Comment on ‘A Wave Traveling over a Hopf Instability Shapes the Cochlear Tuning Curve’

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Since the seminal work by H.L.F. Helmholtz in 1863, to understand the basic principles of hearing has been a great, but still unresolved, challenge for physicists. Some time ago, it has been pointed out (Eguíluz et al., Phys. Rev. Lett. 84, 5232, 2000) that the generic mathematical properties of nonlinear oscillators undergoing a Hopf bifurcation account for the salient characteristics of hearing. Recently, M.O. Magnasco proposed a model of the cochlea (Phys. Rev. Lett. 90, 058101, 2003), which employs Hopf-type instabilities for cochlear amplification. While this model reproduces the input-output behaviour of the cochlea to some extent, the generated model responses deviate significantly from physiological measurements. The reason for the discrepancies between model and experiment are due to the critical choice of the Hopf control parameter close to the bifurcation point \( (\mu = 0) \). The question whether the bifurcation parameter has to be chosen critically or subcritically \( (\mu < 0) \), is central, and has become the subject of a scientific debate. In this contribution, we argue that, for sustained input signals, the control parameter will assume a subcritical value. This leads to model results that are in close agreement with reported experimental data.

Eguíluz et al. \(^\text{[1]}\) have put forward the idea that the salient properties of hearing could be described by a Hopf oscillator system. Their paper, however, left open the actual detailed implementation of this concept within known properties of the cochlea. In a recent contribution \(^\text{[2]}\), M.O. Magnasco attempts to close this gap by complementing the Hopf system with a model of a wave that interacts with the Hopf instabilities as it travels along the cochlea. His results corroborate the generic validity of the Hopf-approach by producing responses that are much closer to measured cochlea data \(^\text{[1,2]}\) if compared with the pure Hopf instabilities \(^\text{[1]}\).

In \(^\text{[2]}\), the Hopf system is considered tuned exactly at the bifurcation point \( \mu = 0 \). While this approach reduces the computation time, it seriously modifies the obtained cochlear response. For the following, we will concentrate on the modifications imposed on the frequency response curves, as they respond more sensitively to modeling details if compared to tuning curves.

The first consequence is that nonlinear responses \( (R \sim F^{1/3}) \) are obtained for sustained sound inputs, irrespective of the stimulus size. This is in contradiction to the constant-gain regime for small stimuli that has previously been outlined (experimentally: bottom curves in Fig. 2 (a) of \(^\text{[2]}\); theoretically: see Ref. \(^\text{[1]}\)).

Secondly, the amplifier bandwidth becomes exceedingly small \( (\Gamma_{3dB} \sim F^{2/3}) \) \(^\text{[1]}\), which leads to abrupt discontinuous model responses. It is true that in nonstationary driving conditions, \( \mu \) may approach or even cross zero \( (\mu > 0) \) in order to reduce the response time for incoming follow-up signals. For sustained signals, however, \( \mu \) will assume a non-zero equilibrium value \(^\text{[3]}\). As the transition points between linear and compressive regime, as well as the amplifier bandwidths, are smooth functions of \( \mu < 0 \), this can consistently be exploited for obtaining realistic response curves \(^\text{[4]}\). We emphasize that the filter-based passive model of \(^\text{[2]}\) already mimicks longitudinal BM coupling. Therefore, the negligence of the longitudinal BM stiffness should not be considered as a substantial cause for the obtained response curve discontinuities. Moreover, also contributions from additional paths with \( \omega \neq \omega_{ch} \) are unable to remove this effect, but instead will merely result in a smoothening of the sharp transition at the response peak. Simulations with models that include passive BM couplings \(^\text{[5]}\) clearly show that the defect persists as long as \( \mu = 0 \) is chosen.

Thirdly, we argue that the choice \( \omega_{ch} > \omega_{pass} \) of the Hopf resonance frequency \(^\text{[6]}\), which is necessary for obtaining the curve forms reported in Fig. 4 b under the condition of \( \mu = 0 \), is unrealistic. It implies that the amplification on the BM takes place on the decaying branch of the passive response, where viscous losses of energy are important. Instead, we propose that the amplification takes place around the passive response peak, where the group velocity becomes small, and a large amount of energy is accumulated in the presence of only moderate viscous forces. This view is corroborated from two-tone suppression experiments, from which the location of amplification can be determined \(^\text{[7]}\).

Our recent modeling approach \(^\text{[8]}\) is based on \( \mu < 0 \) and on a detailed hydrodynamic model of the passive cochlea for the traveling wave. Without any further modifications, this model’s response yields almost perfect agreement with experimental data for low-intensity stimuli (see Fig. 1). The behavior of the response curves on the high frequency branch can be brought even closer to measured data (see Fig. 2 (a) of \(^\text{[2]}\) and Fig. 1 of \(^\text{[1]}\)), by including the observed mechanical forward coupling of outer hair cells \(^\text{[9]}\). The result is a perfect collapse of the response curves on the high frequency branch \(^\text{[4]}\). For stimuli of high intensity, additional effects evidently must be incorporated, as is indicated by the broadened low frequency response of the experimental measurements. In particular, the backward coupling among outer hair cells may become important, as by the interaction of activated Hopf amplifiers, frequencies \( \omega_{ch} > \omega \) will be generated and back-propagated by the coupling. When they are actively amplified, they will lead to the observed shoulder of the low-frequency response. In

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FIG. 1: Local BM frequency response from a Hopf-type cochlea model, where longitudinal BM couplings have been included. Dashed line: passive response. Stimulus frequency: $\omega/2\pi = 1000$ Hz. For two adjacent lines, the stimulus intensity differs by 10 dB.

This behavior is phenomenologically modeled by the filter properties, that lack the detailed relationship to cochlear biophysics proposed in [1].

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