Psychophysical estimates of level-dependent best-frequency shifts in the apical region of the human basilar membrane[a]

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It is now undisputed that the best frequency (BF) of basal basilar-membrane (BM) sites shifts downwards as the stimulus level increases. The direction of the shift for apical sites is, by contrast, less well established. Auditory nerve studies suggest that the BF shifts in opposite directions for apical and basal BM sites with increasing stimulus level. This study attempts to determine if this is the case in humans. Psychophysical tuning curves (PTCs) were measured using forward masking for probe frequencies of 125, 250, 500, and 6000 Hz. The level of a masker tone required to just mask a fixed low-level probe tone was measured for different masker-probe time intervals. The duration of the intervals was adjusted as necessary to obtain PTCs for the widest possible range of masker levels. The BF was identified from function fits to the measured PTCs and it almost always decreased with increasing level. This result is inconsistent with most auditory-nerve observations obtained from other mammals. Several explanations are discussed, including that it may be erroneous to assume that low-frequency PTCs reflect the tuning of apical BM sites exclusively and that the inherent frequency response of the inner hair cell may account for the discrepancy. © *2007 Acoustical Society of America.* [DOI: 10.1121/1.2722046]

I. INTRODUCTION

The basilar membrane (BM) extends from the base to the apex of the cochlea supporting the organ of Corti. Its function is crucial to hearing because it operates as a nonlinear frequency analyzer, at least to a good first approximation (Von Békésy, 1960; Rhode, 1971). Different regions of the BM respond to different frequency components of the acoustic stimulus. Basal regions respond best to high frequencies while apical regions respond best to low frequencies. Actually, any given site on the BM responds to a wide range of frequencies in a filterlike manner, but its response is greatest for one particular frequency, which we will, refer to as the best frequency (BF) (reviewed by Robles and Ruggero, 2001). This report describes a psychophysical approach to investigating how the BF of apical cochlear sites varies with sound level. McFadden (1986) provides a comprehensive review of the topic.

The BF of any given BM site depends on sound level. We will refer to the BF for low-level sounds, near the absolute hearing threshold, as the characteristic frequency (CF). It is now undisputed that the BFs of *basal* sites shift to values lower than the CF as the sound level increases (evidence reviewed by Robles and Ruggero, 2001). By contrast, the direction of the shift for *apical* sites is uncertain, mainly because of the difficulty in recording apical BM responses *in vivo* while maintaining healthy physiological conditions. Indeed, very few studies report *in vivo* recordings of the vibration of apical structures [reviewed by Robles and Ruggero

(2001) and Cooper (2004)]. Of them, only one Cooper and Rhode (1995) reports some BM responses, but they are insufficient to infer the direction of the BF shift. Furthermore, the reliability of all these apical recordings is openly questioned even by their own authors (cf. p. 29 of Cooper, 2004; Robles and Ruggero, 2001). Nevertheless, even if it were possible to make these measurements reliably, the issue remains open as to whether the shift occurs in the same direction for different species.

The direction of the BF shift in lower mammals has been inferred from inner hair cell and auditory nerve responses (Rose *et al.*, 1971; Carney *et al.*, 1999; Carney, 1999; Cheatham and Dallos, 2001). These suggest that the direction of the BF shift depends on the cochlear region: for basal sites (CF > ~ 1.5 kHz), the BF decreases as the sound level increases; for apical sites (CF < ~ 0.75 kHz) the BF increases as the sound level increases; and for intermediate sites (0.75 kHz < CF < 1.5 kHz) no shift occurs. This trend is also supported by furosemide-induced changes in auditory nerve tuning curves (Sewell, 1984). A downward shift in CF was observed when recordings were made from auditory nerve fibers innervating the basal half of the cochlea. However, in fibers with CFs below approximately 800 Hz, an upward shift was recorded.

Psychoacoustic masking methods are widely used to *estimate* some response properties of the human BM (reviewed in Moore, 1998). Specifically, they have been used to investigate the direction of the BF shift in the human cochlea for basal (CFs of 4 and 6 kHz; Moore *et al.*, 2002), intermediate (CFs of 1 and 2 kHz; Moore and Glasberg, 2003; Vogten, 1978), or basal and intermediate sites (CFs ~750 and 2000 Hz; McFadden and Yama, 1983). Overall, the conclu-

sions of these studies match those of BM, inner hair cell, and auditory nerve studies for corresponding cochlear regions. A review of early studies is provided by McFadden (1986).

The direction of the level-dependent BF shift for apical sites of the human cochlea (CFs ≤ 0.5 kHz) has not been explicitly investigated. Yet, knowing the direction of this shift is important to fully understand the level-dependent representation of complex stimuli (including speech) in the human peripheral auditory system as well as to develop more realistic nonlinear models of the human auditory system than those already available (e.g., Lopez-Poveda and Meddis, 2001; Lopez-Poveda, 2005).

