IS TECTORIAL MEMBRANE FILTERING REQUIRED TO EXPLAIN TWO TONE SUPPRESSION AND THE UPWARD SPREAD OF MASKING?

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In this paper we would like to make three key points. *First*, neural two tone suppression (2TS), by low frequency suppressors on high frequency probes, and the upward spread of masking (USM) are alternate measures of the same nonlinear cochlear mechanism. The two have similar (i.e., essentially equal) thresholds and growth rates. *Second*, the thresholds of neural 2TS, and of the USM, as a function of the probe frequency, are nearly independent of frequency, and are close to 65 dB SPL. *Third*, we discuss and model the *level dependence* of 2TS and the USM, which experimentally has previously been found to be about 2.4 dB/dB in both cat and human.

Regarding the *first* point: The dB difference in BM displacement response between a high frequency probe, and a low frequency threshold suppressor, at the probes place, is 10 to 20 dB [13,7,10]. The BM observations are therefore *in basic disagreement* with corresponding neural and psychophysical data, which have *similar* thresholds for excitation and 2TS [9].

Regarding the *second* point: When corrected for the middle ear response, the frequency response slope (i.e., in dB/octave) of the low frequency (basal) portion of the basilar membrane displacement has a slope of about 9 dB/oct, while the neural threshold response has a slope close to 0 dB/oct (i.e., less than 1 dB/oct). This shallow (near zero) basal neural threshold slope shows up as "tails" of neural tuning curves. By transforming neural frequency tuning curves from frequency to place, it is possible to refine and quantify our understanding of this discrepancy. This difference in slope is *in fundamental conflict*.

Regarding the *third* point, the 2.4 dB/dB slope implies that, in the basal "shallow" tail, the excitatory response of a low frequency suppressor (masker) tone "turns down" the gain of the probe at a rate of 1.4 dB/dB, re the suppressor (masker) level. We presume this suppression comes from an outer hair cell (OHC) controlled gain. We argue that a level dependent BM stiffness must act as the nonlinear BM control parameter.

Tuning curve tails: As may be seen for the 6 kHz neuron in Fig. 1, the low frequency tails of high CF threshold neural frequency tuning curves (in the cat) are typically bowl shaped functions of frequency, largely determined by the middle ear pressure transfer function (P_{sv}/P_{ec}). For example, in Figure 18c of Allen (1983), after normalizing by the cochlear microphonic to remove the effect of the middle ear transfer function, the average neural response

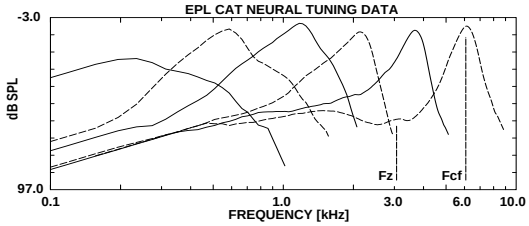

Figure 1. Shown here are a family of cat neural tuning curves, provided by Delgutte and Liberman of Eaton Peabody Laboratory, Boston. These frequency tuning curves were transformed into excitation patterns using the cochlear map of Fig. 2.

slope between 0.3-2.0 kHz was found to be 0 dB/oct, ± 5 dB/oct. *In sharp contrast*, the displacement of the basilar membrane in this same basal region is approximately 9 dB/oct, as shown in the following analysis [see also Allen, 1979].

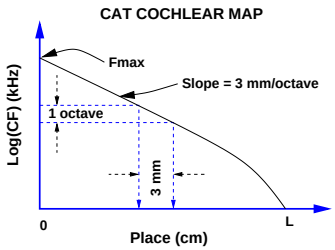

Figure 2. Plot of the cat cochlear map. The slope of 3 mm/oct was established by Liberman by direct measurement. The cochlear map may be used to transform a family of frequency tuning curves into place curves, providing us with estimates of the neural excitation pattern slopes.

By transforming from frequency to place [5], via the *cochlear frequency to place map* shown in Fig. 2, one may find the threshold neural place response for a single tone, thereby removing the effect of the middle ear. For example, in the cat, where the slope of the cochlear map is 3 mm/oct [12], a mechanical [i.e., the BM displacement/scala pressure at the stapes] slope of 9 dB/oct transforms to 3 dB/mm. As shown in Fig. 3 and Table 1, for CFs between 0.25 and 2.0 kHz, this transformation results in *threshold neural place tuning curves* having basal tail response slopes between 0.3-1.3 dB/mm [6].

