

# Basilar-membrane nonlinearity and the growth of forward masking

Christopher J. Plack

*Laboratory of Experimental Psychology, University of Sussex, Brighton BN1 9QG, England*

Andrew J. Oxenham<sup>a)</sup>

*Institute for Perception Research (IPO), P.O. Box 513, 5600 MB Eindhoven, The Netherlands*

(Received 10 June 1997; accepted for publication 19 November 1997)

Forward masking growth functions were measured for pure-tone maskers and signals at 2 and 6 kHz as a function of the silent interval between the masker and signal. The inclusion of conditions involving short signals and short masker-signal intervals ensured that a wide range of signal thresholds were recorded. A consistent pattern was seen across all the results. When the signal level was below about 35 dB SPL the growth of masking was shallow, so that signal threshold increased at a much slower rate than masker level. When the signal level exceeded this value, the masking function steepened, approaching unity (linear growth) at the highest masker and signal levels. The results are inconsistent with an explanation for forward-masking growth in terms of saturating neural adaptation. Instead the data are well described by a model incorporating a simulation of the basilar-membrane response at characteristic frequency (which is almost linear at low levels and compressive at higher levels) followed by a sliding intensity integrator or temporal window. Taken together with previous results, the findings suggest that the principle nonlinearity in temporal masking may be the basilar membrane response function, and that subsequent to this the auditory system behaves as if it were linear in the intensity domain. © 1998 Acoustical Society of America. [S0001-4966(98)02003-7]

PACS numbers: 43.66.Dc, 43.66.Ba, 43.66.Mk [WJ]

## INTRODUCTION

One of the main goals of psychoacoustic research is to provide an account of auditory perception that is physiologically realistic, computationally tractable, and parsimonious. These efforts are complicated by the considerable nonlinearities that are observed in certain aspects of auditory processing. A dramatic example of this nonlinear behavior is forward masking, in which the detectability of a signal is reduced by a masker terminated before the onset of the signal. It is a well-established fact that on-frequency forward masking grows nonlinearly: A given increase in masker level requires a smaller increase in signal level in order for the signal to remain at detection threshold (Jesteadt *et al.*, 1982; Moore and Glasberg, 1983). In other words, the masker becomes relatively less effective as its level is increased. The result is in contrast to that for on-frequency simultaneous masking, in which the signal-to-masker ratio at threshold is almost independent of masker level (Hawkins and Stevens, 1950; Viemeister, 1972).

These findings have been taken as evidence that forward masking is, at least in part, a consequence of nonlinear processes in the auditory nerve; specifically, neural adaptation (Bacon, 1996; Duifhuis, 1973; Jesteadt *et al.*, 1982; Kidd and Feth, 1982). According to this account, the sensitivity of a neuron is reduced after stimulation, leading to a decrease in the detectability of a subsequent signal. Neural adaptation is compressive and saturating (Smith, 1977, 1979), so that the

relative effectiveness of the adaptor decreases with level. These characteristics are consistent, *qualitatively*, with the nonlinearity observed behaviorally in the majority of forward-masking experiments, although more recent physiological studies suggest that the *amount* of forward masking observed in single auditory nerve fibers is not sufficient to account for the *amount* of psychophysical forward masking (e.g., Relkin and Turner, 1988). Even though the adaptation account as described here is based on the response of single neurons measured in isolation, for the present purposes this should be a sufficient analysis. The characteristics of adaptation that are important here (saturation with increasing level, and dependence of adaptation on masker level, not signal level) will apply even if a larger number of neurons are employed in a given forward-masking situation.

An alternative explanation for forward masking is that it is a consequence of more “central” processes relating to the limited temporal resolution of the auditory system: The neural representation of the masker is smoothed over time by an integration device, or temporal window (Festen *et al.*, 1977; Moore *et al.*, 1988; Penner *et al.*, 1972), so that the representation of the masker overlaps with the representation of the signal at some stage in the auditory system. In this account it is the “persistence” of masker excitation that produces the masking (Plomp, 1964; Zwislocki *et al.*, 1959). Classically, however, the temporal window has been taken to be linear, so that the model is unable to account for the nonlinearities observed in forward masking without assuming that the duration of the temporal window is reduced as stimulus level is increased (Plack and Moore, 1990). Not only does this considerably complicate the temporal window model, but it is also inconsistent with other data that suggest that temporal

<sup>a)</sup>Present address: Communication Research Laboratory, Department of Speech–Language Pathology and Audiology, Northeastern University, Boston, MA 02115.

resolution is almost independent of level (Buus and Florentine, 1985; Moore and Glasberg, 1988; Peters *et al.*, 1995; Plomp, 1964; Viemeister, 1979). In addition, a temporal-window model operating on stimulus intensity cannot account for the nonlinear additivity of forward and backward maskers (Penner, 1980).

Despite these failings, the temporal-window model has considerable appeal, mainly perhaps because of its simplicity. It has been suggested that the model can be rescued by assuming that there is a compressive nonlinearity prior to the temporal window (Oxenham and Moore, 1994; Penner, 1980). Furthermore, it has been suggested that the compressive nonlinearity may be related to the nonlinear response of the basilar membrane (Oxenham and Moore, 1994, 1995). In these studies, however, basilar-membrane compression was modeled using a simple (level-invariant) power law. Thus while the additivity of forward and backward masking could be well accounted for, the nonlinear growth of forward masking could not.

Physiological measurements of basilar-membrane vibration have shown that the response to a pure tone at its "nominal" characteristic frequency (CF; defined as the pure-tone frequency that produces the maximum excitation at low levels) is approximately linear for tone levels below about 40 dB SPL (Murugasu and Russell, 1995; Ruggero *et al.*, 1997; Russell and Nilsen, 1997). Above these levels, the response is highly compressive, with a compression ratio of roughly 5:1 (in dB units). It is possible to distinguish two characteristics of basilar-membrane nonlinearity that may determine the compressive behavior at CF. One is the compressive response of the basilar membrane *per se*, which has been linked to an active physiological mechanism. The other is the reduction in the best frequency (BF, the frequency that produces the maximum response) of each place on the basilar membrane as level is increased (McFadden and Yama, 1983; Ruggero *et al.*, 1997; Russell and Nilsen, 1997). As BF shifts downward, the tone fixed at CF (which is no longer the optimum frequency) produces *relatively* less excitation, leading to a compressive response function. The account implies that the response at BF should be less compressive than at CF, and indeed this is observed in some of the basilar membrane measurements (see for example, Ruggero *et al.*, 1997, Fig. 8; Russell and Nilsen, 1997, Fig. 4). Both the compression at BF and the shift in BF may contribute to the measured compression at CF, although it should be emphasized that these characteristics are probably the consequence of a single underlying mechanism.

The nonlinear growth of forward masking can be explained in terms of basilar-membrane nonlinearity as follows (Oxenham and Moore, 1995). Because the amount of masking produced by a forward masker is usually quite small, at least in comparison to simultaneous masking, the threshold signal levels in forward-masking experiments have generally been low. If the masker level is high enough to be in the compressive region of the basilar membrane function, a 10-dB increase in masker level may produce only a 2-dB increase in masker excitation (5:1 compression). If the signal level is always in the low-level, more linear, portion of the basilar-membrane function, then the signal excitation will

increase in proportion to the physical signal level. Assuming that threshold corresponds to a constant internal signal-to-masker ratio, the signal *level* only has to increase by the same amount as the masker *excitation* (i.e., about 2 dB) in order for the signal to remain at threshold (see also Moore, 1996). The hypothesis can account, in principle, for the shallow growth of forward masking. Furthermore, since cochlear damage leads to a loss of basilar-membrane compression, the hypothesis also predicts more linear growth of forward masking in listeners with cochlear hearing impairment. This prediction is consistent with the available data (Oxenham and Moore, 1995, 1997). In further support of the hypothesis, Oxenham and Moore (1997) showed that their modification of the temporal window model, including a simulation of the basilar-membrane response function, provided a good account of the growth of forward masking for both normal and impaired listeners.