The present report describes an attempt to determine the direction of the level-dependent BF shift for apical sites of the human BM. Evidence will be shown that the BF of *both* low- and high-frequency psychophysical tuning curves (PTCs) almost always *decreases* with increasing level. Based on the (conventional) assumption that PTCs reflect BM tuning exclusively, this result would seem inconsistent with the results from most physiological studies in other mammals. It will be discussed that either human cochlear apical responses differ from those of other species or such an assumption may be erroneous for low-frequency PTCs. It will be conjectured that, if the assumption were erroneous, the inherent frequency response of the inner hair cell may account for the apparent discrepancy between psychophysical and physiological results.

II. METHODS

A. Rationale and assumptions

The direction of the level-dependent BF shift was inferred from PTCs for different response criteria (e.g., Chistovich, 1957; Moore, 1978; Moore *et al.*, 1984; reviewed by Moore, 1998). PTCs were measured using tone-on-tone forward masking to avoid potential interactions between the masker and the probe that may complicate the interpretation of the results (Munson and Gardner, 1950; Vogten, 1978; Moore and Glasberg, 1981; Moore, 1998). A pure-tone masker was presented to the listener followed by a fixed-frequency, fixed-level pure-tone probe. The task was to measure the threshold level for maskers of different frequencies that made the probe just detectable. The probe level was *fixed* a few decibels above the listener's absolute threshold for the probe. In these conditions, the threshold masker level is *assumed* to depend on the relative excitation produced by the masker and the probe at the BM place activated by the probe. Because the probe is fixed both in level and frequency, all maskers in any given PTC produce the same excitation on that BM place. For this reason, the resulting PTCs are thought of as iso-response curves and are *assumed* to correspond to BM tuning (or iso-response) curves (cf. Moore, 1998; Yasin and Plack, 2003; Stainsby and Moore, 2006). Consequently, it is assumed that the tip frequency of any given PTC matches approximately that of a corresponding BM tuning curve, and thus both of them will be hereinafter referred to as the BF.

The threshold masker level also depends on the time interval between the masker and the probe. As this interval

increases, the amount of masking decreases and it becomes necessary to increase the masker level to achieve the masking threshold (Zwislocki *et al.*, 1959). Therefore, by *assuming* that the decay of forward masking is independent of masker frequency, it is possible to determine the most effective masker frequency, the BF, at different masker levels by measuring PTCs for increasing masker-probe silent periods.

This approach has important advantages for the purpose of the present study over those in which PTCs are measured for a fixed masker-probe interval and various probe levels (e.g., Vogten, 1978; Kidd and Feth, 1981). Fixing the probe level almost guarantees that the BM region under study is constant for all masker-probe intervals, and thus for all masker levels. Furthermore, the use of a very-low-level probe (just above threshold) minimizes the spread of BM excitation caused by the probe and thus off-frequency listening (Nelson *et al.*, 2001), although off-frequency listening may not be fully eliminated (O'Loughlin and Moore, 1981; see also the following text). Therefore, any change in the behaviorally estimated BF as a result of increasing the masker-probe interval can be reasonably attributed to a level-dependent change in the BF of the BM site whose CF is approximately equal to the probe frequency. Similar assumptions have been made in many other studies that estimated human BM responses behaviorally (e.g., Nelson *et al.*, 2001; Lopez-Poveda *et al.*, 2003; Yasin and Plack, 2003; Plack, 2004; Rosengard *et al.*, 2005; Stainsby and Moore, 2006).

B. Stimuli

PTCs were measured for probe frequencies, f_P, of 125, 250, 500, and 6000 Hz. For each probe frequency, masker frequencies, f_M, ranged from 0.5 to 3 times the probe frequency. Typically 16 masker frequencies were used for each probe frequency although the actual number varied across listeners and masker-probe intervals. Maskers had a fixed duration of 110 ms, including 5-ms raised-cosine onset and offset ramps. The 500- and 6000-Hz probes had 5-ms raised-cosine onset/offset ramps and no steady state portion, hence a total duration of 10 ms. The 125- and 250-Hz probes also had 5-ms onset/offset ramps but a 10-ms steady state, hence a total duration of 20 ms. Longer durations were used for these low-frequency probes in an attempt to decrease the salience of spectral splatter and thus a potential increase in probe detectability by off-frequency listening (Lopez-Poveda *et al.*, 2003; see also the following text). The masker-probe silent intervals, measured from masker offset to probe onset, ranged from 2 to 70 ms. Their actual values differed across listeners and probe frequencies with the aim of measuring PTCs over the widest possible range of masker levels for each listener. These were chosen by trial and error to guarantee that the levels for two masker frequencies, one at the probe frequency and one approximately an octave below it, were still lower than the set maximum level of the system (see the following text). The probe level was fixed at 9 dB above each listener's absolute threshold for the probe.

Stimuli were generated with a Tucker Davis Technologies™ psychoacoustics workstation (System III) at a sampling rate of 24.4 kHz and 24-bit resolution. All stimuli

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TABLE I. Listeners' absolute thresholds for the probes (dB SPL).

