THE OUTER HAIR CELL MOTILITY MUST BE BASED ON A TONIC CHANGE IN THE MEMBRANE VOLTAGE: IMPLICATIONS FOR THE COCHLEAR AMPLIFIER

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Abstract

It has been widely assumed that the function of the OHC is to increase the sensitivity and frequency selectivity of the cochlea via a phasic OHC voltage, which controls the soma length. This action is called the cochlear amplifier. According to this view the length of the OHC is assumed to follow the stimulus to the upper frequency limit of hearing, in a phasic manner (cycle by cycle), adding power at the signal frequency. We propose an alternative view that the OHC controls the dynamic range in a parametric, or tonic manner, via the cells axial stiffness. In this case the change in gain seen by the IHC does not require a phasic response at high frequencies. The OHC could mediate a fast acting gain control, via impedance changes, that follows the OHC membrane tonic voltage envelope. Given a level dependent change in dynamic range (i.e., dynamic range compression), the tuning and sensitivity would necessarily change. Our analysis and conclusions are based upon a re-interpretation of existing mammalian outer hair cell (OHC) studies using a generalized admittance matrix formulation of the OHC, that relates the plasma membrane voltage and current to the soma axial force and velocity.

Traditional view of the OHC's role

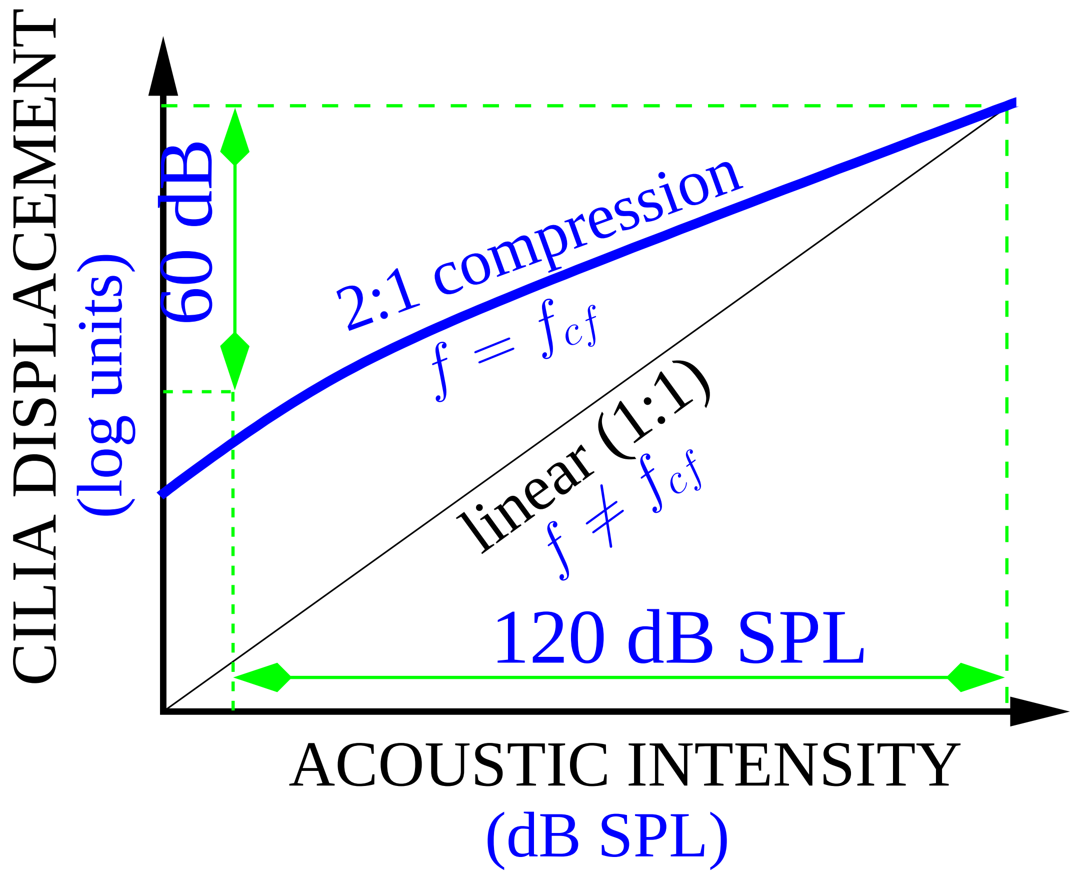
- Power gain based on a phasic cochlear amplifier
  - Increased sensitivity
  - Increase tuning (i.e., narrow bandwidth)
    - ∗ T. Gold 1948, Davis 1983 and many followers

