My 50 years of Cochlear Modeling

MoH Denmark, Jul 25, 2022

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July 23, 2022

Abstract

The goal of this presentation is multi-fold: The *primary goal* is to discuss my present understanding of cochlear function. *Secondary goals* are to review my earlier (1970-1995) cochlear modeling work, along with the roles of four close friends: Egbert De Boer, Steve Neely, Paul Fahey and George Zweig.

To understanding of how the cochlea works, one needs an understanding of the experimental data on: **1**) cochlear function (both basilar (BM) and tectorial membranes (TM), **2**) tympanic membrane, **3**) middle ear (ME), **4**) inner and outer hair cells (IHC, OHC), **5**) auditory nerve (AN), and **6**) cochlear amplifier (CA). My views on these topics have been greatly sharpened by looking back and unifying this complex puzzle. A great deal of progress has been made in the last 50 years.

Conclusions: My recent review of neural tuning curve data from 1985, using nonlinear (NL) distortion product generation, has revealed a deeper understanding of cochlear function. *The most surprising result is that the cochlea is more linear than previously assumed. NL behaviour:* "Low-side" suppression is when the suppressor frequency f_s is at least 1/2 octave lower than the characteristic ("best") frequency (f_{cf}). There is no "low-side" suppression for suppressors below 65 [dB-SPL]Fahey and Allen [1985]. Namely the system acts as if its linear. For suppressors above 65 [dB], the suppression dominates, with a slope of ≈2 [dB/dB]. The "obvious" explanation is that the neural threshold of excitation to both the inner and outer hair cells have approximately the same threshold. *Namely, the suppression threshold of the OHC, which control the NL suppression, are close to, or even equal to, the IHC threshold.*

If the IHC and OHC thresholds are the same in the tail of the tuning curves, then how can the CA function at threshold levels? This is a highly unexpected result, because low-side suppression, as measured on the basilar membrane, has a 20-30 [dB] higher threshold [Cooper, 1996, Geisler and Nuttall, 1997]. *Is the OHC action restricted to the neighborhood of the neuron's best frequency?*

This would require that the neural low-side suppression and loudness recruitment (the reduced loudness of low-intensity sounds in the hearing-impaired ear) are closely related (i.e., must be the same phenomena). The ramifications of this observation seem important as they will impact the diagnosis of cochlear hearing loss, thus the fitting of hearing aids [Allen et al., 2012], [Allen, 1991, 1990; See comment by Lyon, page 332],

In summary: **Low-side suppression acts like an automatic gain control, elevating the loudness threshold with no audible distortion.**

The PDFs cited here is: `https://auditorymodels.org/index.php?n=Main.Publications`.

Goals

- The primary goal is to discuss my present understanding of cochlear function.
- Secondary goals are to review my earlier (1970-1995) cochlear modeling work, along with the roles of four close friends: Egbert De Boer, Steve Neely, Paul Fahey and George Zweig
- To understanding of how the cochlea works, one needs an understanding of the experimental data:
  - sound in the ear canal
  - tympanic membrane,
  - middle ear (ME),
  - cochlear function (both basilar (BM) and tectorial membranes (TM),
  - inner and outer hair cells (IHC, OHC),
  - Low-side 2-tone suppression (DPOAE)
  - auditory nerve (AN)
  - the famous cochlear amplifier (CA).
- My views on these topics have been sharpened by looking back and unifying this complex puzzle. A great deal of progress has been made in the last 50 years.