Listener	Probe frequency and duration			
	125 Hz (20 ms)	250 Hz (20 ms)	500 Hz (10 ms)	6000 Hz (10 ms)
S1	56.0	48.6	36.9	26.1
S2	51.4	52.3	43.9	40.9
S3	59.7	36.0	36.9	30.7

were played monaurally via the system's headphone connections through the same pair of Etymotic ER2 earphones. Listeners sat in a double-walled sound-attenuating room. The sound pressure levels (SPLs) reported below are nominal electrical levels.

C. Procedure

Masker levels at threshold were measured using a two-interval, two-alternative forced-choice paradigm. A two-up, one-down adaptive rule was used to estimate the 71% correct point on the psychometric function (Levitt, 1971). The masker level was increased and decreased by 6 dB for the first two reversals and by 2 dB thereafter. For each measurement, the adaptive procedure continued (typically for 50 to 70 trials) until 12 reversals were recorded. The threshold estimate was taken as the mean of the masker levels for the final ten reversals. The estimate was discarded when the standard deviation (SD) of these ten levels exceeded 6 dB. At least three thresholds were obtained in this way for each condition and their mean was taken as the actual threshold. When the SD of the first three thresholds exceeded 6 dB, a fourth threshold was measured and included in the mean.

The maximum allowed masker level was set to 106 dB SPL. If the adaptive procedure called for a higher level on two consecutive pairs of trials, then the level was set to 106 dB SPL. If the same happened for three consecutive times, the run was aborted.

D. Listeners

PTCs were measured for three listeners, all of whom had normal hearing at the audiometric frequencies according to ANSI (1996). Prior to measuring the PTCs, the listeners' absolute thresholds for the probes were measured with an adaptive two-down one-up adaptive procedure (Levitt, 1971). Each threshold was measured at least three times and the values were averaged. Results are shown in Table I.

E. Determination of the BF and the level at which it occurs

The BF of each PTC was *not* identified directly as the masker frequency with the lowest masker level. Such a procedure might have yielded biased results in a few instances where several masker frequencies had similar levels (±2 dB). Instead, the BFs and the levels at which they occurred (L_{BF}) were obtained by fitting each side of each PTC with a double-rounded exponential (*roex*) function (Patterson *et al.*, 1982). The details of the fitting method can be found in Yasin and Plack (2003).
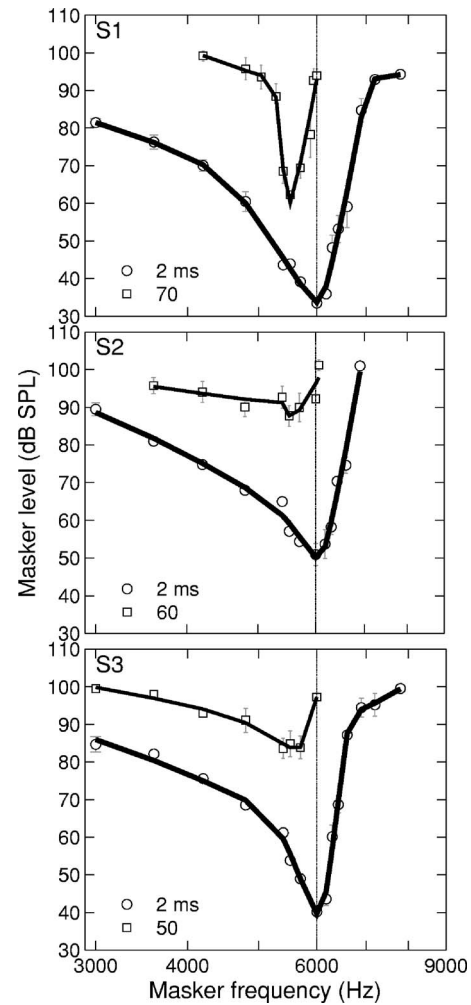

FIG. 1. Psychophysical tuning curves (PTCs) for a probe frequency of 6000 Hz. Each panel illustrates the results for a different listener, as identified by the number in the top-left corner. Symbols illustrate experimental data. Lines illustrate roex fits. PTCs are illustrated for two different masker-probe time intervals (in ms), as indicated by the legend inset on each panel. Error bars illustrate one standard error of the mean. The vertical dashed-dotted line denotes the position of the probe frequency.

III. RESULTS

A. Psychophysical tuning curves

Figures 1–4 depict the PTCs for probe frequencies of 6000, 500, 250, and 125 Hz, respectively. In every figure, each panel illustrates the results for a different listener. Symbols illustrate the experimental PTCs and lines illustrate corresponding *roex* fits.