Traditional view of the OHC's role

- Increased sensitivity
- Increase tuning (i.e., narrow bandwidth)

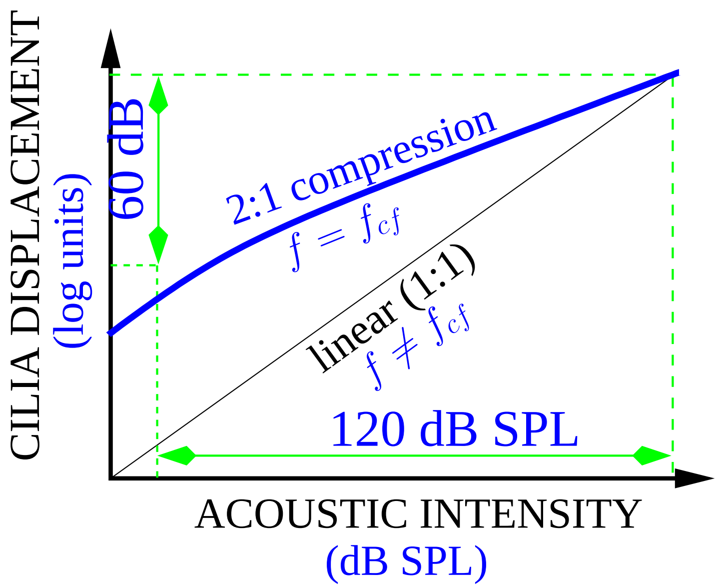
Alternative view of OHC's role

- Frequency dependent compression of the dynamic range



Why is compression necessary?

- Dynamic range of the IHC is less than 63 dB
  - Membrane thermal noise voltage of IHC is given by:
  - $$V_m^{\min} = \sqrt{kT/C_m} \approx 20\ \mu V\ \textit{RMS}$$
  - The maximum RMS IHC membrane voltage is
  - $$V_m^{\max} = V_{stria}/2\sqrt{2} \approx 30\ mV\ \textit{RMS}$$
- 30 mV/20 μV $\Rightarrow$ 63 dB hair cell dynamic range
- 120 dB Acoustic dynamic range is
  - $\Rightarrow$It follows that cochlear compression is essential

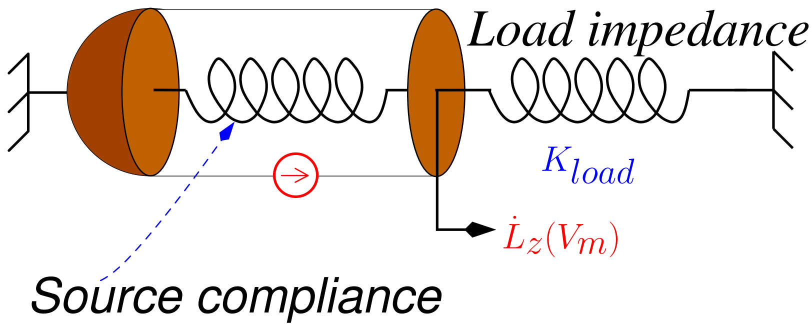


How does cochlear compression work?