The aim of the present experiments was to distinguish between the neural and mechanical explanations for the nonlinear behavior of forward masking. As will be explained, the predictions of the two hypotheses, while similar when signal threshold is low, differ when signal threshold is high. The experiments were designed to exploit this distinction.

## I. GENERAL METHOD

### A. Stimuli

The sinusoidal stimuli were generated digitally on a Silicon Graphics workstation at a sampling rate of 32 kHz, with 16-bit resolution. Anti-aliasing was provided by built-in filters. Analog waveforms were delivered directly via the headphone output on the computer. Level changes were implemented in the digital domain, although for conditions requiring low signal thresholds the built-in analog attenuators were used to decrease the overall output level by up to 18 dB.

### B. Procedure

A 2I, 2AFC paradigm was adopted throughout. In one interval the masker and the signal were presented; in the other interval the masker alone was presented. The inter-stimulus interval was 500 ms. A two-down, one-up adaptive tracking rule was used to estimate the 71% correct point on the psychometric function (Levitt, 1971). The level of the signal was increased and decreased by 4 dB for the first four turnpoints, and by 2 dB thereafter. Sixteen turnpoints were recorded in each experimental block and the threshold estimate was taken as the mean of the values at the last 12 turnpoints. At least four such estimates were made for each listener and the results were averaged.

Listeners were tested individually in an IAC single-walled sound-attenuating booth. Stimuli were presented over one earphone of a Sony MDRV6 headset. Listeners made their responses using the numeric keypad on the computer keyboard. "Lights" were presented in a graphical display on the computer monitor to delineate the observation intervals, and to provide feedback after each trial.

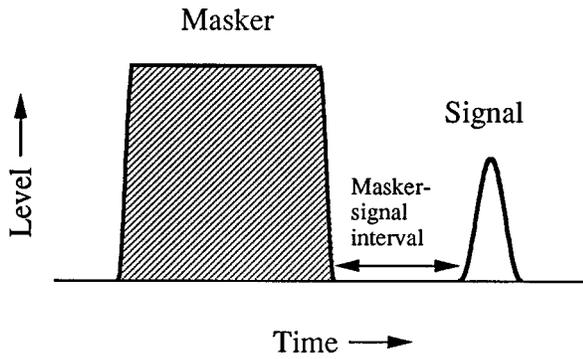


FIG. 1. A schematic illustration of the temporal characteristics of the stimuli.

## II. EXPERIMENT 1: FORWARD MASKING OF 10-MS TONE BURSTS AS A FUNCTION OF LEVEL

### A. Rationale

While the two explanations (neural and mechanical) for the nonlinearity in forward masking produce similar predictions when the signal level is low, the predictions of the hypotheses diverge when the signal level enters the compressive region of the basilar-membrane response function. In terms of the neural adaptation account, the amount of adaptation is dependent only on masker level. This means that the growth of masking should still be shallow at high signal levels, since the adaptation produced by the masker will still be saturated. However, in terms of the basilar-membrane nonlinearity account, if the masker and the signal are *both* being compressed then the effects should cancel out to some degree, so that the masking function should be steeper, i.e., more linear, at high signal levels than at low.

The experiment was designed to test these predictions using a brief signal presented shortly after the masker. The stimulus parameters were chosen to ensure a large amount of masking so that signal threshold at high masker levels would be within the compressive region of the basilar membrane. High signal frequencies were tested, so that the masker and signal would not overlap on the basilar membrane due to “ringing” in the auditory filters (Duifhuis, 1973; Oxenham and Plack, 1997), and so that the spectral spread of the short signal would be small compared to the auditory filter bandwidth.

### B. Conditions

The sinusoidal stimuli are illustrated schematically in Fig. 1. The masker had a steady-state duration of 20 ms with 2-ms raised-cosine onset and offset ramps. The signal had no steady-state portion and 5-ms onset and offset ramps. The masker had the same frequency as the signal and frequencies of 2 and 6 kHz were tested. At each frequency, masker-signal intervals (specified from zero-voltage points) of 2, 20, and 40 ms were tested. At each masker-signal interval, thresholds were measured for masker levels of 30–100 dB SPL in 10-dB steps. In addition, absolute threshold measurements were made in the absence of the masker.

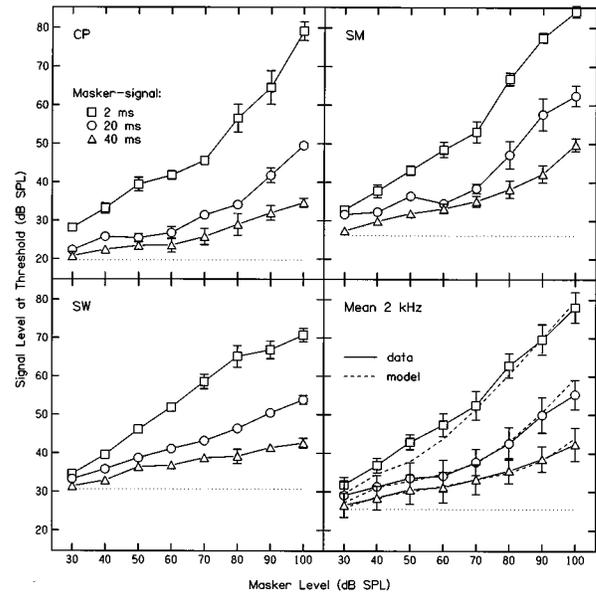


FIG. 2. The individual and mean results from experiment 1 for the 2-kHz signal showing signal threshold as a function of masker level with masker-signal interval as the parameter. The dotted lines show the absolute thresholds for the signal in the absence of the masker. The dashed lines show the predictions of the model described in the text. Error bars show standard errors between replications for the individual data and between listeners for the mean data.

### C. Listeners

Three normally hearing listeners took part. Absolute thresholds for the signal (for CP, SM, and SW, respectively) were 19.7, 26.1, and 30.6 dB SPL at 2 kHz, and 22.3, 29.1, and 17.3 dB SPL at 6 kHz. Listeners were given at least 4 h practice on the task before data collection began.

### D. Results and discussion

The individual and mean data at 2 and 6 kHz are shown in Figs. 2 and 3, respectively. The horizontal dotted lines show the absolute thresholds in the absence of the masker. The dashed lines show the threshold values estimated by a model that will be described later.

The data for the two signal frequencies are broadly similar. For the 2-ms masker-signal interval the masking function is relatively steep (compared to the 20- and 40-ms intervals) over the entire level range, although there is a slight tendency for the function to steepen with increasing masker level, approaching a value of unity at the highest levels. The 20-ms data show an initial very shallow growth of masking, consistent with previous measures of forward masking, followed by an increase in slope. The same pattern is seen for the 40-ms data, although the function first begins to steepen at a higher masker level. The only deviation from this general pattern is for listener SW at 2 kHz, where the 2-ms data appear to flatten off slightly at high masker levels, although this is also where the variability is highest.