USM and neural 2TS thresholds. The frequency, spatial, and magnitude dependence of these basal (tail) threshold responses are consistent with the threshold characteristics of high frequency probes in neural 2TS [8,1,9,14] and psychophysical USM experiments [15]. Namely, as a high level, low frequency, masker (suppressor) is raised in level, the threshold for masking (suppression) of a high frequency probe is coincident with the threshold excitation at the low frequency probe's place (in the base). Said another way, when the cilia excitation in the basal tail approaches threshold levels, the neural, neural 2TS and USM effects are simultaneously at threshold. In spatial terms, *these three thresholds occur at almost the same acoustic intensity over the entire basal tail region of the cochlea*, at about 65 dB SPL [9].

CF	S_1	S_2	S_3
kHz	*SLOPE* (dB/mm)*		
5.0	**	32.7	-66.1
4.0	**	26.3	-69.3
2.0	1.3	15.2	-34.5
1.0	1.2	17.4	-25.6
0.5	0.3	14.8	-34.5
0.25	0.3	17.1	-11.0

Table 1. The definition of S_1, S_2, and S_3 are given in Fig. 3, and are shown as dashed lines superimposed on the neural responses. *Mult by 3 mm/oct to convert to dB/oct **For the CFs at 4 and 5 kHz the data are too limited to make convincing estimates of S_1. Since the effect of the middle ear is much smaller at these frequencies, one may directly confirm the shallow tail with respect to frequency, without the frequency to place transformation.

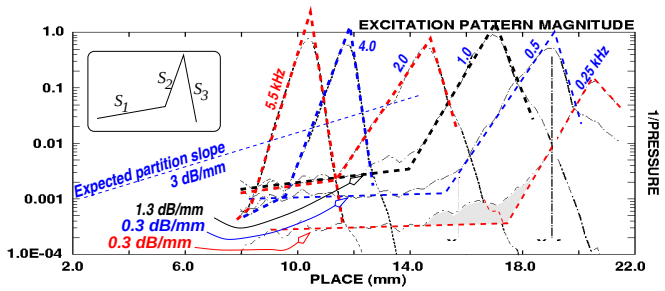

Figure 3. Shown here are the resulting excitation patterns derived from the data of Figures 1 and 2. Straight lines have been placed visually on the curves having slopes as indicated.

From estimates of the human threshold of the USM of Wegel and Lane (1924), we estimate a frequency slope of ≈5 dB/octave for the basal tail (this estimate is imprecise). Since the cochlear map slope in human is 5 mm/octave [11], this corresponds to a slope of ≈1 dB/mm for the excitation response in the basal turns of the human cochlea. Low frequency slopes of 2TS from Abbas and Sachs (1976) and Fahey and Allen (1985) in the cat are less than 1 dB/mm.

Thus in the base of the cochlea, neural tuning curves, USM thresholds, and neural 2TS thresholds each indicate a broad flat tail region, both for human and cat.

A theoretical slope estimate. In the base, the partition stiffness is defined as $K_p(x) \equiv K_p(0)e^{-2ax}$. Assuming a constant partition mass and a 3mm/octave frequency to place map, the value of $a = \ln(2)/3$ for the cat is roughly 0.231 mm^{-1}. From the WKB method, the spatial pressure distribution of a tone stimulus in the base of the cochlea is given by

$$\frac{P(x,\omega)}{P(0,\omega)} = \sqrt{\frac{Z_c(x)}{Z_c(0)}}\; e^{-i\omega \int_{\xi=0}^{x} d\xi/c(\xi)} \qquad (1)$$

$$= e^{-ax/2}\ e^{-i\omega T(x,\omega)}, \tag{2}$$

where the local wave speed is $c(x) = \sqrt{K_p(x)A(x)/\rho}$ and the local characteristic impedance is $Z_c(x) = \sqrt{\rho K_p(x)/A(x)}$. The effective scala area is $A(x)$ and ρ is the scala fluid density. Hair cells are known to be displacement detectors (Hudspeth and Corey, 1977). Above 1 kHz, Dallos has found that inner hair cells (IHC) respond to displacement. OHCs are believed to follow displacement at all frequencies.

