

THE ROLE OF MICROMECHANICS IN EXPLAINING TWO-TONE SUPPRESSION AND THE UPWARD SPREAD OF MASKING

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When a low-frequency tone is above about 65 dB SPL, it is excitatory in the base of the cochlea, leading to a dramatic elevation in the threshold of a high-frequency probe tone, measured either psychophysically or neurally. When measured psychophysically, this effect is called the “upward spread of masking” (USM). USM was first characterized by Fletcher [1] and Wegel and Lane [2]. The USM suppression threshold is between 55 and 65 dB SPL, and the “iso-response growth of masking” is approximately 2.4 dB/dB. The corresponding “rate of suppression” defined as the rate of reduction of the probe relative to the suppressor level, is 1 dB/dB less, namely 1.4 dB/dB. The 1 dB/dB difference follows given the linear growth of the suppressor at the high-frequency probe’s place. When measured neurally this same effect is called (neural) two-tone suppression (Neural-2TS). It was first measured by Kiang and Moxon [3] and Sachs and Abbas [4]. As with USM, Neural-2TS thresholds are about 65 dB SPL, and the iso-rate suppression slope is close to 2.4 dB/dB. Thus 2TS and the USM are two different measures of the same cochlear suppression effect. When 2TS is measured on the basilar membrane (BM) however, the results are very different. Typically the BM-2TS suppression threshold is above 80 dB SPL, and the Fourier component of the low-frequency suppressor tone must be at least 25-35 dB higher than that of the high-frequency probe tone. Unlike neural 2TS, the suppressor level is always much greater than the probe level, at the probe’s characteristic place (CP). The BM-2TS rate of suppression is 1 dB/dB. The discrepancy between 1.4 dB/dB for the neural suppressed slope, and 1 dB/dB on the BM, is key, the latter being the expected result of any saturating nonlinearity. Thus the 2TS/USM disagreement at the BM and at the haircell are in sharp disagreement, both in threshold, as well as slope. We will review this disagreement and discuss how this difference may be resolved using the tectorial membrane as a *base-stop filter*, which forms the BM-cilia displacement transfer function. This is a form of second filter, which in conjunction with a voltage-dependent OHC stiffness, resolves the discrepancy, as well as explaining various other non-linear characteristics.

1 Introduction

Allen and Sen [5] suggested that USM and Neural-2TS are the same phenomenon, observed in the two different paradigms of psychophysical and neural measure-

ments. The similarities in both threshold levels as well as the rate of masking/suppression leads to a unified theory. However, these close similarities are not present when 2TS is observed on the BM. This leads to the conclusion that the physiological basis for BM-2TS must be quite different from that of Neural-2TS/USM.

1.1 Upward-spread of masking

It is evident from USM experiments [2,6] that the growth of masking can be as high as 2.4 dB/dB, meaning that to maintain the probe at its threshold, a 1-dB increase of the masker level requires an increase of the probe by 2.4 dB. To enable further discussion of USM, we define two parameters: a threshold of masking, $I_m^*(f_m, f_p)$ and a growth of masking, ν . The * on I_m indicates the masker intensity is at the suppression threshold level, below which there is no USM effect, f_p is the frequency of the masked probe, and f_m is the frequency of the masker. When the probe frequency is higher than the masker frequency by one half to one octave, I_m^* is close to 65 dB SPL [2]. This important threshold suppression threshold has received scant attention in the masking literature.

Recent studies by Bacon *et al.* [6] and Nelson and Schroder [7] have shown I_m^* to be fairly invariant with respect to the frequency of the probe. The shallow 1-2 dB/octave slope of $I_m^*(f_p)$ may be interpreted as being indicative of the shallow slope of the masker's tail, if we make two assumptions: i) that the neurons at the different characteristic places (CPs) of the probes are similar in sensitivity, and ii) that the masker's response at the CP of the probe is representative of masker's influence on the probe.