Figure 4 shows a scatter plot of the slope of the masking function against signal level at threshold. Each point was obtained by plotting the mean of each two consecutive signal thresholds from the mean data in Figs. 2 and 3 against the

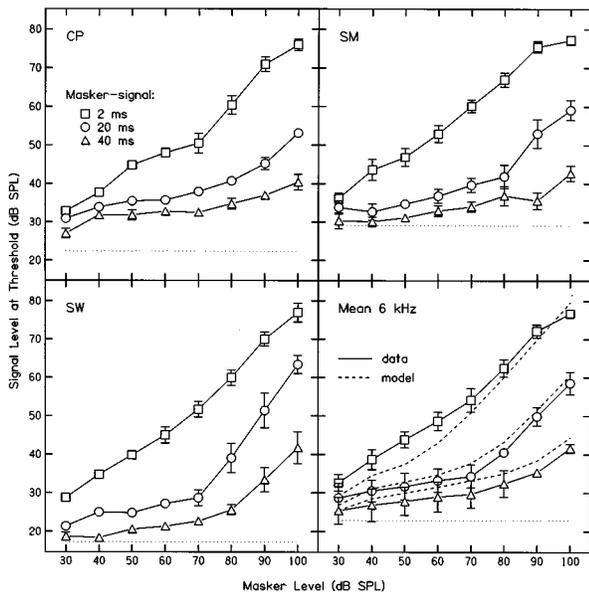


FIG. 3. As Fig. 2 except showing the results from experiment 1 for the 6-kHz signal.

slope of the straight line connecting them. There is a very clear tendency for the slopes to increase with increasing signal level. For signal levels below about 35 dB SPL the slope of the masking function is low, with the values clustered around 0.2 dB/dB. Above this cutoff value the slopes are much greater. The correlation between signal level and slope was measured separately for the 2- and 6-kHz data. In both cases the correlation was positive, strong, and highly significant (respectively:  $r=0.826$ ,  $p<0.001$ ;  $r=0.722$ ,  $p<0.001$ ). Also pertinent is the finding that the correlation between masker level and slope was much weaker ( $r=0.480$ ,  $p<0.02$ , at 2 kHz; and  $r=0.560$ ,  $p<0.01$ , at 6 kHz). It is possible that the correlation with masker level may be largely a result of the correlation between signal level and

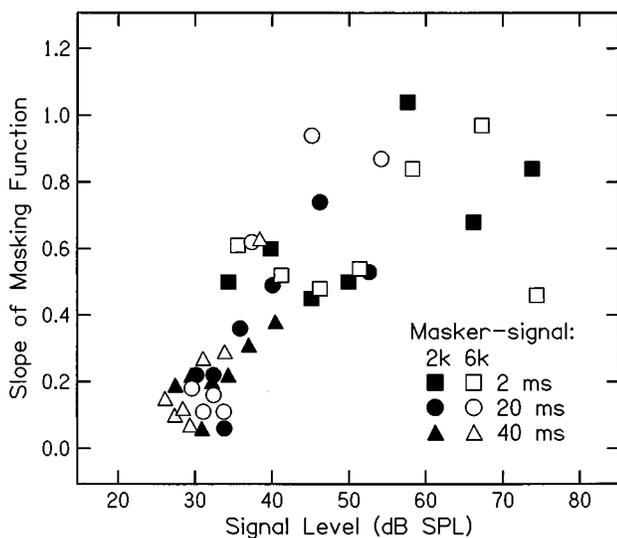


FIG. 4. A scatter plot of signal level at threshold against the slope of the masking function. The data were derived from the mean results of experiment 1 (see text for details).

masker level. A test devised by Williams (1959) was used to determine the significance of the difference in correlations. Grouping the data from 2 and 6 kHz together, it was found that the masking function slope was significantly more highly correlated with signal level than with masker level ( $t=2.691$ ,  $p<0.01$ ). It can be concluded that it is predominantly signal level that determines the shape of the masking function. The analysis supports the view that the masking function steepens because of changes in the compression applied to the signal as threshold level increases.

The shape of the masking function is inconsistent with the hypothesis that the nonlinearities in forward masking are the result of saturating neural adaptation produced by the masker. If the hypothesis were correct then the masking function should be dependent only on masker level, and should be shallow at high masker levels where adaptation is most saturated. Neither of these characteristics are evident in the results. The shape of the masking function is consistent, however, with a basilar membrane input-output function that is steep below 35 dB SPL and shallow (i.e., highly compressive) for levels above this. When the signal is in the linear region and the masker is compressed the masking function is shallow, and when both masker and signal are in the compressive region the masking function is more linear.

### III. EXPERIMENT 2: FORWARD MASKING OF 50-MS TONE BURSTS AS A FUNCTION OF LEVEL

#### A. Rationale

The aim of experiment 2 was to confirm the generality of the results from experiment 1 using longer maskers and signals. The masked threshold for a long signal is lower than that for a short signal, so that the upper, linear, portion of the growth of masking function is less prominent. However, the long signal also has a lower absolute threshold, allowing the masking function to be measured at lower masker levels. This is of interest since, according to the basilar-membrane hypothesis, when both the signal and the masker are at low levels (i.e., within the linear region) the growth of masking should again be linear. Such a pattern is seen in the classic results of Munson and Gardner (1950).

#### B. Conditions

The masker had a steady-state duration of 100 ms with 2-ms raised-cosine onset and offset ramps. The signal had a steady-state duration of 30 ms with 10-ms onset and offset ramps. Signal frequencies of 2 and 6 kHz were tested. At each frequency, masker-signal intervals (specified from zero-voltage points) of 2 and 20 ms were tested. At each masker-signal interval, thresholds were measured for masker levels of 20–100 dB SPL in 10-dB steps. Absolute threshold measurements were made in the absence of the masker.

#### C. Listeners

Three normally hearing listeners took part, only one of whom had taken part in experiment 1. Absolute thresholds for the signal (for DP, SM, and PB, respectively) were 12.9,

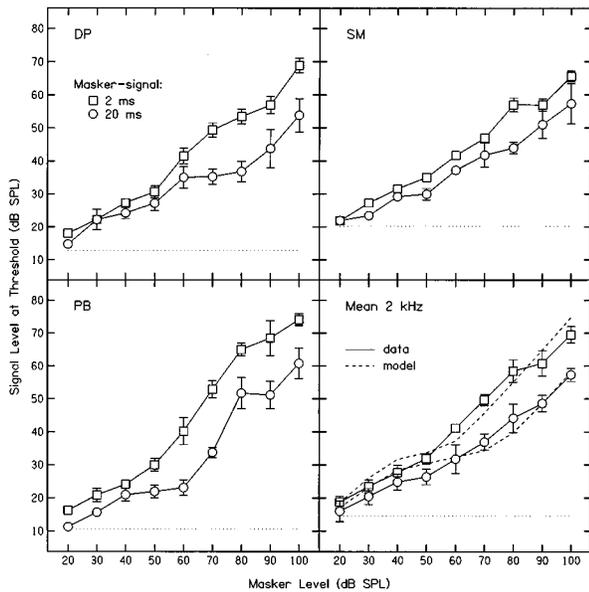


FIG. 5. As Fig. 2 except showing the results from experiment 2 for the 2-kHz signal.

20.2, and 10.6 dB SPL at 2 kHz, and 17.5, 20.7, and 24.2 dB SPL at 6 kHz. Listeners were given at least four hours practice on the task before data collection began.