Let us first examine the results for a probe frequency of 6000 Hz (Fig. 1). The PTCs for the shortest masker-probe interval (2 ms) always had their tips near the probe frequency (i.e., BF~6 kHz) and were asymmetric when plotted on a log scale. That is, they were steeper for frequencies higher than the BF than for lower frequencies. For the longer masker-probe interval, the PTCs became broader for listeners S2 and S3, but narrower for S1. One would expect that the PTCs for the longer masker-probe interval would always be broader than those for the shorter interval. There exist, however, examples where physiological tuning curves get narrower with increasing response criterion, at least over a cer-

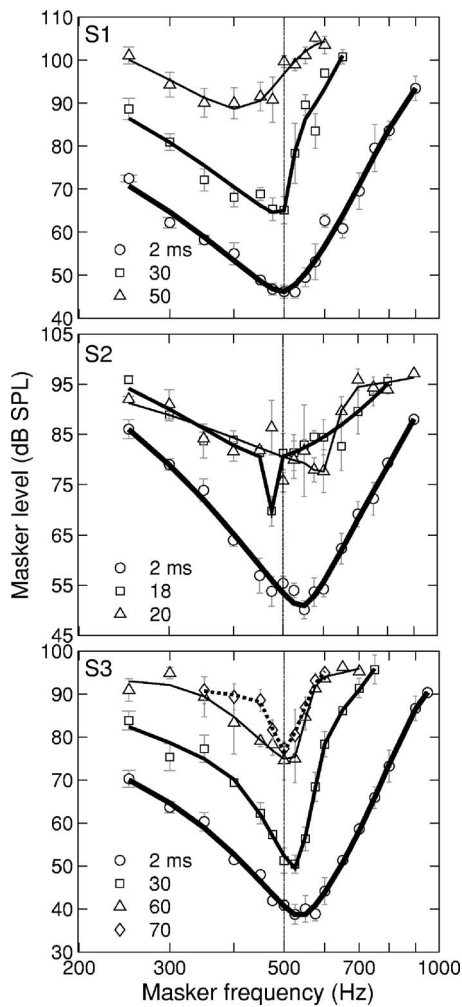Lopez-Poveda *et al.*: Apical cochlear best-frequency shifts

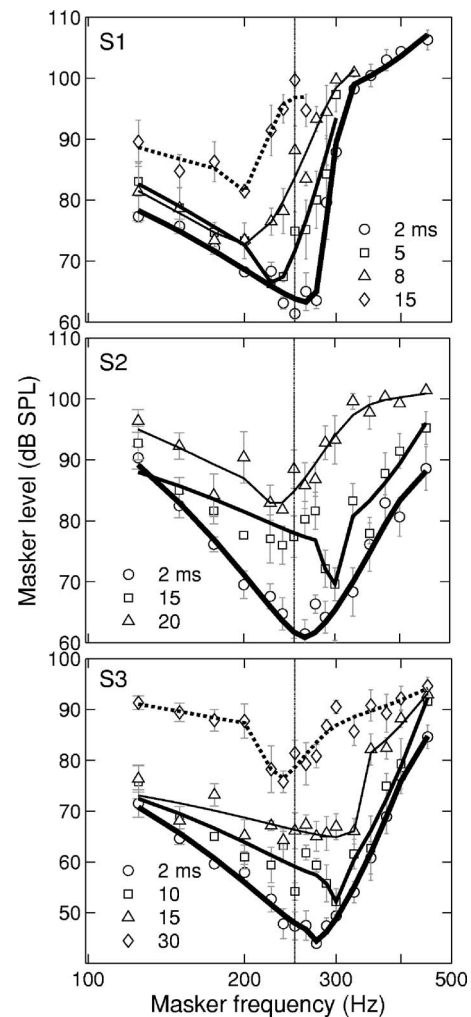FIG. 2. As for Fig. 1 but for probe frequency of 500 Hz.

FIG. 3. As for Fig. 1 but for probe frequency of 250 Hz.

tain range of criteria [for the BM: Fig. 11 of Ruggero *et al.* (1997); for the auditory nerve: Fig. 13 of Evans (1975)]. Therefore, the result for S1 is not unphysiological.

More interesting for the purpose of the present study is that, for all three listeners, the tip frequency of the PTCs decreased as the probe delay increased. That is, the BF decreased as L_{BF} increased. The direction of this shift was consistent with level-dependent BF shifts reported in other species for basal sites of the BM (Ruggero *et al.*, 1997; Rhode and Recio, 2000) and for auditory nerve fibers with CFs above approximately 1.5 kHz (Carney *et al.*, 1999; Carney, 1999). It is also consistent with the direction of the shifts described psychophysically in humans using different methods (Moore *et al.*, 2002).

The PTCs for a probe frequency of 500 Hz (Fig. 2) looked, overall, more symmetric in all conditions than those for $f_P = 6000$ Hz. For the shortest masker-probe interval, the tip frequency was somewhat higher than the probe frequency. It shifted to a slightly different value with increasing L_{BF}. The direction of the shift was different for different listeners. For S1, the BF decreased with increases in the masker-probe interval. For S3, the BF hardly decreased with increasing masker level. For S2, the BF first decreased and then increased as the masker-probe interval increased. BF shifts that reverse in direction with increasing sound level

have been reported (in other species) for the apical region of the cochlear partition (CF~500 Hz) when the velocity of vibration rather than displacement is considered (cf. Fig. 2.3B of Cooper, 2004).

