Inter-relationship between different psychoacoustic measures assumed to be related to the cochlear active mechanism

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The active mechanism in the cochlea is thought to depend on the integrity of the outer hair cells (OHCs). Cochlear hearing loss is usually associated with damage to both inner hair cells (IHCs) and OHCs, with the latter resulting in a reduction in or complete loss of the function of the active mechanism. It is believed that the active mechanism contributes to the sharpness of tuning on the basilar membrane (BM) and is also responsible for compressive input–output functions on the BM. Hence, one would expect a close relationship between measures of sharpness of tuning and measures of compression. This idea was tested by comparing three different measures of the status of the active mechanism, at center frequencies of 2, 4, and 6 kHz, using subjects with normal hearing, with unilateral or highly asymmetric cochlear hearing loss, and with bilateral loss. The first measure, HL_{OHC}, was an indirect measure of the amount of the hearing loss attributable to OHC damage; this was based on loudness matches between the two ears of subjects with unilateral hearing loss and was derived using a loudness model. The second measure was the equivalent rectangular bandwidth (ERB) of the auditory filter, which was estimated using the notched-noise method. The third measure was based on the slopes of growth-of-masking functions obtained in forward masking. The ratio of slopes for a masker centered well below the signal frequency and a masker centered at the signal frequency gives a measure of BM compression at the place corresponding to the signal frequency; a ratio close to 1 indicates little or no compression, while ratios less than 1 indicate that compression is occurring at the signal place. Generally, the results showed the expected pattern. The ERB tended to increase with increasing HL_{OHC}. The ratio of the forward-masking slopes increased from about 0.3 to about 1 as HL_{OHC} increased from 0 to 55 dB. The ratio of the slopes was highly correlated with the ERB ($r=0.92$), indicating that the sharpness of the auditory filter decreases as the compression on the BM decreases. [S0001-4966(99)00211-8]

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INTRODUCTION

It is widely believed that the patterns of vibration on the basilar membrane in a normal ear are strongly influenced by an active mechanism that depends on the operation of the outer hair cells (OHCs); for a review, see Yates (1995). One consequence of this active mechanism is nonlinearity in the input–output functions of the basilar membrane. These functions show marked compression at medium input levels (40 to 80 dB SPL) and become more linear at very low and perhaps at very high levels (Rhode, 1971; Robles *et al.*, 1986; Yates, 1990; Ruggero *et al.*, 1997). The compression occurs only for tones that are reasonably close to the characteristic frequency (CF) for the place whose response is being measured. The response to tones with frequencies well below CF is approximately linear. When the OHCs are destroyed, or rendered inactive by drugs, the input–output functions of the basilar membrane become linear for all frequencies (Ruggero and Rich, 1991; Ruggero *et al.*, 1996).

A second consequence of the active mechanism is connected with the tuning of the basilar membrane. The normal sharp tuning of the basilar membrane at low sound levels is thought to depend on the active mechanism (Sellick *et al.*, 1982; Khanna and Leonard, 1982; Yates, 1995). The sharpness of tuning decreases progressively with increasing sound level, which probably reflects a progressively reducing contribution of the active mechanism. When the OHCs are damaged, or their functioning is impaired, the tuning on the basilar membrane (Sellick *et al.*, 1982; Khanna and Leonard, 1982) or in primary auditory neurons (Evans and Harrison, 1976) becomes broader.

There are many aspects of auditory perception that are thought to be affected by the active mechanism and by the loss of that mechanism when the OHCs are damaged; for

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reviews, see Moore and Oxenham (1998) and Moore (1998). This paper is particularly concerned with three of these aspects. The first is frequency selectivity, as measured behaviorally in masking experiments and quantified in terms of the equivalent rectangular bandwidth (ERB) of the auditory filter (Glasberg and Moore, 1990). It is widely believed that the frequency selectivity revealed in masking experiments depends primarily on the filtering that takes place within the cochlea (Fletcher, 1940; Pickles, 1986; Moore, 1986; Evans *et al.*, 1989). People with cochlear hearing loss usually have ERBs that are markedly greater than normal (Leshowitz *et al.*, 1975; Pick *et al.*, 1977; Glasberg and Moore, 1986; Moore, 1998), and this is thought to reflect damage to the OHCs and the consequent disruption of the active mechanism.

The correlation between the ERB and the audiometric threshold at the test frequency is not high (Pick *et al.*, 1977; Glasberg and Moore, 1986; Laroche *et al.*, 1992; Moore, 1998), and the scatter of the ERB values for hearing losses in the range 50–70 dB can be considerable. This scatter may reflect the fact that elevation in absolute threshold can arise both from outer hair-cell damage and from inner hair-cell damage (Liberman and Dodds, 1984; Liberman *et al.*, 1986; Borg *et al.*, 1995; Moore, 1998); the former results in reduced basilar-membrane vibration for a given input sound level together with reduced sharpness of tuning, while the latter results in less efficient transduction of the basilar-membrane vibration into neural activity. In theory, the ERB of the auditory filter should be highly correlated with the amount of outer hair-cell damage, since the tuning on the basilar membrane appears to depend strongly on outer hair-cell function. However, IHC damage is thought not to affect the tuning on the basilar membrane (Liberman and Dodds, 1984; Liberman *et al.*, 1986). Therefore, the ERB should not necessarily be correlated with the amount of inner hair-cell damage, unless outer and inner hair-cell damage are themselves highly correlated. One aim of this paper is to assess the correlation between the ERB of the auditory filter and an estimate of outer hair-cell damage based on loudness measurements (see below for details). We also examine the correlation between the ERB and a more direct measure of basilar-membrane compression that has been described by Oxenham and Plack (1997).

The second psychoacoustic factor of interest for the present paper is the loudness recruitment that is usually associated with cochlear hearing loss (Fowler, 1936; Steinberg and Gardner, 1937). This may be described as follows. The absolute threshold is higher than normal. However, when a sound is increased in level above the absolute threshold, the rate of growth of loudness level with increasing sound level is greater than normal. When the level is sufficiently high, usually around 90 to 100 dB SPL, the loudness reaches its ''normal'' value; the sound appears as loud to the person with impaired hearing as it would to a normally hearing person. With further increases in sound level above 90–100 dB SPL, the loudness grows in an almost normal manner.

Two factors have been suggested to contribute to loudness recruitment. The first is a reduction in, or loss of, the compressive nonlinearity in the input–output function of the basilar membrane (Yates, 1990; Moore and Glasberg, 1997). In an ear where the damage is confined largely to the OHCs, with inner hair cells (IHCs) intact, the transformation from basilar-membrane velocity or amplitude to neural activity (spike rate) probably remains largely normal (Yates, 1990; Patuzzi, 1992). However, in an ear with damage to the IHCs as well, the transduction process may also be affected (Yates, 1990; Liberman *et al.*, 1986).

If the input–output function on the basilar membrane is steeper (less compressive) than normal in an ear with outer hair-cell damage, this would be expected to lead to an increased rate of growth of loudness level with increasing sound level. However, the magnitude of the basilar-membrane response at high sound levels can be roughly the same in a normal and an impaired ear (Ruggero and Rich, 1991; but see Ruggero *et al.*, 1997). This could explain why the loudness in an impaired ear usually ''catches up'' with that in a normal ear at sound levels around 90–100 dB SPL.

Another factor that may contribute to loudness recruitment is reduced frequency selectivity. For a sinusoidal stimulus, reduced frequency selectivity leads to an excitation pattern which is broader (spreads over a greater range of CFs) in an impaired than in a normal ear. Kiang *et al.* (1970) and Evans (1975) suggested that this might be the main factor contributing to loudness recruitment. They suggested that, once the level of a sound exceeds threshold, the excitation in an ear with cochlear damage spreads more rapidly than normal across the array of neurons, and this leads to the abnormally rapid growth of loudness with increasing level. However, experiments using filtered noise to mask signal-evoked excitation at CFs remote from the signal frequency indicate that reduced frequency selectivity is not a major contributor to loudness recruitment (Moore *et al.*, 1985; Hellman, 1978; Hellman and Meiselman, 1986); such noise has only a small effect on the perceived loudness of the signal. Although spread of excitation may play a small role, the loss of compressive nonlinearity on the basilar membrane seems to be a more dominant factor.

This conclusion is reinforced by a model of loudness perception applied to cochlear hearing loss, as proposed by Moore and Glasberg (1997). The model attempts to partition the overall hearing loss between the loss due to outer hair-cell damage, called HL_{OHC}, and the loss due to inner hair-cell damage, called HL_{IHC}; the sum of HL_{OHC} and HL_{IHC} is equal to the total hearing loss, HL_{TOTAL}. HL_{OHC} is associated with loss of compression and reduced frequency selectivity, while HL_{IHC} is associated simply with reduced sensitivity. The model accounts well for measures of loudness recruitment in people with unilateral cochlear hearing loss. It also accounts for the fact that changes in loudness with stimulus bandwidth (Zwicker *et al.*, 1957) are smaller in hearing-impaired than in normally hearing people (Florentine and Zwicker, 1979; Bonding, 1979; Bonding and Elberling, 1980; Moore *et al.*, 1999).

The model starts by calculation of an excitation pattern for the sound under consideration. Excitation patterns are calculated for a normal ear in a manner similar to that described by Glasberg and Moore (1990). The excitation patterns are made broader (but change less with level) as HL_{OHC}

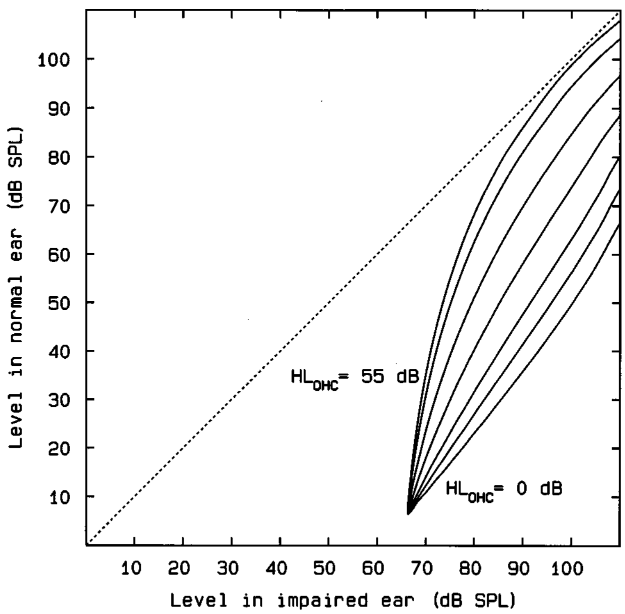

FIG. 1. The effect on loudness-matching functions of changing the value of the parameter HL_{OHC} for a hypothetical subject with a flat hearing loss of 60 dB in one ear and normal hearing in the other ear. The value of HL_{OHC} was 0, 10, 20, 30, 40, 50, or 55 dB.

increases, but they do not depend on the value of HL_{IHC}. The excitation pattern is then transformed to a specific loudness pattern. The total area under the specific loudness pattern gives the predicted overall loudness. The transformation from excitation to specific loudness at a given frequency is normally compressive, but it is made progressively less compressive as HL_{OHC} increases; again, it does not depend on HL_{IHC}. The effects of inner hair-cell loss are modeled simply by attenuating the excitation level at a given frequency by the value of HL_{IHC} at that frequency, prior to the transformation to specific loudness.

Figure 1 illustrates the effect of varying the parameter HL_{OHC} for a hypothetical subject with a flat hearing loss of 60 dB at all frequencies in one ear, with the other ear having completely normal audiometric thresholds. The figure shows the predicted sound levels required to match the loudness of a 1-kHz sinusoid between the two ears. To generate these predictions, the loudness was calculated as a function of level for each ear separately, and the loudness functions were used to calculate the levels giving equal loudness in the two ears. The slopes of the functions vary with HL_{OHC}. They have a downward curvature for large values of HL_{OHC}, but become almost straight for moderate values of HL_{OHC}, and even have a slight upward curvature for very small values of HL_{OHC}. Empirically measured loudness growth functions can vary markedly in slope and in curvature across subjects, even for subjects with similar absolute thresholds (Hellman and Meiselman, 1990, 1993; Kiessling *et al.*, 1993; Moore and Glasberg, 1997), and variations in the parameter HL_{OHC} allow the model to fit this observed range. The method of deriving the values of HL_{OHC} as a function of frequency for individual subjects is described later.

Moore and Glasberg (1997) obtained estimates of HL_{OHC} as a function of CF for several subjects with unilateral or highly asymmetric cochlear hearing loss. The estimates were based on loudness matches of tones presented alternately to the two ears. Some of those subjects were used in the present experiment, so that we could examine the relationship between the HL_{OHC} estimates and the estimates of the ERBs of their auditory filters obtained using notched-noise masking (Glasberg and Moore, 1990; Stone *et al.*, 1992). If both the HL_{OHC} values and the ERBs depend on the degree to which the active mechanism is operative, then the two should be highly correlated.

