My 50 years of Cochlear Modeling

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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 in the last 50 years have been sharpened, unifying this complex puzzle. A great deal of progress has been made over this time
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 (BF)?*
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, 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 understand the cochlea, one needs experimental data on the following:
  - $P_{ec}(f)$: sound in the ear canal at frequency f
  - ME: middle ear
  - BM: basilar membranes
  - TM: tympanic membrane,
  - IHC, OHC: inner and outer hair cells
  - DP: Distortion product
  - DPOAE: Low-side 2-tone suppression distortion product f_{dp}
  - AN: auditory nerve
  - BF: best frequncy of neural tuning curve f_{bf}
  - CA: cochlear amplifier
- 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.*

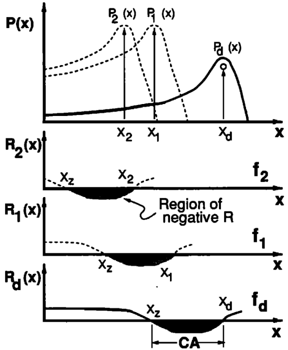
- Using the distorion product method we can discover how it works

Four experiments

- Four different key experiments are summarized:
  1. The **"Allen-Fahey experiment"**: Measure the gain of the CA [Allen and Fahey, 1992, **AF-92]**
  2. The **"Second-Filter experiment"** [Fahey and Allen, 1985, **FA-85]**
  3. The **"2d cochlear-map experiment"**: Tuning of DPoae responses [Allen and Fahey, 1993, AF-93]
     There is a strange correlation $\approx 1/2$ oct $< BF$ (where the tail and tip join)
     This led support to the *resonant-TM 2d filter hypothesis* [Allen and Sen, 1999]
  4. Kim, Siegel, Molnar (1979): **"Kim-Phase population experiment"**:
     Phase of a single tone is measured for a large number of tuning curves [Kim et al., 1979, KSM-79]
     The phase has a π phase shift at the 2d-cochlear map frequency (AF-93)
- My views on these four topics have been sharpened by reflection on their relationship
  A great deal of progress has been made in the last 50 years.

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 $(X_z < X_2(f_2) < X_1(f_1) \ll X_d(f_d))$

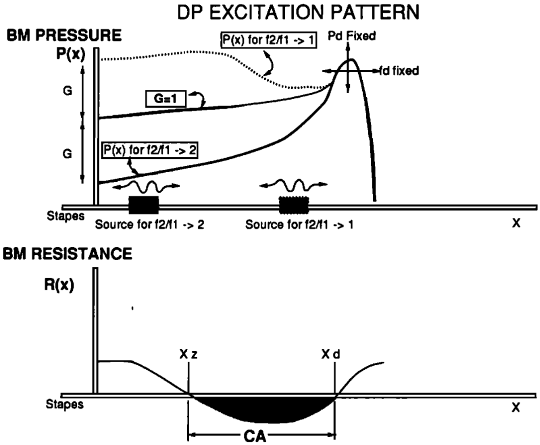
Exp-I (AF-92): Measure the gain of the Cochlear Amplifier (CA)

- Basic idea: move the acoustic source from the ear canal onto the BM, by using DPOAEs
- Record from a neuron having BF frequency f_{bf}
- Fixed the DP frequency $f_d = f_1 - (f_2 - f_1)$ equal to f_{bf}
- Fixed the DP pressure @ neurons threshold
- Vary the source location at $X_2(f_2)$ along the BM @ $X_2(f_2) < X_d(f_d)$.
- Move source through the region of negative resistance (region of CA gain)
- Measure the EC pressure $P_{ec}(f_2)$ as a function of $X_2(f_2)$

The gain of the CA is quantified as $P_{ec}(X_2)$

Measureing the gain of the CA via a BM DPOAE–SOURCE

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



- Please Google: "Allen-Fahey experiment" (open discussion 5 mins?)

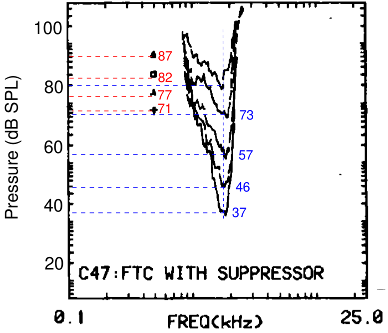
Exp-II (FA-85): Neural low-side suppression measured (2d-filter)

Experimental data:

- FA-85 measured Low-side neural suppression threshold and showed that:
  the neural detection threshold $\approx$ low-side suppresison thresholds
- Cooper (1996) and Geisler-Nuttal (1997) measured the low-side suppression on the BM and found a threshold difference between 20 and 30 dB
- It is an unequivaqual conclusion that there must be a "second-filter" action between BM neural response

Example of Low-side suppression (FA-85)

