Pitfalls in behavioral estimates of basilar-membrane compression in humans[a]

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Psychoacoustic estimates of basilar-membrane compression often compare on- and off-frequency forward masking. Such estimates involve assuming that the recovery from forward masking for a given signal frequency is independent of masker frequency. To test this assumption, thresholds for a brief 4-kHz signal were measured as a function of masker-signal delay. Comparisons were made between on-frequency (4 kHz) and off-frequency (either 2.4 or 4.4 kHz) maskers, adjusted in level to produce the same amount of masking at a 0-ms delay between masker offset and signal onset. Consistent with the assumption, forward-masking recovery from a moderate-level (83 dB SPL) 2.4-kHz masker and a high-level (92 dB SPL) 4.4-kHz masker was the same as from the equivalent on-frequency maskers. In contrast, recovery from a high-level (92 dB SPL) 2.4-kHz forward masker was slower than from the equivalent on-frequency masker. The results were used to simulate temporal masking curves, taking into account the differences in on- and off-frequency masking recoveries at high levels. The predictions suggest that compression estimates assuming frequency-independent masking recovery may overestimate compression by as much as a factor of 2. The results suggest caution in interpreting forward-masking data in terms of basilar-membrane compression, particularly when high-level maskers are involved.
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I. INTRODUCTION

Psychophysical methods for estimating gain and compression in the healthy human cochlea have received considerable attention over the past decade (e.g., Oxenham and Plack, 1997; Nelson *et al.*, 2001; Lopez-Poveda *et al.*, 2003; Plack *et al.*, 2004; Rosengard *et al.*, 2005). These methods are attractive because they provide a potential window into the characteristics of the basilar-membrane (BM) response in humans, which cannot be measured directly. A number of different psychophysical paradigms have been used. In one, termed growth of masking (GOM), the level of a forward masker required to just mask a brief tonal signal is measured as a function of signal level, with the gap between masker offset and signal onset held constant (Oxenham and Plack, 1997). In another paradigm, termed the temporal masking curve (TMC) method, the level of a forward masker required to just mask a brief tonal signal is measured as a function of the gap between the masker offset and the signal onset, with the level of the signal held at a low constant value (Nelson *et al.*, 2001; Lopez-Poveda *et al.*, 2003; Plack *et al.*, 2004; Rosengard *et al.*, 2005). In both paradigms, on-frequency masking functions, where the masker and signal are at the same frequency, are compared with off-frequency masking functions, where the masker frequency is well below that of the signal.

Because these measures are indirect, they rely on a number of assumptions. First, all the techniques assume that the signal is detected when it evokes excitation at or near a place along the BM with a characteristic frequency (CF) equal to the signal frequency (CF_s) that is sufficient to produce a certain criterion increase in the decision variable over the value representing the response to a masker alone. This assumption allows conclusions to be drawn about the response at the CF_s, based on the signal's masked threshold. The conditions necessary for this assumption to hold are maintained by presenting the signal in the presence of a spectrally shaped noise designed to limit the audible spread of the signal's excitation (e.g., Oxenham and Plack, 1997) or by limiting the signal to a very low level, so that its spread of excitation along the BM remains minimal (e.g., Nelson *et al.*, 2001). A second assumption, which is also necessary for both the GOM and TMC paradigms, is that the response of the BM at CF_s is linear when presented with tones well below the signal frequency. This assumption is based on physiological findings in other mammals, showing that the BM response to tones more than half an octave below the CF of the place of measurement is linear, at least in the base of the cochlea (e.g., Rhode and Robles, 1974; Murugasu and Russell, 1995; Ruggero *et al.*, 1997). A third assumption is that the effectiveness of a forward masker after a given delay from its offset is determined by cochlear filtering at the signal place, and that once filtering has occurred, all maskers with the same temporal envelope characteristics have an equivalent masking effect, regardless of their spectral com-

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position. In other words, the masker excitation at CF_s determines the signal threshold, regardless of the masker spectrum.

This third assumption has no direct physiological support, although for simultaneous masking it forms the basis of the well-known power spectrum model of masking (e.g., Fletcher, 1940). From a physiological standpoint, given the complex interactions that occur between inhibitory and excitatory inputs as early as the cochlear nucleus (e.g., Wickesberg and Oertel, 1988; Ryugo and Parks, 2003), it seems at least possible that such an assumption may not hold. Nevertheless, early studies using these assumptions have derived estimates of BM input-output functions that are in good agreement with direct physiological measures in other mammals (e.g., Oxenham and Plack, 1997; Nelson *et al.*, 2001). Furthermore, the effect of cochlear hearing loss on these estimates (e.g., Oxenham and Plack, 1997; Plack *et al.*, 2004) seems to be in line with physiological measures in other species following cochlear damage or dysfunction (Ruggero *et al.*, 1997).

Incorporated within the third assumption is the prediction that the recovery from forward masking for a given signal frequency is independent of masker frequency, once masker effectiveness has been equated. For instance, if two forward maskers of the same duration but different frequencies (or with different spectral content) produce the same amount of masking at one masker-signal delay, then they should also produce the same amount of masking at any other delay. This assumption is necessary for the TMC method, in which on- and off-frequency masker levels at threshold are compared over a large range of masker-signal delays. With this method, the comparison between on- and off-frequency masker levels can be used to derive BM input-output curves only if it is assumed that the "internal" recovery from forward masking (i.e., after the effects of peripheral filtering and compression) is the same for both on- and off-frequency maskers.

Unlike the first two assumptions, the third—of masker-independent recovery from forward masking—can be tested psychophysically. There are some studies that have compared forward masking at different signal frequencies, using both on-frequency (Jesteadt *et al.*, 1982) and off-frequency (Stainsby and Moore, 2006) maskers. However, these do not address the question of whether the rate of recovery from forward masking changes with masker frequency when the signal frequency is kept constant. We are aware of only one psychophysical study that has addressed this question directly. Nelson and Pavlov (1989) used a 1-kHz signal that was fixed at a level just above the quiet threshold. They measured the TMC, i.e., the level of a forward masker needed to just mask the signal as a function of the masker-signal delay, for masker frequencies of 900, 1000, and 1100 Hz. Although the TMCs appeared to have different slopes for the different masker frequencies, after incorporating a simple normalization based on the presumed attenuation of the masker level by the auditory filter centered on the signal frequency, the data for all three masker frequencies could be fitted very well by one line. Nelson and Pavlov (1989) concluded that the apparent differences between the original slopes were due to the difference between masker levels that were needed to produce the same output of the filter centered on the signal frequency. However, because all the masker frequencies were within 10% of the signal frequency, none of the conditions provides a very strong test of masker-frequency independence for forward masking. In particular, to render this assumption valid for behavioral measures of BM input-output functions, the test would need to include masker frequencies that were well below the signal frequency, to approximate the off-frequency maskers used in the GOM and TMC paradigms. Thus, to our knowledge, no physiological or behavioral study has yet provided convincing support for the assumption, as used by most psychophysical methods for estimating BM gain and compression in humans, that the recovery from forward masking for a given signal is independent of masker frequency.