#### D. Results and discussion

The individual and mean data at 2 and 6 kHz are shown in Figs. 5 and 6, respectively. The mean results at 6 kHz are similar to the on-frequency results of Munson and Gardner (1950) at 1 kHz. There is an initial, relatively steep, increase in signal threshold over the lowest three masker levels; a broad, shallow mid-level region; and a dramatic steepening in the masking function at high masker levels. The steepening begins at a lower masker level for the 2-ms data. The

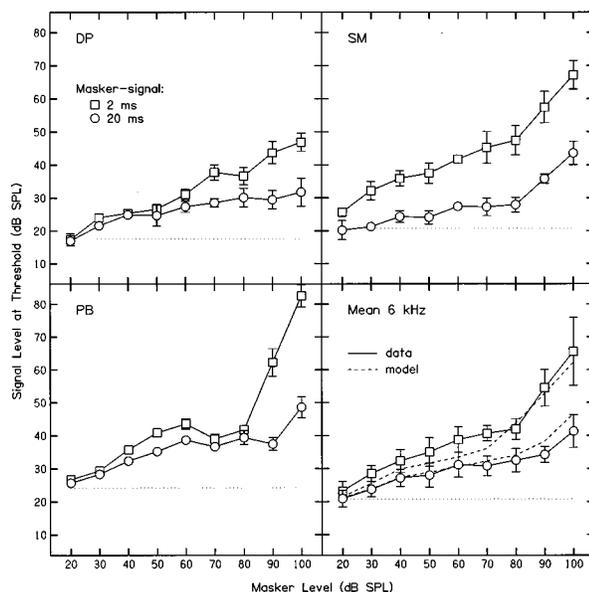


FIG. 6. As Fig. 2 except showing the results from experiment 2 for the 6-kHz signal.

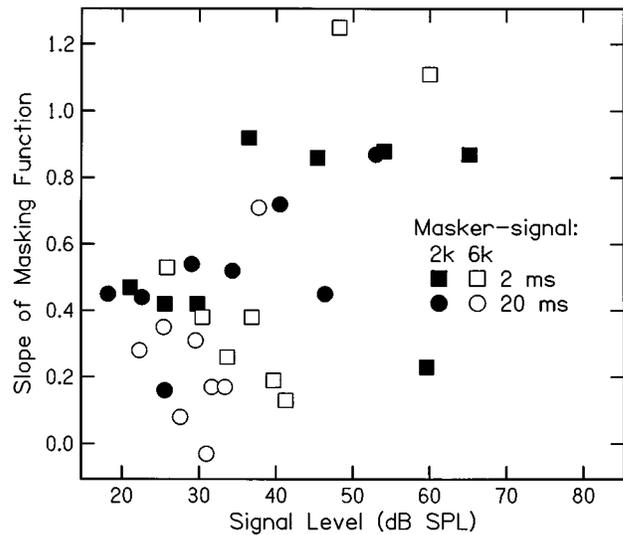


FIG. 7. As Fig. 4 except showing a scatter plot derived from the mean results of experiment 2.

masking functions at 2 kHz are relatively steep throughout the level range, although there is also a tendency for the functions to steepen with increasing masker level.

Figure 7 shows a scatter plot of the slope of the mean masking function against signal level. Once again, there is a clear tendency for the slopes to increase with increasing signal level, although the effect is more variable than it was in experiment 1. Part of this variability is possibly a result of the increase in slope for low masker levels. The correlation between signal level and slope was measured separately for the 2- and 6-kHz data. At both frequencies the correlation was positive and significant (respectively:  $r=0.486$ ,  $p < 0.05$ ;  $r=0.628$ ,  $p < 0.005$ ). Again, the overall correlation with masker level was weaker, although only marginally so at 2 kHz ( $r=0.452$ ,  $p < 0.1$ , at 2 kHz; and  $r=0.391$ ,  $p > 0.1$ , at 6 kHz). Grouping the data from 2 and 6 kHz together, it was found that masking function slope was significantly more highly correlated with signal level than with masker level ( $t=1.768$ ,  $p < 0.05$ ).

Considering only masker levels up to 70 dB, at 6 kHz there was a significant *negative* correlation between masker level and slope ( $r = -0.622$ ;  $p < 0.05$ ). This confirms that the lower part of the masking function, where both masker and signal levels are within the linear region, has a more linear slope than the masking function at medium masker levels. Because of the earlier steepening in the growth of masking function at 2 kHz, the negative correlation was not seen over the same range of masker levels for this data set. Overall, however, the results are consistent with the basilar-membrane hypothesis and confirm that the nonlinear growth of forward masking is not explicable in terms of saturating neural adaptation.

As can be seen in Fig. 6, the results for the highest masker levels at 6 kHz were highly variable between listeners. Widin and Viemeister (1979) also comment on the large variation in thresholds between their listeners. In some respects this is to be expected. First, a slight between-listener variation in the shape of the basilar-membrane function, for

instance, the level at which the basilar membrane changes from being linear to compressive, can have a dramatic effect on signal thresholds. For example, if the transition from the linear to the compressive region is at 35 dB, then the masking function would become almost linear for signal levels above this, perhaps resulting in an increase in signal threshold from 35 to 55 dB for a 20-dB increase in masker level. If the transition level is 40 dB, however, the masking function should be shallow up to this value, so the signal threshold may only increase from 35 to 39 dB for the same 20-dB increase in masker level (given 5:1 compression). In other words, a 5-dB between-listener variation in the transition level (well within the range of values observed physiologically) can produce a 16-dB between-listener variation in signal threshold that was not evident for a masker level 20 dB lower. Similarly, any variation in the efficiency of the detection mechanism between listeners has a much larger effect at high levels, because of the compression. If the internal signal-to-masker ratio at threshold is increased by 2 dB, the physical signal level has to be increased by 10 dB under 5:1 compression.

While all the individual results in Fig. 6 vary at high levels, the largest discrepancy is seen in the results for listener PB, where there is a dramatic steepening in the growth function for the 2-ms masker-signal interval at high levels. The slope here is greater than unity and is not compatible with a basilar membrane function that is equally compressive above a low-level cutoff point. While the results for this listener may be attributable to random variation, there is an alternative explanation. Until recently, physiological measurements of the basilar membrane response at CF often showed a three stage function, with a linear low-level region, a compressive mid-level region, and a linear high-level region (Ruggero, 1992; Ruggero and Rich, 1991; Ruggero *et al.*, 1993). The absence of compression at very high levels has been linked to a reduction in sensitivity caused by a deterioration in the physiological condition of the animal (Ruggero *et al.*, 1997). If PB's hearing is very slightly impaired at 6 kHz (indeed, his absolute threshold was the highest of the three listeners), then it is conceivable that his basilar-membrane function followed the steep-shallow-steep pattern. This being the case, when the masker enters the high-level linear region and the signal is in the compressive region then the masking function should become very steep (greater than linear) since now the signal threshold needs to increase at a much higher rate than masker level to overcome the compression (the reverse of the situation for low signal levels and medium masker levels). It is possible that PB's results may be explained in this way, although this does not appear to be a general rule. For the 2-kHz data in experiment 1, for example, SW has the highest absolute threshold of the three listeners, but a shallower slope at high levels (see Fig. 2). In any case, PB's data are clearly not consistent with the adaptation account.

Although there were clear individual differences in the 6-kHz condition in experiment 2, the remaining results were reasonably consistent between listeners, at least in terms of the overall form of the data, and the subsequent analysis will focus on the mean data. If the mechanical hypothesis is ac-

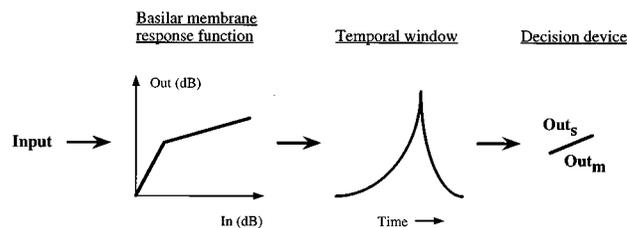


FIG. 8. An illustration of the processing stages of the model described in the text.

cepted, it is reasonable to regard the mean data as providing a first approximation to the “average” basilar-membrane response, while acknowledging that the shape of the function may differ between individuals.