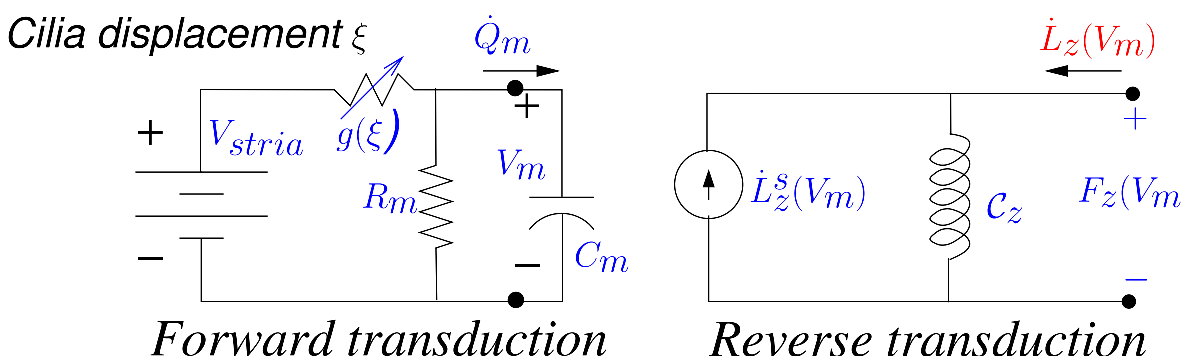
- We need an OHC model to answer this.
  - The following is a chronological review of OHC models,
  - from the Thévenin point of view.

Thévenin OHC Models 1985

- Simple Electromotility Brownell 1985
- Voltage controlled membrane Area motor:
- Assuming constant cell volume $\Delta L = \frac{2L}{A}\Delta A$