The aim of this study was to test the hypothesis that the rate of recovery from forward masking is the same for different masker frequencies, once masker effectiveness has been equated at a given masker-signal delay. A confirmation of the hypothesis would strengthen the theoretical underpinnings of compression measures based on TMCs, which rely on the assumption when deriving BM input-output functions. On the other hand, if the hypothesis is not supported, the accuracy of at least some of the derived behavioral estimates of BM input-output functions may be questioned.

II. FORWARD MASKING FOLLOWING ON- AND OFF-FREQUENCY MASKERS

A. Stimuli and procedure

The signal was always a 10-ms 4-kHz tone, gated on and off with 5 ms raised-cosine ramps (no steady-state portion). Detection thresholds were measured for the signal using a three-alternative forced-choice (3AFC) procedure, coupled with an adaptive tracking technique that estimated the 70.7% correct point on the psychometric function (Levitt, 1971). The threshold level of the signal was measured in quiet, in a simultaneous background noise, and in the presence of sinusoidal forward maskers.

1. Thresholds in quiet

In the quiet condition, the signal appeared randomly in one of the three observations intervals while the other two contained silence. The three intervals were marked by lights on a computer screen. At the beginning of each run, the signal was set to a level at which it was clearly audible. The signal level was decreased by 8 dB after two consecutive correct responses and increased by the same step size after each incorrect response until the second reversal was obtained. The step size was then reduced to 4 dB until the fourth reversal. After that, the step was further reduced to 2 dB for the remaining eight reversals. A run terminated after 12 reversals and a threshold estimate was obtained by averaging the signal levels at the last eight reversals. Three thresholds obtained from single runs were averaged to compute the final threshold estimate for each subject. In this and all subsequently described tasks, visual feedback indicating the correct response was provided after each trial.

2. Thresholds in simultaneous masking by noise

In all the forward-masking experiments, a simultaneous low-level background noise was added to reduce any potential "off-frequency listening" (e.g., O'Loughlin and Moore, 1981). The noise consisted of two bands spectrally placed around the signal frequency. The lower-frequency band extended from 2260 to 3200 Hz (a half-octave band) and the higher-frequency band extended from 5200 to 6200 Hz. As the signal level was varied adaptively, the overall noise level was also varied to remain 20 dB below the level required to mask the signal.

To determine the necessary noise levels during the adaptive procedure, the growth of simultaneous masking for the 10-ms 4-kHz signal was measured as a function of the noise level, prior to the main experiment. The 3AFC procedure and the steps used in adaptive tracking were the same as for measuring the threshold for detecting the signal in quiet. In each trial, the noise was turned on 300 ms before the beginning of the first observation interval. The noise continued throughout the three observation intervals and ended with the offset of the signal in the third interval (or where the signal offset would have been if the signal had been presented in the third interval). A new sample of noise was drawn for every trial. Thresholds were measured for overall noise levels between 10 and 80 dB SPL.

Once thresholds had been measured over this range of masker levels, the masked signal thresholds were plotted as a function of the simultaneous masker level for each subject individually and were fitted by a quadratic equation with the coefficients estimated from a least-squares fit. During the forward-masking experiments, the noise level on each trial was set by computing the level based on the quadratic fit to the current signal level, and subtracting 20 dB from the obtained value.

3. Forward-masking thresholds

The recovery from forward masking was measured for the 4-kHz signal presented after a 150-ms forward masker (total duration), gated on and off with 5-ms raised-cosine ramps. The recovery curves were measured for a 4-kHz (on-frequency) masker, and for three off-frequency maskers, two below the signal, with a frequency of 2.4 kHz, and one above the signal, with a frequency of 4.4 kHz. The levels of the 2.4-kHz maskers (below the signal frequency) were 92 and 83 dB SPL (90 and 83 dB SPL for S1); the level of the 4.4-kHz masker (above the signal frequency) was 92 dB SPL. For each off-frequency masker, the level of the on-frequency masker was found that produced a similar masked threshold at a 0-ms delay between the masker offset and the signal onset. To determine the necessary on-frequency masker level, the following steps were performed separately for each off-frequency masker and each subject:

(1) For the off-frequency masker, the masker-signal delay was set to 0 ms and the signal level was varied adaptively to find the masked threshold. The stepping rule in adapting signal levels was the same as for measuring detection of the signal in quiet. Three threshold estimates were obtained and averaged. When the standard deviation of the mean exceeded 6 dB, three additional estimates were obtained and all the single-run thresholds were averaged to obtain the final estimate. On rare occasions when there was a clear outlier (a threshold that was more than 10 dB higher than any of the other single-run estimates), the discrepant threshold was not included in the mean.

(2) The 4-kHz signal was set to a level corresponding to the masked threshold obtained in step 1. The signal was preceded by a 4-kHz (on-frequency) masker and the delay between the masker offset and the signal onset was 0 ms. In the 3AFC task, the on-frequency masker level was varied adaptively to find the level needed just to mask the signal. The step sizes in adapting the masker level were the same as for measuring detection of the signal in quiet, except that the masker level was increased after two consecutive correct responses and decreased after each incorrect response. The masker level at threshold was computed by averaging three to six single-run estimates. As in step 1, occasional outliers (masker levels lower by more than 10 dB than any other estimate) were excluded from the mean.

(3) The level of the 4-kHz masker was set to the value obtained as the final threshold estimate in step 2. A 4-kHz signal was presented after a 0-ms delay, and its level was varied adaptively as in step 1 to find masked threshold. Three single-run threshold estimates were averaged to compute the final estimate. The final estimate was compared with the mean threshold obtained in step 1. If the estimate fell within ± 2 dB of the value obtained in step 1, the masking produced by the 4-kHz masker was considered equivalent to that of the off-frequency masker. In cases where the masked threshold fell outside that range of signal levels, the measurement was repeated with the level of the 4-kHz masker increased or decreased relative to the level obtained in step 2. The level adjustments were made on a trial-and-error basis, but typically one additional adjustment was sufficient to obtain a signal level at threshold that fell in the ± 2 dB range around the level obtained in step 1. In such cases, the "adjusted" 4-kHz masker level was considered equivalent to that of the off-frequency masker.

Upon completion of steps 1–3, recovery functions were measured with the masker levels fixed and the signal level varied adaptively, for masker-signal offset-onset delays ranging from 0 to 115 ms. For half the listeners, recovery functions were first measured for the 92-dB 2.4-kHz masker and the equivalent (at a 0-ms delay) 4-kHz masker. The recovery functions for the 83-dB 2.4-kHz masker and the equivalent 4-kHz masker were measured subsequently. For the other half of the listeners, testing was carried out in the reverse order. For listener S6, recovery functions were first measured in the condition involving the 4.4-kHz masker. This listener was later tested using the two 2.4-kHz maskers. Listeners S1–S3 were tested with the 4.4-kHz masker after they completed the conditions involving the 2.4-kHz maskers. Thus, the experiment consisted of three masking conditions, each involving the measurement of two recovery functions, one