The third factor of interest for this paper is the magnitude of compression on the basilar membrane, estimated by measuring growth-of-masking functions in forward masking. Oxenham and Plack (1997) investigated forward masking for a 6-kHz sinusoidal signal and a masker of the same frequency or one octave lower. Forward masking was used to prevent interactions between the masker and the signal on the basilar membrane, which can lead to nonlinear effects such as suppression and combination tone generation. For the on-frequency case (signal frequency equal to masker frequency), they showed that under certain conditions, if the signal is made very brief and the time delay between the masker and signal is very short, the level of the signal at threshold is approximately equal to the masker level. Under these conditions, the growth-of-masking function (masker level as a function of signal level) has a slope of 1; each 10-dB increase in signal level requires a 10-dB increase in masker level. For the off-frequency case (masker frequency equal to 3 kHz instead of 6 kHz), the growth-of-masking function had a slope much less than 1; a 40-dB increase in signal level required only a 10-dB increase in signal level. This can be explained in the following way: the signal threshold depends on the response evoked by the masker at the signal CF. The growth of response on the basilar membrane for tones well below the CF is linear. Thus, the signal is subject to compression while the masker is not. This gives rise to the shallow growth-of-masking function. The slope value of around 0.25 corresponds to a compression of about 4 to 1, which is in good agreement with the estimates of Oxenham and Moore (1994, 1995). For midrange levels, Oxenham and Plack found even more compression, with a slope of about 0.16.

Even when the slope of the growth-of-masking function for the on-frequency case (signal frequency equals masker frequency) is not equal to 1, the compression on the basilar membrane can still be estimated from the ratio of slopes for the on-frequency case and the off-frequency case (Oxenham and Plack, 1997), and that is the approach taken in the present study. For brevity, in the remainder of this paper, we will refer to this quantity simply as the ''ratio of slopes.''

If the compression on the basilar membrane is lost as a consequence of cochlear hearing loss, then the growth-of-masking functions in forward masking (in dB per dB) should have slopes close to unity, except when the signal is very close to its absolute threshold (Oxenham and Moore, 1997; Moore and Oxenham, 1998). Furthermore, the slopes should remain close to unity, regardless of the relative frequencies of the masker and signal, as all frequencies should be processed linearly. Empirical data have confirmed these predictions (Oxenham and Moore, 1995, 1997; Oxenham and

TABLE I. Comparison of different compression-related measures at 2 kHz. The column headed HL gives the absolute threshold in dB HL. Values of HL_{OHC} were estimated from loudness matches between the two ears. Values of the ERB were estimated from notched-noise masking. The slope ratio is the slope of the growth-of-masking function in forward masking for a masker one octave below the signal frequency divided by the slope for a masker at the signal frequency. Parentheses indicate that at least one of the slope values was based on three or less points covering a small range of signal levels; there is a large possible error associated with these slope ratios.

Subject	Ear	HL	HL_{OHC}	ERB	Slope ratio
DF	Better	9	7	0.16	0.42
DF	Worse	60	30	0.75	0.73
AW	Better	26	21	0.16	0.38
AW	Worse	75	55	0.45	0.67
VF	Better	22	18	0.19	0.65
VF	Worse	60	50	>1	1.28
DT	Better	53		0.71	1.02
AR	Better	62		0.50	1.14
VW	Better	66		0.48	(>1)

Plack, 1997). In this paper, we consider several cases of hearing loss where there was probably some remaining outer hair-cell function, and hence some residual compression on the basilar membrane. Thus, we could examine the relationship between the estimated threshold elevation due to outer hair-cell damage (HL_{OHC}) and the amount of residual compression, as estimated from the ratio of slopes.

In summary, the aim of this study was to compare several psychoacoustic measures that are thought to be related to the functioning of the active mechanism in the cochlea. These measures were: the absolute threshold in dB HL; the estimated amount of the hearing loss attributable to outer hair-cell damage, HL_{OHC}; the ERB of the auditory filter as estimated from masking with notched noise; and the compression on the basilar membrane as estimated from the ratio of slopes. In addition, psychophysical tuning curves PTCs (Chistovich, 1957; Small, 1959; Moore, 1978) were obtained to check for the possibility of ''dead regions,'' i.e., regions in the cochlea where the IHCs or neurons are destroyed or nonfunctional. When the signal is presented at a frequency corresponding to a dead region, the tip of the PTC is shifted away from the signal frequency (Thornton and Abbas, 1980; Florentine and Houtsma, 1983; Moore, 1998).

I. METHOD

A. Subjects

Three groups of subjects were tested. The first was composed of six normally hearing subjects; all had thresholds better than 15 dB HL at the standard audiometric frequencies from 250 to 8000 Hz. Their ages ranged from 19 to 48 years (mean 29). They were tested only in the experiment measuring the ratio of slopes in forward masking. The second group consisted of three subjects with unilateral or highly asymmetric hearing loss. The third group consisted of three subjects with bilateral hearing loss. The ages of the hearing-impaired subjects ranged from 48 to 85 years (mean 67). All losses were diagnosed as being of cochlear origin as indicated by: lack of an air-bone gap, signs of loudness recruitment; normal tympanograms, and normal acoustic reflex thresholds. The subjects with highly asymmetric losses were tested separately in each ear. When the worse ear was being tested, pink noise with a spectrum level of 25 dB at 1 kHz was presented to the better ear, to prevent ''cross hearing.'' Only the better ear was tested for the subjects with bilateral losses. The absolute thresholds of the ears tested are specified in dB HL at 2, 4, and 6 kHz (the test frequencies used in the experiments) in Tables I–III. The other quantities given in the tables will be described later.

All of the subjects (both hearing impaired and normally hearing) had previous experience in psychoacoustic tests, including masking experiments. They were given practice in each task until their performance appeared to be stable. This generally took 2–4 h per task.

TABLE II. As Table I, but for a frequency of 4 kHz.

Subject	Ear	HL	HL_{OHC}	ERB	Slope ratio
DF	Better	14	11	0.16	0.55
DF	Worse	55	35	0.44	(0.67)
AW	Better	39	31	0.21	0.60
AW	Worse	66	55	0.48	0.74
VF	Better	10	8	0.14	0.34
VF	Worse	54	45	0.53	0.76
DT	Better	62		0.55	1.03
AR	Better	60		0.36	0.62
VW	Better	57		0.21	(1.07)

TABLE III. As Table I, but for a frequency of 6 kHz.

Subject	Ear	HL	HL_{OHC}	ERB	Slope ratio
DF	Better	35	28	0.16	0.55
DF	Worse	65	65	1.05	1.35
AW	Better	49	39	0.22	0.45
AW	Worse	75	55	1.07	1.41
VF	Better	18	14	0.165	0.28
VF	Worse	47	45	0.27	0.79
DT	Better	57		0.82	0.96
AR	Better	47		0.21	0.48
VW	Better	67		0.84	1.32

B. Stimulus generation

Except for measurements of the ratio of slopes in forward masking, all stimuli were generated digitally using a Tucker-Davis Technologies (TDT) System II, controlled by a PC, using a sampling rate of 32 000 or 50 000 Hz. For generation of the notched-noise maskers used to estimate the ERB of the auditory filter, the stimuli were initially specified in the frequency domain, and were transformed into the time domain via an inverse Fourier transform, using a routine supplied by Tucker-Davis. The spectral values were specified at 1-Hz intervals up to approximately 16 000 Hz, and a 1-s noise buffer was generated. The three noise bursts for a given trial were taken as consecutive segments from that buffer. A new noise buffer was generated for every trial. The spectral slopes were essentially infinite. Stimuli were converted to analog form using two channels of a TDT DD1, one for the signal and one for the masker.

For measurements of the ratio of slopes in forward masking, the sinusoidal signal and masker were generated using two Farnell DSG1 signal generators, and were gated using TDT SW2 gates. For all measurements, the levels of the signal and masker were controlled by TDT PA4 programmable attenuators, and signal and masker were mixed (TDT SM3) before being passed to a headphone buffer (TDT HB6), a final manual attenuator (Hatfield 2125), and one earpiece of a headphone. Most of the data were gathered using a Sennheiser HD414 earphone. However, the notched-noise masking data at 6 kHz were gathered using an Etymōtic Research ER2 insert earphone, which gives a flatter response at the eardrum. Also, some of the psychophysical tuning curves for a signal frequency of 6 kHz were obtained using the ER2 earphone.

C. General procedure

Thresholds were measured using a two- or three-alternative forced-choice, three-down one-up procedure tracking the 79.4%-point on the psychometric function. A three-alternative procedure was used for measurements of notched-noise masking and PTCs. A two-alternative procedure was used for measurements of absolute threshold and forward masking (this was done for consistency with the previous work of Oxenham and Plack, 1997). Observation intervals were marked by lights on the response box and feedback was provided after each trial by a light indicating the correct interval. Twelve turnpoints were obtained in a given run, and the threshold estimate for that run was taken as the mean value of the levels at the last eight turnpoints. The step size was usually 5 dB up to the first four turnpoints, and 2 dB thereafter. At least two runs were obtained for each condition. When the thresholds for those two runs differed by more than 2 dB, at least one additional run was obtained.

D. Absolute thresholds

Absolute thresholds were initially measured using the above procedure, using sinusoidal stimuli with 200-ms steady-state and 10-ms raised-cosine rise/fall times. Sound levels were specified in dB SPL at the eardrum, using a previously obtained calibration of the HD414 earphones based on probe microphone measurements (Rastronics Portarem 2000 system) in ten ears. They were converted to thresholds in dB HL, using the values for the monaural absolute threshold at the eardrum specified in Moore *et al.* (1997).

E. Estimation of the values of HL_{OHC}

The estimates of the values of HL_{OHC} were taken from Moore and Glasberg (1997), who tested five subjects with highly asymmetric hearing loss, three of whom were tested in the present experiment. The HL_{OHC} estimates were based on loudness matches between the two ears of the subjects with highly asymmetric hearing loss, using sinusoidal stimuli covering a wide range of frequencies. The value of the parameter HL_{OHC} at each frequency was adjusted so that the loudness-matching functions predicted by the model fitted the data as closely as possible. In general, the steeper the loudness growth in a given ear at a given frequency, the greater the value of HL_{OHC} at that frequency. However, the loudness growth at a given frequency can be somewhat affected by the value of HL_{OHC} at other frequencies, as the model assumes that the overall loudness of a sound is related to the total area under the specific loudness pattern (Zwicker and Scharf, 1965). The values of HL_{OHC} were adjusted so as to give the best overall fit to the data, rather than to optimize the fit at any single frequency. To a first approximation, the value of HL_{OHC} at a given frequency can be regarded as a quantitative estimate of the amount of loudness recruitment at that frequency.

It should be noted that the values of HL_{OHC} could not be derived independently for the two ears of a given subject, as they were based on loudness matches between the two ears. Where there was a hearing loss in the better ear, it was assumed that the value of HL_{OHC} for that ear was 80% of the total hearing loss, which was argued by Moore and Glasberg (1997) to be a typical value for mild hearing losses (losses around 40 dB HL). The hearing losses in the better ear were usually small, and the value assumed for the better ear at a given frequency had only a small effect on the value fitted for the impaired ear of the same subject at that same frequency. The values of HL_{OHC} are given in Tables I–III. Estimates of HL_{OHC} were not available for the subjects with bilateral hearing loss (DT, AR, and VW).

F. Estimation of the ERB of the auditory filter using notched-noise masking

The ERB of the auditory filter was estimated using an abbreviated version of the notched-noise method (Patterson, 1976; Patterson and Nimmo-Smith, 1980; Glasberg and Moore, 1990) described by Stone *et al.* (1992). Thresholds for detecting a sinusoid with frequency f_c (2, 4, or 6 kHz) were measured in the presence of a masker with a spectral notch around f_c. The width of the notch was systematically varied. The notch was placed both symmetrically and asymmetrically about f_c. In practice, each masker actually consisted of two noise bands, one above and one below f_c, each with a bandwidth of $0.4f_c$. The deviation in frequency of the nearer edge of each noise band from f_c is expressed relative to f_c and denoted by Δ. Values of Δ for the lower and upper bands, respectively, were: 0 and 0; 0.2 and 0.2; 0.4 and 0.4; 0.2 and 0.4; 0.4 and 0.2. The spectrum level within the passband of each noise band was 50 dB (*re* 20 μPa).

On each trial, the noise was presented in three bursts, each with 10-ms raised-cosine rise/fall times and a 200-ms steady-state portion. The interval between bursts was 500 ms. The signal was presented synchronously with one of the noise bursts, chosen at random on each trial. The starting signal level was about 10 dB above the estimated masked threshold determined in pilot experiments.