- 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, 1990]

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

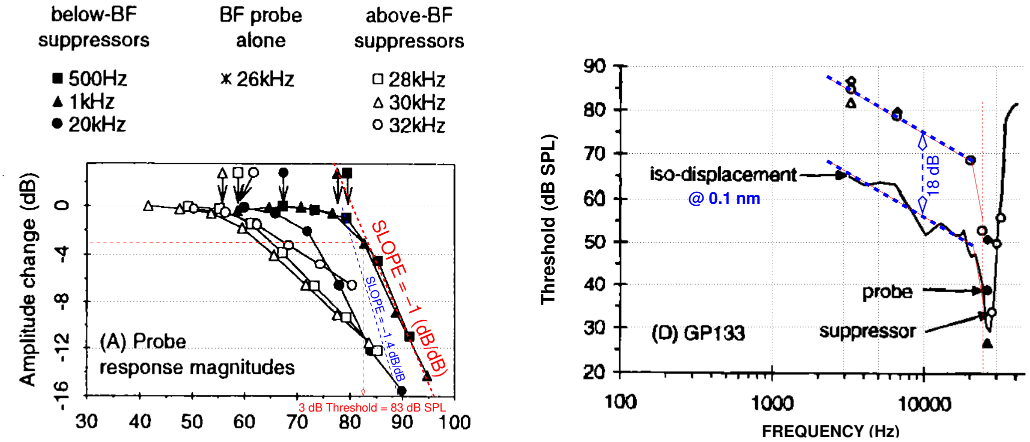


Figure: *LEFT: BM Suppression of a 26 [kHz] probe by Low-side suppressors @ 0.5, 1, 20 [kHz] RIGHT: BM Suppression as a function of frequency The BM low-side suppression is very different from the neural data of AF-93: 1) The detection and suppression threshold are 18 [dB] apart, and 2) it depends on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

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

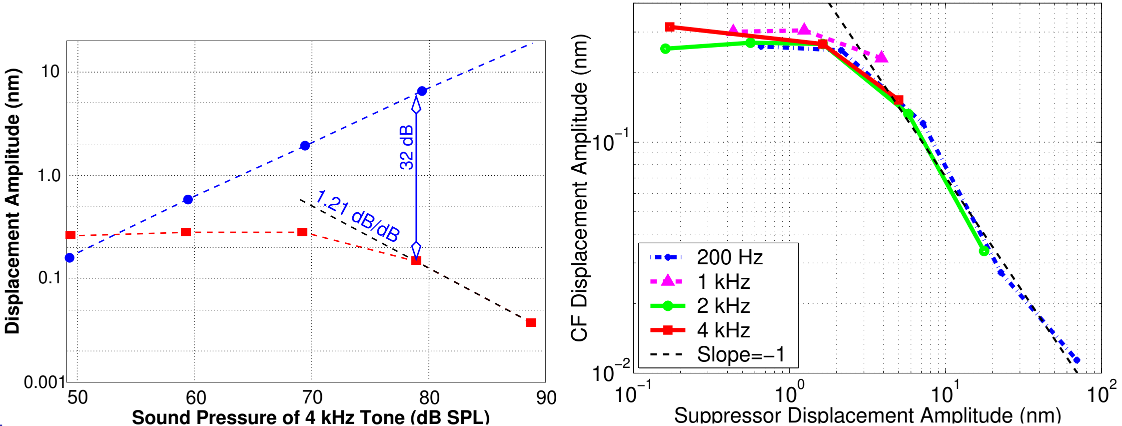
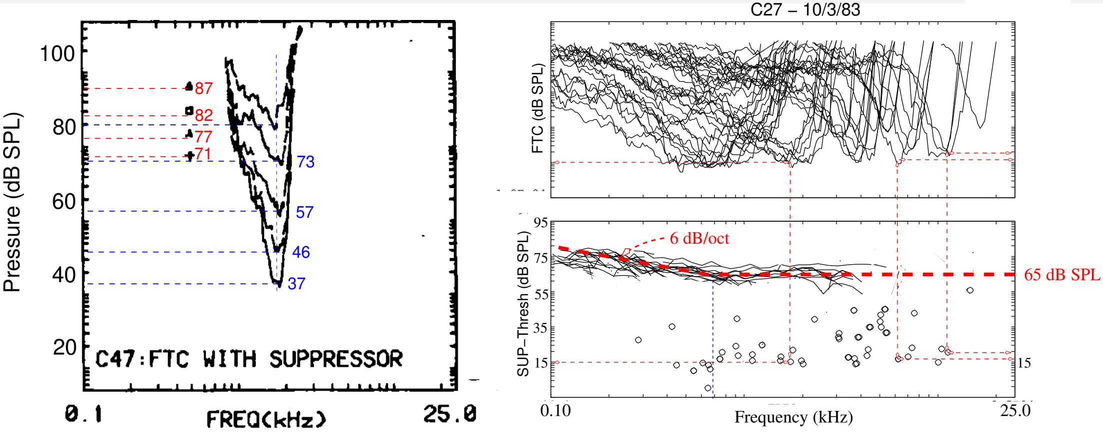