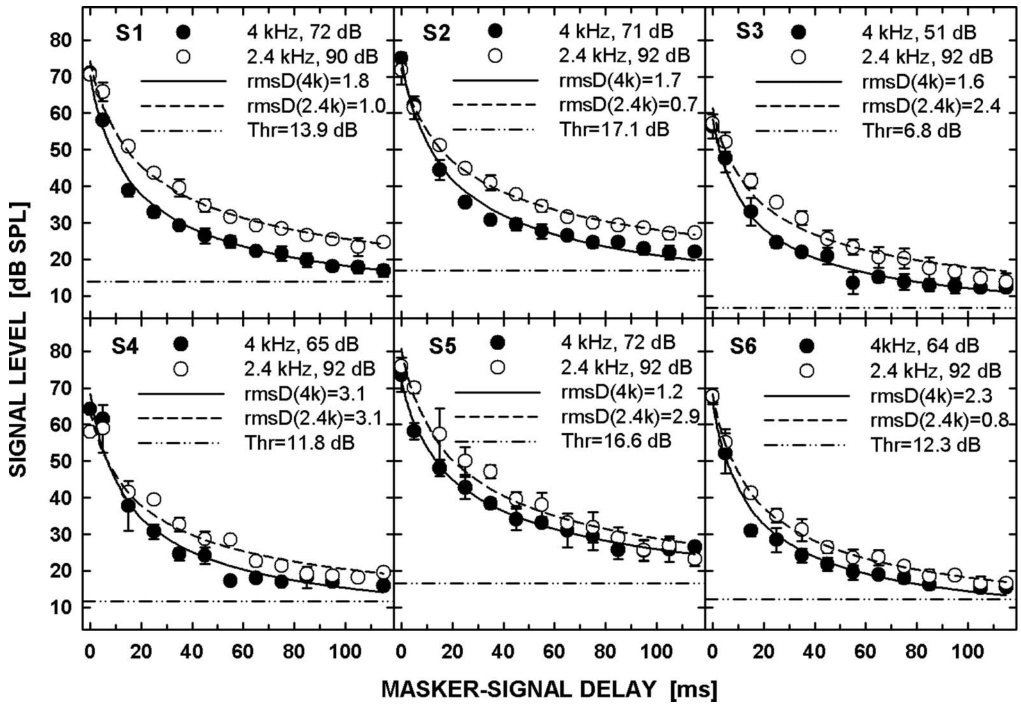

FIG. 1. Recovery from forward masking in the LF_HL condition, i.e., for a 2.4-kHz masker presented at 92 dB SPL (open symbols) and a 4-kHz masker that produced similar masked thresholds at a 0-ms delay (filled symbols). The dashed and solid lines show power-function fits to the data for the 2.4- and 4-kHz maskers, respectively. Value of rms deviations (rmsD) are provided in the legend, for each fitted function. The dashed-dotted line shows threshold for detecting the 4-kHz signal in quiet.

for an off-frequency masker and the other for an on-frequency masker. The condition involving a 92-dB SPL 2.4-kHz masker will be referred to as the low-frequency high-level (LF_HL) condition; the condition involving an 83-dB SPL 2.4-kHz masker will be referred to as the low-frequency low-level (LF_LL) condition, and the condition involving a 92-dB SPL 4.4-kHz masker will be referred to as the high-frequency high-level (HF_HL) condition.

For a given condition, the masker order (on- or off-frequency masker first) was selected randomly for the measurement of each recovery function and for each subject. Once the masker frequency was selected, the recovery function was measured with the masker-signal delay chosen randomly for each repetition. A new random order was selected for each repetition of each condition. Three to six threshold estimates were obtained for each delay. The rule for eliminating outliers was the same as for step 1 listed above. About 5% of runs were discarded as outliers.

Off-frequency listening was controlled by the presence of the background noise, as described above. Precautions were also taken to reduce or eliminate the effect of temporal confusion that has been shown to affect the amount of on-frequency forward masking at short masker-signal delays (Moore and Glasberg, 1982; Neff, 1986). A 70-dB SPL 7-kHz tone was gated on and off with the masker, and was presented to the contralateral ear. The tone served as a cue that marked the temporal beginning and end of the masker. The contralateral tone was used in all conditions, including the measurement of growth of simultaneous masking for the short signal presented in background noise.

All the stimuli were generated digitally on a personal computer with a sampling rate of 48 kHz and played out via a 24-bit LynxStudio Lynx22 sound card. The stimuli were presented via the left earphone of a Sennheiser HD 580 headset, except for the contralateral cuing tone, which was presented via the right earphone. The listeners were tested in a double-walled sound-attenuating booth and responded via a computer keyboard or mouse.

B. Listeners

Seven listeners participated in the study. All had normal hearing as evidenced by their quiet thresholds measured using an ANSI certified audiometer (Madsen Conera). The listeners had thresholds that were below 15 dB HL for audiometric frequencies between 0.25 and 8 kHz. All the listeners were paid for their participation, except S1 who is the first author. Not every listener participated in every condition: Listeners S1–S6 completed conditions LF_HL and LF_LL, and four listeners from that group (S1–S3 and S6) and an additional listener (S7) completed condition HF_HL. The listeners received at least 2 h of practice before the data collection commenced.

C. Results

Functions representing recovery from forward masking in the LF_HL condition for the six listeners are shown in Fig. 1. Each panel shows data from one listener. Masked thresholds for a 92-dB SPL 2.4-kHz masker, plotted as a function of masker-signal delay, are shown by the open circles. Masked thresholds for the 4-kHz masker that produced an equivalent masked threshold at a 0-ms delay are shown by the filled circles. For convenience, such an on-frequency masker will be referred to hereafter as an "equivalent

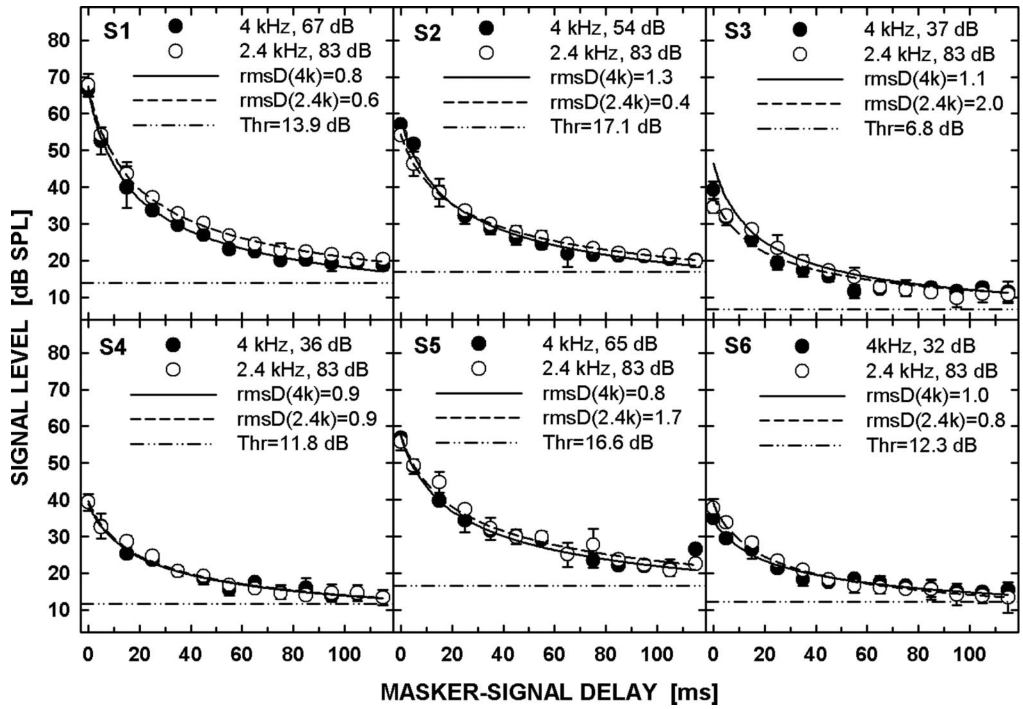

FIG. 2. As Fig. 1 except for the LF_LL condition, in which the 2.4-kHz masker was presented at 83 dB SPL.

masker" even if it did not produce the same masked thresholds at delays other than 0 ms. The levels of the equivalent 4-kHz masker are presented in the legend for each listener. The dashed horizontal line represents the threshold for detecting the 10-ms 4-kHz signal in quiet.