#### IV. THE REVISED TEMPORAL-WINDOW MODEL

In order to provide a quantitative test of the basilar-membrane hypothesis, a version of the temporal-window model was implemented that could estimate signal thresholds in forward-masking paradigms. In its present form the model consists of three stages: a level-dependent compressor, a sliding temporal integrator, and a decision device (see Fig. 8). As the masker and the signal were pure tones with the same frequency, and since the temporal smearing due to ringing was considered to be negligible at the CFs tested, the effects of the auditory filter were ignored for the present purposes.

The model assumes that the detectability of the signal is determined by the response at the place on the basilar membrane with CF equal to the signal frequency. Since the early years of research on frequency selectivity, models of masking have often made this assumption (Fletcher, 1940; Moore, 1995), and it would seem to be a reasonable one to make in the present case, where the spectrum of the signal is small compared to the critical band and hence the utility of “off-frequency listening” (Johnson-Davies and Patterson, 1979) is minimized. The model also assumes that threshold is determined by the ratio of signal intensity to masker intensity at some central stage in the auditory system. Again, this is an assumption commonly used in models of masking, and is consistent with the finding that the Weber fraction for intensity discrimination is approximately constant over a wide range of levels (Viemeister, 1988). In terms of traditional signal detection theory (Green and Swets, 1966), the approach assumes that the standard deviation of the internal representation is proportional to its mean.

##### A. Stage 1: The compressor

This stage simulates the nonlinear input-output function of the basilar membrane. The most recent direct measurements of basilar-membrane vibration have shown that the response at CF can be divided into two level regions: A roughly linear region for input levels below about 40 dB SPL, and a compressive region for higher levels (Murugasu and Russell, 1995; Ruggero *et al.*, 1997; Russell and Nilsen, 1997). It was decided to produce a rough approximation to the overall response function using two straight lines on dB/dB coordinates.

In an earlier article (Oxenham and Plack, 1997) the response of the basilar membrane was measured behaviorally using a forward masker an octave below the signal frequency. The experiment was a modification of an earlier procedure that used the growth of simultaneous masking to estimate basilar-membrane response functions (Nelson and Schroder, 1997; Stelmachowicz *et al.*, 1987; Yates *et al.*, 1990). The reasoning is that the excitation produced by the low-frequency masker should grow linearly at the CF corresponding to signal frequency (Murugasu and Russell, 1995; Yates *et al.*, 1990), so that the change in masker level with signal level provides an estimate of the amount of signal compression at CF. In other words, the plot of masker level at threshold as a function of signal level is an estimate of the basilar-membrane input-output function. The results obtained were consistent with physiological measurements.

The mean masker levels obtained by Oxenham and Plack at 6 kHz, for signal levels of 30–80 dB SPL, were used to estimate the nonlinear function in the first stage of the model. Because the 4-ms signal used in the main experiment of Oxenham and Plack had a high absolute threshold, meaningful masker thresholds could only be measured for signals levels of 40 dB SPL and greater. Therefore, for the purposes of the present analysis, for signal levels above 35 dB SPL the results for the 4-ms signal were used, but for the lower signal levels of 30 and 35 dB SPL the results for a 14-ms signal were used, with the masker levels at threshold decreased by a constant 6.56 dB. This was the mean difference between the masker levels needed to mask the 4-ms and 14-ms signals at signal levels of 40, 45, 50, 55, and 60 dB SPL. The manipulation corrects for the greater detectability of the longer signal.

The data were fitted with two straight lines, with the slope of the lines and the position of the “knee” in the function where the two lines meet as free parameters. The value of these free parameters was found that minimized the squared deviations of the experimental results from the fitted function. It was found that the Oxenham and Plack data were well fit by two straight lines with slopes of 0.78 and 0.16 on dB/dB coordinates. The lines meet at a signal level of 45 dB SPL. This value is 10 dB above the cutoff value of 35 dB SPL suggested by the present data from experiment 1; it was decided to use the latter value here. Both values are within the range observed physiologically.

Following this somewhat crude analysis, the compressive function in the first stage of the temporal window model is given by:

$$L_{\text{out}} = 0.78 L_{\text{in}} \quad (L_{\text{in}} \leq 35 \text{ dB SPL}) \quad (1)$$

$$L_{\text{out}} = 0.16 L_{\text{in}} + 21.7 \quad (L_{\text{in}} > 35 \text{ dB SPL}), \quad (2)$$

where  $L_{\text{in}}$  is input level expressed in dB SPL, and  $L_{\text{out}}$  is the output of the compressive function expressed in dB. The constant of 21.7 is added to Eq. (2) so that  $L_{\text{out}}$  is the same for Eqs. (1) and (2) when  $L_{\text{in}} = 35$ . The output of this stage is expressed in units of intensity. This is consistent with the transfer function of auditory nerve fibers, for which firing rate has been found to be linearly related to stimulus intensity (Yates *et al.*, 1990).

## B. Stage 2: The temporal window

In the second stage the waveform is smoothed by a sliding temporal integrator, or temporal window. The output of this stage is the integrated product of the input waveform (in units of intensity) with the temporal window, as a function of the center time of the window. (This is equivalent to a convolution of the input waveform with the time-reversed temporal window.) The shape of the temporal window is described by a combination of exponential functions:

$$W(t) = 0.975 \exp(t/4) + 0.025 \exp(t/29) \quad (3)$$

for times before the center of the window ( $t=0$ ) and

$$W(t) = \exp(-t/3.5) \quad (4)$$

for times after the center of the window, where  $W(t)$  is an intensity-weighting function and  $t$  is time measured relative to the center (or maximum) of the weighting function (in ms). These equations are taken from Oxenham and Moore (1994) with the parameters derived for listener AO.

The temporal window simulates masking by causing the masker and the signal to effectively overlap in time. The shape of the temporal window determines the relative threshold values for different masker-signal intervals in forward masking, and also determines the effect of increases in masker duration.

## C. Stage 3: The decision device

The decision device is particular to the task being simulated. In the present case, the statistic used is simply the ratio of the output of the window in response to the signal to the output in response to the masker (the signal-to-masker ratio), referred to subsequently, in dB units, as the parameter  $k$ . The fitting procedure described below uses an adaptive algorithm to find the optimum value of  $k$  as a function of the center time of the window.  $k_{\text{thr}}$  is the optimum value of  $k$  at signal threshold, and is a measure of the efficiency of the decision mechanism.

Although it has taken a few lines to describe, the temporal-window model is in essence an extremely simple description of auditory processing, which ignores all the complications and nonlinearities of neural physiology in favor of a scheme based around a simple intensity integrator. It should be emphasized that the primary purpose of the model described here is to provide a quantitative evaluation of the mechanical hypothesis, and not to provide an all-encompassing description of temporal masking. Other factors, including the temporal effects of auditory filtering and possible “cognitive” influences, would have to be taken into consideration to account for thresholds in all possible conditions.

## D. Implementing the model

The model was fitted to the present results in the following way. For each condition, digital representations of the intensity envelope of the masker and of the signal were generated. The masker level was set at the value for the particular condition but the signal level was varied by the fitting procedure. A continuous intensity envelope was added to the

masker to act as a “noise floor.” This simulates the influence of absolute threshold for the lowest masker levels. The effect of the noise floor is relatively insignificant except for the lowest signal levels. The level of the noise floor was chosen so that, in the absence of the masker, the thresholds predicted by the model were similar to the mean absolute thresholds for the signal in quiet. The levels used for simulating the results of experiment 1 were 19 dB at 2 kHz and 17 dB at 6 kHz. The levels used for simulating the results of experiment 2 were 6 dB at 2 kHz and 15 dB at 6 kHz. The predicted absolute thresholds at 2 and 6 kHz, respectively, were 25.2 and 23.3 dB for the experiment 1 simulations, and 14.4 and 20.7 dB for the experiment 2 simulations.