The filter shapes were derived from the data using the method described by Patterson and Nimmo-Smith (1980) and later modified by Glasberg and Moore (1990). The auditory filter was assumed to have the form of the roex(*p*,*r*) filter described by Patterson *et al.* (1982)

$$W(g)=(1-r)(1+pg)\exp(-pg)+r, \tag{1}$$

where g is the normalized frequency deviation from the center of the filter (deviation from center frequency divided by center frequency), p is a parameter determining the slope of the filter skirts, and r is a parameter that places a dynamic range limitation on the filter. The value of p was allowed to differ for the upper and lower halves of the filter. The upper and lower p values are called p_u and p_l, respectively. The value of r was assumed to be the same for the two sides of the filter. Thus, the filter shape was defined by three parameters. The fitting procedure works by finding the values of p_u, p_l, and r that give the best fit to the data; see Glasberg and Moore (1990) for details. These best-fitting values define the filter shape. The fitting procedure took into account the transfer function of the earphone (i.e., the sound level at the eardrum as a function of frequency for a fixed input voltage), and also the assumed transfer function through the middle ear; the middle-ear transfer function was as specified in Moore *et al.* (1997).

When the auditory filter is very broad, as it often is in hearing-impaired persons, the asymmetry of the auditory filter is not well defined by the data obtained using the abbreviated notched-noise method, although the bandwidth of the filter is reasonably well defined. Therefore, in the present paper we present only the ERBs of the auditory filters determined from the fitted values of the three parameters.

G. Estimation of the ratio of slopes

Growth-of-masking functions in forward masking were measured for three signal frequencies (2, 4, and 6 kHz), with a sinusoidal masker centered either at the signal frequency or one octave below it. Following Oxenham and Plack (1997), within a given run the signal level was fixed and the masker level was varied to determine the masked threshold. The fixed signal level ranged from about 10 dB above the absolute threshold to 90 or 95 dB SPL. The absolute threshold for the brief signal was initially measured using a two-alternative forced-choice procedure. The initial level of the masker was about 10 dB below the level needed to mask the signal, as estimated in pilot experiments. The masker was presented in two bursts with 100-ms steady-state portions, 2-ms raised-cosine rise/fall ramps, and 500-ms interburst interval. The signal was presented following one of the two bursts, selected randomly on each trial. Data were initially gathered using a signal with a raised-cosine envelope of total duration 4 ms, i.e., there were two 2-ms ramps, with no steady-state portion. The silent interval between the masker and signal was 2 ms. This signal duration was probably long enough to minimize audible spectral splatter at 4 and 6 kHz (Oxenham, 1997). However, we later became concerned that the results for the 2-kHz signal might have been influenced by spectral splatter. Hence, the conditions using the 2-kHz signal were rerun with a longer signal duration. The total signal duration was increased to 10 ms (two 5-ms ramps). The masker onset and offset ramps were also increased to 5 ms, and the masker–signal silent interval was decreased to 0 ms.

H. Psychophysical tuning curves

As mentioned earlier, psychophysical tuning curves (PTCs) were obtained mainly to check for the existence of ''dead regions'' where there are no functional IHCs or neurons. In such cases, the tip of the PTC should be shifted away from the signal frequency. The PTCs were determined in simultaneous masking, and the timing of the stimuli was exactly as described for the notched-noise masking experiment. The signal was a sinusoid presented 10 dB above the absolute threshold. The masker was an 80-Hz-wide noise band, generated using the same method as described for the notched-noise masker. A noise band was used as the masker rather than a sinusoid, to reduce the influence of beats on the results. The exact masker frequencies were chosen individually for each subject, so as to define the position of the tip of the tuning curve with reasonable accuracy. Owing to limitations in the availability of subject VF, it was not possible to obtain PTCs for her.

II. RESULTS

A. Psychophysical tuning curves

The results of the PTC measurements are described first, as the outcome of these affected the subsequent analyses. As mentioned above, the main point of the PTC measurements was to determine whether any of the subjects had dead regions corresponding to any of the signal frequencies. In the great majority of cases, the tips of the PTCs fell at or close to the signal frequency, providing no evidence for dead regions. However, there was one exception. For the worse ear of subject DF, the tuning curve for the signal frequency of 2000 Hz was rather flat, but showed a small minimum close to 4000 Hz. However, the results were also very variable, especially across sessions. It is likely that she had a dead region in the low to middle frequencies, although the exact boundary of this region was difficult to determine. In the figures and correlational analyses that follow, the results for the worse ear of DF for a signal frequency of 2000 Hz are excluded.

Generally, there was a reasonable correspondence between the sharpness of the PTCs and the ERBs of the auditory filters measured using notched-noise masking (see below). However, some of the PTCs showed irregularities around the tips, possibly reflecting cues based on temporal interactions of the signal and masker (Moore *et al.*, 1998). Hence, in the rest of this paper we concentrate on the ERB values, as we believe that these were less affected than the PTCs by factors such as off-frequency listening (Johnson-Davies and Patterson, 1979; O'Loughlin and Moore, 1981a, 1981b) and temporal interactions between the signal and masker.

B. ERB values

The ERB values are given in Tables I–III. They are expressed as a proportion of the center frequency. The ERB values are plotted as a function of the absolute thresholds in dB HL in Fig. 2. The solid symbols at the far left show the mean ERB values for normally hearing subjects as specified in Glasberg and Moore (1990); note that these were derived using a larger number of notch widths than for the present experiments. The ERB values for the ears tested in the present experiment are only slightly greater than normal for absolute thresholds up to 35 dB HL, but tend to increase above that. As has been found in earlier studies (Pick *et al.*,

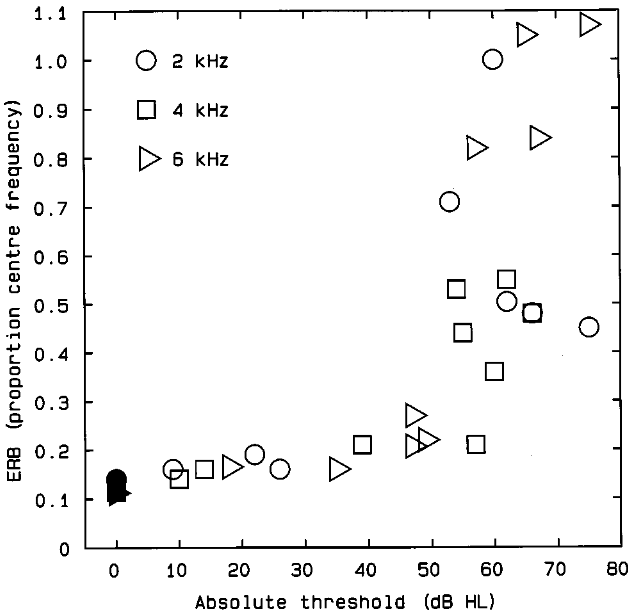

FIG. 2. The ERB of the auditory filter, expressed as a proportion of center frequency and plotted as a function of the absolute threshold in dB HL at the test frequency. Each symbol represents results for one frequency, as indicated in the figure. The solid symbols at the far left show mean ERBs for normally hearing subjects, given by Glasberg and Moore (1990).

1977; Glasberg and Moore, 1986; Laroche *et al.*, 1992; Moore, 1998), for absolute thresholds in the range 45–80 dB HL, the scatter in the ERB values is considerable. For example, in the range from 50 to 60 dB HL, the ERB values range from 0.21 to 1. Considering only cases where the absolute threshold was greater than 35 dB HL, roughly the hearing loss at which the ERB values start to increase, the (Pearson) correlation between the ERBs and the absolute thresholds is 0.58 ($n=19, p<0.01$).

Figure 3 shows the relationship between the ERBs and the values of HL_{OHC} (upper panel) or HL_{IHC} (lower panel). The former were estimated from the loudness-matching data of Moore and Glasberg (1997). The values of HL_{IHC} were obtained simply by subtracting the values of HL_{OHC} from the overall hearing loss at the same center frequency. For example, for a hearing loss of 55 dB at a specific frequency, if HL_{OHC} was 40 dB, then HL_{IHC} would be 15 dB. The ERB values tend to increase with increasing HL_{OHC}, as expected. Considering only cases where HL_{OHC} was greater than 25 dB HL, roughly the value at which the ERB values start to increase, the correlation between the ERBs and the values of HL_{OHC} is 0.75 ($n=11, p<0.01$). This correlation is higher than the correlation between the ERBs and the absolute thresholds, although the difference between the two correlations is not statistically significant according to the test described by Howell (1997); $z=0.72, p>0.05$. In contrast, the ERBs show no clear relationship to the values of HL_{IHC}. The correlation between these two quantities (excluding the mean results for the normal ears) is 0.38 ($n=18$, not significant). The correlation between the ERBs and the values of HL_{IHC} was not increased by excluding cases where HL_{IHC} was below a certain limit.

The results are consistent with our expectation that the ERB values would be more closely related to the values of

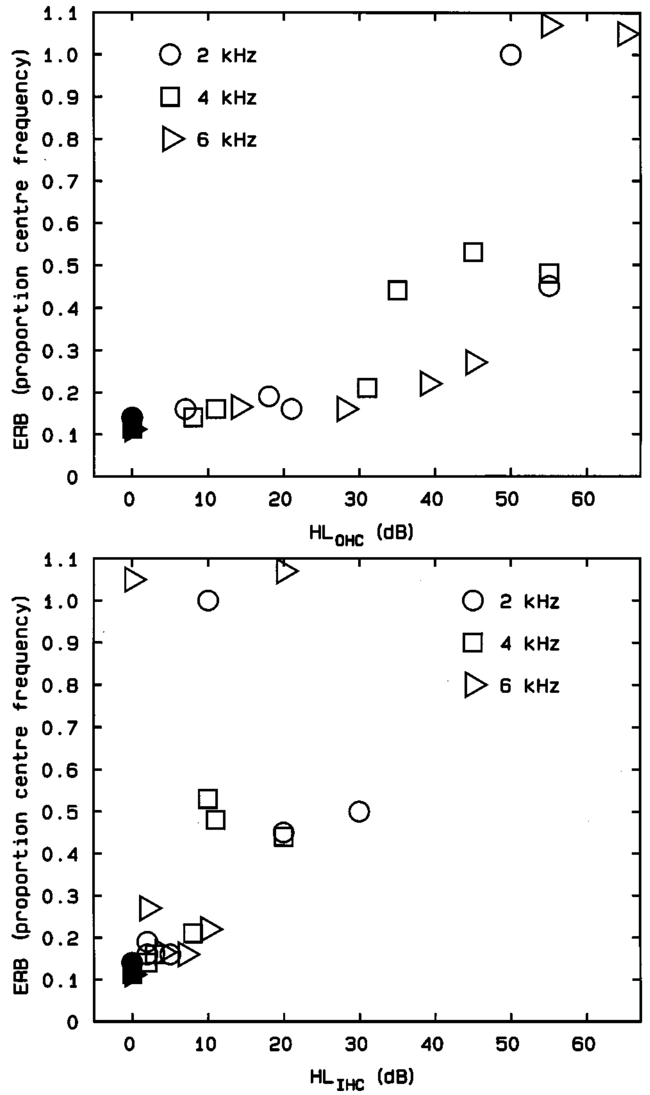

FIG. 3. The ERB of the auditory filter plotted as a function of HL_{OHC} (upper panel) or HL_{IHC} (lower panel).

HL_{OHC} than to the absolute thresholds, although the difference in correlation (ERB versus HL_{TOTAL} compared to ERB versus HL_{OHC}) failed to reach statistical significance. However, the ERB values plotted as a function of HL_{OHC} still show considerable scatter. This may reflect errors of measurement, especially in the estimates of HL_{OHC}. These were derived indirectly using the loudness model, based on loudness-matching data. Scatter in the original data was sometimes considerable, and this could easily have led to errors of 20% or so in the estimated values of HL_{OHC} ($\pm$20% was the typical range of values of HL_{OHC} over which a reasonable fit to the data could be obtained).