At the 0-ms delay, the two maskers produced very similar amounts of masking, as intended. As the delay increased, the two functions diverged for all listeners, and thresholds for the off-frequency masker fell above those obtained for the on-frequency masker. This indicates that the rate of recovery was slower for the off-frequency masker than for the on-frequency masker. For four listeners (S3–S6), masked thresholds for the two maskers became similar at the longest masker-signal delays. For the on-frequency masker, the masked threshold remained constant for masker-signal delays greater than 55 ms for S3 and S4, and delays greater than 85 ms for S5, despite the fact that recovery was not yet complete. Over the same range of delays, the threshold for the off-frequency masker continued to decrease. Because the on-frequency masking reflected by this residual threshold elevation exhibited extremely slow recovery and was not consistently present in the data of all the listeners, the data should probably not be interpreted as reflecting faster recovery for the off-frequency masker at long delays.[1] The solid lines in Fig. 1 represent power-function fits to the data. The fitted function was defined as

$$L_s = a(d/10)^{-b}, \qquad (1)$$

where L_S represents the signal level (dB SPL) at masked threshold predicted by the fitted function, d is the delay (milliseconds) between the masker offset and the signal offset, and a and b are free parameters that were adjusted to produce the best fit using the least-squares method. Parameter b determines the rate of recovery from forward masking. The offset-offset interval (rather than the offset-onset interval) was selected to avoid values of zero, which produce an undefined value of L_s.

Data for the LF_LL condition are presented in Fig. 2. The open symbols show masked thresholds obtained for the 83-dB SPL 2.4-kHz masker and the filled symbols show thresholds for the equivalent 4-kHz masker. In contrast to the LF_HL condition, the two maskers produced similar thresholds at all delays between the masker and the signal, suggesting the same rate of recovery from forward masking for the lower-level (83 dB SPL) off-frequency masker and equivalent on-frequency masker.

Figure 3 shows comparisons between the values of parameter b that determined the recovery rates in Eq. (1) for the on- (filled bars) and off-frequency (unfilled bars) maskers. The left and right panels show the comparisons for the LF_HL and LF_LL conditions, respectively.

For the LF_HL condition, the values of exponent b are smaller for the 2.4-kHz masker, indicating a slower rate of recovery than for the equivalent 4-kHz masker, for all the listeners except S5. A paired t-test comparing b values for the two maskers confirmed that the difference was significant [$t(5)=4.37$, $p=0.007$]. This result indicates that, despite producing the same amount of masking at the selected masker-signal delay of 0 ms, the rate of recovery from forward masking differed between the two maskers. Because the signal frequency was the same in both cases, and because the range of signal levels was very similar, effects of peripheral compression cannot explain the observed differences between the recovery rates.

In the LF_LL condition, three listeners showed a slightly slower recovery for the 2.4-kHz masker (S1, S2, and S3), but the other three showed either no difference between the re-

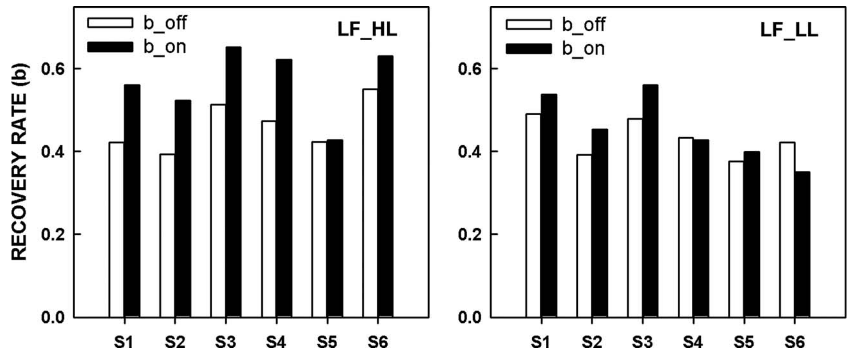

FIG. 3. Values of exponent b in Eq. (1) that characterizes the rate of recovery from forward masking for a 2.4-kHz masker (open bars) and a 4-kHz masker that produced similar masked threshold at a 0-ms delay (filled bars). Values of parameter b are shown for the LF_HL condition (left panel) and the LF_LL condition (right panel).

covery rates for the two maskers or a slight difference in the opposite direction. A paired t-test showed that the difference between the values of exponents b for the two maskers was not significant in this condition $[t(5)=1.02,\ p=0.35]$. Thus, in contrast to the results from the LF_HL condition, data from the lower masker level generally follow a pattern that is consistent with the assumption of equal rates of recovery, independent of masker frequency.

The final condition, HF_HL, allowed us to test whether the different on- and off-frequency decay curves found in the LF_HL condition were due solely to the high sound pressure level of the masker, or whether the results also depended on masker frequency. Figure 4 shows recovery functions for the HF_HL condition obtained for five listeners. Open symbols represent masked thresholds plotted as a function of the delay between the masker offset and the signal onset, for the 92-dB SPL 4.4-kHz masker. Filled symbols show thresholds for the equivalent 4-kHz masker. Equation (1) was fitted to the data and the values of exponent b were estimated. The rates of recovery for the 4- and 4.4-kHz maskers were very similar for all the listeners with the exception of S7. A paired t-test revealed no significant difference between the b-values for the two maskers $[t(4)=0.133,\ p=0.9]$. As with the LF_LL condition, the results from the HF_HL condition are consistent with the hypothesis that the recovery from forward masking is independent of masker frequency. Thus, it appears that a high off-frequency masker level is not sufficient in itself to produce different on- and off-frequency decay curves.

