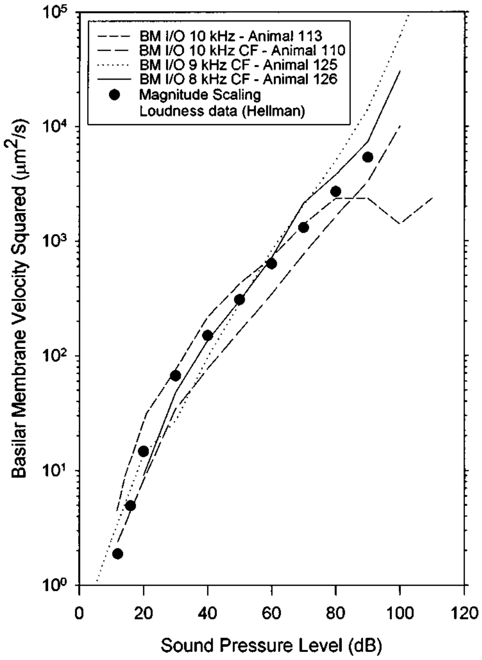

FIG. 7. A comparison of the square of the BM I/O function and the loudness function for a 3.0-kHz tone. The BM I/O functions are from Ruggero *et al.* (1997). The loudness function is from Hellman (1976). The loudness function was arbitrarily scaled so that the magnitude of the datum for 40 dB SPL was centered among squared velocities for the four BM I/O functions.

than one) in normal hearing and increase to a value of one when the active process is eliminated completely. Further studies need to be conducted to examine the appropriateness of either of these models for conditions of hearing loss and simulated hearing loss.

Finally, it is of interest to note that the average slope of the BM I/O functions in Ruggero *et al.*'s (1997) study is 0.32. This value is about half the value reported typically for magnitude scaling procedures (average$=$0.6) (Scharf, 1978). Assuming that loudness is determined in large part by the BM I/O function, the slope difference may be due to the finding that IHCs square the output of the BM (Goodman *et al.*, 1982). To examine this idea, the square of basilar membrane velocity for Ruggero *et al.*'s (1997) BM data was plotted as a function of level and compared with an archival loudness function for a 3.0-kHz tone obtained by Hellman (1976) using magnitude estimation and magnitude production. The functions in Fig. 7 plotted in this manner show a striking resemblance. Thus if the link between the BM I/O function and loudness is real and interspecies differences are minimal, the slope of the loudness magnitude scaling function may be accounted for at the level of the cochlea. This is in contrast to the report by Zeng *et al.* (1998) who argue that central factors play a large role in determining the shape of the loudness function. They assume that loudness compression is a peripheral process that occurs at the level of the BM and is followed by more central (i.e., at the level of the brain) loudness exponentiation expansion which recovers the original 100-dB dynamic range of the input stimulus. For the comparison in Fig. 7, we found it unnecessary to assume a central exponentiation-expansive process to account for the discrepancy between the loudness function and the BM I/O function.

V. CONCLUSIONS

(1) There is a striking resemblance between BM I/O functions and ones derived from loudness-matching functions for long-duration tones between an ear with normal hearing and one with threshold shift of 60 dB or more.

(2) Despite the similarity between BM I/O functions and ones derived from matching functions, there are some notable differences. Namely: (a) the loudness-matching function continues to steepen for hearing losses as great as 80 dB which results in a derived BM I/O function that becomes more compressive as the hearing loss increases. According to some measurements, the gain of the active process is thought to be 60–65 dB and a tight coupling between loudness and BM I/O functions would predict that the loudness function would not become steeper for losses exceeding the active gain of the system (Moore and Glasberg, 1997). (b) The loudness-matching function became steeper as the duration of a tone in noise was shortened resulting in the derived BM I/O function becoming more compressive. If broadband noise linearizes the cochlear response, tonal duration, in the range of values selected for this study, is not predicted to affect the slope of the derived BM I/O function.