C. Forward masking with on-frequency and off-frequency maskers

The individual results for the normally hearing subjects using the signal with 4-ms total duration are shown in Figs. 4 and 5. The masker level is plotted on the ordinate, because the masker level was varied to determine the threshold. For the on-frequency condition (masker frequency equals signal frequency—solid symbols), the masker level at threshold is

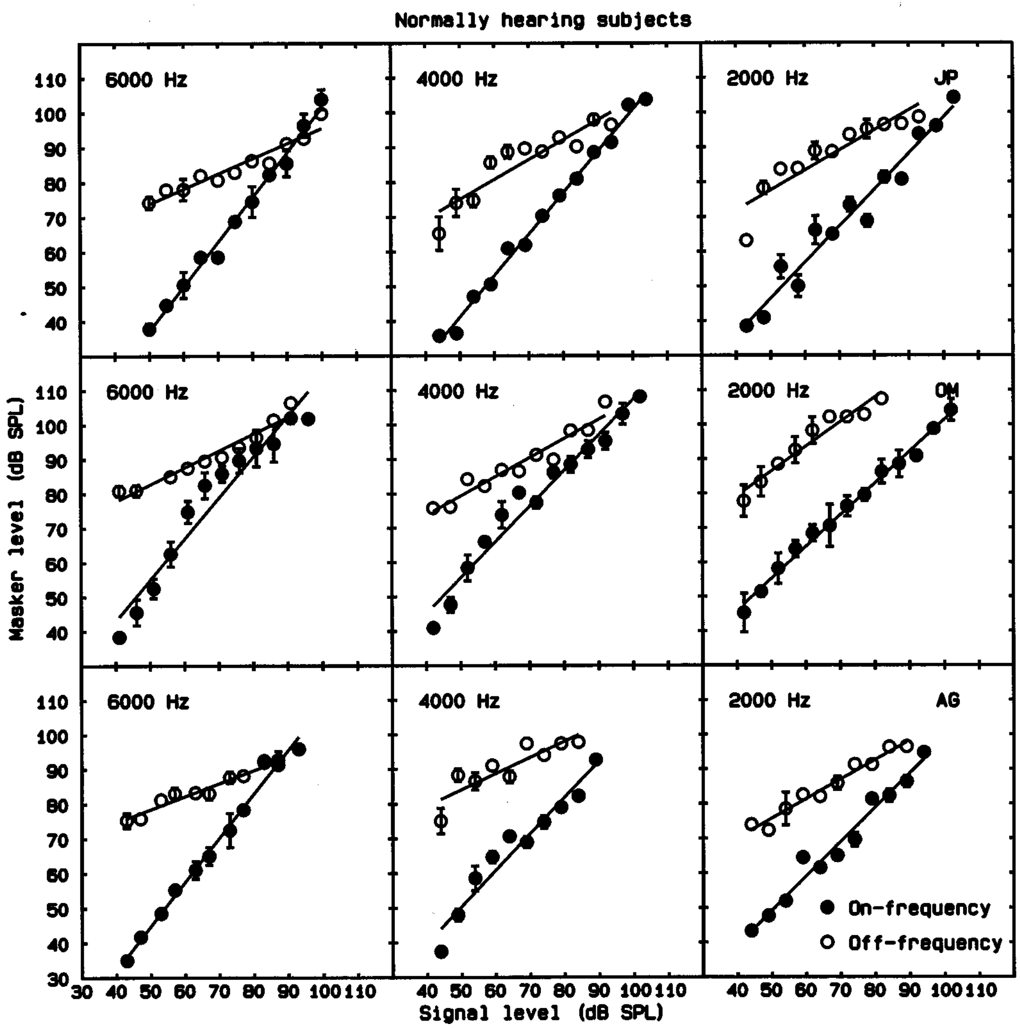

FIG. 4. Growth-of-masking functions in forward masking for normally hearing subjects JP, OM, and AG. The masker level required for threshold is plotted as a function of the signal level. Results for the on-frequency masker are shown by filled circles, and results for the off-frequency masker are shown by open circles. Each column shows results for one signal frequency and each row shows results for one subject. Error bars indicate ± one standard deviation across runs. Error bars are not shown where they would be smaller than the symbols.

usually roughly equal to the signal level, and the slopes of the fitted linear regression lines are close to unity. This is consistent with the data of Oxenham and Plack (Oxenham and Plack, 1997; Plack and Oxenham, 1998). Slopes close to unity have sometimes been taken as evidence for ''confusion'' of the signal with the masker (Moore and Glasberg, 1982, 1985; Neff, 1985, 1986). However, for our stimuli we believe it likely that the slopes close to unity reflect the short signal duration and brief masker–signal interval (which meant that the signal and masker levels were similar), rather than confusion. In fact, on average the slopes are slightly greater than unity, especially at 4000 and 6000 Hz; slope values are given later in Table IV. This means that the masker level required for threshold grows slightly more rapidly with increasing level than the signal level. For very low signal levels, approaching the absolute threshold, the functions sometimes become a little steeper, as expected. The lines were fitted to the data excluding the lowest data point (where the signal was only 10 dB above absolute threshold), but the slope values were almost the same when this point was included. The proportion of variance in the data accounted for by the fitted lines was between 0.79 and 0.996 (means 0.95, 0.90, and 0.95 at 2000, 4000, and 6000 Hz, respectively).

For the off-frequency maskers (one octave below the signal frequency—open circles), the functions have slopes markedly less than unity, especially for midrange levels. Again, this is consistent with the data of Oxenham and Plack (1997). However, for the 2000-Hz signal, the slopes are not always greatly different for the on-frequency and off-frequency maskers; see, for example, the results of subjects OM, DV, and RK. As mentioned earlier, we suspected that the results at 2000 Hz might have been influenced by spectral splatter. Splatter could affect the results in two ways. First, the spectrum of the 4-ms 2000-Hz signal contained energy at frequencies well above 2000 Hz. When the signal level was well above the absolute threshold, the level of the 1000-Hz masker needed to mask this splatter might have been greater than the level needed to mask the energy centered around 2000 Hz. Second, spectral splatter produced by the 2-ms offset ramp of the masker might have had a mask-

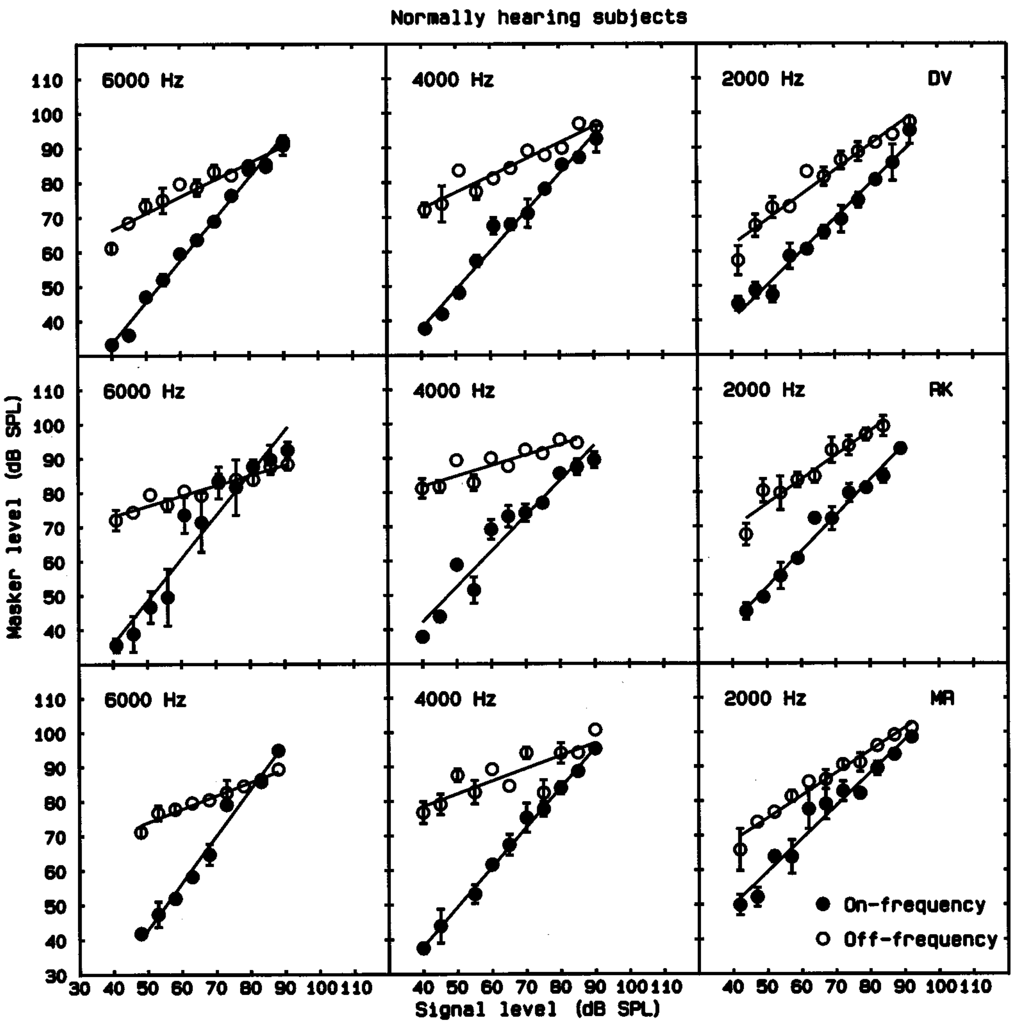

FIG. 5. As Fig. 4, but for normally hearing subjects DV, RK, and MR.

ing effect, reducing the masker level needed to mask the signal.

Figure 6 compares the results for the 2000-Hz signal with 4-ms total duration (2-ms ramps) and the 2000-Hz signal with 10-ms duration (5-ms ramps). Recall that the masker–signal interval was 2 ms for the former and 0 ms for the latter. Also, the offset ramp of the masker had a duration of 2 ms for the former and 5 ms for the latter. The proportion of variance in the data accounted for by the fitted lines for the longer signal duration was between 0.96 and 0.99 (mean 0.97). For the on-frequency masker, the masker level required at threshold was somewhat higher for the longer signal, as expected, but the slopes of the growth-of-masking functions were only slightly affected by the signal duration. The mean slope across the six subjects (standard deviation across subjects in parentheses) was 0.99 (0.047) for the 4-ms signal and 1.11 (0.084) for the 10-ms signal. The small increase is consistent with earlier work on the effect of signal duration or delay in forward masking, except that the earlier work usually measured signal threshold as a function of masker level, so the slope decreased with increasing duration or delay (Weber and Green, 1978; Jesteadt *et al.*, 1982; Moore, 1981; Moore and Glasberg, 1983).

For the off-frequency masker, the slope was sometimes markedly less for the 10-ms signal than for the 4-ms signal. This was especially true for subjects DV and RK. The main effect of the change in timing was that the masker level at threshold increased markedly for the longer signal. This is probably explicable in terms of two factors. The first is the normal ''decay of masking'' that occurs in forward masking as the signal duration is increased. The second is connected with the fact that the masker offset ramp had a longer duration for the longer signal. This longer offset ramp would have produced less spectral splatter, making it much less likely that the splatter produced at the masker offset would have a significant masking effect. As the masking would then have been determined by the on-frequency energy in the masker, the masker level at threshold had to be increased.

Since it seems likely that the results at 2000 Hz were affected by spectral splatter for the 4-ms signal but were not (or were affected much less) for the 10-ms signal, the results for the latter will be used in further analyses. Linear regression lines were fitted to the growth-of-masking functions for the off-frequency masker, excluding the lowest data point, for which the signal level would have been only 10 dB above the absolute threshold. The slopes and slope ratios of the

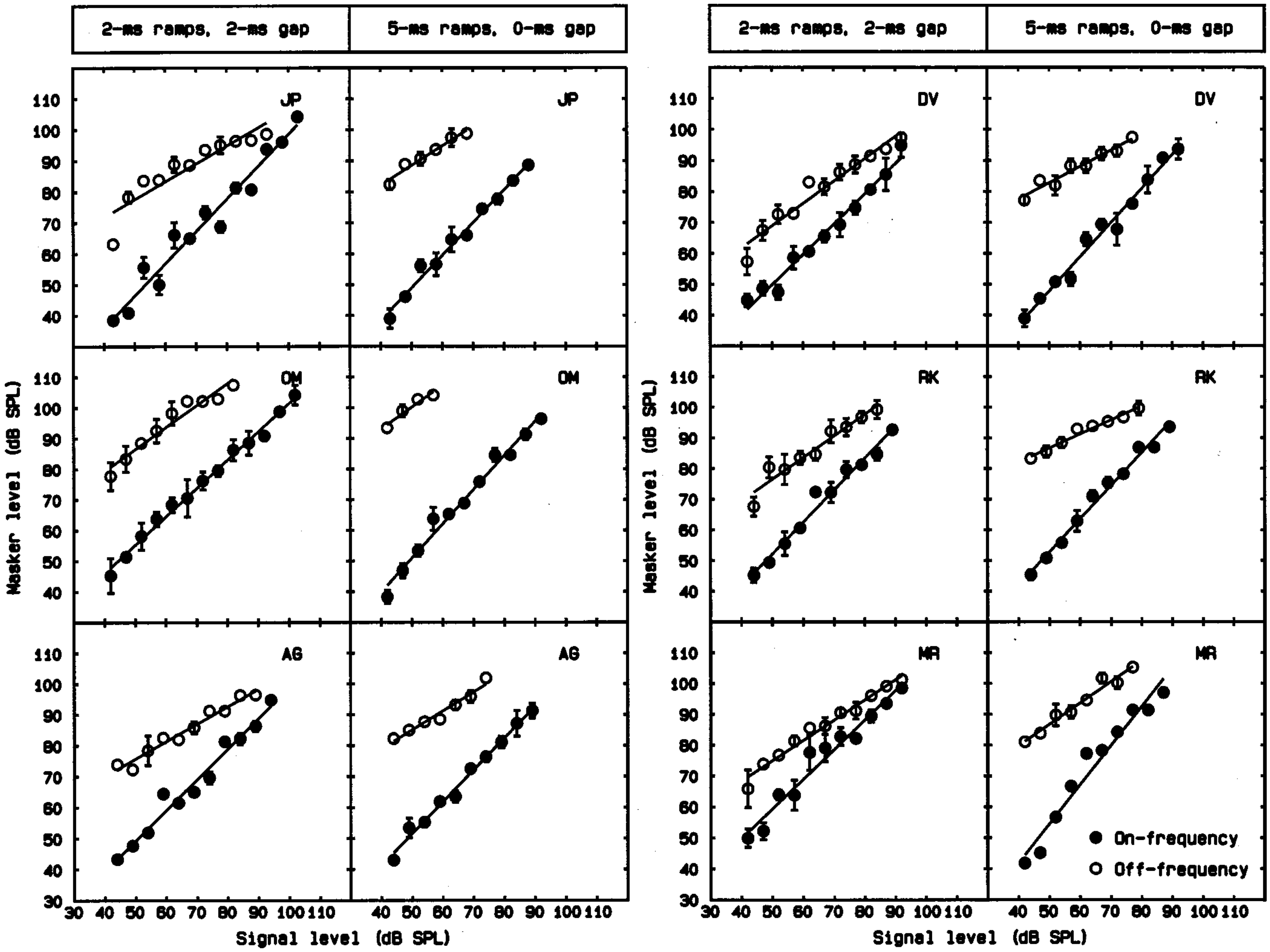

FIG. 6. Comparison of growth-of-masking functions in forward masking for two temporal configurations of the masker and signal; the configuration is indicated at the top of each column. Results are shown for six normally hearing subjects. The signal frequency was 2 kHz.