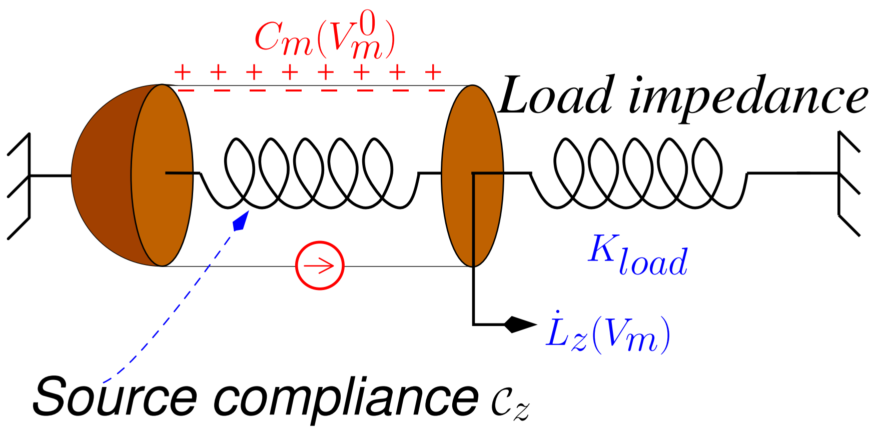


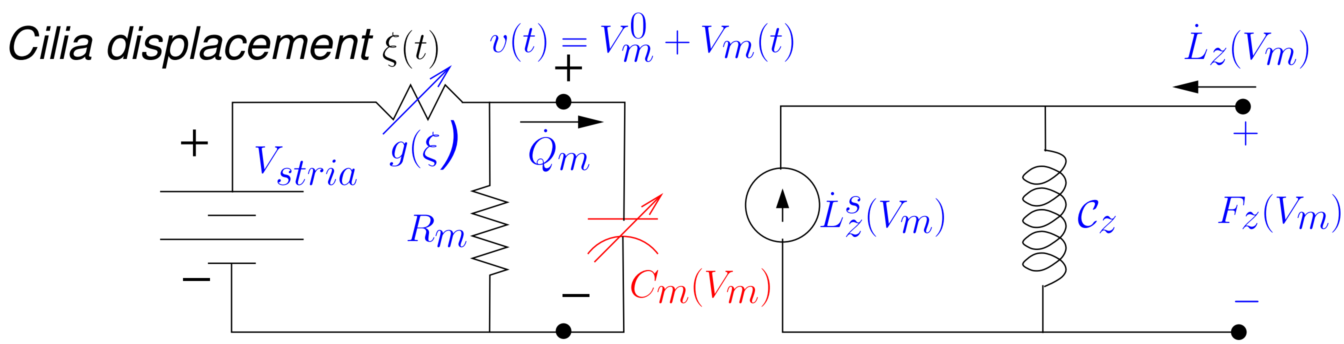
$\frac{\Delta L_z}{L_z} \approx 4\%$



Thévenin OHC Models 1989

- Nonlinear Capacitance Ashmore 1989
  - Area motor and Charge movement are coupled, via
  - Voltage dependent (2-state?) membrane molecules
  - Dallos *1991,1993*, Mountain and Hubbard 1994





$$\left|\frac{\Delta C_m}{C_m}\right| \approx 40\%$$

Thévenin OHC Models 1999

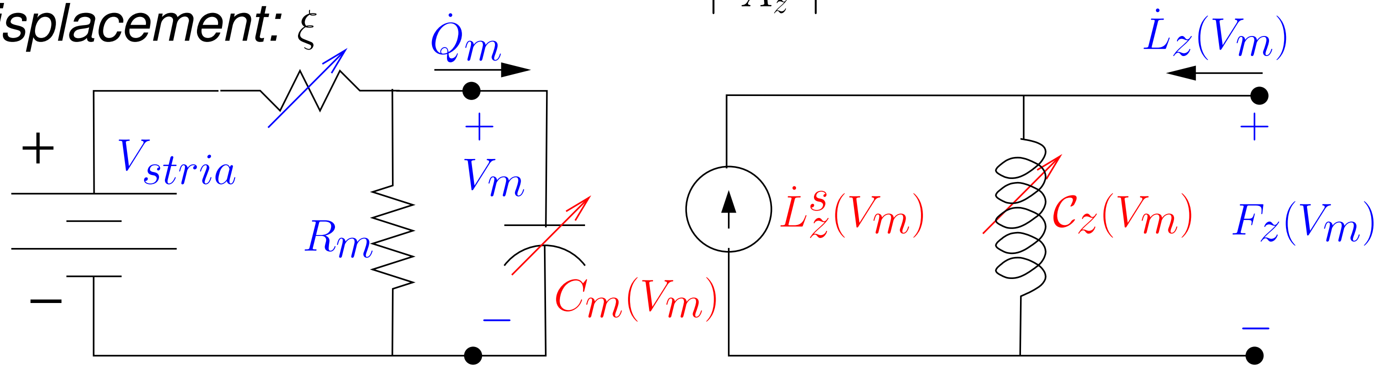
- NL Soma Stiffness depends on V_m He and Dallos 1999