In summary, for two of the three conditions (LF_LL and HF_HL), recovery from forward masking was found to be the same for on- and off-frequency maskers. However, for the LF_HL condition, this was not the case; instead, the 92-dB SPL off-frequency masker produced a slower recovery from forward masking than the on-frequency masker, even though both produced the same amount of masking at a 0-ms

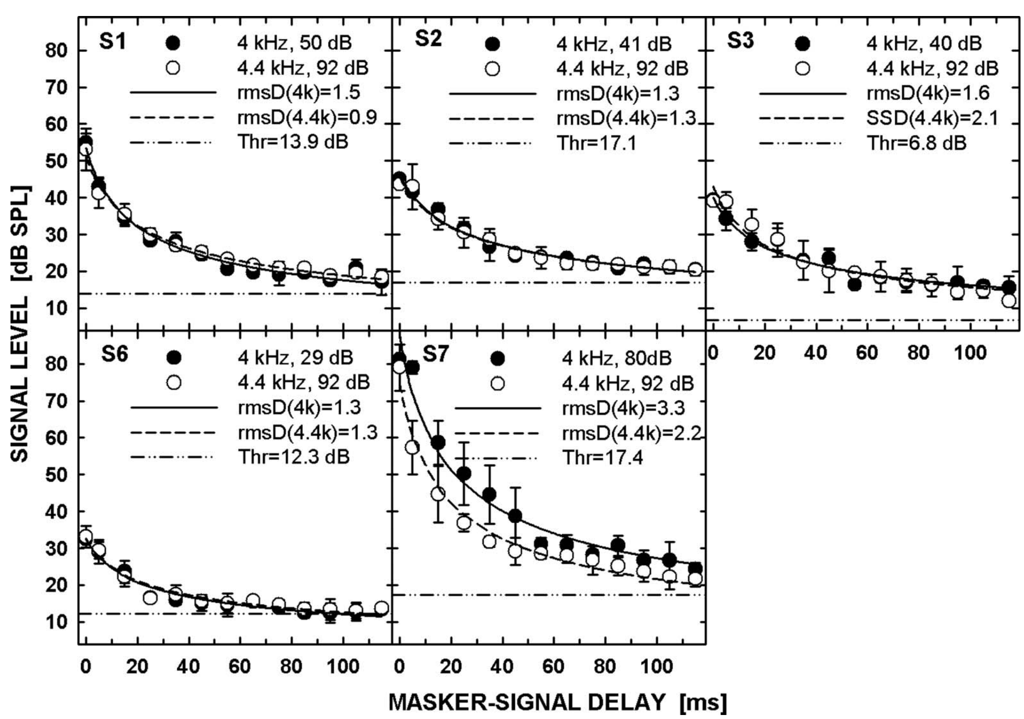

FIG. 4. Recovery from forward masking in the HF_HL condition, i.e., for a 4.4-kHz masker presented at 92 dB SPL (open symbols) and a 4-kHz masker that produced similar masked threshold at a 0-ms delay (filled symbols). Otherwise as Fig. 1.

masker-signal delay. The LF_HL and LF_LL conditions are directly relevant to studies that have estimated BM compression using psychophysical TMC method, as they rely on comparing on-frequency and off-frequency forward-masking thresholds with the off-frequency masker well below the signal frequency and often at high levels (as in our LF_HL condition).

D. Discussion

The listeners in our study exhibited a slower recovery rate for the high-level 2.4-kHz masker than for the 4-kHz masker that produced an equivalent amount of masking at a 0-ms delay. At face value, the results may have important implications for behavioral estimates of BM compression and gain in humans obtained by comparing the slopes of on- and off-frequency TMCs. But first, other potential explanations, not involving different underlying rates of decay of forward masking, should be considered.

One potential explanation is that the contralateral 70-dB SPL 7-kHz tone was not effective in eliminating the effect of temporal confusion on the recovery rates. For the on-frequency masker, perceptual similarity between the masker and the signal could increase the amount of forward masking for the shortest masker-signal delays (Moore and Glasberg, 1982; Neff, 1986). As the delay increased, the effect of similarity would diminish leading to a steeper slope of the recovery function. For the off-frequency masker, the pitch of the signal was distinctly different from that of the masker, and thus the slope of the recovery function would not be affected by temporal confusion at short masker-signal delays. However, it is not clear why temporal confusion could produce a difference between on- and off-frequency maskers in the LF_HL condition, but not in the LF_LL or HF_HL condition. In all conditions, the level of the cuing tone was either similar to or higher than the level of the on-frequency masker, ensuring that the cue tone was clearly audible and salient. Also, comparing across conditions (especially LF_HL and LF_LL), no consistent relationship between the similarity of levels of the masker and the cue and the presence of a difference between recovery rates for the on- and off-frequency maskers is apparent. For example, the on-frequency masker levels for S1, S4, and S6 in Fig. 1, where the difference in recovery was observed, were similar to the on-frequency masker levels for S1, S2, and S5 in Fig. 2, where no difference was observed.

Another potential explanation involves the basalward shift in the peak of the BM traveling wave with increasing stimulus level (e.g., Ruggero *et al.*, 1997). For the high-level 2.4-kHz masker, the peak of the excitation pattern produced by the signal might shift apically with decreasing signal level during the course of recovery toward the peak of the excitation pattern produced by the masker. This could lead to a slower recovery rate. For the on-frequency masker, as the masker-signal delay increased, the peak of the excitation pattern produced by the signal would also shift apically and therefore away from the peak of the excitation pattern produced by the masker, making the signal more detectable at a given masker-signal delay and thus leading to a faster recovery from forward masking. The difference between the rates of recovery for the on- and off-frequency maskers might not be observed in the LF_LL and HF_HL conditions because the maximum signal level at threshold may have been too low for substantial peak migration to occur during the course of recovery. This potential problem would not occur for TMC measurements because the signal is typically kept at a fixed low level, and so reflects the response of a fixed place along the BM, whether or not that place represents the peak of excitation produced by an on-frequency masker.

A number of animal studies have investigated the shift of the peak of BM vibrations with increasing level in the basal end of the cochlea using different paradigms. When isointensity curves are measured, i.e., when a given place on the BM is stimulated with equal-intensity tones of differing frequency, the plot of the BM responses as a function of frequency of the stimulating tone exhibits a gradual shift in the position of the peak response toward lower frequencies with increasing level of the stimulus (Ruggero *et al.*, 1997; Ruggero *et al.*, 2000). These isolevel functions can be considered as equivalent to the responses of the auditory filter for different levels of the stimulus, if they are measured at frequencies for which the contributions of the outer and middle ear transfer functions are negligible. In contrast, when responses to a tone with a fixed frequency are measured at different places on the BM around the CF, for different levels of the test tone, the spatial patterns of BM responses exhibit broadening on the basal side with increasing level but the position of the peak of these patterns shifts toward the base only for levels of 90 dB SPL or higher (Russell and Nilsen, 1997; Ren, 2002). The spatial patterns can be thought of as equivalent to the excitation patterns produced by a tone presented at different levels. Thus, there is consensus regarding peak migration between the different experimental paradigms at very high levels (90 dB SPL or more) but not at lower levels. The lack of consensus over a wide range of levels may simply reflect differences between species since different animals were used with different experimental paradigms. However, the data of Nilsen and Russell (2000) suggest they may reflect differences between animals even within the same species. Nilsen and Russell (2000) measured spatial patterns of BM responses in two animals (guinea pigs) and found that one exhibited a peak shift only at very high levels (90 and 100 dB SPL), consistent with their earlier reports while the other exhibited a peak shift for a stimulus level as low as 60 dB SPL, although the position of the shifted peak did not change for levels between 60 and 90 dB SPL.