The PTCs for probe frequencies of 250 and 125 Hz (Figs. 3 and 4, respectively) were alike, but they differed qualitatively from those at 500 Hz. These PTCs appeared more asymmetric than those at 500 Hz, with their high-frequency slopes being steeper than the low-frequency ones (e.g., S1 for a probe frequency of 250 Hz). At 250 Hz (Fig. 3), the BF for the shortest masker-probe interval was slightly higher than the probe frequency for all three listeners. The BF decreased monotonically with increasing masker level for listener S1 only. For listeners S2 and S3, the BF first increased and then decreased with increasing masker level. At 125 Hz (Fig. 4), the BF for the shortest masker-probe interval was slightly higher than the probe frequency for S3 and S1, respectively. Remarkably, for S2 the BF (231.3 Hz) was almost twice the probe frequency (125 Hz). Also, the high-frequency tails of these PTCs became unusually shallower as the masker-probe interval increased. Possible reasons for these results are discussed in the following text. At 125 Hz, the BF decreased monotonically with increasing masker level for all three listeners (Fig. 4).
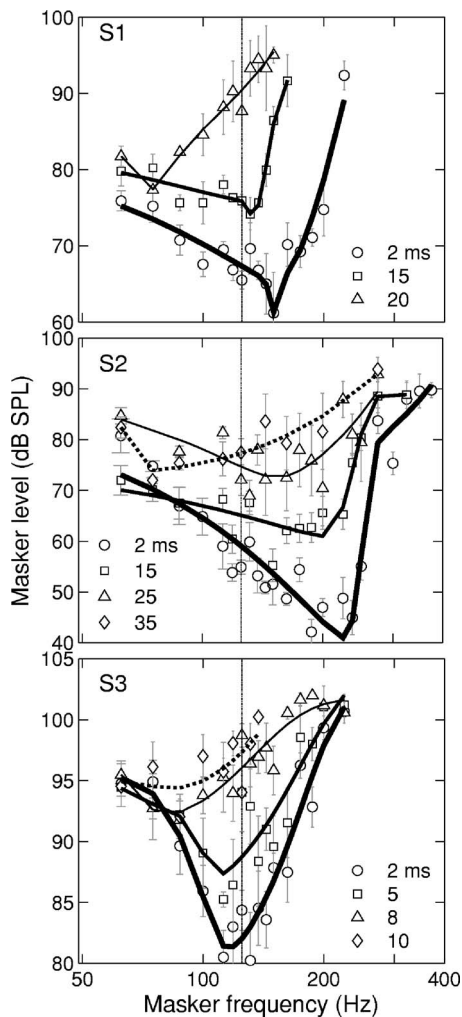
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FIG. 4. As for Fig. 1 but for probe frequency of 125 Hz.

B. The direction and magnitude of level-dependent BF shifts

Figure 5 summarizes the main results pertaining to the relationship between the BFs and their corresponding levels, L_{BF}, as determined by the roex fits. Each panel illustrates the results for a different probe frequency. Each symbol illustrates the results for a different listener [as indicated by inset in Fig. 5(d)]. The figure plots deviations of the BF with respect to the probe frequency (in octaves) against L_{BF} relative to the probe level. This form of representation serves two purposes: (a) to identify the direction of any level-dependent BF shift, and (b) to quantify the extent of the shift and compare it across probe frequencies.

Figure 5 shows three striking results. First, the BF is always lower at the highest than at the lowest masker levels, except for S2 at 500 Hz, although in some cases (S2 at 500 Hz; S2 and S3 at 250 Hz) the BF varies nonmonotonically with increasing masker level. These results are inconsistent with most physiological observations in other mammalian species that monotonic level-dependent BF shifts occur in opposite directions for apical and basal cochlear sites (Rose *et al.*, 1971; Carney *et al.*, 1999; Carney, 1999; Cheatham and Dallos, 2001). Second, the magnitude of the behaviorally estimated relative BF shift is considerably greater for the lowest probe frequency tested. Third, in several instances the probe frequency is lower than the BF at the lowest masker levels and sometimes even when the masker level equals the probe level [i.e., the plots do not go across the (0, 0) point]. The latter is somewhat surprising because one would expect that the BF be equal to the probe fre-
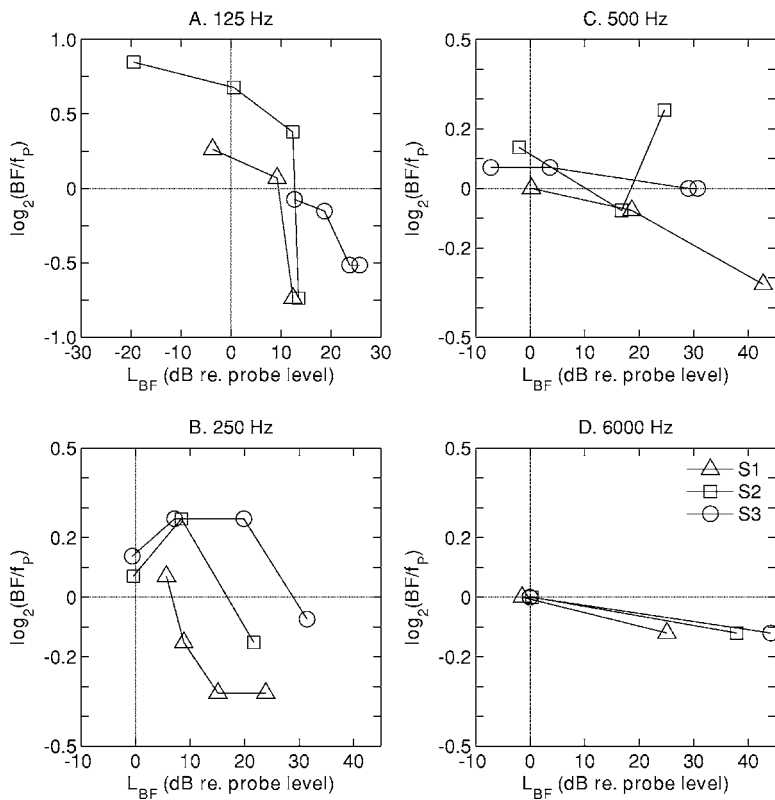