The model was fitted to the mean data independently for each signal frequency from each experiment. The fitting procedure predicted data values based on a given value of  $k_{thr}$ . It was assumed that the temporal window was centered on the time that produced the highest value of  $k$ , i.e., the maximum detectability. The center time was usually on the offset ramp of the signal. The parameter  $k_{thr}$  was varied adaptively to find the value (to the nearest 0.05 dB) that minimized the sum of the squared deviations of the predicted data values from the measured values. The signal thresholds derived with this optimum value of  $k_{thr}$  were taken as the predictions of the model.

The only free parameter in the fitting procedure itself was the parameter  $k_{thr}$  although clearly the knee in the compressive function was also constrained by the data (to a limited extent) and the level of the noise floor was constrained by the absolute threshold measurements. Aside from these three, all the other parameters in the fit were taken from independent measures of basilar-membrane nonlinearity and of temporal resolution, selected before data collection began.

## E. Evaluating the model

The thresholds predicted by the model are shown by the dashed lines in Figs. 2, 3, 5, and 6. Consider first the fits to the data from experiment 1 (Figs. 2 and 3). The model accounts very well for the overall shape of the data at both frequencies, although it is slightly more accurate at 2 kHz than at 6 kHz. The only consistent deviation of the predictions from the data is for the 50- and 60-dB masker levels for a 2-ms masker-signal interval. The optimum values of  $k_{thr}$  at 2 and 6 kHz were  $-0.15$  and  $-0.05$  dB, respectively.

The results of experiment 2 are also reasonably well described by the model (Figs. 5 and 6). The model captures the initial steep growth from absolute threshold in the 6-kHz data, although it underestimates somewhat the signal thresholds in the mid-level region for the 2-ms masker-signal interval. The model also captures the steeper, more linear function at 2 kHz. This is achieved by simply using a high value of  $k_{thr}$ : 5.75 dB compared to 3.65 dB at 6 kHz. When  $k_{thr}$  is high, the signal threshold is increased so that the signal level enters the compressive region at a lower masker level, leading to a more linear function overall.

When both the signal and the masker are in the linear portion of the basilar-membrane function (levels below about 35 dB) then it might be expected that the slope of the masking function would be unity. However, both the data and the

simulations show a slope shallower than unity, albeit steeper than at medium masker levels. The results can be explained in terms of the proximity of absolute threshold, represented by the noise floor in the simulation. When the signal level is close to absolute threshold, a substantial part of the masking is attributable to the fixed-level noise floor, so that changes in masker level have a smaller effect on signal threshold than would be the case if the noise floor were absent. The result is a masking slope shallower than unity even when both masker and signal are in the linear region of the response function.

Both the values of  $k_{thr}$  derived from the experiment 2 data are higher than those derived from the experiment 1 data. While it is not unreasonable to attribute this variation solely to the different listeners used in the two experiments, fits to the individual data of the listener (SM) who was common to both experiments revealed that this was not the case. For these fits the noise floor was adjusted to match the listener's absolute thresholds (see above), but otherwise the model was the same as that fitted to the mean data. The resulting values of  $k_{thr}$  at 2 and 6 kHz were 0.05 and 0.25 dB for experiment 1, and 5.55 and 4.20 dB for experiment 2. In other words, the results of the fitting procedure suggest that there was some additional performance deficit associated with the stimulus configuration used in experiment 2. The deficit is not simply a consequence of the longer masker having more energy, since this should be taken into account by the integration of the temporal window (Oxenham and Moore, 1994). One possibility is that the long masker used in experiment 2 made it hard to focus attention on the subsequent signal. Moore and Glasberg (1982) provided evidence that temporal uncertainty may affect thresholds in forward masking by demonstrating that performance can be improved by gating a “cue” stimulus with the masker or the signal. Another possibility, however, is that the parameters of the temporal window used in the model were inaccurate. To illustrate this idea, the mean 2-kHz data from experiments 1 and 2 were fitted with the time constant for the skirt of the window [the number 29 in Eq. (3)] increased by a factor of 3. The manipulation increases the amount of energy that is integrated from the long forward masker in experiment 2. The optimum values of  $k_{thr}$  in the new fits were much more similar between the two experiments ( $-3.4$  and  $-2.1$  dB, respectively), although the overall goodness of fit was worse. It is possible that a temporal-window shape could be found that would enable all the data to be fit reasonably well with a single value of  $k_{thr}$ . The window shape used here was derived using a different initial compression and this factor can have a large effect on the estimated shape of the window.

Overall, the results appear to be broadly consistent with the temporal-window model: The mean data can be described using a very small number of free parameters. In all the simulations, the same basilar-membrane function and the same temporal-window function were used. The level of the noise floor was determined by the absolute threshold measurements. The only parameter allowed to vary between the different frequencies and experiments was the efficiency of the detector mechanism,  $k_{thr}$ .

The sum-of-squared deviations of the predicted values from the measured values was 79 dB<sup>2</sup> for the 2-kHz data

from experiment 1. When the slope of the compressive part of the basilar membrane function in the model was increased by 50% from 0.16 to 0.24 the best sum-of-squared deviations that could be obtained for this data set increased to 390 dB<sup>2</sup>. In other words, the predictions are highly sensitive to the overall form of the basilar membrane function. Since the function used in the simulations was derived from an independent measure of basilar membrane nonlinearity (Oxenham and Plack, 1997), the analysis adds further support to the hypothesis that the nonlinearities in forward masking are the result of basilar-membrane nonlinearities, as opposed to other nonlinearities in the auditory pathway.

## F. Modeling results from other studies

As a final test of the general applicability of the model, the data from three other studies of forward masking growth using sinusoidal maskers and signals (Jesteadt *et al.*, 1982, Fig. 1; Kidd and Feth, 1981, Fig. 3; Moore and Glasberg, 1983, Table A1) were fit with the temporal-window model. It was decided to only use data for signal frequencies of 2 kHz and above, since the form of the basilar-membrane function, which is crucial for the success of the model, is not known for lower frequencies. In these three papers the results are quoted in units of dB SL, i.e., level above absolute threshold. For the present purposes the values were converted into dB SPL by adding 15 dB, which was the mean absolute threshold from experiment 2 at 2 kHz. Although the mean absolute thresholds from the individual papers differed slightly from this value, it was hoped that using the same mean threshold might correct for any calibration differences between the studies. For example, if the responses of the headphones at high frequencies varied substantially between the different studies then this may be reflected by differences in the absolute thresholds, and hence differences in the masked thresholds when expressed in dB SPL. The current approach assumes that the “true” mean absolute threshold in each case was the same as that measured in experiment 2 at 2 kHz. In effect, the mean absolute thresholds are being used to calibrate the individual experiments.

The stimulus parameters in the three studies were fairly similar. The signal duration was 20 ms in each case. Kidd and Feth used a 300-ms masker and a masker-signal interval of 10 ms. Jesteadt *et al.* also used a 300-ms masker and Moore and Glasberg used a 210-ms masker. The latter two studies used a range of masker-signal intervals.

The data were fitted using the procedure described earlier, with the noise floor fixed at 6 dB (as for the 2-kHz results from experiment 2). A different value of  $k_{thr}$  was derived for each set of data. The transformed data and the predictions of the model are illustrated in Fig. 9. It can be seen that the model fits the data fairly well. The biggest discrepancy is for the data of Jesteadt *et al.* where the model underestimates the threshold for the 60-dB masker with a delay of 5 ms. It will be remembered that a similar discrepancy was seen in the predictions of the results from experiment 1. The model also underestimates the thresholds for the 20-dB masker for the 4-kHz data of Moore and Glasberg. It would appear that the noise floor used by the model is too low in this case.