lines fitted to the growth-of-masking functions are shown in Table IV. Following the convention used by Oxenham and Plack (1997), the ratios are expressed as the slope for the off-frequency masker divided by the slope for the on-frequency masker. Thus, smaller numbers indicate more basilar-membrane compression. For example, a ratio of 0.3 means that the basilar-membrane response at CF grows by about 3 dB for each 10-dB increase in signal level.

The slope ratios at 6000 Hz are slightly larger than those found by Oxenham and Plack (1997). However, they estimated the slopes of the growth-of-masking functions only for signal levels between 50 and 80 dB SPL. Fitting our data in the same way resulted in slope ratios close to theirs. Their ratios may be regarded as estimates of the slope of the basilar membrane input–output function over the range where the compression is maximal. Our ratios indicate the slope of the input–output function averaged over a somewhat wider intensity range.

The slope ratios increase with decreasing frequency, which is consistent with physiological and psychoacoustical measurements indicating less basilar-membrane compression at lower frequencies (Yates, 1990, 1995; Neely, 1993; Rhode and Cooper, 1996; Hicks and Bacon, 1999). However, Oxenham and Plack (1997) also measured growth-of-masking functions for a 2000-Hz signal, but only for the off-frequency masker. They found somewhat shallower growth-of-masking functions than reported here, consistent with

TABLE IV. Slopes and slope ratios of the growth-of-masking functions in forward masking for the normally hearing subjects (first six rows), for the mean of the normally hearing subjects, and for the better ears of the subjects with asymmetric hearing loss.

	Frequency								
	6000 Hz			4000 Hz			2000 Hz		
Subject	On	Off	Ratio	On	Off	Ratio	On	Off	Ratio
JP	1.28	0.43	0.34	1.19	0.57	0.48	1.06	0.64	0.60
OM	1.18	0.49	0.41	1.12	0.60	0.53	1.12	0.72	0.64
AG	1.27	0.37	0.29	1.21	0.67	0.55	1.03	0.62	0.60
DV	1.19	0.48	0.40	1.11	0.47	0.42	1.10	0.52	0.47
RK	1.24	0.30	0.24	1.03	0.30	0.29	1.08	0.46	0.43
MR	1.36	0.39	0.29	1.15	0.37	0.32	1.27	0.69	0.54
Mean	1.25	0.41	0.33	1.14	0.50	0.42	1.11	0.61	0.55
AW	1.52	0.69	0.45	1.26	0.76	0.60	1.34	0.51	0.38
DF	1.07	0.60	0.55	1.28	0.70	0.55	1.18	0.50	0.42
VF	1.47	0.41	0.28	1.39	0.47	0.34	0.99	0.64	0.65

similar midlevel compression at 2000 and 6000 Hz. A possible factor contributing to the difference between the two studies was their use of a high-pass background noise. This was designed to prevent off-frequency listening. In our experiments, when the masker frequency was below the signal frequency, the signal might have been detected mainly using a region of the basilar membrane with CF somewhat above the signal frequency. The response of such a region would be less compressive than for the CF region. Also, as pointed out by Oxenham and Plack (1997), the results for the off-frequency masker when the signal frequency was 2000 Hz may have been influenced by the acoustic reflex. At high masker levels, the reflex was probably activated, and it would have attenuated the 1000-Hz masker more than the 2000-Hz signal. As a result, the masker level required for threshold would have increased. This effect would be absent for lower masker levels, so the overall effect would be a steeper growth-of-masking function. Thus, the slope ratios at 2000 Hz may underestimate the true amount of basilar-membrane compression.

For some subjects (e.g., JP, RK, and MR), the growth-of-masking functions for the on-frequency masker at 6000 Hz lay above those for the off-frequency masker, for masker levels above 90 dB SPL. In other words, the on-frequency masker had to be higher in level than the off-frequency masker to achieve a given amount of masking. It should be noted, however, that the levels plotted in Figs. 4–6 are nominal levels, assuming that the earphones produced equal eardrum sound levels at all frequencies for a given input voltage. This was not, in fact, the case. The Sennheiser HD414 earphones are designed to have a ''diffuse field'' response, and the frequency response measured at the eardrum shows a 10–12-dB peak for frequencies around 3000 Hz. Thus, the effective level of the off-frequency masker would have been about 10–12 dB higher than the nominal level plotted in the figures. Allowing for this, the growth-of-masking functions for the off-frequency and on-frequency maskers would not actually cross over, but they would converge at very high levels, consistent with an almost low-pass characteristic of basilar-membrane filtering at very high levels (Ruggero *et al.*, 1997).

Due to limited availability of the hearing-impaired subjects, it was not possible to test them at 2000 Hz with the longer signal duration. However, we feel that the results for the impaired ears were unlikely to be affected by spectral splatter, owing to the reduced frequency selectivity and reduced dynamic range associated with cochlear hearing loss. The results for the better ears of the subjects with unilateral or highly asymmetric hearing losses are shown in Fig. 7; slope values are given in Table IV. The proportion of variance in the data accounted for by the fitted lines was between 0.59 and 0.996 (means 0.92, 0.89, and 0.95 at 2000, 4000, and 6000 Hz, respectively). The results resemble those for the normally hearing subjects in general form. Even though the results at 2000 Hz were obtained with the shorter signal, there are still substantial slope differences between the on-frequency and off-frequency cases. The slope ratios are given in Tables I–IV. They mostly fall within the range of those for the normally hearing subjects (obtained with the longer signal at 2000 Hz), although, on average, the ratios are slightly larger, indicating less compression.

The results for the worse ears of the subjects with unilateral or highly asymmetric hearing losses are shown in Fig. 8. The proportion of variance in the data accounted for by the fitted lines was between 0.88 and 1.0 (means 0.95, 0.93, and 0.94 at 2000, 4000, and 6000 Hz, respectively). The results cover a much smaller range of levels than for the normal ears, as the subjects had only a limited dynamic range. The lowest signal level used was usually 10 dB above the absolute threshold for the signal, and the highest signal level was chosen so that the masker level did not exceed the uncomfortable loudness level. This limited range of levels made it more difficult to determine the slopes of the growth-of-masking functions accurately. Nevertheless, it is clear that the slopes for the off-frequency maskers are generally steeper than those found for the better ears of the same subjects or for the normally hearing subjects. The slopes for the on-frequency maskers, however, are close to unity, similar to those for the normally hearing subjects. Thus, the slope ratios, shown in Tables I–III, are markedly greater than for the better ears of the same subjects or for the normally hearing subjects. These results are consistent with those of Oxenham and Plack (1997).

The results for the bilaterally hearing-impaired subjects are shown in Fig. 9. The proportion of variance in the data accounted for by the fitted lines was between 0.91 and 1.0 (means 0.99, 0.97, and 0.99 at 2000, 4000, and 6000 Hz, respectively). Again, in some cases it was only possible to obtain results over a very limited range of signal levels, making it difficult to estimate the slopes of the growth-of-masking functions, especially for the off-frequency masker. But, the general pattern of results is similar to that for the worse ears of the unilaterally impaired subjects; the slopes for the off-frequency maskers are not generally markedly smaller than those for the on-frequency maskers. The slope ratios are given in Tables I–III. Mostly, they are close to unity, indicating little or no compression. But, there is evidence of residual compression for subject AR at 6000 and 4000 Hz.

Figure 10 shows the slope ratios plotted as a function of the absolute threshold at the test frequency. Filled symbols show the mean results for the normally hearing subjects, while open symbols show the results for the subjects with unilateral or bilateral hearing impairment. There is a clear trend for the slope ratios to increase with increasing hearing loss, for losses above about 35 dB. The correlation between the slope ratios and the absolute thresholds, excluding cases where the absolute threshold was below 35 dB HI, was 0.56 ($n=17, p<0.02$). The relatively low correlation reflects the large scatter in the slope ratios for a given hearing loss, especially around 60 dB HL. This might happen because the absolute threshold is affected by both IHC and OHC loss, but the slope ratio is related mainly to the latter.

Figure 11 shows the slope ratios plotted as a function of HL_{OHC} (upper panel) and HL_{IHC} (lower panel). The slope ratios tend to increase with increasing HL_{OHC}, as expected. Considering only cases where HL_{OHC} was greater than 25 dB HL, roughly the value at which the ratios start to increase,

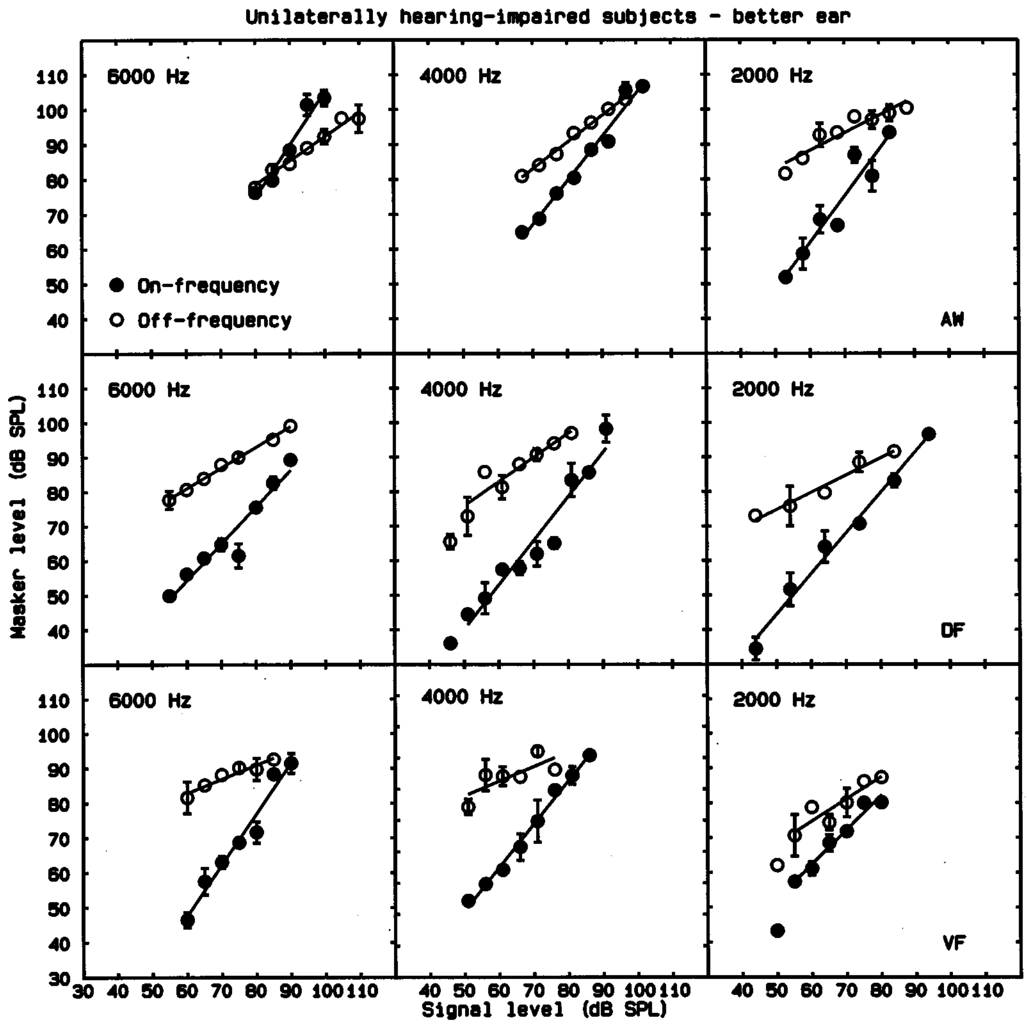

FIG. 7. As Fig. 4, but showing results for the better ears of three subjects with unilateral or highly asymmetric hearing loss.

the correlation between the slope ratios and the values of HL_{OHC} is 0.68 ($n=11, p=0.01$). This correlation is higher than the correlation between the HL_{OHC} values and the absolute thresholds, although the difference between the two correlations is not statistically significant according to the test described by Howell (1997); $z=0.46, p>0.05$. In contrast, the slope ratios show no clear relationship to the values of HL_{IHC}. The correlation between these two quantities (excluding the mean results for the normal ears) is 0.262 ($n=17$, not significant).