The cochlea

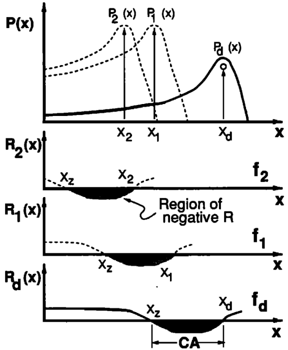
- The cochlea is a complex organ, the source of hearing

Figure: *Great picture showing the two cochlear ducts, the Basilar membrane (BM), and the organ of Corti (OoC). The OHC and IHC are buried between the tectorial and basilar membranes.*

- Using the distorion product method we can discover how it works

Low-side suppression: Definition of DPOAEs *[Allen and Fahey, 1992]*

- Two primary frequencies @ $f_2 > f_1 \gg f_d$ create NL DPOAE @ $f_d = f_1 - (f_2 - f_1) = 2f_1 - f_2$



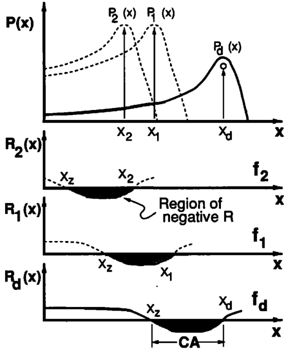
- The two tones "mix" in the region between $X_2 < X_1$, but mostly near X_2
- The regions of the CA is assumed to be the three shaded region $(X_z < X_2(f_2) < X_1(f_1) \ll X_d(f_d))$

Experiment I: Measure the gain of the Cochlear Amplifier (CA)

- The basic idea is to move the acoustic source from the ear canal onto the BM, by using DPOAEs at fixed frequency $f_d = f_1 - (f_2 - f_1)$ variable place $X_d(f_2)$
- By varying f_2, the source at $X_2(f_2)$ may be placed anywhere on the BM @ $X_2(f_2) < X_d(f_d)$.
- This variable source may be move through the region of negative resistace (region of CA gain), to explore the magnitude the the CA as a function of "place"
- The gain of the CA is then explored as a function of the source location X_2.

We measuring the gain of the CA by varying the BM source location: The CA gain at X_2 is the ear canal f_d pressure for a fixed neural response

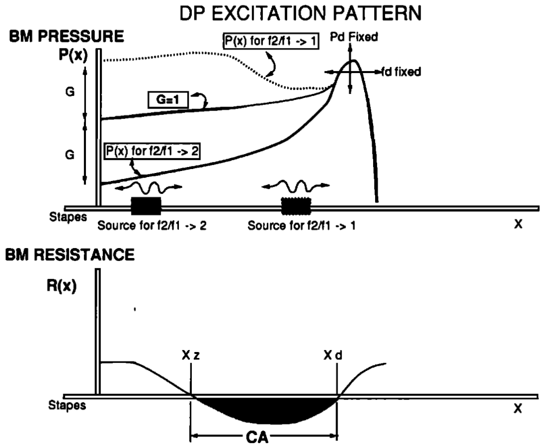
- The source is at $X_2(f_2)$ results in a NL BM DPOAE signal at $X_d(f_d)$



- THis DPOAE signal is detected by the neuron having its BF at the DPOAE frequence f_d

Measureing the gain of the CA
Using a DPOAE–SOURCE on the BM

- Please Google: "Allen-Fahey experiment"



- Use a DPOAE source on BM @ "place" $X_2(f_2)$, determined by f_2, and a neuron as the detector

Experiment II: Neural low-side suppression measured

- [Fahey and Allen, 1985] (FA-85)
- Cooper (1996) and Geisler-Nuttal (1997) measured the low-side suppression on the BM and found a threshold difference between 20 and 30 dB
- FA-85 measured Low-side suppression with a neural paradigm and found the neural detection threshold and the low-side suppresison thresholds to be equal
- It is an unequivaqual conclusiong that there must be a "second-filter" action between BM neural response

Low-side suppression on the BM [Cooper, 1996]