$$\frac{\Delta K_z(V_m)}{K_z} \approx 400\%$$

- Every element is voltage dependent!
  - $\Rightarrow$ Area and stiffness motor

$$\left|\frac{\Delta A_z}{A_z}\right| = 2\%$$

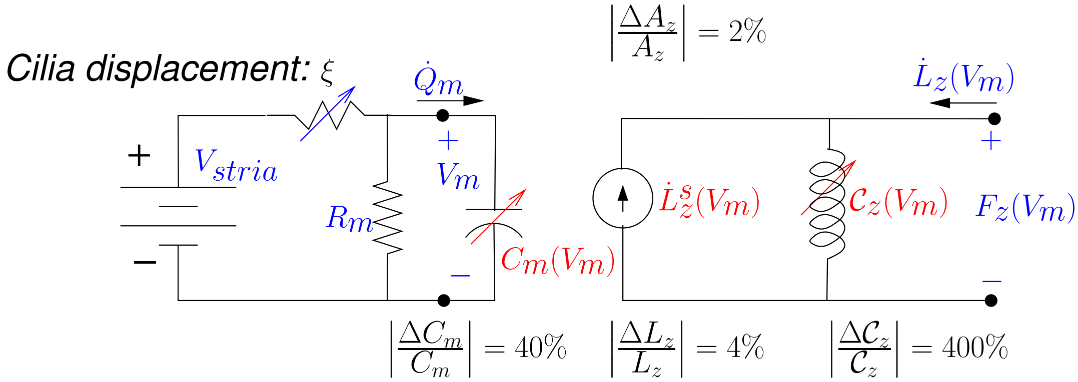
Cilia displacement: ξ



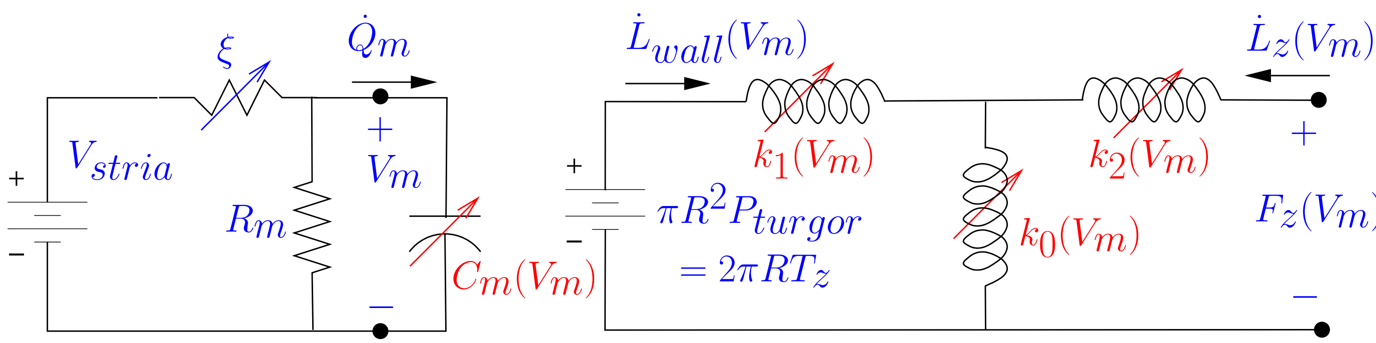
$$\left|\frac{\Delta C_m}{C_m}\right| = 40\% \quad \left|\frac{\Delta L_z}{L_z}\right| = 4\% \quad \left|\frac{\Delta \mathcal{C}_z}{\mathcal{C}_z}\right| = 400\%$$