Interestingly, psychophysical human data appear to show similar discrepancies depending on the paradigm used. While tuning curves measured at high frequencies typically exhibit a shift of the best frequency, i.e., the frequency corresponding to the position of the tip of the tuning curve, toward lower frequencies (e.g., Lopez-Poveda *et al.*, 2007), other masking paradigms often show spread of excitation toward high frequencies, but no evidence of a change in peak position except at very high levels (see McFadden, 1986 for a review). Moore *et al.* (2002) measured masking patterns in forward masking and showed evidence of a level-dependent

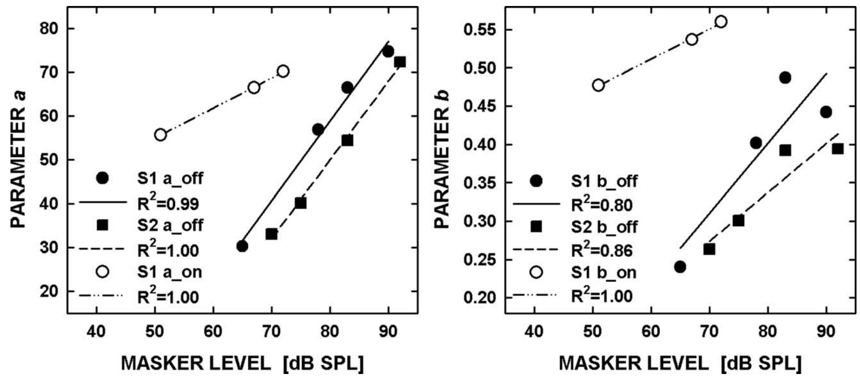

FIG. 5. Values of parameters a (left panel) and b (right panel) providing the best fit to the forward-masking data by the function described by Eq. (1), plotted as a function of the level of the off-frequency masker (filled symbols) and the on-frequency masker (open symbols). Circles (filled and open) represent the data for S1 and squares for S2. The solid, dashed, and dashed-dotted lines represent linear regression fits to the data.

peak shift for a 6-kHz masker, although the limited number of subjects (two) and the variability in the data preclude strong conclusions. For a 4-kHz masker (the frequency used in our study), their data did *not* exhibit a level-dependent peak shift. Likewise, masking patterns measured by Wojtczak and Viemeister (2006) did not provide evidence for a peak shift, except when the level of a 4-kHz masker was 93 dB SPL.

In all conditions tested in our study, including the LF_HL condition, the signal level at masked threshold did not exceed 80 dB SPL. In view of the previously published data, an explanation in terms of the BM-response peak shift, although appealing, is not supported by data from physiological and psychophysical studies that have explicitly investigated the level dependence of the spectral position of the peak of the excitation pattern.

In summary, two potential factors, "confusion" and BM peak shift, appear unlikely to have contributed to the different masking curves found for the on-frequency and high-level low-frequency maskers. Instead, the results may reflect a true difference in decay of the internal effect of the two maskers. If that is the case, then our findings may have important implications for the BM compression estimates obtained using the TMC method. The following section explores the extent to which the differential forward-masking recovery functions measured here might lead to errors in the estimated BM input-output functions.

III. EVALUATION OF POTENTIAL ERRORS IN COMPRESSION ESTIMATES

When TMCs are measured to derive the BM response and estimate cochlear compression, the signal level is fixed at a low value, typically 10–15 dB SL, and the on- and off-frequency masker levels needed to just mask the signal are measured at different masker-signal delays (Nelson *et al.*, 2001; Lopez-Poveda *et al.*, 2003; Plack *et al.*, 2004). The present experiment showed that the decay of forward masking for a given signal is not always independent of masker frequency. Because this result contradicts an assumption of the procedure that allows BM input-output functions to be derived from TMC data, it is possible that some systematic errors may have resulted. In this section, we attempt to evaluate the extent to which TMC-based estimates of BM compression may be affected by this assumption.

A. Methods

To evaluate the potential error that results from the observed difference in recovery rates, TMCs were simulated using our data. In order to derive TMCs, with a fixed signal level and a variable masker level, from our data, with a fixed masker level and a variable signal level, some interpolation of the data was necessary. In particular, it was assumed that parameters a and b in Eq. (1) are linear functions of masker level (see below for justification of this). Linear regression fits to the values of a and b, plotted as a function of masker level, were obtained separately for each masker frequency and each listener. In most cases, the regression lines were fitted to just two data points, i.e., two values of a and two values of b, obtained separately for the 4-kHz masker and the 2.4-kHz masker in the LF_LL and LF_HL conditions. For listeners S1 and S2, additional data (not shown) were collected. The recovery of forward masking was measured for the 2.4-kHz masker at levels of 78 and 65 dB SPL for listener S1 and at masker levels of 75 and 70 dB SPL for listener S2. For S1, the recovery function was also measured for the 4-kHz masker at a level of 51 dB SPL. These additional data provided further estimates for parameters a and b. In these selected cases, the regression lines were fitted to three (S1, 4-kHz masker) or four data points (S1 and S2, 2.4-kHz masker). Parameters a and b obtained from regression lines were used to generate recovery functions described by Eq. (1) for masker levels selected from the range between those used in the LF_LL and LF_HL conditions in 1-dB steps, separately for the 4- and 2.4-kHz masker. For S1 and S2, the range of levels was extended down to the lowest masker levels used to measure recovery functions for these two listeners. The additional data collected for S1 and S2 provided us with some test as to whether our assumption of linear variation of parameters a and b with masker level was reasonable. Figure 5 shows values of parameters a and b plotted as a function of masker level along with the linear regression lines, for cases where more than two points per function were available. The regression lines provided excellent fits to parameter a plotted as a function of masker level, for both

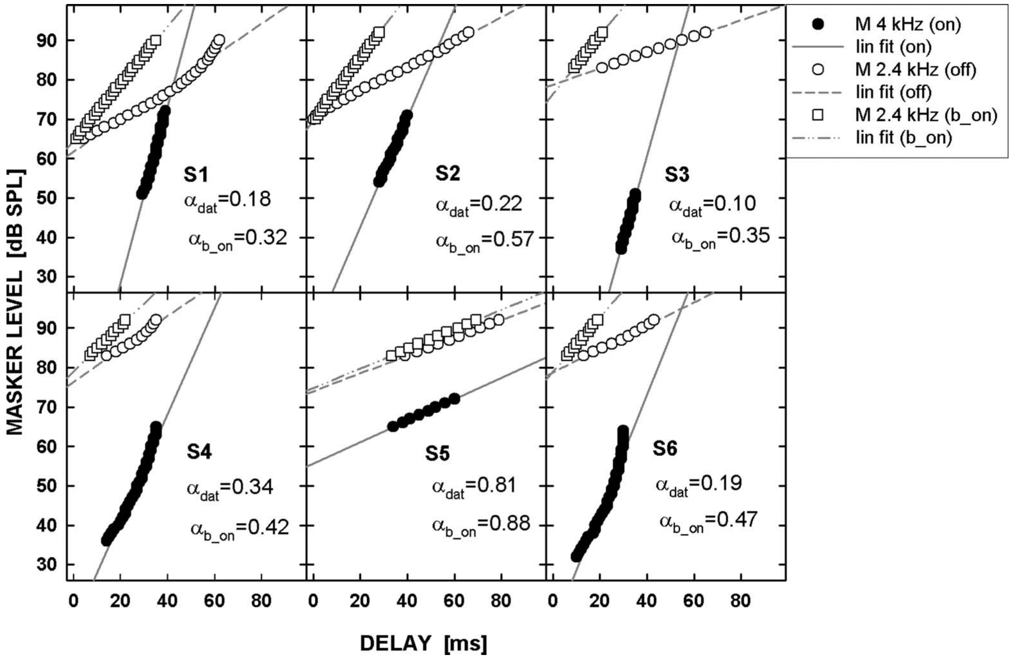

FIG. 6. Temporal masking curves simulated using parameters of best-fitting power functions to the data in Figs. 1 and 2, for the 4-kHz masker (filled circles) and the 2.4-kHz masker (open circles). The temporal masking curve for the 2.4-kHz masker simulated with the value of parameter b for the 4-kHz masker is shown by the open squares. The solid, dashed, and dashed-dotted lines show linear regression fits to each curve. The insert shows compression exponent α_{dat}, estimated from the simulated TMCs by computing the ratio of the slopes of the dashed (off-frequency TMC) and solid (on-frequency TMC) lines, and exponent α_{b_on}, estimated from the ratio of the slopes of the dashed-dotted line (off-frequency TMC simulated with parameter b for the 4-kHz masker) and the solid line (on-frequency TMC).