D. Relationship between the ERBs and the slope ratios

Figure 12 shows the relationship between the ERBs and the slope ratios. The solid symbols show the mean results for the normally hearing subjects, while open symbols show the results for the subjects with unilateral or bilateral hearing impairment. The two quantities are clearly closely related. The correlation (excluding the mean results for the normally hearing subjects) is 0.92 ($n=24, p<0.001$). It is interesting that the correlation between the ERBs and the slope ratios is higher than the correlation between the ERBs and the values of HL_{OHC}, although the difference between the two correlations fails to reach the 5% significance level, according to the test described by Howell (1997) ($z=1.54, p=0.1$). The correlation between the ERBs and the slope ratios is also higher than the correlation between the slope ratios and the values of HL_{OHC} and this difference is marginally significant ($z=1.88, p=0.06$). We also applied a test of the significance of the difference between two correlations described by Williams (1959). This test is applicable when comparing two correlations where one of the quantities is common to the two correlations. For example, when comparing the correlation of the slope ratio with the ERB and the correlation of HL_{OHC} with the ERB, the ERB values are common to the two. The test requires that equal numbers of samples contribute to each correlation, so we applied the test to the data for both ears of the unilaterally impaired subjects (the only ones for whom HL_{OHC} estimates were available), but excluding the data for the worse ear of DF at 2 kHz. The correlation of the slope ratio with the ERB, 0.952, was significantly higher than the correlation of the slope ratio with HL_{OHC}, 0.776 ($t=3.05, p<0.005$). In addition, the correlation of the slope ratio with the ERB was significantly higher than the correlation of the ERB with HL_{OHC}, 0.785 ($t=2.85, p<0.01$).

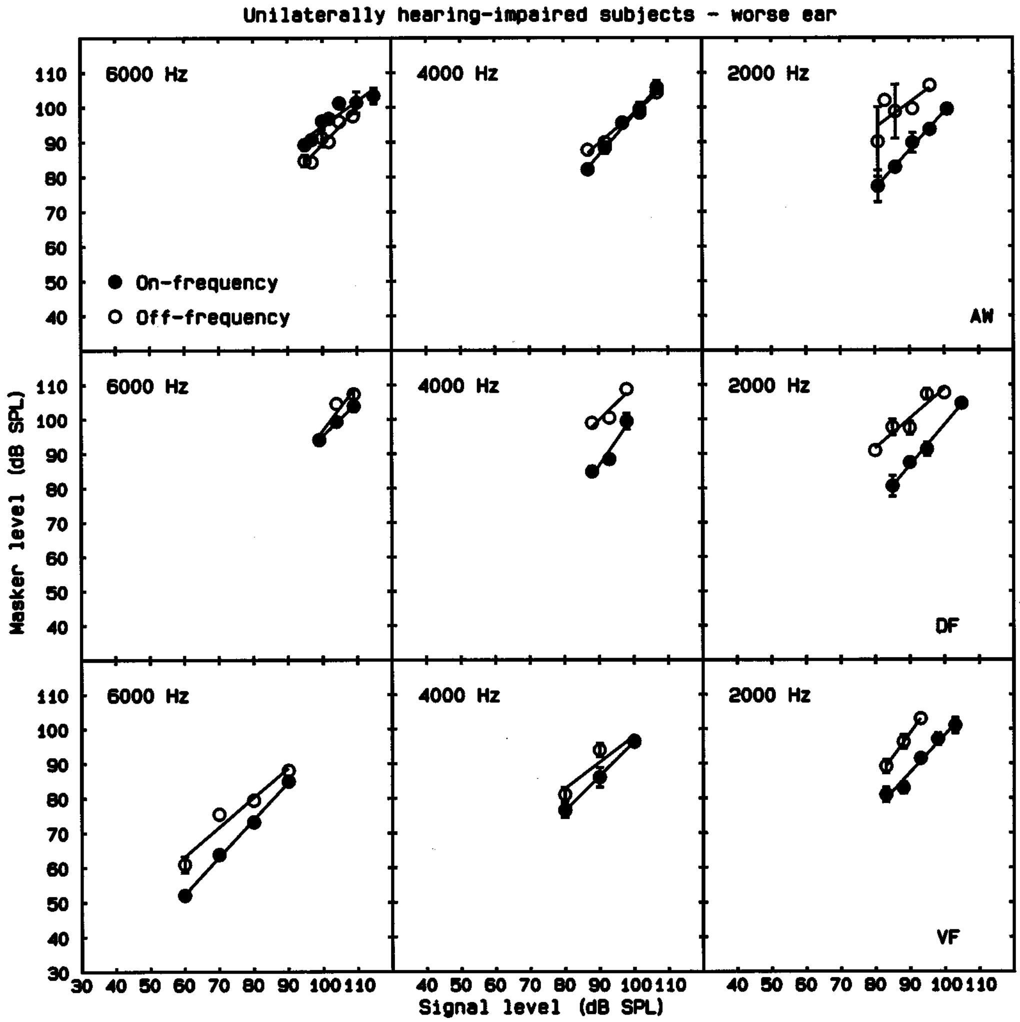

FIG. 8. As Fig. 4, but showing results for the worse ears of three subjects with unilateral or highly asymmetric hearing loss.

III. DISCUSSION

The experiments described in this study, together with the loudness-matching results of Moore and Glasberg (1997), provide three independently derived measures (the ERB, the value of HL_{OHC} and the slope ratio) that are significantly correlated with each other across different frequencies and hearing-impaired listeners. The correlation between the ERB and the slope ratio is particularly high (0.92). In contrast, the correlations between the absolute threshold and either the ERB (0.58) or the slope ratio (0.56) are considerably lower. These differences in correlation are significant, according to the test described by Howell (1997): for the former, $z=2.94, p<0.005$; for the latter, $z=2.85, p<0.005$. These findings are consistent with the ideas outlined in the Introduction, namely that cochlear hearing loss comprises at least two components, each with effects on hearing that are to a certain extent separable. The first component may be ascribed to the functioning of the cochlear active mechanism; damage to the OHCs reduces the level-dependent and frequency-selective gain of this mechanism. This would be expected to lead not only to elevated thresholds, but would also affect the ERB, the slope ratio, and loudness recruitment (estimated by parameter HL_{OHC}). The high correlation found between the ERB and the slope ratio is consistent with the idea that both reflect this first component. The second component may reflect damage to the IHCs, and hence a reduction in transduction efficiency. While this component could increase absolute thresholds, it would not be expected to affect frequency selectivity (as estimated by the ERB) or compression at CF (as estimated by the slope ratio). Thus, the lower correlation between overall hearing loss and either the ERB or the slope ratio may be due to the overall hearing loss being affected by both components, while the ERB and the slope ratio are only affected by the first component.

The correlations between the parameter HL_{OHC} and either the ERB (0.75) or the slope ratio (0.68) are both significant, but are nonetheless lower than the correlation between the ERB and slope ratio (0.92). As discussed above, this may be due to errors in estimating HL_{OHC}. In addition, HL_{OHC} is derived from loudness judgments. The function relating sound intensity to loudness is complex and may be determined by many factors beyond the initial acoustic to mechanical transduction in the cochlea. Moore and Glasberg (1997), following Launer (1995; Launer *et al.*, 1997), assumed that hearing loss due to inner hair-cell damage, represented by the quantity HL_{IHC}, could be modeled as a level-independent attenuation of the excitation level. This may be an oversimplification. For instance, damaged IHCs might re-

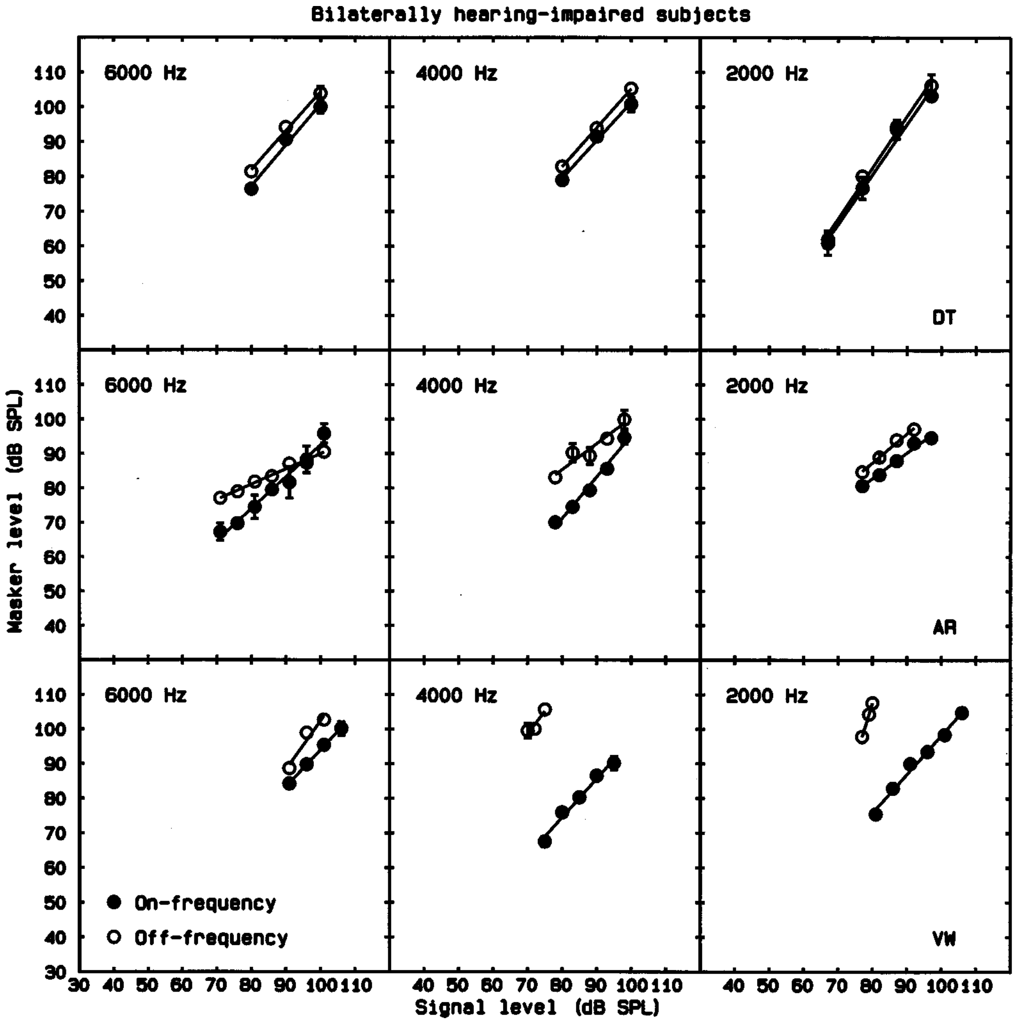

FIG. 9. As Fig. 4, but showing results for the better ears of three subjects with bilateral hearing loss.

spond very weakly to low-level stimulation, but respond nearly normally to high-level stimulation. This would elevate absolute thresholds, but might not affect loudness at high levels. The result would be something akin to loudness recruitment, but it would not be expected to lead to reduced frequency selectivity or reduced BM compression. Thus, there exists the possibility for a dissociation of the amount of loudness recruitment and the ERB or the slope ratio, which is not accounted for in the two-component model of cochlear hearing loss. In summary, while the ERB and the slope ratio should not be affected by IHC damage, it is at least conceivable that loudness recruitment may be, to some extent. This may explain the somewhat lower correlations associated with HL_{OHC}.