Thévenin OHC Models

- Area and stiffness motor 1999



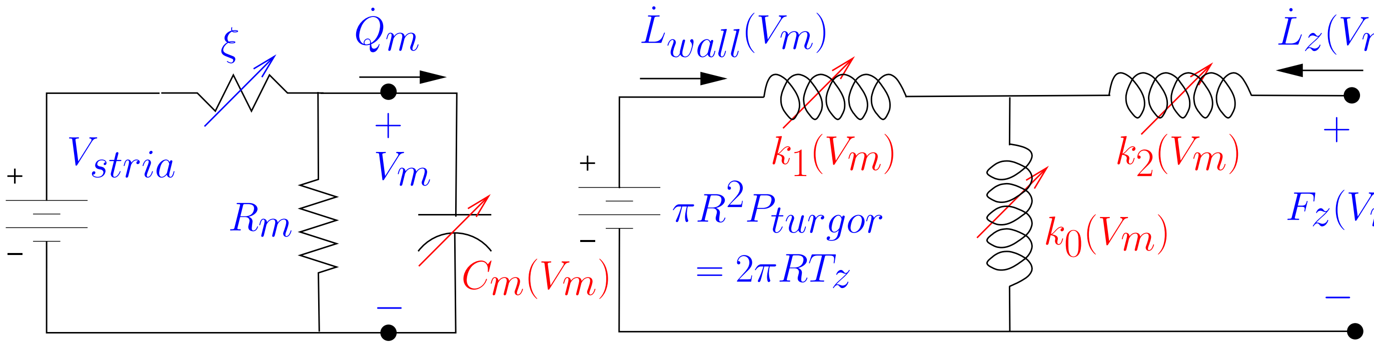
- Simplified model: NO area motor 2002



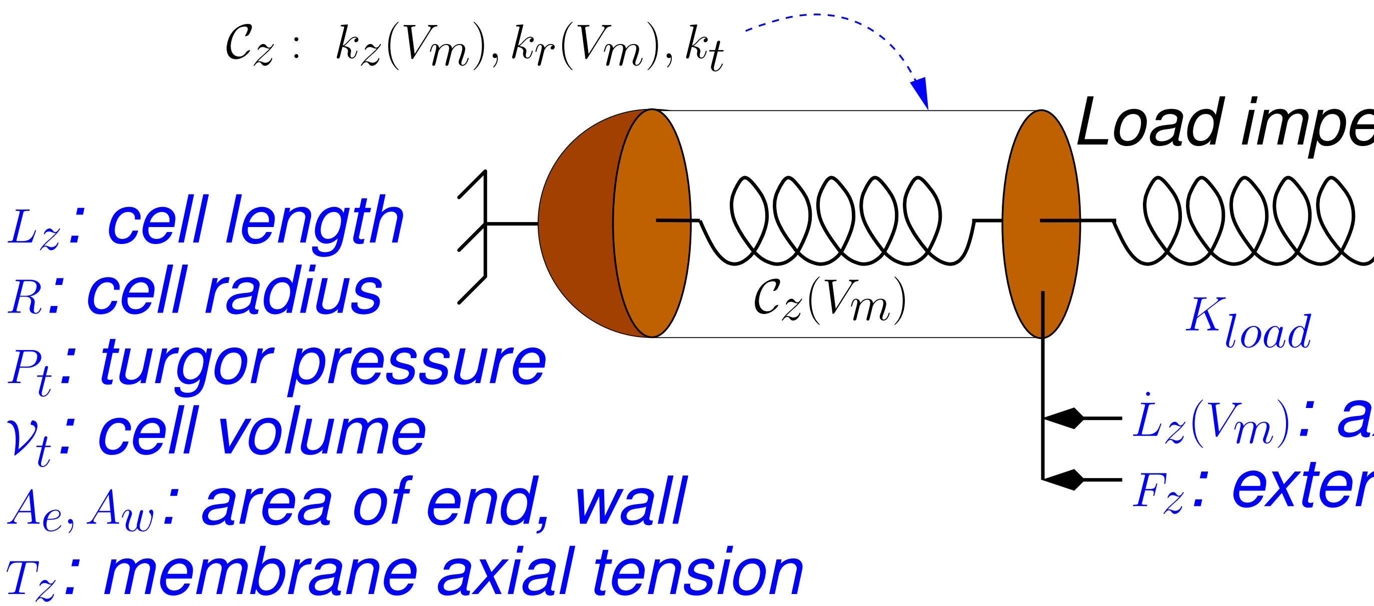
  - The turgor pressure P_t is the mechanical energy source
- The OHC is a voltage dependent spring

Proposed Model 2002

- Voltage dependence of $k_z(V_m)$ and $k_t(V_m)$ with P_t constant:

