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Title:
Where is the Energy Stored? Energy Flow in the Eardrum Can Account for Long Transmission Delays in the Frog

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Abstract:
Transmission from the external ear to auditory nerve can introduce appreciable delay, given the cascade of transduction and transmission processes that occur. Much of this lag can be attributed to filtering by the frequency-selective elements in the ear. That is, resonance takes time: the sharper the tuning, the longer the delay. However, one vertebrate group has proved to be an outlier: anuran amphibians' (frogs and toads) ears exhibit comparatively long delays (several milliseconds), yet relatively broad tuning. These delays have been partially attributed to the middle ear (ME), though their biomechanical origins remain unclear. The present study used scanning laser doppler vibrometery to map surface velocity over the tympanic membrane (TyM) of anesthetized adult bullfrogs (Rana catesbeiana). Three females and one male were studied. Stimuli consisting of constant-voltage frequency sweeps (duration: 700 ms; sweep range: 0.2-8.0 kHz) repeated once every second were delivered via a loudspeaker placed 18 cm away from the TyM. Stimulus generation and data acquisition were controlled by Polytec software; subsequent analysis was done using customized software written in MATLAB. We also investigated TyM motion by measuring the pressure ratio across the TyM, the effects of ossicular interruption, and changes due to physiological state of TyM ('dry-out'). Mechanical responses showed varying degrees of radial symmetry in a frequency-dependent fashion. Our main finding is the general observation of a circularly-symmetric inward-traveling wave at intermediate frequencies on the TyM surface, starting at the outer edges and propagating inward with decreasing amplitude towards the center (the site of the ossicular attachment). For low stimulus frequencies (~0.5 kHz), the entire membrane vibrates in a simple (0,1) mode. At higher frequencies (> 2.5 kHz), intermediate nodes become apparent, suggestive of standing waves. A large pressure drop was apparent across the TyM, and ossicular interruption appears to have had relatively little effect on the measured responses. The delays we observed on the bullfrog TyM, approximately an order of magnitude longer than those observed for gerbil, appear to arise from a slow, mechanical inward-traveling wave. These motions can account for a substantial fraction of the relatively long delays previously observed in the anuran inner ear, and can help inform models of mammalian TyM biomechanics.