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## Slow to hear: Traveling waves on the eardrum

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The purpose of the ear is to convey incoming acoustic energy from the world around us into the central nervous system. This process however can introduce (appreciable) delay, given the cascade of transduction processes that occur. From sound to synapse, much of this lag can be attributed to filtering by the frequencyselective 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 (frogs and toads) ears exhibit comparably long delays (several milliseconds), yet relatively broad tuning. These delays have been partially attributed to the middle ear (ME), though the biomechanical origin remains uncertain. The present study sought to determine the genesis of this additional group delay by using scanning laser doppler vibrometery to map surface velocity over the tympanic membrane (TyM) of anesthetized bullfrogs (Rana catesbeiana). Our main finding is the general observation of a circularly-symmetric inward-traveling wave on the TyM surface, starting at the outer edges of the TyM and propagating inward with decreasing amplitude towards the center (the site of the ossicular attachment). Presumably these TyM waves stem from mechanical constraints associated with being a semi-aquatic species with a relatively large tympanum. We investigated some of these constraints by measuring the pressure ratio across the TyM, the effects of ossicular interruption, the changes due to physiological state of TyM ('dry-out'), and by calculating the middle-ear input impedance. In summary, the present study demonstrates the existence of a slow, mechanical inward-traveling wave on the TyM surface that generates and can account for a substantial fraction of the relatively long delays previously observed in the anuran inner ear.

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