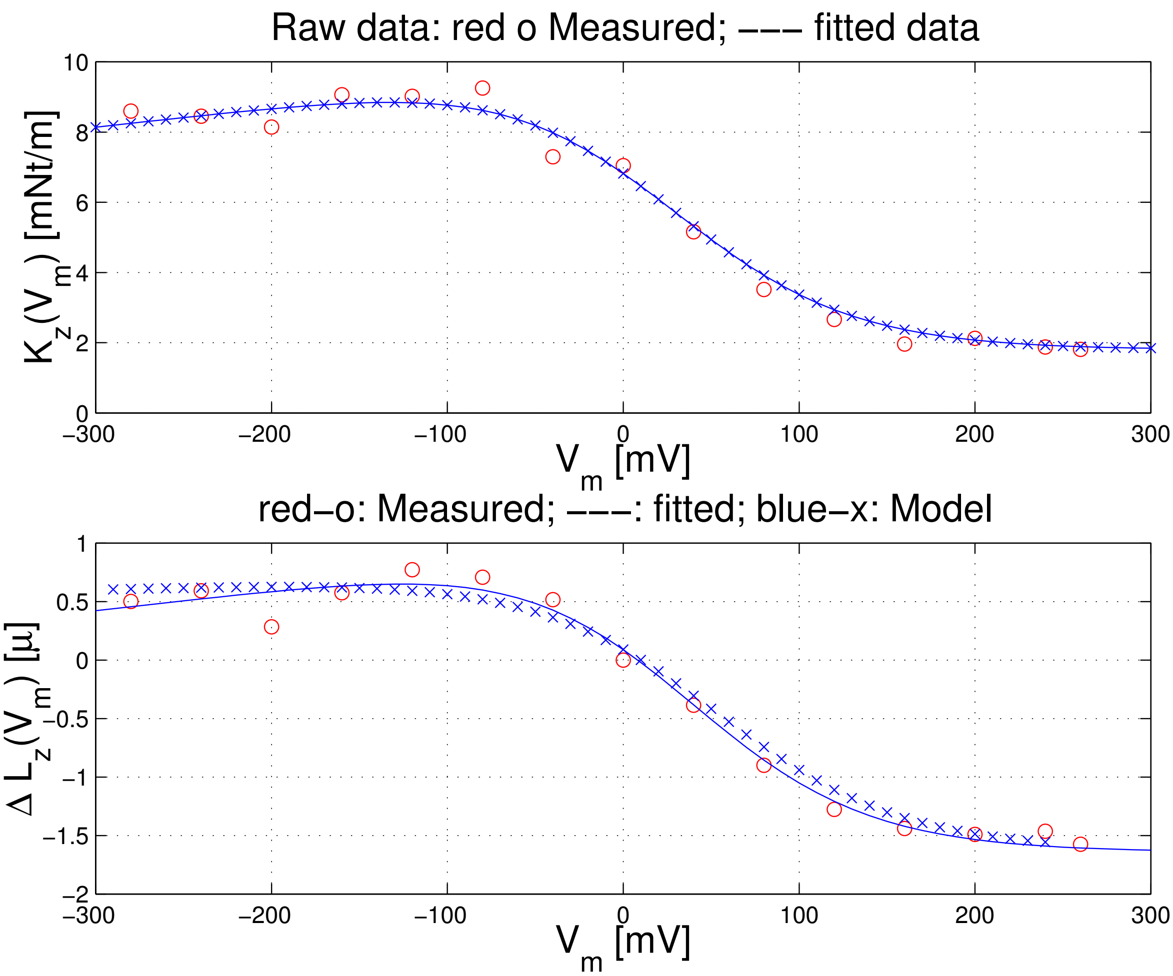


- Definitions for: $[k_r,\ k_z,\ k_t]$, $[F_z,\ L_z]$, $[A_e,\ A_w]$, $[P_t,\ \dot{\mathcal{V}}_t]$, T_z, R



Model Results

- Match to $K_z(V_m)$ and $\Delta L_z(V_m)$



Summary

- Model of a voltage dependent membrane stiffness accounts for all known OHC properties!
  - Relative length change $\frac{\Delta L_z}{L_z} \approx 4\%$ 1985
  - Relative Capacitance change $\frac{\Delta C_m}{C_m} \approx 40\%$ 1989
  - Axial stiffness change $\frac{\Delta K_z}{K_z} \approx 400\%$ 1999
  - The OHC is a voltage controlled stiffness.
- The model OHC has no "area motor"
- The model OHC is not piezoelectric
  - The wagging tail $\Delta L_z(V_m)$ is not the dog $K_z(V_m)$.
- "Length change, or electromotility, is a simple consequenc of stiffness change."
  - –Dallos & He 2001

–Compression is modulated by OHC stiffness, via tonic (DC) voltage changes

QUESTIONS?