For low-frequency maskers greater than about $2I_m^*$, the probe level must be increased much more than a corresponding linear increase in the masker level. This effect is quantified by the slope of the masking growth ν . To quantify this effect, we further define $I_p^*(I_m, f_m, f_p)$ to be the threshold intensity of the probe of frequency f_p , given a masker level I_m at frequency f_m . Thus, for a probe tone with frequency at least an octave higher than the masker tone ($f_p > 2f_m$):

$$\frac{I_p^*(I_m, f_m, f_p)}{I_p^*(I_m = 0)} \simeq \max \left[1, \left(\frac{I_m}{I_m^*} \right)^\nu \right] \quad (1)$$

The max function in Eq. 1 takes into account the masking effect at masking levels below $2I_m^*$. There is almost no masking in this region, as the probe saturates any effect that the masker might have, and we can approximate it as zero dB. Taking logs of both sides, and expressing the intensity on a dB-SL scale:

$$\beta_p^*(I_m, f_m, f_p) \simeq \max [0, (\beta_m - \beta_m^*(f_p)) \nu], \quad \text{where } \beta = 10 \log(I/I^*) \quad (2)$$

The parameter ν describes the “strength” of the masking, in terms of the slope of the masking curves, in dB/dB. It ranges from 1 dB/dB (linear growth) to about 2.4 dB/dB. Most studies show the maximum slope to be between 2 and 3 dB/dB. This slope is directly related to the compressive nonlinearity of the cochlea.

1.2 Neural two-tone suppression

Neural-2TS is the effect whereby the neural discharge rate of a neuron tuned to a probe tone is reduced by the presence of a suppressor tone of different frequency. The probe tone is typically introduced at 6 to 10 dB above the neuron’s threshold. The ability of the suppressor tone to reduce the discharge rate of the probe neuron depends mainly on the suppressing tone’s intensity and on its frequency relative to the CF. Suppression is most effective when the suppressor frequency is lower than CF, and we shall concentrate on this case.

Neural-2TS experiments [8,9] using suppressor frequencies lower than the CF (probe) tone have found suppressor thresholds of 65 dB SPL and maximum iso-rates of suppression of around 2.4 dB/dB. These values are strikingly similar to the USM parameters I_m^* and ν . This similarity has led us to the conclusion that USM and 2TS are due to the same physical phenomena. Traditionally, the two phenomena have been treated separately.

A most interesting aspect of Neural-2TS is that the CF probe neuron is not necessarily excited [10] when the suppressor frequency is at least an octave lower than the CF even though the suppressor tone level may be at the threshold level (60-70 dB SPL) of suppressing the probe response.

1.3 Basilar-membrane two-tone suppression

2TS can also be observed mechanically on the BM (BM-2TS). The differences in BM-2TS and Neural-2TS/USM observations clearly demonstrate that mechanical structures other than the BM must be involved in neural coding: that neural response cannot simply be explained by the BM response alone.

The first line of evidence is the contrast between the response of the suppressor at the probes place, at the suppression threshold level $I_s^*(f_s, f_p)$ ($f_p \gg f_s$). In the neural case the suppressor does not typically excite the basally tuned probe at the suppression threshold. This is in contrast to BM-2TS case where the suppressor greatly increases the BM response at the probes CP. For example, in the neural case a 1-kHz tone at 65 dB will just start to suppress a 5-kHz neuron at its CF-threshold. On the BM, it takes an 80-dB SPL 1-kHz tone to just start suppressing a 5-kHz probe. Furthermore, the low-frequency suppressor dominates the BM response at the 5-kHz place. Under no conditions will the BM

RMS response at the probes place be reduced due to an increase in the suppressor. Namely, on the BM, the total response due to the CF and suppressor tone is always greater than the response of the CF tone alone [11]. Because of this it is necessary to apply a *Fourier analysis* to resolve the probe component on the BM to observe any probe suppression. This is quantitatively dramatically different from Neural-2TS, where the total discharge rate is typically reduced with the application of a *non-excitatory suppressor tone*.

So there are two differences: First the BM-2TS the suppressor must be more than 80 dB SPL before it suppress the probe tone [11,14], whereas with neural-2TS, 65 dB is the nominal value [10]. When the suppressor is 80 dB, the amount of suppression seen by the neuron is about $(80-65) \cdot 2.4 = 36$ dB, which is close to the maximum amount of suppression (< 50 dB). Second, to account for the large difference in the response of the suppressor at the probe's CP, there must be a high-pass filter in the transduction path, to reduce the suppressor level to the OHC threshold [12-14]. If we assume that OHCs are slightly more sensitive than IHCs, then neurons will not respond at the threshold of suppression, as observed.