It follows, from Eq. 2 and Hooke's Law [i.e., $P(x,\omega) = K_p(x)D(x,\omega)$], that the magnitude of the BM displacement $|D(x,\omega)|$ must vary as $e^{3ax/2}$. This corresponds to a BM displacement slope of about $20\log_{10}(e^{3a/2}) = 3$ dB/mm (i.e., 9 dB/oct) in the basal tail.[a] This slope is typical of experimental BM transfer functions [4].

Neural 2TS and USM thresholds: Fahey and Allen (1985) found the pure tone neural tail and basal neural 2TS thresholds to be 65 dB SPL for low frequency suppressors between 0.8 and 5 kHz. Unpublished data extends this published upper frequency limit to 14 kHz.

In stark contrast, recent BM 2TS measurements by Ruggero *et al.* (1992), Cooper (1996), and Geisler and Nuttall (1997), have shown unequivocally that the neural and BM 2TS thresholds are *significantly* different (unlike the cat neuron, where they are the same). For example, Ruggero *et al.* say (page 1096)

> ... if neural rate threshold actually corresponds to a constant displacement ($\approx$ 2 nm) ..., then mechanical suppression thresholds would substantially exceed neural excitation thresholds and would stand in disagreement with findings on neural rate suppression.

Using a 0.1 nm displacement criterion, Cooper found basal excitation thresholds near 65 dB and 2TS thresholds near 85 dB SPL. Cooper says (page 3095)

> Indeed, the direct comparisons shown ... indicate that most of the low-frequency mechanical suppression thresholds were between 10 and 20 dB above the iso-displacement tuning curves[,] which corresponded to "neural thresholds" at the site's [CF].

That is, Cooper's BM results placed the threshold of BM suppression about 1 order of magnitude higher in level than the Fahey and Allen 2TS thresholds, both in absolute terms, and relative to the 0.1 nm threshold. The Geisler and Nuttall (1997) study confirms these findings (see their Fig. 2). A second unequivocal finding of the studies [7,10] is that nonlinear suppression is dependent on BM displacement rather than velocity.

[a] For this calculation we have taken the area constant. Weaver measured $A(x)$ for three human cochleas, and two showed a small decrease with x. Including this decrease would make the BM displacement slope larger, *strengthening* the argument presented here.

In summary, we have highlighted two important differences between neural and BM experimental data: *(i)* As detailed in Table 1, there is a discrepancy in the relative slopes of neural threshold response and BM displacement of between 3 and 10 in the basal tail (0.3-1 dB/mm vs. 3 dB/mm) [6]. *(ii)* The dB difference in the threshold intensity for neural 2TS and neural excitation thresholds is close to 0 dB over a wide range of frequencies, but differ by 10 to 20 dB when measured on the BM. *We believe these two problems are related.*[b]

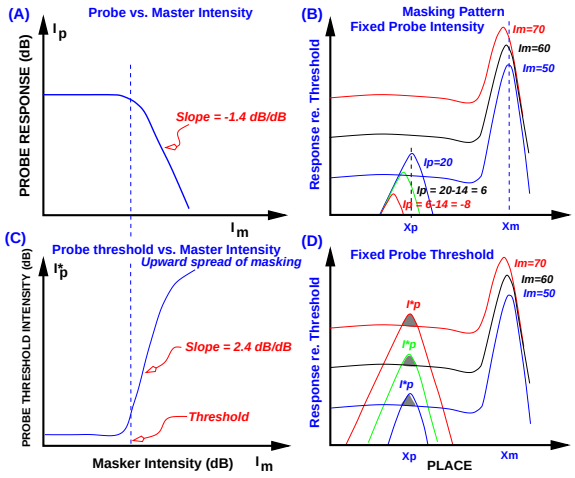

Figure 4. Panels (A,B) depict (in a cartoon format) what must happen to the hair cell cilia response of a high frequency probe tone as a low frequency excitatory suppressor tone is increased in intensity. (A) depicts the level function for the suppressed response of the probe, as a function of the suppressor intensity. Panels (C,D) depict the probe after an adjustment back to its detection threshold. (C) shows the level function for the threshold probe intensity as a function of the suppressor intensity.