Figure: *LEFT: Data similar to that of [Cooper, 1996] showing low-side suppression on the BM. The suppressed tone frequency is 17[kHz]. There is no suppression at 69 dB and 6 [dB] for the 4 [kHz] tone is increased from by 10 dB from 69 to 79 [dB-SPL] compared to 0 [dB/dB] as seen neurally in AF-85. Inthis 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].*

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

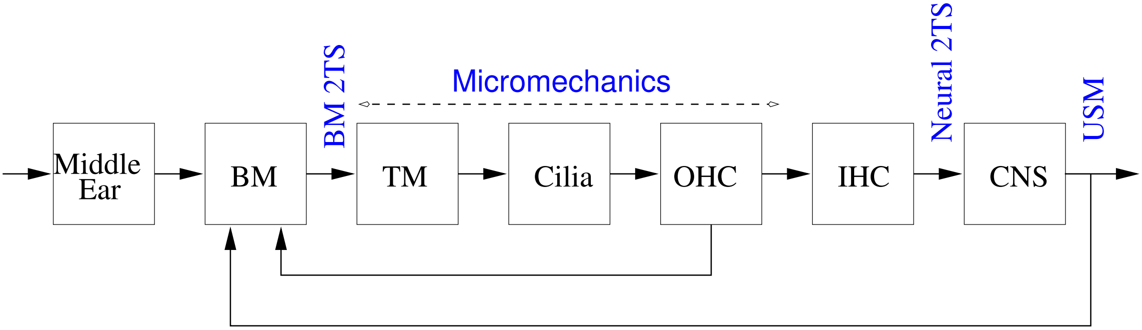


Figure: *Sound enters via the middle ear, travels down the BM and TM, excites the cilia of the OHC, IHC → AN*

If the two thresholds differ, that difference must be due to the TM

Exp-III (AF-93): Slopes of cat neural tuning curves *[dB/oct]*

- Above CF $f > f_{CF}$ and below CF $f < f_{CF}$ the BF, as a function of the BF Allen [1983]
- The 2d cochlear map function is defined where tail and tip meet below BF [Allen and Fahey, 1993]

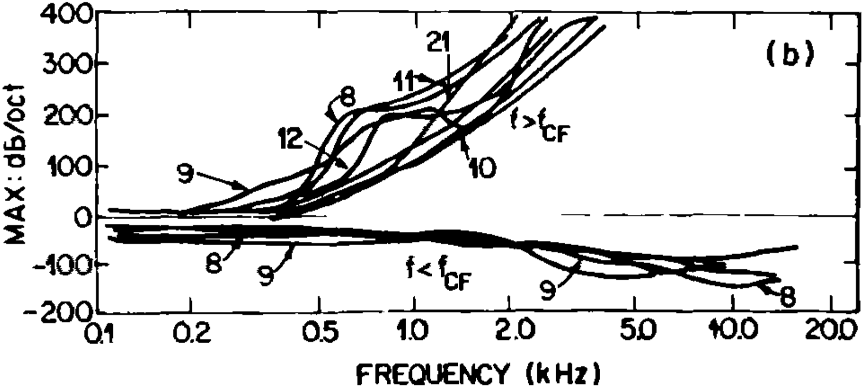


Figure: *Neural tuning curve slopes above and below BF (Cat)*

Exp-IV (KSM-79): Single-tone neural population study [Kim et al., 1979]