The second line of evidence involves the growth of suppression, as characterized by parameter ν , defined in Eq. 1. The maximum suppression in Neural-2TS is about 2.4 dB/dB [9,10]. Both Geisler and Nuttall [11] and Cooper [14] found BM suppression slopes of 1 dB/dB. In contrast, Ruggero *et al.* [15] found the maximum suppression of BM-2TS to be approximately 1.42 dB/dB (measured using iso-velocity analysis).

There is a huge discrepancy therefore between the Geisler [11] and Cooper [14] results, and Ruggero's [15] (1 vs. 1.42 dB/dB) and between the BM and neural results (1 vs. 2.4 dB/dB). The difference between a 1 and 2.4 dB/dB suppression amounts to 10 dB and 24 dB of suppression for a 10 dB change in suppressor level (more than a factor of 4 deviation for every factor of 3 change in level!).

A third important observation of both the Cooper [14] and Geisler [11] studies was that the displacement (of the OHC cilia) rather than the velocity must control the nonlinear response. This is simply proved by looking at how the iso-suppression response depends on the stimulus as a function of frequency. When BM displacement is used as the control, the suppression is independent of frequency. However when velocity is the control, the suppression threshold depends on frequency. One must conclude that the OHC stimulation is proportional to the BM displacement, not its velocity. When Ruggero [15] uses BM velocity as the relevant variable in his characterization of suppression, he is viewing the response through a 6 dB/octave highpass filter. This has important implications to the interpretation of his results, since, as we concluded above, that it takes a high-pass filter to bring the neural and BM measurements into alignment.

What then is BM-2TS due to if it is not the same as Neural-2TS? A most plausible theory, first suggested by Geisler and Nuttall [11], is that BM-2TS is due to a saturating non-linearity in the OHC response. An alternative conjecture is that the BM-2TS is strongly coupled to OHC cilia responses, and that the simple interpretation of the BM measurements, as being proportional to the BM volume velocity, is a poor assumption. It would be easy to imagine that what is being measured with the laser is not BM volume velocity, but some combination of modes of the micromechanics (i.e., some combination of the BM and the TM responses). We might expect that in a tightly coupled system some reflection of these micromechanical mechanisms in the BM response.

These three discrepancies between BM-2TS and USM/Neural-2TS of (i) suppressor threshold level, (ii) growth of suppression and (iii) the fact that in Neural-2TS unlike BM-2TS, the neural response is typically lower than the probe alone, provides sufficient evidence to suggest that the two phenomena are quite different. Each of these poses a *serious* problem for theories which suggest that neural response is directly related to BM mechanics. The usual explanation is that the suppressor response is being filtered by secondary structures in the cochlea. It is thus reasonable to conclude that BM mechanics is not simply related to the neural response, but is modified by the micromechanics of the organ of Corti.

2 Models and Results

To explain the USM/2TS phenomenon, we hypothesize that the micromechanics of the cochlea acts as a *base-stop filter* on the BM tail response. The term “base-stop” means that the filter attenuates basal to the CP. This filter results in an IHC and OHC cilia excitation pattern that is nearly independent of place, basal to the CP. When viewed in the frequency domain, this base-stop filter is equivalent to a high-pass filter, which converts the 9-dB/octave slope of the BM “tail” response to an almost frequency invariant (flat) neural tuning curve tail response. Such low-frequency flat tails are quite common in high-frequency neural tuning curves.

In the model, as shown in Figure 1, we assume that the place-independent excitatory stimulus tail of the low-frequency masker, which grows linearly with masker intensity, changes the stiffness of the BM at the place of the probe (the high-frequency CF tone), causing the suppression of the probe. Working this backwards, this means that the low-frequency flat tail excitation must suppress the high-frequency probe with a growth rate of ≈ 1.4 dB/dB (Fig. 1A). Figure 1B shows that as the flat tail response increases, linearly with level, the probe is being suppressed.