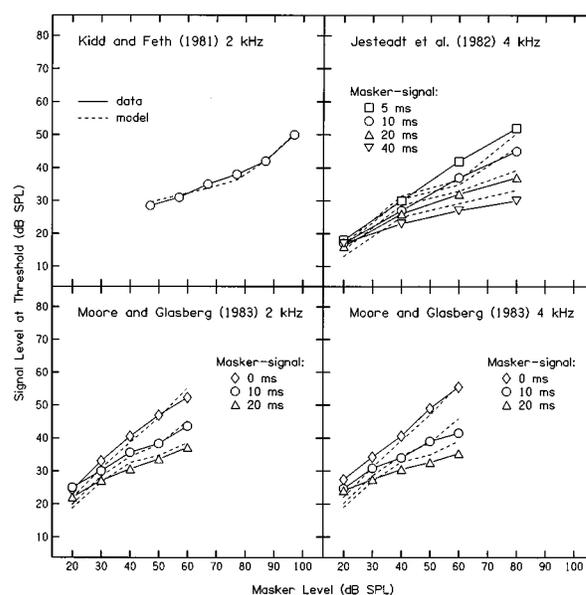


FIG. 9. Mean results from three previous forward-masking studies together with the predictions of the model described in the text.

The values of  $k_{thr}$  were  $-2.25$  dB for the data of Kidd and Feth,  $-0.30$  dB for the data of Jesteadt *et al.*, and  $2.70$  and  $2.85$  dB for the 2- and 4-kHz data of Moore and Glasberg, respectively. Although  $k_{thr}$  does vary between studies, the variability is not great, and the values are broadly consistent with those derived from the present study. There was little variation in  $k_{thr}$  with frequency for the data of Moore and Glasberg.

## V. GENERAL DISCUSSION

### A. Previous forward-masking studies

While (to the authors’ knowledge) the present experiments are unique in terms of the stimulus configurations employed (to ensure high signal thresholds while avoiding temporal overlap on the basilar membrane), there are other forward-masking studies that also provide support for the hypothesis presented here. Oxenham and Plack (1997) measured forward-masking functions with a 6-kHz masker and a very brief 6-kHz signal. Because of the large amount of masking produced by the design, the signal level at threshold was roughly equal to masker level. They found a nearly linear masking function at all levels, which is entirely consistent with the model: When the signal and masker are at similar levels they are both compressed (or not compressed) equally, and the masking function is linear, just as in simultaneous masking.

Other studies have generally measured low signal thresholds which are not expected to lead to a dramatic steepening in the growth function. Some of these were examined in Sec. IV F. Using noise maskers, Moore and Glasberg (1983) found a slight steepening in the growth function at high masker levels. Across the different masker-signal intervals they used, the steepening appears to be related to signal level, consistent with the basilar-membrane hypothesis. Similarly, the data of Jesteadt *et al.* (1982), Kidd and

Feth (1981), and Widin and Viemeister (1979) show a steepening in the masking function as masker-signal delay is decreased and signal threshold is increased, although the shortest masker-signal intervals used by these authors may have resulted in a temporal overlap of the masker and signal on the basilar membrane, particularly at low frequencies where the temporal response of the auditory filter is longer (Kiang *et al.*, 1965). Some of the results of Kidd and Feth in particular (see Fig. 5 in their article) are similar in form to those reported here. Other studies (Bacon and Jesteadt, 1987; Kidd and Feth, 1982) have shown a steepening in the growth function as signal threshold is increased due to an increase in masker duration. As described earlier, the classic data of Munson and Gardner (1950), with the more linear low-level region, also offer support for the basilar-membrane account.

Finally, the fact that sensorineural hearing-impaired listeners show more linear forward-masking functions (Oxenham and Moore, 1995, 1997) provides quite strong evidence that the nonlinearities in forward masking are a consequence of healthy, nonlinear, cochlear function.

### B. Is the central auditory system intensity linear?

In the present experiments and subsequent analysis it has been shown that a simple model incorporating a compressive function and an intensity integrator can account, quantitatively, for the nonlinear growth of forward masking. Oxenham and Moore (1994) have demonstrated that a very similar approach can account for both the increase in signal threshold with increasing forward-masker duration (Kidd and Feth, 1982) and for the nonlinear additivity of forward and backward masking (Penner, 1980). Both of these phenomena are examples of the nonlinear summation of masker intensity over time. In contrast, hearing-impaired listeners, who are assumed to have more linear basilar-membrane functions, show a *linear* additivity of intensity in these situations (Oxenham and Moore, 1995). Taken together, the results suggest that the principle nonlinearity in temporal masking (at least for the range of masker-signal intervals studied here) is the basilar-membrane response function. While a saturating neural nonlinearity cannot account for the present results, it is conceivable that forward masking is due in part to some form of linear adaptation rather than to a persistence of activity. Unlike the temporal-window model, however, an explanation based on adaptation cannot account for backward masking, or for the additivity of forward and backward masking.

The simple hypothesis described here has important consequences since it implies that, after the compressive basilar membrane, the auditory system may behave *as if* it were intensity linear with respect to temporal masking. Despite the severe nonlinearities involved in neural transduction, synaptic transmission, and neural spike generation, when the auditory system integrates activity over time it seems to use a transform that is equivalent to integrating intensity. This may prove to be a very useful property with regard to modeling normal and impaired hearing. Furthermore, it has been shown that auditory-nerve firing rate is proportional to stimulus intensity after the effects of the basilar membrane

have been factored out (Yates *et al.*, 1990). The implication may be that the auditory system integrates by effectively counting neural spikes.

### C. Applications of the approach

Oxenham and Plack (1997) measured the masker level needed to forward mask a signal an octave above as a function of signal level. They argued that the function provides a direct estimate of the CF basilar-membrane response to the signal. In a similar way, the present experiments suggest that the growth of on-frequency forward masking provides an estimate of the basilar-membrane response to the masker. The approach assumes that the basilar-membrane response function is approximately linear at low levels, and that threshold corresponds to a constant “internal” signal-to-masker ratio. As long as the signal level is within the linear region, then the growth of signal threshold with masker level should be equivalent to the basilar membrane input-output function in response to the masker. The particular stimuli chosen by Munson and Gardner (1950) may be ideal for these type of measurements. They used a 400-ms masker and an 80-ms signal separated by a 20-ms silent interval. The long masker ensured a reasonable amount of masking and the long signal ensured a low absolute threshold and hence a reasonable dynamic range within the low-level region. The 20-ms masker-signal interval was sufficient to avoid an overlap of responses on the basilar membrane. The growth of masking they observed for a 1-kHz masker and signal for masker levels up to about 80 dB SPL is similar to recent physiological measurements of the basilar membrane response at CF.

Unfortunately, the technique of using an on-frequency forward masker requires a large dynamic range so that the masker and the signal can be in clearly distinct regions of the basilar-membrane function. While it may prove to be a useful tool for measuring peripheral nonlinearity in normal listeners, it has little application to the study of impaired hearing.

### VI. CONCLUSIONS

The main findings presented in this article can be summarized as follows:

- (1) The function relating signal threshold to forward-masker level is shallow for signal levels below about 35 dB SPL, but becomes steeper at higher levels. There is a highly significant positive correlation between signal threshold level and masking function slope, but the correlation between masker level and masking function slope is weaker: Signal level seems to be the principle determinant of masking function slope.
- (2) The steepening with level and dependence of slope on signal level are inconsistent with an explanation for the growth of forward masking in terms of saturating neural adaptation.
- (3) The data can be described by a simple model involving a nonlinear transfer function (representing the response function of the basilar membrane) and a sliding intensity integrator, or temporal window. The success of the ap-

proach here and elsewhere suggests that the principle nonlinearity in temporal masking may be the basilar-membrane response function, and that subsequent to this the auditory system behaves as if it were linear in the intensity domain.