FIG. 5. The estimated BF as a function of the estimated L_{BF}. The BF is plotted relative to the probe frequency (f_P) in octaves. Positive/negative values indicate that the BF is higher/lower than the probe frequency, respectively. Different symbols illustrate the results for different listeners as indicated by the inset in the bottom, right panel. Each panel illustrates the results for a different probe frequency. Note that different probe durations were used for probe frequencies below and above 500 Hz (Sec. II B), and that different masker-probe intervals were used for different listeners (see Figs. 1–4).

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quency when the relative level between the masker and the probe is 0 dB. Interpretations of these results and their implications are discussed below.

One last remark: an alternative way of estimating the BF and L_{BF} would have been to equate them to the frequency of the most effective masker (i.e., the masker requiring the lowest level instead of L_{BF} estimated from *roex* fits) and the level at which it occurs, respectively. This was done and the results (not shown) confirmed the main conclusions drawn from Fig. 5.

IV. DISCUSSION

The goal of this study was to characterize the direction of level-dependent BF shifts in the *apical* region of the *human* BM. Specifically we sought to assess whether the direction of the shift conforms to that inferred from auditory nerve studies in other mammals (Rose *et al.*, 1971; Carney *et al.*, 1999; Carney, 1999). Those physiological studies suggest that, with increases in the stimulus level, the BF decreases for basal sites but increases for apical sites. The present results (summarized in Fig. 5) appear inconsistent with this conclusion as the BF of PTCs decreased with increasing level for low (<500 Hz) and high (6 kHz) probe frequencies and the BF shift was sometimes nonmonotonic.

A. Comparisons with other psychoacoustical and physiological results

To our knowledge, no other study has been carried out to date with identical motivations or methods. Allowing for the differences in motivations and methods, however, the present findings agree in part with those from other masking studies. Kidd and Feth (1981), for instance, reported PTCs for several probe frequencies and levels. Their PTCs were measured using a similar method to the one employed here except that they fixed the masker-probe interval (at 10 ms) and considered two probe levels: 10 and 20 dB SL. The tip frequency of their 250-Hz PTCs decreased when the masker level increased by ~25 dB as a result of increasing the probe level (see Fig. 1 in Kidd and Feth, 1981). The present 250-Hz PTCs have BFs that either decrease monotonically (S1) or vary nonmonotonically (S2 and S3) with increasing masker level [Fig. 5(b)]. Nevertheless, their BFs decrease when the masker level increases over a range comparable to that of Kidd and Feth and therefore the two studies are mostly consistent in this respect. No BF shift occurred in the 500-Hz PTCs of Kidd and Feth.

The present results are consistent with previously reported masking patterns for low- and high-frequency tonal maskers. It has long been known that the peak of the masking pattern shifts to higher frequencies with increasing the level of a *high*-frequency (≥1 kHz) masker (e.g., Munson and Gardner, 1950; Ehmer and Ehmer, 1969; Kidd and Feth, 1981). This shift is consistent with the idea that the peak of the BM traveling wave caused by the masker moves towards the base of the cochlea with increasing the masker level. Hence, it is consistent with the observation that the BF for a given cochlear site decreases with increasing level. Less well appreciated, however, is that a similar shift in the peak of the

masking pattern occurs for masker frequencies ≤500 Hz (Table I in Ehmer and Ehmer, 1969; Tobias, 1977; Fig. 2 in Kidd and Feth, 1981; reviewed by McFadden, 1986). This is consistent with the idea that the BF of *apical* cochlear sites decreases with increasing level as occurs for basal sites.

That said, this earlier behavioral evidence must be taken with caution, as the results of Tobias (1977) were almost certainly affected by masker-probe interactions (e.g., beats, suppression) (Munson and Gardner, 1950; Vogten, 1978; Moore and Glasberg, 1981) and those of Kidd and Feth (1981) and Ehmer and Ehmer (1969) by off-frequency listening [the effects of off-frequency listening in estimates of level-dependent BF shifts are amply discussed on p. 73 of Moore and Glasberg (2003)]. Note that masker-probe interactions are minimized in the present results thanks to using nonsimultaneous masking. The use of a fixed, low-level probe also minimized off-frequency listening (Nelson *et al.*, 2001), although the fact that the BF shift was not zero when the masker and the probe had identical levels at low probe frequencies [Figs. 5(a) and 5(b)] indicates that off-frequency listening may have still occurred here for some listeners (see the following text).

