Energy Propagation via Traveling Waves on the Bullfrog Tympanic Membrane

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Introduction

Frogs are amazing. For example, they may turn into a prince when thrown against a wall (or kissed, depending on the story's version). Also amazing, and unique among tetrapods, is the relatively long delay associated with forward transmission of sounds through the tympanic middle ear (~30x longer than in gerbil). The largest fraction of this delay is between the external sound pressure and the induced motion at the center of the tympanic membrane (TyM), where the single, middle-ear ossicle is attached. The present study sought to investigate the basis for this lag by mapping the velocity profile of the TyM using laser Doppler vibrometry.

Methods

Recordings were obtained from the tympani of adult American bullfrogs (*R. catesbeiana*) under free-field conditions. After the induction of anesthesia, the frog was placed inside a double-walled sound-attenuating chamber. A scanning laser Doppler vibrometer that allows the acquisition of vibration velocity across a user-defined grid, was used to map responses over the entire TyM surface. Stimuli were presented from a speaker which was in line with the incident laser beam, and positioned ~20 cm from the TyM. A microphone was placed in close proximity of the ipsilateral TyM, and its signal served as a reference to vibrometric recordings. Stimulus waveforms were tailored to study energy propagation along the tympanum, and consisted either of frequency sweeps or tone complexes with multiple inharmonic frequency components.

Results & Discussion

Our main finding is the presence of traveling waves on the surface of the TyM. These waves start at the edges of the tympanum and (slowly) propagate inward to the membrane's center (where the single is attached). These waves occur over a range of stimulus frequencies that corresponds to the range of bullfrog hearing (500 – 1700 Hz). For higher frequencies, the TyM vibrations show patterns that are more complex. To capture the essential features, we propose a relatively simple model in which the TyM is a distributed segment of a transmission line, which couples the surrounding ear to the center of the TyM (i.e. the middle ear ossicle and inner ear). At those frequencies where the characteristic impedances of the transitions are well matched, the response is dominated by a (slow) traveling wave. Mismatches between these impedances cause (partial) reflection of the propagating energy, resulting in multiple waves that propagate in opposite directions. Their interference causes standing waves or a response that is more complex.