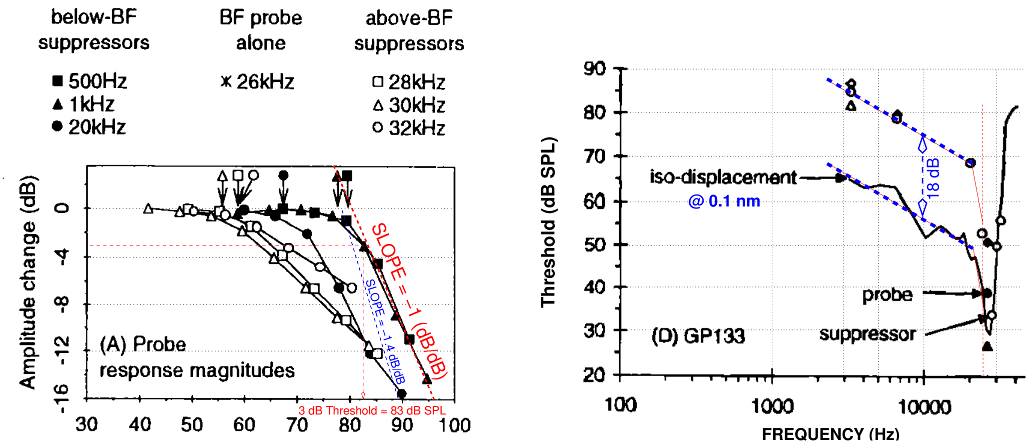


Figure: *LEFT: BM Suppression of a 26 [kHz] probe by Low-side suppressors @ 0.5, 1, 20 [kHz] RIGHT: BM Suppression as a function of frequency The BM low-side suppression is very different from the neural data of AF-93: 1) The detection and suppression threshold are 18 [dB] apart, and 2) it depends on frequency [Cooper, 1996]*

Low-side suppression on the BM [Geisler and Nuttall, 1997]

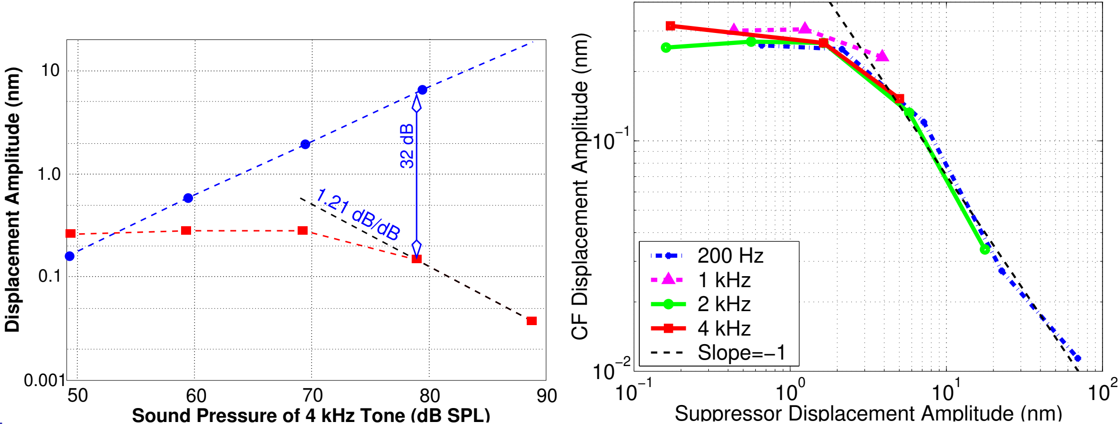
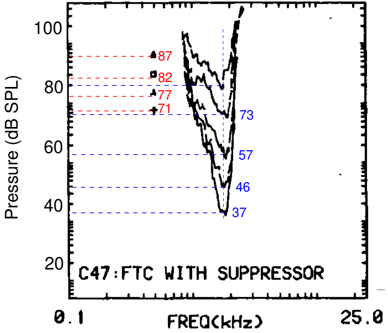


Figure: *LEFT: Data similar to that of [Cooper, 1996] showing low-side suppression on the BM. The suppressed tone frequency is 17[kHz]. There is no suppression at 69 dB and 6 [dB] for the 4 [kHz] tone is increased from by 10 dB from 69 to 79 [dB-SPL] compared to 0 [dB/dB] as seen neurally in AF-85. Inthis case the low-side suppression threshold difference at 0.1 [nm] is 32 [dB]. RIGHT: The BM low-side suppression is very different from the neural data of AF-93: 1) The detection and suppression threshold are 18 [dB] apart, and 2) it depends on frequency [Geisler and Nuttall, 1997].*