(3) On average, the slope of the BM I/O function is one-half the slope of loudness functions obtained using magnitude scaling procedures for long-duration tones. Given that IHCs square the output of the BM (Goodman *et al.*, 1982), the slope of the cochlear output function in log units would double and be consistent with loudness scaling data. Thus the slope of the loudness magnitude scaling function follows the output of the cochlea for long-duration tones.

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[1] Loudness between roughly 30 and 90 dB SPL is described by a simple power law:

$$L=kP^{0.6}, \tag{1}$$

where L is loudness (in sones), P is pressure (N/m^2), and k is a scaling constant (Scharf, 1978). If units of power are used, the exponent is 0.3.

[2] A modified power function (e.g., Zwislocki, 1965) provides a better fit to loudness-matching data than a linear function; however, the slope obtained from a linear regression summarizes the main effect of threshold shift and provides a method for summarizing and comparing different conditions in a manner that is interpreted easily (e.g., Stevens, 1966).

[3] Ruggero *et al.* (1997) measured BM I/O functions in chinchilla for CFs between 9.0 and 10.0 kHz. Chinchilla hearing sensitivity is excellent at these frequencies. The mean threshold for frequencies of 8.0 kHz and 11.0 kHz is 7 dB SPL for six studies (Fay, 1988). Hearing sensitivity for humans at 4.0 kHz (Fay, 1988), the test frequency in the present study, and the one used for comparison with the chinchilla results, is also excellent.

[4] Detection thresholds for subject 3 (S3) were not measured for the 2-ms,

low-level noise condition. Her derived slopes for this condition are plotted in Fig. 6 at the group-mean threshold for this condition, but these points were not used in calculating the proportion of variance accounted for by the regression lines.

[5] Moore and Glasberg (1997) assumed for their model predictions for comparison with Miskolczy-Fodor's (1960) data that complete OHC loss results in a 55-dB loss of sensitivity. They state that assuming a 65-dB loss of sensitivity for complete OHC loss would yield results more consistent with Miskolczy-Fodor's (1960) data for 80 dB SPL losses. A study of BM I/O functions derived from single-unit data by Cooper and Yates (1994) showed that frequencies above 2.0 kHz show more gain than lower frequencies, which is the basis for Moore and Glasberg's (1997) assumption of two gain values corresponding to the loss of OHC. However, even this greater amount of gain associated with OHC loss would not account for loudness slope increases that occur for losses between 65 and 80 dB SPL as reported in Hellman and Meiselman's (1993) study.

[6] The slope of the loudness function for tones in noise is also dependent on noise bandwidth. For long-duration tones, Hellman (1970, 1972) showed that given the same noise spectrum level and the same thresholds, the slope of the loudness-matching function, and hence the slope of the loudness function, changed with variations in the noise bandwidth. The noise bandwidth was held constant in the present study and the use of a broadband noise produces loudness recruitment functions nearly identical to those seen in cochlear hearing loss (Hellman, 1988).

[7] A single psychometric function slope describes tonal detection in quiet and in noise between roughly 0.5 and 4.0 kHz. Green and Swets (1966) show psychometric functions for tonal detection for a wide range of durations in noise (10 ms, 100 ms, and 1000 ms) for various frequencies (0.25 Hz–6.0 Hz). Watson *et al.* (1972) measured psychometric functions for detection of a 150-ms tone in quiet for various frequencies (0.125–4.0 kHz). Viemeister and Schlauch (unpublished data) measured psychometric functions for detection for tones in quiet and in noise in the same listeners. The slope of the psychometric function, within the resolution of our confidence limits, did not vary with duration (10 ms, 20 ms, 40 ms, 80 ms, and 160 ms) and frequency (0.5 Hz, 2.0 Hz, and 4.0 kHz). Viemeister and Schlauch's result corroborates Green and Swets' (1966) result and extends Watson *et al.*'s (1972) result to shorter tonal durations.

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