the on- and off-frequency maskers. Parameter b was well fitted by a regression line only for the on-frequency masker (open circles, dashed-dotted line). For the off-frequency masker, there was a clear departure of b from a linear function of level at masker levels between 83 and 92 dB SPL. The results in Fig. 5 demonstrate that, in general, the linear interpolation of the parameters in Eq. (1) was justified. However, by using the values of parameter b from the fitted line rather than raw data for the 2.4-kHz masker, we slightly underestimated the potential error in calculating compression for listeners S1 and S2.

B. Results

For each masker level, the delay corresponding to a masked signal threshold of 15 dB SL was found, which effectively simulates the TMC. Figure 6 shows TMCs obtained by plotting the level of the masker against the delay at which that masker produced threshold for detecting the signal at 15 dB SL. The filled circles represent the simulated TMC for a 4-kHz (on-frequency) masker. The open circles represent the simulated TMC for a 2.4-kHz (off-frequency) masker derived directly from the data. This off-frequency TMC would be observed if masker levels at threshold were measured as a function of the masker-signal delay in a typical TMC paradigm. The open squares represent the off-frequency TMC that would be obtained if the recovery rate for the 2.4-kHz masker were the same function of masker level as that for the 4-kHz masker, consistent with the assumption used by the psychophysical methods for deriving compression from TMCs. Thus, the difference between the slopes of the two off-frequency TMCs (open circles versus open squares) directly represents the contribution of the factor that differentially affects psychophysical recovery rates for the on- versus off-frequency masker, but that is *not* related to the difference in peripheral compression.

Straight line fits to the simulated TMCs were used to compute the compression exponents that are provided in the inset in each panel. Exponent α_{dat} represents the compression that would be estimated from the TMC method, provided our simulations accurately represent the results of a task in which the masker level rather than the signal level is measured as a function of the masker-signal delay. For five listeners, the values of α_{dat} were in the range between 0.1 and 0.34, with a mean value of 0.21. This value is in good agreement with compression exponents obtained from TMCs measured for the same signal frequency of 4-kHz, i.e., 0.26 in the study of Lopez-Poveda *et al.* (2003), 0.2 in Plack *et al.* (2004), and 0.23 in Rosengard *et al.* (2005). However, our data indicate that these compression estimates may be affected by a difference between the rates of recovery for the on- and off-frequency maskers that cannot be attributed to differences in compression. Exponent α_{b_on} was obtained from the ratio of the slopes of the straight-line fits to the simulated TMCs shown by the open squares and filled circles. The exponent represents the estimate of compression that would be obtained if the factor that differentially affects the slopes of recovery functions but that is not due to the difference in compression were eliminated in the TMC method. In other words, the compression exponent α_{b_on} would be observed if the assumption of equal recovery rates were valid for the equivalent 2.4- and 4-kHz maskers. The values of α_{b_on} are between 0.32 and 0.57 with the mean value of 0.43, which is about a factor of 2 larger than the mean value of the compression exponents estimated from a TMC method for the same five listeners. (Data for S5 were excluded from the above comparisons because these data showed very little compression in any condition, which is unusual in a person with normal hearing.) Studies estimating compression based on TMCs have often reported the minimum slope of a third-order polynomial fit to the derived BM input-output functions as a measure of compression. BM input-output functions (not shown here) derived from the simulated TMCs in Fig. 6 were fitted with a third-order polynomial and the minimum slopes were computed for each listener (except S5). The average minimum compression exponent α_{dat} was 0.13, a little lower than the average compression exponents reported in other studies but still well within the range of exponents observed for different individuals. The average "corrected" exponent α_{b_on} was 0.28, which is a little higher but also within the range of individual exponents. The exponents obtained from the third-order polynomial fit to the BM input-output function support the conclusion that compression based on the measured TMCs may be, on average, overestimated by about a factor of 2. It is important to note that this difference does not depend critically on the method used to fit the data. Since the off-frequency TMCs were generally well fitted by a straight line over the range of overlapping delays, the corrected and uncorrected compression estimates decreased by the same factor when the third-order polynomial fit was used.

IV. GENERAL DISCUSSION

A. Comparisons with other studies and implications

Previously reported compression exponents in humans agree with the "uncorrected" estimates, α_{dat}, and also are very similar to the often-reported compression of 0.2 observed in direct measurements of BM responses in guinea pig (Nuttall and Dolan, 1996) and in chinchilla (e.g., Ruggero, *et al.* 1997; Rhode and Recio, 2000). Thus, it may appear that our corrected compression estimates, α_{b_on}, imply responses at the base of the human cochlea that are less compressive than responses in the cochleas of other species. Although differences in the exact amount of compression among different species would not be surprising, given differences in the mechanical characteristics of the BM, such a conclusion is not warranted given the variability of compression estimates across humans and across animals. Compression of 0.2 in animal studies has typically been observed in only one or two cochleas selected from a larger number of sensitive cochleas within the species. In fact, most BM responses measured by Ruggero *et al.* (1997) had slopes between 0.3 and 0.5, and the two cochleas for which the slope was 0.2 at medium input levels exhibited a *decrease* (negative slope) or saturation of the response (no change) with increasing input level [see Fig. 3 of Ruggero *et al.* (1997)].

Our findings are consistent with certain aspects of data from the study by Rosengard *et al.* (2005), which compared slopes of the BM-response functions derived with a 4-kHz signal using two methods, GOM and TMC, in the same listeners. The TMCs measured by Rosengard *et al.* (2005) often contained levels of the off-frequency masker (2.2 kHz) that were in the range between 80 and 100 dB SPL. In contrast, the GOM functions for the off-frequency masker rarely reached levels higher than 85 dB SPL. Interestingly, for four out of five normal-hearing listeners, compression measured at 4 kHz was stronger when estimated from the TMCs than when estimated from GOM. This result is generally consistent with the finding that compression is overestimated when high levels of the off-frequency masker are used.