The slope of 2TS and USM: Suppression and USM super-threshold data are exquisitely interesting. Delgutte (1990) found a 2TS slope of 2.4 dB for every dB of suppressor level. We have estimated the same slopes of 2.4 dB/dB from Wegel and Lane's 1924 USM IO functions (level of a 2-4 kHz probe, at threshold, as a function of a 400 Hz masker's intensity).[c]

We show a summarizing cartoon (Fig. 4) to help explain and summarize our view of the data. Panels (A,B) depict the response of a fixed probe, to a low frequency masker, at three masker intensities. In (B) we depict the IO function of the probe, with a slope of $1.4 = 2.4 - 1$ dB/dB. The probe must be attenuated by 1.4 dB for every dB of suppressor (masker) level. Since the probe (its intensity is fixed) is not returned to threshold, its slope must be –1.4 dB/dB. In (C,D) we see the same situation, except the probe is returned to threshold. The IO function in this case is $2.4 = 1.4 + 1$ dB/dB since it

[b] Suppression on the BM has not yet been measured as a function of the probe frequency. If the CF is level dependent, as we believe, then this would be an important experiment.
[c] The slopes for the experimental BM data seem to be uncertain.

must overcome the basal linear masker growth. In summary, as the masker is increased by 1 dB, the probe is attenuated by 1.4 dB. To return the probe to threshold, it must be increased by 1.4 dB to overcome the attenuation, and another 1 dB to overcome the masker level increase, giving a total of 2.4 dB/dB. What remains unexplained is how the masker can reduce the gain of the probe in this manner.

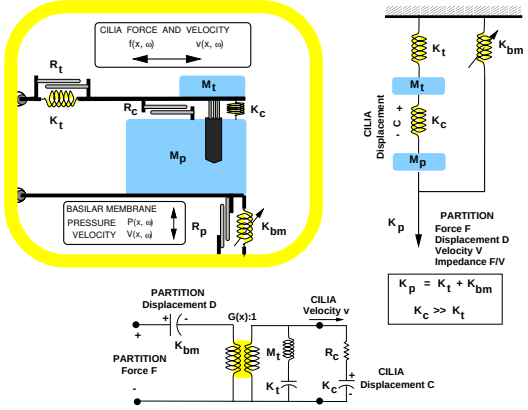

Figure 5. If the partition stiffness $K_p(x)$ is dominated by the stiffness of the tectorial membrane $K_t(x)$ at high intensities, and the OHCs induced stiffness (a dynamic nonlinear component of the stiffness) at low intensities, then a simple model can satisfy all the required conditions simultaneously.

A robust solution: We propose that the micromechanics of the tectorial membrane (TM) transforms the BM displacement slope of 3 dB/mm to a cilia excitation which has almost constant place dependence (<0.3 dB/mm in cat). From Fig. 5 it follows that the cilia to BM displacement ratio is $H_c \equiv C/D = K_t/(K_c + K_t)$. It is required, by the TM model [3], that the cilia be much stiffer than the TM ($K_c >> K_t$), thereby attenuating the cilia response in the base. Thus $H_c \approx K_t/K_c << 1$.

If the TM to cilia stiffness ratio $K_t(x)/K_c(x)$ were to vary as $e^{-3ax/2}$ it would compensate for the $e^{3ax/2}$ dependence of the BM displacement. If two springs are in series, and one is much stiffer, the total stiffness is dominated by the smaller stiffness, namely $K_t K_c/(K_t + K_c) \approx K_t$. The partition stiffness is therefore $K_p \approx K_t + K_{bm}(C)$. The second term is the dynamic OHC component of the stiffness which depends on the cilia displacement C, and is approximately equal to K_t in quiet (i.e., $C = 0$), and at very high intensities, or in a dead ear, approaches zero. This gives us enough equations to determine every element uniquely, in a manner that is consistent with our requirements. It follows that the cilia stiffness must be $K_c(x) = K_p(0)e^{-ax/2}$. The fact that OHC cilia increase in length [from 4 to 6 μm in the cat] is qualitatively consistent with this decreasing $K_c(x)$.

Under these conditions, *(1)* the TM stiffness is proportional to e^{-2ax} [i.e., $K_t \propto K_p(x)$]; *(2)* at high intensities, $K_t(x)$ determines the partition

stiffness $K_p(x)$; *(3)* the transduction "filter" $H_c(x, f)$ cancels the 3 dB/mm (9 dB/oct) BM displacement growth giving a cilia response with a close to zero slope. Since the partition stiffness is mainly determined by the TM stiffness, [plus an equal dynamic, nonlinear component due to the OHCs at low intensities $K_{bm}(C)$], this choice of parameters naturally accounts for the necessary correlation in the partition and TM stiffness variation.

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