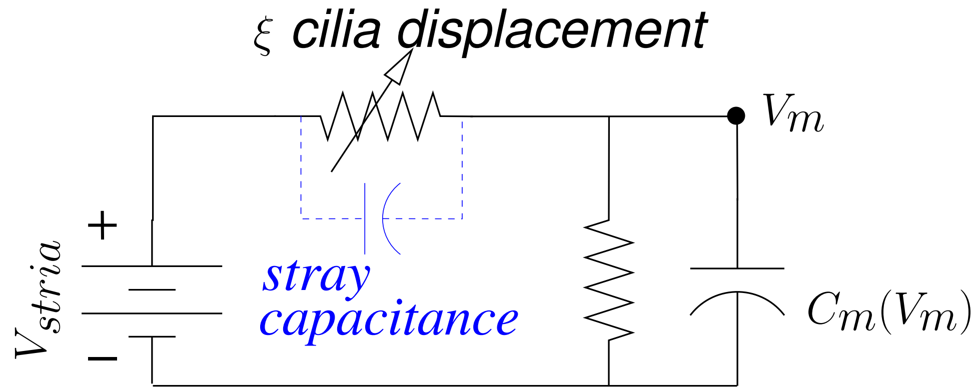
Microchamber Experiments

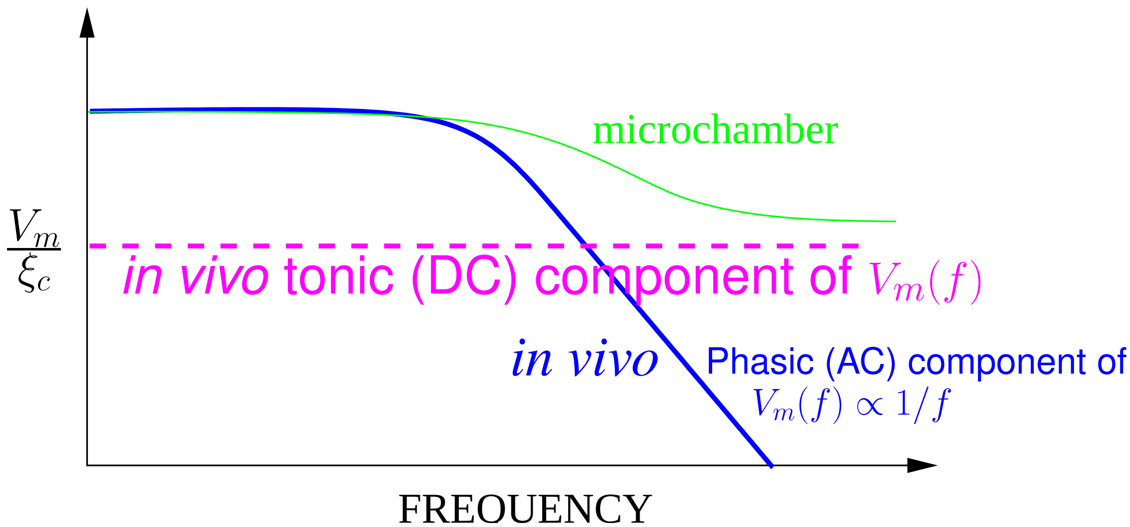
- Method for measuring at high frequencies:
- Based on microchamber "capacitive divider"

- V_m constant as $f \to \infty$
  - $\Delta L_z(V_m), C_m(V_m)$ and $K_z(V_m)$ are wideband ($>$ 25 kHz)

Membrane voltage must be lowpass

- If the Davis hair cell model is correct, $V_m \propto 1/f$





Tonic response dominates the phasic

- Since the phasic voltage $V_m(f) \propto 1/f$,
  - the tonic component [$V_m(f < f_c) \approx$ const.] must dominate at high stimulus frequencies $f >> f_c$
- The tonic V_m changes with efferent stimulation
  - $\Rightarrow$the tonic component can change the BM sensitivity
- Both arguments lead to the conclusion that:
  - $\Rightarrow$ BM compression is controlled by the tonic component

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