Psychoacoustic measures associated with basilar-membrane compression may well have clinical applications. For example, complete loss of basilar-membrane compression would probably be associated with strong loudness recruitment and a limited dynamic range, indicating the need for a hearing aid incorporating some form of automatic gain control or compression. While loudness recruitment can be measured clinically, using subjective loudness judgments (Pascoe, 1978; Hellbrück and Moser, 1985; Allen and Jeng, 1990; Kiessling *et al.*, 1993; Cox *et al.*, 1997), there is controversy about the validity and reliability of these procedures (Elberling, 1999). Estimates of loudness obtained by numerical ratings or categorical ratings can be strongly influenced by factors such as the range of stimuli used and the instructions given (Heller, 1991; Hellbrück, 1993; Hohmann, 1993). Often, listeners distribute their responses across the range of available categories whatever range of stimulus levels is used (Garner, 1954). Even for normal listeners, the variability of loudness judgments for a given sound level can be considerable (Elberling and Nielsen, 1993; Kiessling, 1997; Elberling, 1999). Given the uncertainty about the validity and reliability of loudness scaling procedures, it might be preferable to use a more objective measure of basilar-membrane compression, such as the ratio of slopes estimated in forward masking, or the ERB of the auditory filter estimated using notched-noise masking. In a clinical setting, it would not be necessary to measure the growth-of-masking functions using a large number of signal levels, as was done in the present experiment. Rather, reasonably accurate slope estimates could be obtained using just two signal levels, one 10 dB above and one 30 dB above the absolute threshold. In our experiments, it was always possible to use a signal at 30 dB above the absolute threshold without the masker becom-

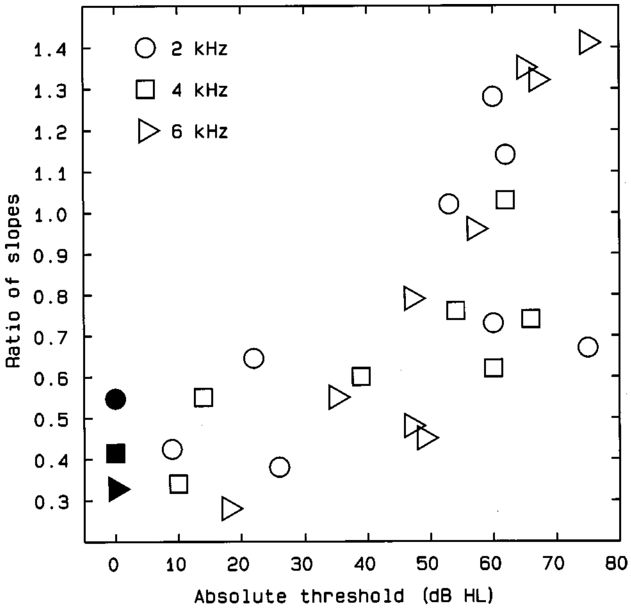

FIG. 10. Ratio of the slopes of the growth-of-masking functions in forward masking, plotted as a function of absolute threshold in dB HL at the test frequency. Each symbol represents results for one frequency, as indicated in the figure. The solid symbols at the far left show the mean ratios for the six normally hearing subjects. Small numbers indicate strong basilar-membrane compression, while numbers around 1 indicate little or no compression.

ing uncomfortably loud, although this might not be possible in cases of severe to profound hearing loss.

Another clinical application is in the estimation of inner hair-cell damage. There is evidence that inner hair-cell damage is associated with particular difficulty in understanding speech, especially when background noise is present (Killion, 1997; Hogan and Turner, 1998; Moore, 1998). Hearing-impaired persons with extensive inner hair-cell damage over a certain range of CFs may receive little or no benefit from amplification in that frequency range (Murray and Byrne, 1986; Hogan and Turner, 1998). Inner hair-cell damage could be estimated indirectly by estimating the hearing loss due to outer hair-cell damage from the ratio of slopes, and then subtracting that estimate from the overall loss. However, further work is needed to determine whether such an approach would be useful in clinical practice.

IV. SUMMARY AND CONCLUSIONS

We have examined the relationship between three different measures of the status of the cochlear active mechanism, at center frequencies of 2, 4, and 6 kHz, using subjects with normal hearing, with unilateral or highly asymmetric cochlear hearing loss, and with bilateral loss. The first measure, HL_{OHC}, was an indirect measure of the amount of the hearing loss attributable to OHC damage; this was based on loudness matches between the two ears of subjects with unilateral hearing loss and was derived using a loudness model. The steeper the rate of loudness growth in a given ear at a given frequency, the greater the estimate of HL_{OHC}. The second measure was the ERB of the auditory filter, which was estimated using the notched-noise method. The third measure was based on the ratios of the slopes of growth-of-masking functions obtained in forward masking for off-frequency and on-frequency maskers; small ratios indicate strong compression. The results show the following:

(1) For the hearing-impaired subjects, the ERB of the auditory filter was correlated with the absolute threshold at the test frequency ($r=0.58$ for hearing losses greater than 35 dB), but it was more highly correlated with HL_{OHC} ($r=0.75$ for values of HL_{OHC} greater than 25 dB). However, the difference between the two correlations failed to reach statistical significance. The ERB was not significantly correlated with HL_{IHC}, the estimated amount of the hearing loss attributable to inner hair-cell damage ($r=0.38$).

(2) For normally hearing subjects, the ratio of slopes in forward masking had mean values of 0.33, 0.42, and 0.55 at 6, 4, and 2 kHz, respectively. This may indicate that basilar-membrane compression decreases with decreasing frequency. However, the results at 2 kHz may have been affected by activation of the acoustic reflex which would tend to increase the ratio of slopes.

(3) For the subjects with hearing impairment, the ratio of

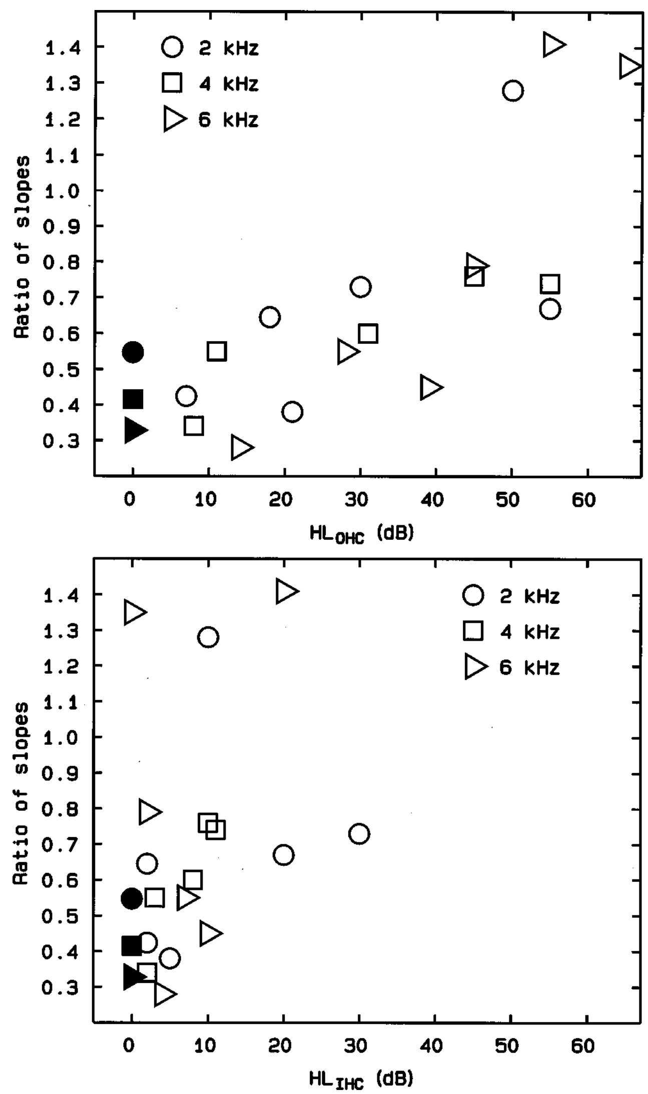

FIG. 11. Ratio of the slopes of the growth-of-masking functions in forward masking, plotted as a function of HL_{OHC} (upper panel) or HL_{IHC} (lower panel).

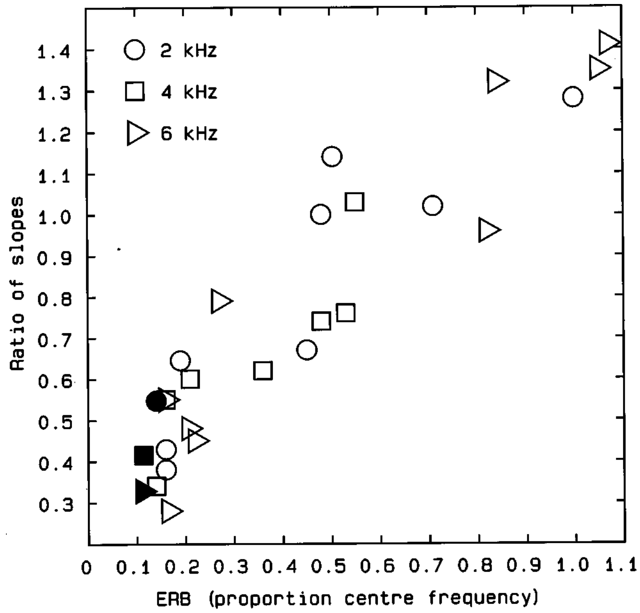

FIG. 12. Ratio of the slopes of the growth-of-masking functions in forward masking, plotted as a function of the ERB of the auditory filter. Each symbol represents results for one frequency, as indicated in the figure. The solid symbols at the far left show the mean ratios for the six normally hearing subjects, plotted as a function of the ERB values for normally hearing subjects given by Glasberg and Moore (1990).

slopes in forward masking was correlated with the absolute threshold at the test frequency ($r=0.56$ for hearing losses greater than 35 dB), but it was more highly correlated with HL_{OHC} ($r=0.68$ for values of HL_{OHC} greater than 25 dB). However, the difference between the two correlations failed to reach statistical significance. The ratio of slopes was not significantly correlated with HL_{IHC} ($r=0.26$).

(4) The ERB of the auditory filter was highly correlated with the ratio of slopes ($r=0.92$). This suggests that both of these measures give a reasonably direct measure of the status of the active mechanism at a given CF. The sharpness of tuning declines progressively as the amount of basilar-membrane compression decreases.

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Allen, J. B., and Jeng, P. S. (**1990**). ''Loudness growth in 1/2-octave bands (LGOB); a procedure for the assessment of loudness,'' J. Acoust. Soc. Am. **88**, 745–753.

Bonding, P. (**1979**). ''Critical bandwidth in loudness summation in sensorineural hearing loss,'' Br. J. Audiol. **13**, 23–30.

Bonding, P., and Elberling, C. (**1980**). ''Loudness summation across frequency under masking and in sensorineural hearing loss,'' Audiology **19**, 57–74.

Borg, E., Canlon, B., and Engström, B. (**1995**). ''Noise-induced hearing loss—Literature review and experiments in rabbits,'' Scand. Audiol. **24**, Suppl. 40, 1–147.

Chistovich, L. A. (**1957**). ''Frequency characteristics of masking effect,'' Biophys. J. **2**, 743–755.

Cox, R. M., Alexander, G. C., Taylor, I. M., and Gray, G. A. (**1997**). ''The contour test of loudness perception,'' Ear Hear. **18**, 388–400.

Elberling, C. (**1999**). ''Loudness scaling revisited,'' J. Am. Acad. Audiol **10**, 248–260.

Elberling, C., and Nielsen, C. (**1993**). ''The dynamics of speech and the auditory dynamic range in sensorineural hearing impairment,'' in *Recent Developments in Hearing Instrument Technology*, edited by J. Beilin and G. R. Jensen (Stougaard Jensen, Copenhagen).

Evans, E. F. (**1975**). ''The sharpening of frequency selectivity in the normal and abnormal cochlea,'' Audiology **14**, 419–442.

Evans, E. F., and Harrison, R. V. (**1976**). ''Correlation between outer hair cell damage and deterioration of cochlear nerve tuning properties in the guinea pig,'' J. Physiol. (London) **252**, 43–44.

Evans, E. F., Pratt, S. R., and Cooper, N. P. (**1989**). ''Correspondence between behavioural and physiological frequency selectivity in the guinea pig,'' Br. J. Audiol. **23**, 151–152.

Fletcher, H. (**1940**). ''Auditory patterns,'' Rev. Mod. Phys. **12**, 47–65.

Florentine, M., and Houtsma, A. J. M. (**1983**). ''Tuning curves and pitch matches in a listener with a unilateral, low-frequency hearing loss,'' J. Acoust. Soc. Am. **73**, 961–965.

Florentine, M., and Zwicker, E. (**1979**). ''A model of loudness summation applied to noise-induced hearing loss,'' Hearing Res. **1**, 121–132.