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

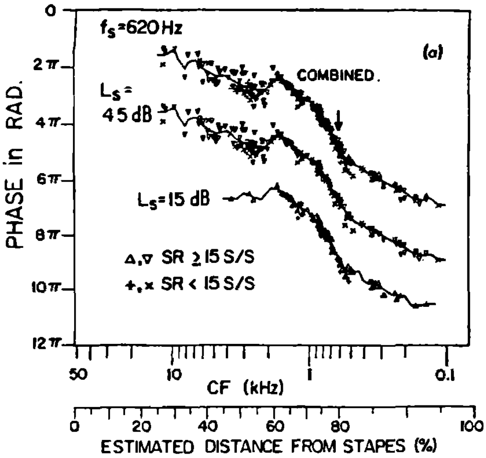


Figure: *Population study: phase results [Allen, 1980]*

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

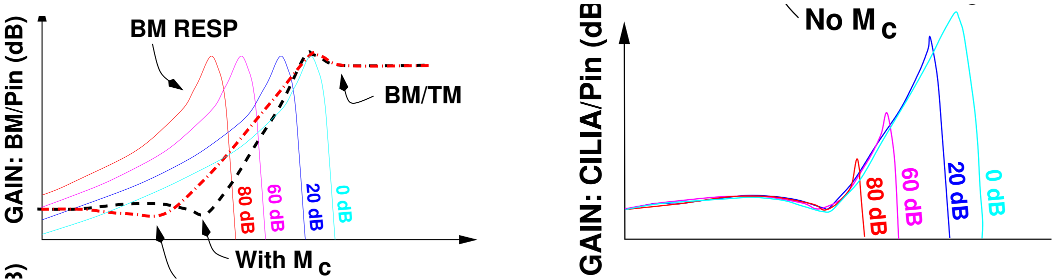


Figure: *“Second filter” on TM at 2d cochlear map frequency.*

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

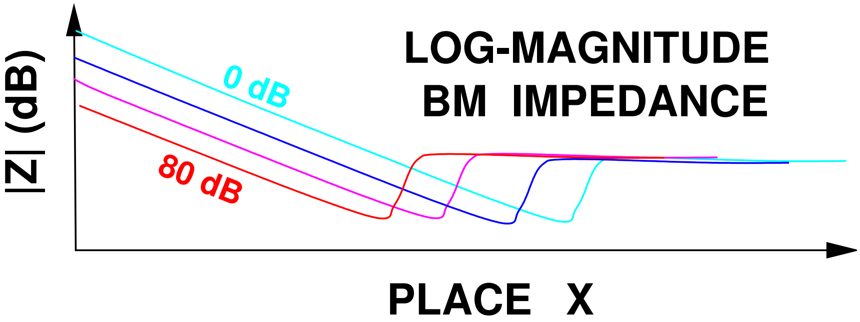


Figure: *OHC stiffness decreases with increasing SPL [Dallos et al]*

Nonlinear BM "migration" model

- Big picture of NL cochlear model

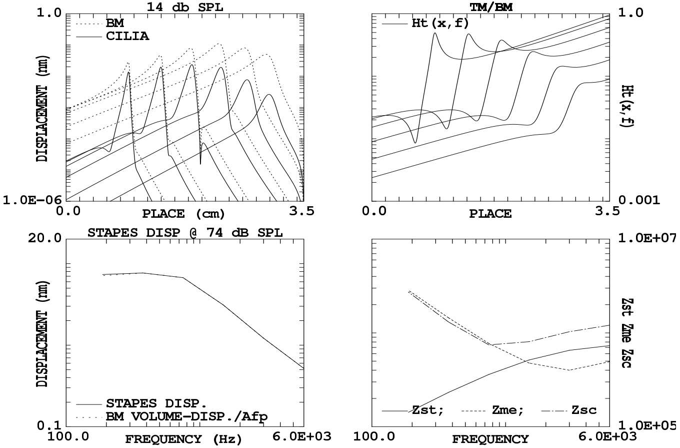


Figure: *Migration figure.*

Model output Sen and Allen [2006]

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

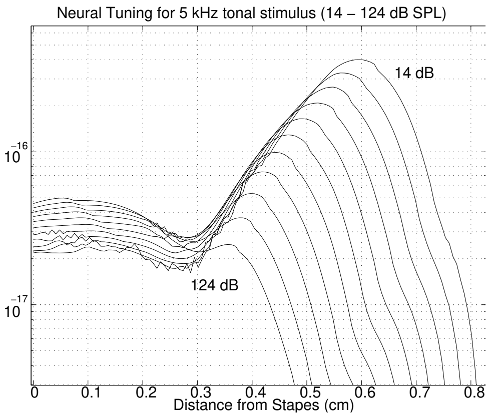


Figure: *Results of the Sen-Allen time-domain model for a single input tone with varying level.*

Cartoon of Low-side suppression Allen [2001]

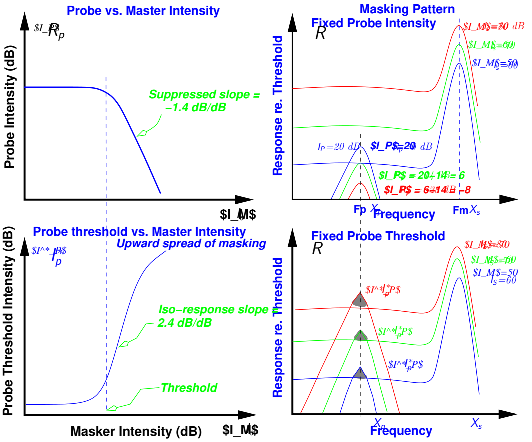


Figure: *Cartoon shown a cartoon-model showing low-side suppression. Excitation is equal to suppression threshold.*

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 an improved understanding of Cochlear function
- There is NO (i.e., 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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Copies of my documents

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