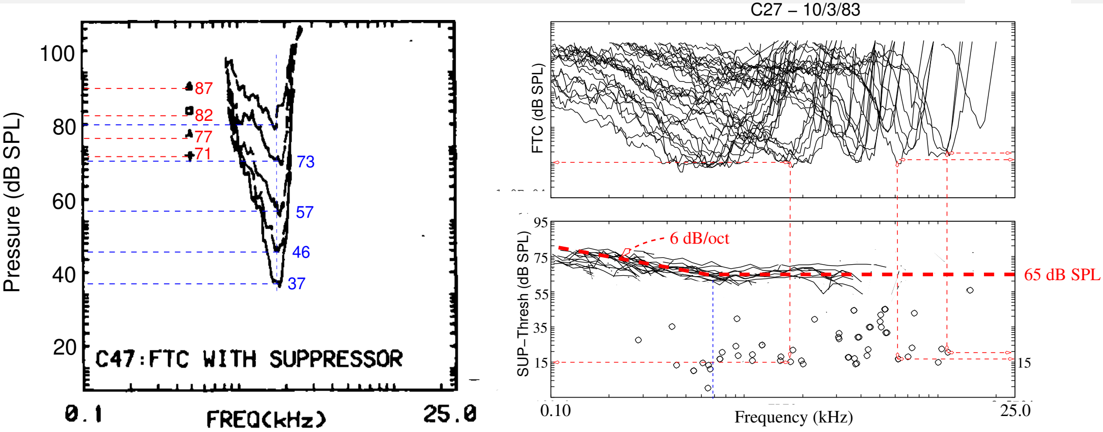
Example of Low-side suppression

- BF= 1.8 kHz, $f_2 = 500$ [Hz], $f_1 = (1800+500)/2 = 650$ [Hz]



- There is no low-side suppression below 65 [dB-SPL]
- Suppression Slope = 2.2 [dB/dB] above 65 dB-SPL [Delgutte, 1990a,b]

There is no low-side suppression below 65 [dB-SPL]



- The bold-red dashed line is the locus of Low-side suppression thresholds (@65 [dB-SPL])
- 65 [dB-SPL] is also the excitation threhold in the low-frequency Tuning curve "tail"
- Excitation and suppression thresholds are similar (or identical?) (Amazing, or obvious?)

Block model of Cochlear function

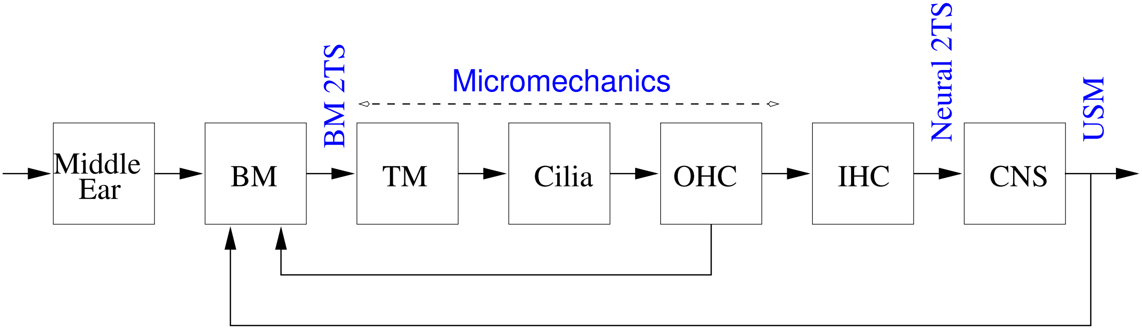


Figure: *Sound enters via the middle ear, travels down the BM and TM, excites the cilia of the OHC, IHC → AN*

Slopes of cat neural tuning curves *[dB/oct]* from Allen [1983]

- Above CF $f > f_{CF}$ and below CF $f < f_{CF}$ the BF, as a function of the BF