Fowler, E. P. (**1936**). ''A method for the early detection of otosclerosis,'' Arch. Otolaryngol. **24**, 731–741.

Garner, W. R. (**1954**). ''Context effects and the validity of loudness scales,'' J. Exp. Psychol. **48**, 218–224.

Glasberg, B. R., and Moore, B. C. J. (**1986**). ''Auditory filter shapes in subjects with unilateral and bilateral cochlear impairments,'' J. Acoust. Soc. Am. **79**, 1020–1033.

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

Hellbrück, J. (**1993**). *Hören* (Hogrefe Verlag, Göttingen).

Hellbrück, J., and Moser, L. M. (**1985**). ''Hörgeräte Audiometrie: Ein computer-unterstütztes psychologisches Verfahren zur Hörgeräteanpassung,'' Psychol. Beitr. **27**, 494–509.

Heller, O. (**1991**). ''Oriented category scaling of loudness and speech audiometric validation,'' in *Contributions to Psychological Acoustics*, edited by A. Schick (BIS, Oldenburg).

Hellman, R. P. (**1978**). ''Dependence of loudness growth on skirts of excitation patterns,'' J. Acoust. Soc. Am. **63**, 1114–1119.

Hellman, R. P., and Meiselman, C. H. (**1986**). ''Is high-frequency hearing necessary for normal loudness growth at low frequencies?,'' 12th ICA Paper B11-5.

Hellman, R. P., and Meiselman, C. H. (**1990**). ''Loudness relations for individual and groups in normal and impaired hearing,'' J. Acoust. Soc. Am. **88**, 2596–2606.

Hellman, R. P., and Meiselman, C. H. (**1993**). ''Rate of loudness growth for pure tones in normal and impaired hearing,'' J. Acoust. Soc. Am. **93**, 966–975.

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

Hogan, C. A., and Turner, C. W. (**1998**). ''High-frequency audibility: Benefits for hearing-impaired listeners,'' J. Acoust. Soc. Am. **104**, 432–441.

Hohmann, V. (**1993**). *Dynamikkompression für Hörgeräte-Psychoakustische Grundlagen und Algorithmen* (VDI-Verlag, Düsseldorf).

Howell, D. C. (**1997**). *Statistical Methods for Psychology*, 4th ed. (Duxbury, Belmont, CA).

Jesteadt, W., Bacon, S. P., and Lehman, J. R. (**1982**). ''Forward masking as a function of frequency, masker level, and signal delay,'' J. Acoust. Soc. Am. **71**, 950–962.

Johnson-Davies, D., and Patterson, R. D. (**1979**). ''Psychophysical tuning curves: restricting the listening band to the signal region,'' J. Acoust. Soc. Am. **65**, 675–770.

Khanna, S. M., and Leonard, D. G. B. (**1982**). ''Basilar membrane tuning in the cat cochlea,'' Science **215**, 305–306.

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

Kiessling, J. (**1997**). ''Scaling methods for the selection, fitting and evaluation of hearing aids,'' in *Psychoacoustics, Speech and Hearing Aids*, edited by B. Kollmeier (World Scientific, Singapore).

Kiessling, J., Steffens, T., and Wagner, I. (**1993**). ''Untersuchungen zur praktischen Anwendbarkeit der Lautheitsskalierung,'' Audi. Akust. **4/93**, 100–115.

Killion, M. C. (**1997**). ''Hearing aids: Past, present and future: Moving toward normal conversations in noise,'' Br. J. Audiol. **31**, 141–148.

Laroche, C., Hétu, R., Quoc, H. T., Josserand, B., and Glasberg, B. (**1992**). ''Frequency selectivity in workers with noise-induced hearing loss,'' Hearing Res. **64**, 61–72.

Launer, S. (**1995**). ''Loudness perception in listeners with sensorineural hearing impairment,'' Ph.D. thesis, Oldenburg, Germany.

Launer, S., Hohmann, V., and Kollmeier, B. (**1997**). ''Modeling loudness growth and loudness summation in hearing-impaired listeners,'' in *Modeling Sensorineural Hearing Loss*, edited by W. Jesteadt (Erlbaum, Mahwah, NJ).

Leshowitz, B., Linstrom, R., and Zurek, P. (**1975**). ''Psychophysical tuning curves in normal and impaired ears,'' J. Acoust. Soc. Am. **58**, S71.

Liberman, M. C., and Dodds, L. W. (**1984**). ''Single neuron labeling and chronic cochlea pathology. III. Stereocilia damage and alterations in threshold tuning curves,'' Hearing Res. **16**, 54–74.

Liberman, M. C., Dodds, L. W., and Learson, D. A. (**1986**). ''Structure-function correlation in noise-damaged ears: A light and electron-microscopic study,'' in *Basic and Applied Aspects of Noise-Induced Hearing Loss*, edited by R. J. Salvi, D. Henderson, R. P. Hamernik, and V. Colletti (Plenum, New York).

Moore, B. C. J. (**1978**). ''Psychophysical tuning curves measured in simultaneous and forward masking,'' J. Acoust. Soc. Am. **63**, 524–532.

Moore, B. C. J. (**1981**). ''Interactions of masker bandwidth with signal duration and delay in forward masking,'' J. Acoust. Soc. Am. **70**, 62–68.

Moore, B. C. J. (**1986**). ''Parallels between frequency selectivity measured psychophysically and in cochlear mechanics,'' Scand. Audiol. Suppl. **25**, 139–152.

Moore, B. C. J. (**1998**). *Cochlear Hearing Loss* (Whurr, London).

Moore, B. C. J., Alcántara, J. I., and Dau, T. (**1998**). ''Masking patterns for sinusoidal and narrowband noise maskers,'' J. Acoust. Soc. Am. **104**, 1023–1038.

Moore, B. C. J., and Glasberg, B. R. (**1982**). ''Contralateral and ipsilateral cueing in forward masking,'' J. Acoust. Soc. Am. **71**, 942–945.

Moore, B. C. J., and Glasberg, B. R. (**1983**). ''Growth of forward masking for sinusoidal and noise maskers as a function of signal delay: implications for suppression in noise,'' J. Acoust. Soc. Am. **73**, 1249–1259.

Moore, B. C. J., and Glasberg, B. R. (**1985**). ''The danger of using narrow-band noise maskers to measure suppression,'' J. Acoust. Soc. Am. **77**, 2137–2141.

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

Moore, B. C. J., Glasberg, B. R., and Baer, T. (**1997**). ''A model for the prediction of thresholds, loudness and partial loudness,'' J. Audio Eng. Soc. **45**, 224–240.

Moore, B. C. J., Glasberg, B. R., Hess, R. F., and Birchall, J. P. (**1985**). ''Effects of flanking noise bands on the rate of growth of loudness of tones in normal and recruiting ears,'' J. Acoust. Soc. Am. **77**, 1505–1515.

Moore, B. C. J., Glasberg, B. R., and Vickers, D. A. (**1999**). ''Further evaluation of a model of loudness perception applied to cochlear hearing loss,'' J. Acoust. Soc. Am. **106**, 898–907.

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

Murray, N., and Byrne, D. (**1986**). ''Performance of hearing-impaired and normal hearing listeners with various high-frequency cut-offs in hearing aids,'' Aust. J. Audiol. **8**, 21–28.

Neely, S. T. (**1993**). ''A model of cochlear mechanics with outer hair cell motility,'' J. Acoust. Soc. Am. **94**, 137–146.

Neff, D. L. (**1985**). ''Stimulus parameters governing confusion effects in forward masking,'' J. Acoust. Soc. Am. **78**, 1966–1976.

Neff, D. L. (**1986**). ''Confusion effects with sinusoidal and narrowband-noise forward maskers,'' J. Acoust. Soc. Am. **79**, 1519–1529.

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

O'Loughlin, B. J., and Moore, B. C. J. (**1981b**). ''Off-frequency listening: effects on psychoacoustical tuning curves obtained in simultaneous and forward masking,'' J. Acoust. Soc. Am. **69**, 1119–1125.

Oxenham, A. J. (**1997**). ''Increment and decrement detection in sinusoids as a measure of temporal resolution,'' J. Acoust. Soc. Am. **102**, 1779–1790.

Oxenham, A. J., and Moore, B. C. J. (**1994**). ''Modeling the additivity of nonsimultaneous masking,'' Hearing Res. **80**, 105–118.

Oxenham, A. J., and Moore, B. C. J. (**1995**). ''Additivity of masking in normally hearing and hearing-impaired subjects,'' J. Acoust. Soc. Am. **98**, 1921–1935.

Oxenham, A. J., and Moore, B. C. J. (**1997**). ''Modeling the effects of peripheral nonlinearity in listeners with normal and impaired hearing,'' in *Modeling Sensorineural Hearing Loss*, edited by W. Jesteadt (Erlbaum, Mahwah, New Jersey).

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

Pascoe, D. P. (**1978**). ''An approach to hearing aid selection,'' Hearing Inst. **29**, 12–16.

Patterson, R. D. (**1976**). ''Auditory filter shapes derived with noise stimuli,'' J. Acoust. Soc. Am. **59**, 640–654.

Patterson, R. D., and Nimmo-Smith, I. (**1980**). ''Off-frequency listening and auditory filter asymmetry,'' J. Acoust. Soc. Am. **67**, 229–245.

Patterson, R. D., Nimmo-Smith, I., Weber, D. L., and Milroy, R. (**1982**). ''The deterioration of hearing with age: frequency selectivity, the critical ratio, the audiogram, and speech threshold,'' J. Acoust. Soc. Am. **72**, 1788–1803.

Patuzzi, R. B. (**1992**). ''Effects of noise on auditory nerve fiber response,'' in *Noise Induced Hearing Loss*, edited by A. Dancer, D. Henderson, R. Salvi, and R. Hamernik (Mosby Year Book, St. Louis).

Pick, G., Evans, E. F., and Wilson, J. P. (**1977**). ''Frequency resolution in patients with hearing loss of cochlear origin,'' in *Psychophysics and Physiology of Hearing*, edited by E. F. Evans and J. P. Wilson (Academic, London).

Pickles, J. O. (**1986**). ''The neurophysiological basis of frequency selectivity,'' in *Frequency Selectivity in Hearing*, edited by B. C. J. Moore (Academic, London).

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

Rhode, W. S. (**1971**). ''Observations of the vibration of the basilar membrane in squirrel monkeys using the Mössbauer technique,'' J. Acoust. Soc. Am. **49**, 1218–1231.

Rhode, W. S., and Cooper, N. P. (**1996**). ''Nonlinear mechanics in the apical turn of the chinchilla cochlea *in vivo*,'' Aud. Neurosci. **3**, 101–121.

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

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

Ruggero, M. A., Rich, N. C., Recio, A., Narayan, S. S., and Robles, L. (**1997**). ''Basilar-membrane responses to tones at the base of the chinchilla cochlea,'' J. Acoust. Soc. Am. **101**, 2151–2163.

Ruggero, M. A., Rich, N. C., Robles, L., and Recio, A. (**1996**). ''The effects of acoustic trauma, other cochlea injury and death on basilar membrane responses to sound,'' in *Scientific Basis of Noise-Induced Hearing Loss*, edited by A. Axelsson, H. Borchgrevink, R. P. Hamernik, P. A. Hellstrom, D. Henderson, and R. J. Salvi (Thieme, Stockholm).

Sellick, P. M., Patuzzi, R., and 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.

Steinberg, J. C., and Gardner, M. B. (**1937**). ''The dependency of hearing impairment on sound intensity,'' J. Acoust. Soc. Am. **9**, 11–23.

Stone, M. A., Glasberg, B. R., and Moore, B. C. J. (**1992**). ''Simplified measurement of impaired auditory filter shapes using the notched-noise method,'' Br. J. Audiol. **26**, 329–334.

Thornton, A. R., and Abbas, P. J. (**1980**). ''Low-frequency hearing loss: perception of filtered speech, psychophysical tuning curves, and masking,'' J. Acoust. Soc. Am. **67**, 638–643.

Weber, D. L., and Green, D. M. (**1978**). ''Temporal factors and suppression effects in backward and forward masking,'' J. Acoust. Soc. Am. **64**, 1392–1399.

Williams, E. J. (**1959**). ''The comparison of regression variables,'' J. Royal. Stat. Soc. (B) **21**, 396–399.

Yates, G. K. (**1990**). ''Basilar membrane nonlinearity and its influence on auditory nerve rate-intensity functions,'' Hearing Res. **50**, 145–162.
Yates, G. K. (**1995**). ''Cochlear structure and function,'' in *Hearing*, edited by B. C. J. Moore (Academic, San Diego).
Zwicker, E., Flottorp, G., and Stevens, S. S. (**1957**). ''Critical bandwidth in loudness summation,'' J. Acoust. Soc. Am. **29**, 548–557.
Zwicker, E., and Scharf, B. (**1965**). ''A model of loudness summation,'' Psychol. Rev. **72**, 3–26.