Psychophysical methods for estimating compression are often used to compare the BM-response growth between listeners with normal and impaired hearing. Because the off-frequency TMC measured at 4 kHz likely represents linear processing (Lopez-Poveda *et al.*, 2003), the slope of the off-frequency TMC should be similar for the two groups of listeners. However, the off-frequency TMCs for hearing-impaired listeners generally exhibit shallower slopes than those measured for listeners with normal hearing (Plack *et al.*, 2004; Rosengard *et al.*, 2005). It is possible that the shallower slopes simply reflect slower temporal processing in hearing-impaired listeners, given that the two groups of listeners were not matched with respect to the listeners' age. The effect of age might have played a role, as a number of studies have shown age-related deficits in temporal auditory processing (e.g., Mendelson and Ricketts, 2001; Fitzgibbons *et al.*, 2007). However, slower temporal processing would likely affect the on- and off-frequency TMCs approximately equally and thus would not affect the estimated compression. In light of our findings, the shallower slopes of the off-frequency TMCs in hearing-impaired listeners may have resulted from higher off-frequency masker levels compared with those used for listeners with normal hearing over the same range of masker-signal delays. In addition, the necessity to use very high off-frequency masker levels may have introduced a difference between the recovery rates for the on- and off-frequency maskers that was not due to the difference in compression. If that were the case, previously reported amounts of compression in the hearing-impaired listeners may also have been overestimated.

Our findings suggest that it would be prudent to avoid using masker levels that are higher than about 83 dB SPL in the measurement of a TMC. However, this may not always be possible, since it would greatly reduce the dynamic range available for deriving the BM response in normal-hearing listeners and would often make it impossible to measure an off-frequency TMC for hearing-impaired listeners.

B. Alternative methods for estimating compression

Because the difference between the recovery rates for the on- and off-frequency maskers is level dependent, compression estimates obtained from GOM may also be affected by the different recovery rates if high off-frequency masker levels are used. GOMs are typically measured using a single short masker-signal delay (Oxenham and Plack, 1997), and thus the potential errors in compression estimates are likely to be smaller than those from the TMCs measured over a wide range of delays. However, the method based on GOM may be inadequate for estimating compression in frequency regions below about 4 kHz, due to the possibility that the response to the off-frequency masker at the CF_s place is compressive at lower frequencies (e.g., Lopez-Poveda *et al.*, 2003).

Additivity of forward masking may provide a desirable alternative method because it avoids comparisons between the effects of on- and off-frequency maskers (Plack and O'Hanlon, 2003; Plack *et al.*, 2006). The mean compression estimates of 0.17 in the study by Plack and O'Hanlon (2003) and 0.21 in the study by Plack *et al.* (2006) fall in between the average compression exponents α_{dat} and α_{b_on} obtained from the third-order polynomial fits to the BM input-output functions derived from the TMCs shown in Fig. 6. However, it should be noted that the method for estimating compression from additivity of forward masking relies on an assumption of linear summation of the effects of two (or more) forward maskers. At a low signal level (10 dB SL), combining the effects of two equally effective forward maskers leads to a compression estimate that is nearly equal to 1 (Plack and O'Hanlon, 2003). Assuming that the BM-response growth is linear at low levels, this result supports the assumption of linear additivity. It is harder to demonstrate linear additivity of forward masking over a range of medium and high levels, for which the BM response becomes compressive. Some support can be found in the data from listeners with severe cochlear hearing losses (Oxenham and Moore, 1995). Instead of using two forward maskers, a forward and a backward masker were combined in that study and masked thresholds for two equally effective maskers presented together were compared with the masked threshold observed for either masker separately. When equally effective forward and backward maskers were combined, the hearing-impaired listeners exhibited a much smaller shift in threshold relative to the threshold for a single masker than the normal-hearing listeners, consistent with more linear processing. However, in many cases the shift was less than 3 dB at lower SLs and in most of the hearing-impaired listeners, the threshold shift exceeded 3 dB at higher levels. The latter might indicate some residual compression of the BM response even in the presence of a cochlear hearing loss (Plack *et al.*, 2004; Rosengrad *et al.*, 2005). The interpretation of the data for the hearing-impaired subjects in the study of Oxenham and Moore (1995) may also be complicated by the fact that backward masking is poorly understood and tends to diminish after training. Thus, an equally effective backward masker may have become less effective during the course of the experiment. Perhaps the strongest support for linear additivity of the effects of two forward maskers is from a recent study of Plack *et al.* (2007). That study demonstrated that a combined effect of masker M1 presented at a level necessary to mask a signal with a level of L_s+x dB and masker M2 presented at a level needed to mask the signal with a level of L_s dB was the same as the combined effect of M1 presented at a level necessary to mask an L_s dB signal and M2 presented at a level needed to mask an L_s+x dB signal. This commutative behavior is consistent with linear additivity of the effects of two forward maskers. Plack *et al.* (2007) showed that commutation worked for levels up to 70 dB SPL. Thus, at present there is no clear reason to suspect that additivity of masking experiments yield inaccurate estimates of compression. Comparison of compression estimates from additivity of forward masking and the "revised" TMC estimates should be made using the same listeners to determine if the two measures do indeed produce consistent results.

C. Potential mechanisms

The difference in recovery was observed in the LF_HL condition but not in the LF_LL and HF_HL conditions, suggesting that factors such as off-frequency listening and temporal confusion probably cannot account for this result.

It is possible that the difference between recovery rates in the LF_HL condition is mediated by mechanisms at higher levels of the auditory pathways. However, without knowing the site of origin and the mechanisms that contribute to forward masking it is hard to pinpoint the cause of the observed effect. Further research is needed to assess a possible involvement of efferent activity (Shore, 1998; Guinan, 2006) or activation of the middle ear acoustic reflex (Møller, 2000). Higher-level interactions between excitatory and inhibitory inputs characterized by different delays (e.g., Oertel, 1983) could also lead to frequency dependence of the rate of recovery from forward masking.

V. CONCLUSIONS

The purpose of this study was to test the hypothesis that the rate of recovery from forward masking for a given signal is the same for different masker frequencies, provided that the maskers are equally effective at a given masker-signal delay. This hypothesis is at the core of some psychoacoustic methods for estimating BM compression in humans, in particular, the TMC method. The following conclusions can be drawn from the data.

(1) When a high-level (90–92 dB SPL) off-frequency masker was nearly an octave below the signal frequency (LF_HL condition), different recovery rates were observed for the equivalent on- and off-frequency maskers. In contrast, no difference between the recovery rates was found for lower levels of the low-frequency masker (83 dB SPL) or for high-frequency maskers (4.4 kHz) at the same high level (92 dB SPL).
(2) Simulated TMCs, obtained using the parameters of recovery functions fitted to masked thresholds, provide compression estimates which suggest that compression from TMCs may be overestimated by as much as a factor of 2 when high-level off-frequency maskers are used.
(3) Since the difference between the rates of recovery from forward masking depended on the level of a 2.4-kHz masker, the TMC and GOM methods may overestimate compression when high levels of the off-frequency masker are used, although the potential error is likely to be smaller for the GOM-based estimates.
(4) The results suggest that caution should be exercised in interpreting TMC data in terms of BM compression, particularly when the off-frequency masker levels exceed about 85 dB SPL.

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[1]A function defined by a sum of two exponentials was initially fitted to each listener's data. The shorter time constants were always greater for the off-frequency masker than for the on-frequency masker. The longer time constants did not consistently follow the same trend across listeners. For listeners S3, S4, and S5 the longer time constant was greater for the on-frequency masker, but it was extremely long ($>10^{10}$ ms). This suggests that a mechanism other than that underlying forward masking at shorter delays played a role in threshold elevation for these three listeners.

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