## ACKNOWLEDGMENTS

We are most grateful to Armin Kohlrausch for helpful comments on an earlier version of this manuscript, and to three anonymous reviewers whose careful criticism improved the clarity and content of the article. The first author was supported by a Royal Society University Research Fellowship and the second author by a Wellcome Trust Research Fellowship (0044215/Z/95/Z).

- Bacon, S. P. (1996). "Comments on 'Manipulations of the duration and relative onsets of two-tone forward maskers' [J. Acoust. Soc. Am. **94**, 1269–1274 (1993)]." J. Acoust. Soc. Am. **99**, 3246–3248.
- Bacon, S. P., and Jesteadt, W. (1987). "Effects of pure-tone forward masker duration on psychophysical measures of frequency selectivity." J. Acoust. Soc. Am. **82**, 1925–1932.
- Bus, S., and Florentine, M. (1985). "Gap detection in normal and impaired listeners: The effect of level and frequency." in *Time Resolution in Auditory Systems*, edited by A. Michelsen (Springer-Verlag, New York), pp. 159–179.
- Duifhuis, H. (1973). "Consequences of peripheral frequency selectivity for nonsimultaneous masking." J. Acoust. Soc. Am. **49**, 1155–1162.
- Festen, J. M., Houtgast, T., Plomp, R., and Smoorenburg, G. F. (1977). "Relations between interindividual differences of auditory functions." in *Psychophysics and Physiology of Hearing*, edited by E. F. Evans and J. P. Wilson (Academic, London).
- Fletcher, H. (1940). "Auditory patterns." Rev. Mod. Phys. **12**, 47–65.
- Green, D. M., and Swets, J. A. (1966). *Signal Detection Theory and Psychophysics* (Wiley, New York).
- Hawkins, J. E., and Stevens, S. S. (1950). "The masking of pure tones and of speech by white noise." J. Acoust. Soc. Am. **22**, 6–13.
- 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. B., and Patterson, R. D. (1979). "Psychophysical tuning curves: Restricting the listening band to the signal region." J. Acoust. Soc. Am. **65**, 765–770.
- Kiang, N. Y.-S., Wantanabe, T., Thomas, E. C., and Clark, L. F. (1965). "Discharge patterns of single fibers in the cat's auditory nerve." Res. Monogr. No. 35 (MIT, Cambridge, MA).
- Kidd, G., and Feth, L. L. (1981). "Patterns of residual masking." Hearing Res. **5**, 49–67.
- Kidd, G., and Feth, L. L. (1982). "Effects of masker duration in pure-tone forward masking." J. Acoust. Soc. Am. **72**, 1384–1386.
- Levitt, H. (1971). "Transformed up-down methods in psychoacoustics." J. Acoust. Soc. Am. **49**, 467–477.
- McFadden, D., and Yama, M. F. (1983). "Upward shifts in the masking pattern with increasing masker intensity." J. Acoust. Soc. Am. **74**, 1185–1189.
- Moore, B. C. J. (1995). "Frequency analysis and masking." in *Hearing*, edited by B. C. J. Moore (Academic, New York), pp. 161–205.
- Moore, B. C. J. (1996). *An Introduction to the Psychology of Hearing* (Academic, New York).
- 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. (1988). "Gap detection with sinusoids and noise in normal, impaired, and electrically stimulated ears." J. Acoust. Soc. Am. **83**, 1093–1101.
- Moore, B. C. J., Glasberg, B. R., Plack, C. J., and Biswas, A. K. (1988). "The shape of the ear's temporal window." J. Acoust. Soc. Am. **83**, 1102–1116.
- Munson, W. A., and Gardner, M. B. (1950). "Loudness patterns—a new approach." J. Acoust. Soc. Am. **22**, 177–190.
- Murugasu, E., and Russell, I. J. (1995). "Salicylate ototoxicity: The effects on basilar membrane displacement, cochlear microphonics, and neural responses in the basal turn of the guinea pig cochlea." Aud. Neurosci. **1**, 139–150.
- Nelson, D. A., and Schroder, A. C. (1997). "Linearized response growth inferred from growth-of-masking slopes in ears with cochlear hearing loss." J. Acoust. Soc. Am. **101**, 2186–2201.
- 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**, 1921–1934.
- 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, Hillsdale, NJ).
- 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.
- Penner, M. J. (1980). "The coding of intensity and the interaction of forward and backward masking." J. Acoust. Soc. Am. **67**, 608–616.
- Penner, M. J., Robinson, C. E., and Green, D. M. (1972). "The critical masking interval." J. Acoust. Soc. Am. **52**, 1661–1668.
- Peters, R. W., Moore, B. C. J., and Glasberg, B. R. (1995). "Effects of level and frequency on the detection of decrements and increments in sinusoids." J. Acoust. Soc. Am. **97**, 3791–3799.
- Plack, C. J., and Moore, B. C. J. (1990). "Temporal window shape as a function of frequency and level." J. Acoust. Soc. Am. **87**, 2178–2187.
- Plomp, R. (1964). "The rate of decay of auditory sensation." J. Acoust. Soc. Am. **36**, 277–282.
- Relkin, E. M., and Turner, C. W. (1988). "A reexamination of forward masking in the auditory nerve." J. Acoust. Soc. Am. **84**, 584–591.
- Ruggero, M. A. (1992). "Responses to sound of the basilar membrane of the mammalian cochlea." Curr. Op. Neurobiol. **2**, 449–456.
- 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., and Recio, A. (1993). "Alteration of basilar membrane responses to sound by acoustic overstimulation." in *Biophysics of Hair Cell Sensory Systems*, edited by H. Duifhuis, J. W. Horst, P. v. Dijk, and S. M. v. Netten (World Scientific, Singapore), pp. 258–264.
- 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.
- Russell, I. J., and Nilsen, K. E. (1997). "The location of the cochlear amplifier: Spatial representation of a single tone on the guinea pig basilar membrane." Proc. Natl. Acad. Sci. USA **94**, 2660–2664.
- Smith, R. L. (1977). "Short-term adaptation in auditory nerve fibers: Some poststimulatory effects." J. Neurophysiol. **40**, 1098–1112.
- Smith, R. L. (1979). "Adaptation, saturation, and physiological masking in single auditory-nerve fibers." J. Acoust. Soc. Am. **65**, 166–178.
- Stelmachowicz, P. G., Lewis, D. E., Larson, L. L., and Jesteadt, W. (1987). "Growth of masking as a measure of response growth in hearing-impaired listeners." J. Acoust. Soc. Am. **81**, 1881–1887.
- Viemeister, N. F. (1972). "Intensity discrimination of pulsed sinusoids: The effects of filtered noise." J. Acoust. Soc. Am. **51**, 1256–1269.
- Viemeister, N. F. (1988). "Intensity coding and the dynamic range problem." Hearing Res. **34**, 267–274.
- Viemeister, N. F. (1979). "Temporal modulation transfer functions based upon modulation thresholds." J. Acoust. Soc. Am. **66**, 1364–1380.
- Widin, G. P., and Viemeister, N. F. (1979). "Pure-tone forward masking." J. Acoust. Soc. Am. **66**, 388–395.
- Williams, E. J. (1959). "The comparison of regression variables." J. Royal Stat. Soc. (B) **21**, 396–399.
- Yates, G. K., Winter, I. M., and Robertson, D. (1990). "Basilar membrane nonlinearity determines auditory nerve rate-intensity functions and cochlear dynamic range." Hearing Res. **45**, 203–220.
- Zwislocki, J., Pirodda, E., and Rubin, H. (1959). "On some poststimulatory effects at the threshold of audibility." J. Acoust. Soc. Am. **31**, 9–14.