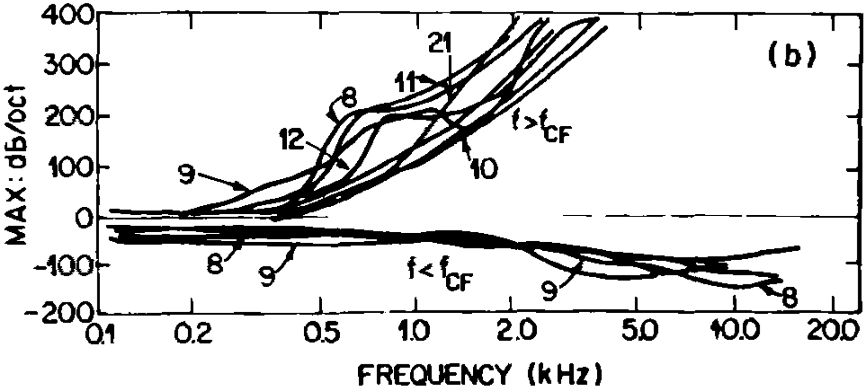


Figure: *Migration figure.*

Cat neural population study for a single tone at 620 [Hz]

- Note the π phase shift just below 2 [kHz]. The arrow represents the tone frequency.

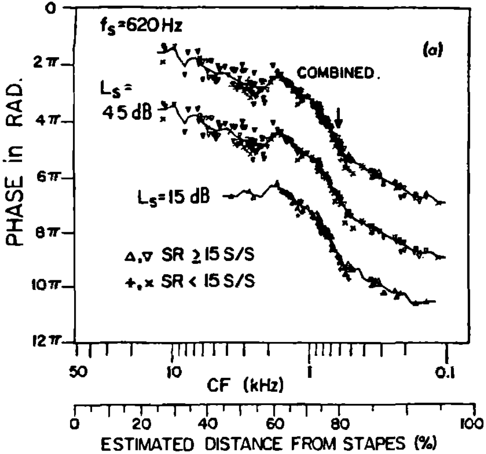


Figure: *Migration figure.*

Nonlinear BM "migration" model

- Model tuning curves as a function of input level: 0, 20, 60, 80 *[dB-SPL]*
  LEFT: BM response with TM 2d-filter model.
  RIGHT: NL model as a function of level

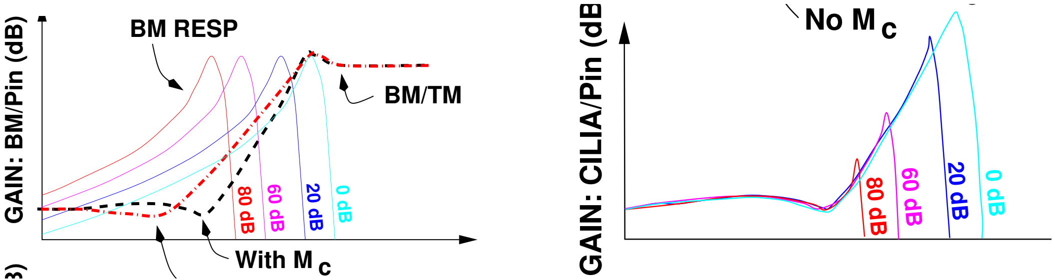


Figure: *Migration figure.*

Nonlinear BM “migration” model

- BM Impedance as a function of input level: Note basal drop in stiffness with level
- The models assumes the OHC change the BM stiffness 2x with increasing input level

