

Connecting the nonlinear building-blocks inside the ear with their environment

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Receptor cells in each sensory system convert different types of energy into an electrochemical nerve impulse which can be processed by the brain. In the case of hearing this transduction is performed by the *hair cells*. These receptor cells are responsible for the conversion of mechanical movements (air's vibrations) into an electrical signal (see Fig 1). The hair cell's mechano-electrical transduction process is highly non-linear and has been experimentally characterized only during the last few years¹. Hair cells should amplify the incoming (mechanical) signal in order to distinguish it from background noise. This amplification process results in the exquisite capabilities of the auditory system^{1,2}. Consequently, it can be said that the hair cells are the nonlinear building-blocks of the ear.

In the last few years a small number of mathematical models have been proposed that describe the transduction process occurring in the hair-cells^{1,2}. Those models are rather complicated and include many parameters with poorly known values. Moreover, the analysis of those models has relayed only on numerical simulations. In this work we characterize the dynamics of these models and show that they are all topologically equivalent (see Fig. 2). We also propose a simpler mathematical model describing the dynamics of the hair-cells. This *minimal model* arises from a simplified description of the main biophysical processes taking place inside the hair-cell bundles. We showed in a recent publication in PNAS³ that the dynamics of the minimal model can be treated analytically to a large degree and that it is very rich. Furthermore, the dynamics of the minimal model is topologically equivalent³ to the other, more complex, models (see Fig. 2).

Hair cells in the auditory, vestibular, and lateral-line systems of vertebrates receive inputs through a remarkable variety of accessory structures that impose complex mechanical loads on the mechanoreceptive hair bundles. Although the physiological and morphological properties of the hair bundles in each organ are specialized for detecting the relevant inputs, we suggest that the mechanical load on the bundles also adjusts their responsiveness to external signals.

We augment the minimal model to explore how the mechanical environment can regulate a bundle's innate behavior and response to input³. We find that an unloaded hair bundle can behave very differently from one subjected to a mechanical load. Depending on how it is loaded, a hair bundle can function as a switch, active oscillator, quiescent resonator, or low-pass filter. Moreover, a bundle displays a sharply tuned, nonlinear, and

sensitive response for some loading conditions and an untuned or weakly tuned, linear, and insensitive response under other circumstances. Our simple characterization of active hair-bundle motility explains qualitatively most of the observed features of bundle motion from different organs and organisms³.

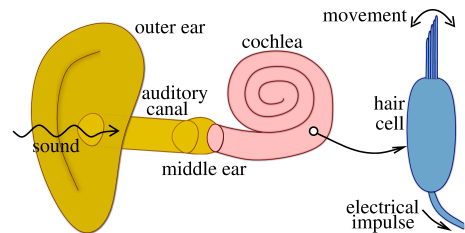


FIG. 1. Schematic view of the location of the hair cells in the inner ear and the mechano-electrical transduction process.

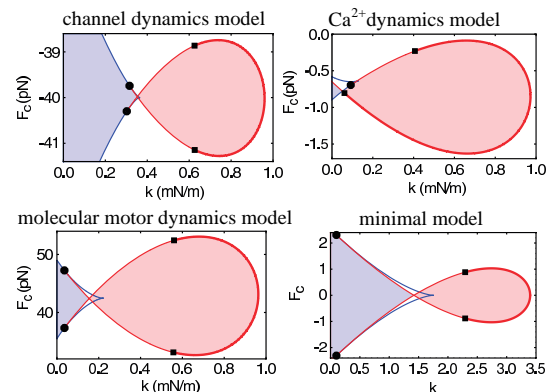


FIG. 2. State diagram for three standard models of the hair cell and our minimal model. Note that all four models are qualitatively equivalent. In the horizontal axis the stiffness is plotted and in the vertical the external force applied in the hair bundle. In the red areas the system oscillates spontaneously and in the blue ones it behaves as a bistable switch.

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¹ A.J. Hudspeth, *Making an Effort to Listen: Mechanical Amplification in the Ear*, *Neuron* **59**, 530 (2008)

² Martin, in *Active Processes and Otoacoustic Emission*, Manley, Fay and Popper Eds., Springer (2007)

³ D. Ó Maoiléidigh, E.M. Nicola and A.J. Hudspeth, *The diverse effects of mechanical loading on active hair bundles*, *Proc. Natl. Acad. Sci. USA*, **109**, 1943-1948 (2012).