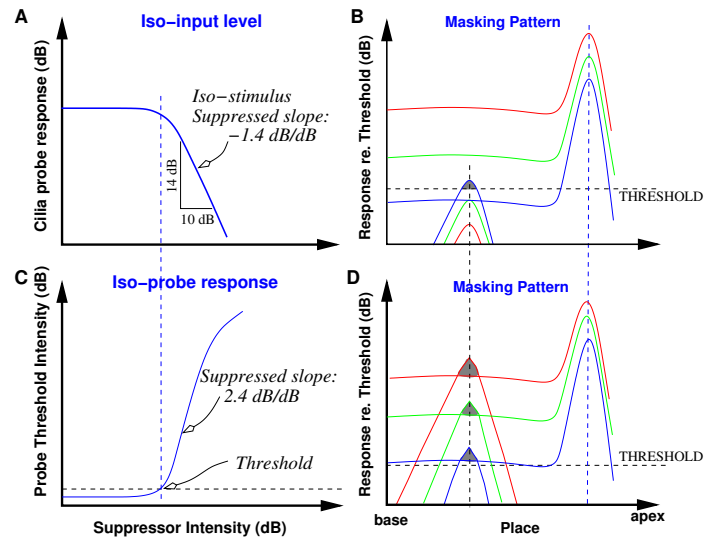


Figure 1. A cartoon explaining the unified theory of USM and 2TS.

In the USM measurement paradigm, the probe level must overcome both the suppression effect and the linear growth of the tail. This is shown in Figure 1D. In order for it to overcome both of these effects, USM must grow at a rate of as much as $1.4 + 1 = 2.4$ dB/dB, as shown in Figure 1C.

In USM, asking the subject to increase the probe tone such that it is just perceivable, is the psychophysical equivalent of iso-discharge rate of the nerve fibers, at the CF of the probe. Neural-2TS observations, which use such an iso-rate measurement to calculate the growth of suppression, have a maximum growth rate of 2.4 dB/dB. As in the USM case, the underlying suppression must be at a rate which is 1 dB/dB lower than the iso-response observation.

3 Summary

Central to any unified theory of USM and Neural-2TS is the ability of the low-frequency suppressor/masker's tail response to turn down the gain of the high-frequency CF probe tone, without exciting the high-frequency neuron. This gain control can be modeled using a voltage controlled axial stiffness of the OHC. Since the longest cilia of the OHCs are firmly attached to the TM, the effective stimulus is the displacement. We assume that the BM stiffness depends on the

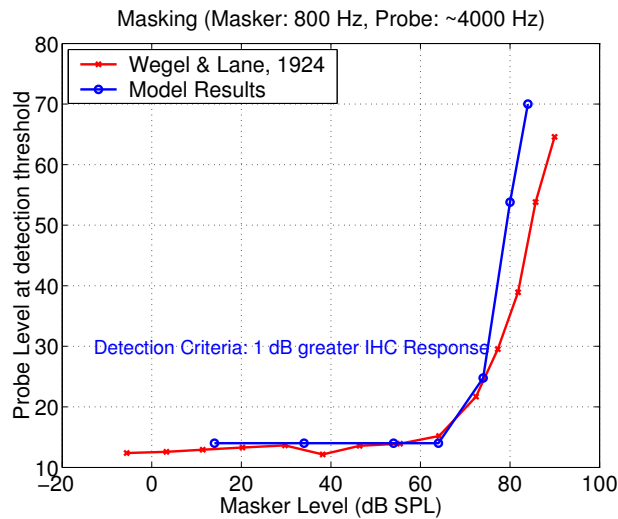


Figure 2. USM from model and Wegel and Lane [2]. The masker and probe frequency in the model is 800 Hz and 15 kHz, respectively. Wegel and Lane's data is for the masker at 400 Hz and the probe at 8 kHz.

axial stiffness of the OHC, causing a migration of the CP of the BM response. The result of this migration in BM response, when viewed through the base-stop transduction filtering of the TM, is to compress the neural response. The tightly coupled micromechanics is reflected in the BM response measurements. This shows up as a response mixture of a BM volume velocity modified by the TM filtering. Figure 2 shows our model results in producing USM. Our results, when compared to the data from Wegel and Lane [2], provide a good fit.

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