The present human results appear inconsistent with those from earlier auditory nerve studies in other species (Carney *et al.*, 1999; Carney, 1999; Rose *et al.*, 1971), but are consistent with the *mechanical* data of Cooper and Rhode (1997) for a cochlear site with a CF~500 Hz. These data show that the BF of cochlear partition motion decreases with increases in the stimulus level, at least when the amplitude of vibration is expressed in units of displacement (see Fig. 2.4B in Cooper, 2004). As for inner hair cells, the ac receptor potential of apical units (CF<1000 Hz) peaks at a frequency that decreases with increasing sound level (Figs. 3 and 4 in Dallos, 1986; Fig. 10A in Dallos, 1985). Interestingly, dc (Fig. 10C in Dallos, 1985) and average (Fig. 3 in Cheatham and Dallos, 2001) inner hair cell receptor potential responses indicate upward BF shifts with increasing level.

B. Conjectures on the discrepancy between psychoacoustical and physiological results

1. Distortion, energy splatter, and off-frequency effects

Earphone harmonic distortion might have contributed to the observed downward BF shifts. The first harmonic of low-frequency, high-level maskers might have contributed, together with the masker, to masking the probe and, given that distortion is greater at high levels, its contribution would have increased with increasing masker level. This effect, however, would be small (if at all existent) because the SPL of the first harmonic was always 46 dB lower than the fundamental (as measured at the output of the earphones with a sound level meter placed on a Zwislocki coupler), even for the maximum output SPL of the system.

The 5-ms ramps on the probes might have been too short to prevent off-frequency probe detection by energy splatter. This might explain why the BFs differed from the probe frequency when they should have been equal (Fig. 5), particularly for PTCs below 500 Hz. If the significance of

this effect varied across listeners, it might also explain the remarkable large difference observed for S2 at 125 Hz. Possibly this effect could have been further reduced by increasing the ramps on the probes. However, off-frequency listening is an inherent difficulty with tonal forward masking and must always be considered in interpreting the results (Kidd and Feth, 1981; O'Loughlin and Moore, 1981).

Similarly, the 5-ms ramps on the masker might have been too short to prevent off-frequency masking by masker-energy splatter. This might account, at least in part, for the downward BF shifts observed at 125 Hz because energy splatter would be greater for high-level, low-frequency maskers. This, however, could have happened *only* if the splatter of masker energy were toward the base of the cochlea with increasing masker level, which is still in conflict with the apicalward shift of the peak of BM traveling wave with increasing level suggested by most physiological studies in other mammals. One possible explanation is that the response characteristics of the apical region of the *human* BM differ from those of the mammalian species for which auditory nerve and inner hair cell responses exist. This, however, seems unlikely given that at least one of the relevant auditory nerve studies (Rose *et al.*, 1971) was carried out in a primate species. Alternatively, our current interpretation of PTCs (or of auditory nerve responses) may be incorrect, at least for apical sites.

2. Influence by the acoustic reflexes

Low-frequency PTCs may have been influenced by the middle-ear acoustic reflex (Møller, 2000). The reflex starts to operate for levels around 75–78 dB *hearing level* (Neumann *et al.*, 1996) and attenuates incoming sounds to the cochlea. If it had been activated by the masker, its effect would not have decayed entirely by the time that the probe was presented. This may have made the probe inaudible at masker levels at which it would have been audible without the reflex. The reflex would be more likely (and strongly) activated by masker frequencies in the tails of the PTCs because their levels are higher. In the present task, where the probe *had* to be detected, this might have led to masker levels lower than they would have been without the reflex and hence might have "broadened" the PTCs. It is possible that this contributed to reducing the slope of the high-frequency tails of some PTCs for the longer masker-probe intervals (e.g., S2 and S3 in Fig. 4). On the other hand, the reflex might have been activated also during the later portion of the masker, thus reducing its ability to mask the probe. Therefore, the reflex might have *shaped* the PTCs through a complex combination of its effects, on the masker and on the probe.

It is doubtful, however, that activation of the acoustic reflex accounts for the downward BF shifts with increasing level observed at 125 and 250 Hz (Fig. 5). First, the BFs for all listeners and conditions occurred at SPLs below the threshold level of reflex activation [75–78 dB HL according to Neumann *et al.* (1996)]. Also, the threshold SPL of reflex activation decreases with increasing frequency from 100 to 500 Hz (cf. Fig. 12.9 of Møller, 2000). Therefore, the above-mentioned "broadening" effect of the reflex would be stronger on the high- than on the low-frequency tails of low-

frequency PTCs. If anything, this would shift the BF upward relative to what would be measured without the reflex.