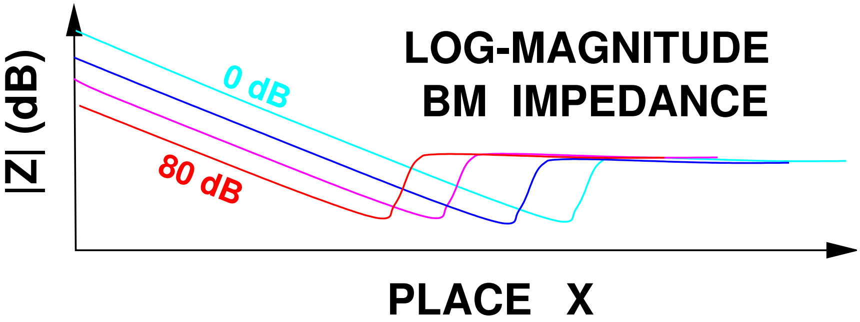


Figure: *Migration figure.*

Nonlinear BM "migration" model

- Big picture of NL cochlear model

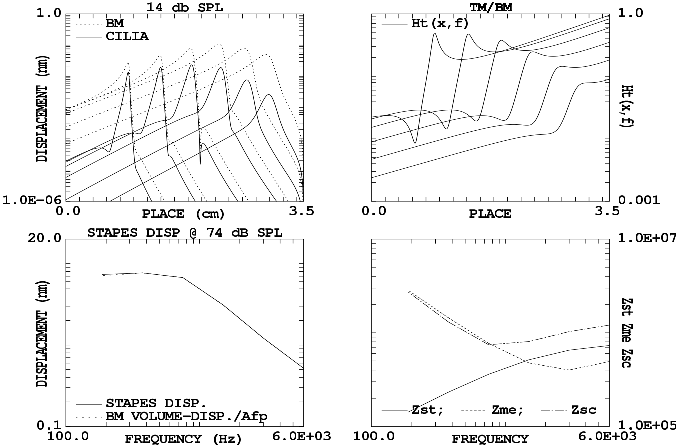


Figure: *Migration figure.*

Model output Sen and Allen [2006]

- Input signal is a pure tone from 14-124 [dB-SPL]

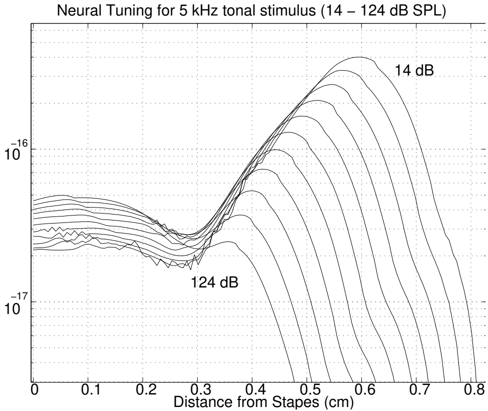


Figure: *Results of the Sen-Allen time-domain model for a single input tone with varying level.*

Cartoon of Low-side suppression Allen [2001]

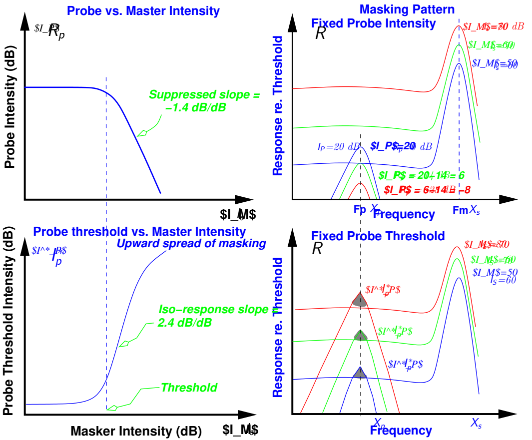


Figure: *Cartoon shown a cartoon-model showing low-side suppression. Excitation is equal to suppression threshold.*

My 50 years of Conclusions

- Present view of cochlear tuning (BM vs Neural are very different $\rightarrow$ Second filter)
- The use of DPOAEs is key to our understanding of the cochlea
- the cochlea is much more linear in its filtering properties than we previously assumed
- Low-side suppression opens the door to a full understanding of Cochlear function
- There is NO (zero) Suppression below 65 dB-SPL!
- Above 65 dB-SPL, the suppression ≈ 2 [dB/dB]!
- IHC (Linear) & OHC (NL) have nearly identical (equal) thresholds!
- Neural and BM low-side suppression differ by 20 [dB]!

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