It is also unlikely that the activation of the olivocochlear efferent system (Guinan, 1996) accounts for the observed BF shifts because the activation of medial olivocochlear efferents reduces the sensitivity of low-CF auditory nerve without affecting their BFs (cf. Fig. 1 of Guinan and Gifford, 1988).

3. Influence by the inherent inner-hair-cell frequency response

As explained above, the ac component of the receptor potential of apical inner hair cells (CF < 1000 Hz) peaks at a frequency that *decreases* with increasing sound level (Figs. 3 and 4 in Dallos, 1986; Fig. 10A in Dallos, 1985). This occurs even when the BF of the associated BM response is level independent (Shamma *et al.*, 1986). If the amount of (forward) masking at low frequencies were proportional to the amplitude of the ac receptor potential, this might explain the downward BF shift observed in the present PTCs and in earlier data, at least qualitatively. It might also explain, at least in part, why the present human results indicate a downward BF shift with increases in sound level while primate auditory-nerve iso-intensity responses indicate an upward BF shift (Rose *et al.*, 1971). The reason would be that auditory nerve iso-intensity functions plot the *average* discharge rate of the fibers, which is thought to be proportional to the dc (or average) receptor potential (Robles and Ruggero, 2001) and this peaks at frequencies that *increase* with increasing level (Fig. 10C in Dallos, 1985; Shamma *et al.*, 1986; Fig. 3 in Cheatham and Dallos, 2001). In summary, human low-frequency PTCs may reflect the tuning of the ac component of the inner hair cell receptor potential, which differs from that of the associated BM (Shamma *et al.*, 1986) and auditory nerve *average* responses.

It is uncertain how this might happen but a possible mechanism relates to the contribution of auditory-nerve post-stimulus recovery to forward masking (e.g., Harris and Dallos, 1979; Meddis and O'Mard, 2006). The magnitude of this effect is commonly thought to depend on the *average* discharge rate evoked by the masker. While this is almost certainly true for high-frequency maskers (Harris and Dallos, 1979, p. 1090), it is conceivable that for very low frequency maskers, the amount of masking depends on the (*peak*) discharge rate over, say, the last cycle of the masker, which would depend on the peak receptor potential. This needs experimental confirmation but appears plausible because in response to very low frequency masker and probes, fibers would discharge on every semicycle of the stimulus and would have time to recover partly from firing during the other semicycle. This would occur even when the stimulus greatly exceeds the SPL that elicits saturation (average) discharge rates (Rose *et al.*, 1971). Therefore, the fibers' response to the probe might be particularly conditioned by their peak discharge over the preceding masker cycle.

The same would not apply to high-frequency stimuli. For high-frequency stimuli the ac component of the receptor potential is highly attenuated relative to the dc component (Sellick and Russell, 1980). Thus, both behavioral and physiological frequency responses would "necessarily" follow the

dc component of the receptor potential. The dc response of the isolated inner hair cell (i.e., without the influence of BM tuning) is approximately frequency independent (e.g., Fig. 12A in Lopez-Poveda and Eustaquio-Martin, 2006). Consequently, PTCs and auditory nerve responses would reflect the tuning of BM responses more or less directly, as is commonly assumed.

Even if this conjecture were true, however, an important issue would remain puzzling. Evidence for a BF increase with increasing level comes not only from average-rate frequency response functions of auditory nerve fibers (Rose *et al.*, 1971). It also comes from the analysis of the instantaneous frequency of the fibers' impulse responses (Carney *et al.*, 1999; Carney, 1999) and this is likely independent of the magnitude of the ac or the dc components of the receptor potential of inner hair cells.

V. SUMMARY AND CONCLUSIONS

It has been shown that the tip frequency of low-frequency PTCs (<500 Hz) decreases with increases in the level at which the tip occurs, albeit sometimes nonmonotonically. Based on the conventional interpretation of PTCs, this would imply that the BF of BM apical sites decreases with increasing level, an interpretation that appears inconsistent with well-established evidence drawn from the analysis of the responses of low-CF auditory nerve fibers in other mammals. The reason for the inconsistency is uncertain. Activation of the middle-ear acoustic reflex probably contributed to shaping the PTCs, but it is doubtful that this accounts for the observed downward BF shifts with increasing level. It is possible that human apical cochlear responses differ from those of other mammals (including some primates). If this were the case, the observed apical downward BF shifts with increasing level might be partly due to off-frequency masking by masker-energy splatter. An alternative explanation would be that for low-frequency stimuli the amount of masking depends on the amplitude of the ac component of the inner hair cell receptor potential. This peaks at a frequency that decreases with increasing level even when the BF of the associated BM response is level independent and when the average isointensity response of auditory fibers indicates an upward BF shift with increasing level (Shamma *et al.*, 1986). This conjecture needs proof.

In any case, the evidence shown indicates that it may be erroneous to make inferences about the level-dependent frequency response properties of the *apical* region of the BM from low-frequency PTCs (or masking patterns). Further, it also may be erroneous to make such inferences from the average frequency response characteristics of low-CF inner hair cells or auditory nerve fibers (Shamma *et al.*, 1986).

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