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Underwater Sound Localization using Internally Coupled Ears (ICE)

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ABSTRACT

Internally coupled ears or for short ICE [1-4], where an interaural cavity acoustically couples the eardrums, are an anatomical trait present in more than half of all terrestrial vertebrates. The superposition of outside and internal pressure on the two eardrums results in internal instead of interaural time and level differences, which are keys to sound localization. Although ICE is primarily a low-frequency terrestrial adaptation, the African clawed frog Xenopus laevis is a fully aquatic species with a distinct air-filled canal between the ears. In water, the speed of sound is four times that in air. Unlike terrestrial animals with ICE, the Xenopus interaural cavity is also medially connected to the lungs. By modeling the inflated lungs as a Helmholtz resonator [5], we demonstrate their effect in improving hearing in a low-frequency regime, while simultaneously enhancing sound localization in a disjoint high-frequency regime, corresponding to the frequency ranges of male advertisement calls. In conjunction with its unique plate-like eardrums, we show how Xenopus uses its ICE-like interaural coupling to generate considerable internal level differences between eardrum vibrations and thus overcomes the challenges of underwater sound-localization. Taken together, the two arguments of Helmholtz resonator and plate-like eardrums show [6] the potency of ICE and are interpreted accordingly.

Keywords: Underwater hearing, sound localization, Xenopus, phonotaxis

1. INTRODUCTION

Being fully aquatic, the clawed frog *Xenopus* faces two problems: (i) how to get food and (ii) how to find a sexual partner. The food consists of flies that drop onto the water surface during night. The frog's lateral-line system is well suited to localize them. Under water and for far-away sources, however, the lateral line system is not effective as its range is of the same order as the frog‘s length. Thus sound comes in, allowing for long-range localization. Moreover, what the animal actually hears is not the external interaural time and level difference, ITD & ILD, but the *internal* time and level difference, iTD & iLD, which result from the internal coupling; cf. Fig. 1. ICE has two distinct modes of operation. First, increase of the time difference that the animal actually perceives in a low-frequency range by a factor of about 4. The precise value depends on the properties of the eardrum and the interaural cavity volume [3,4]**.** The iTD plateau ends at (typically) 500–700 Hz. Since water has a sound velocity that is four times that in air and the interaural distance is small (cm), iTDs are not a feasible means of sound localization. Second, just above the eardrum's fundamental frequency f_0 there is an outspoken iLD maximum for directions $\pm 90^{o}$. It may be as large as 15-20 dB. Of course straight on gives iLD = 0, whereas ILD $\equiv$ 0 for whatever direction.

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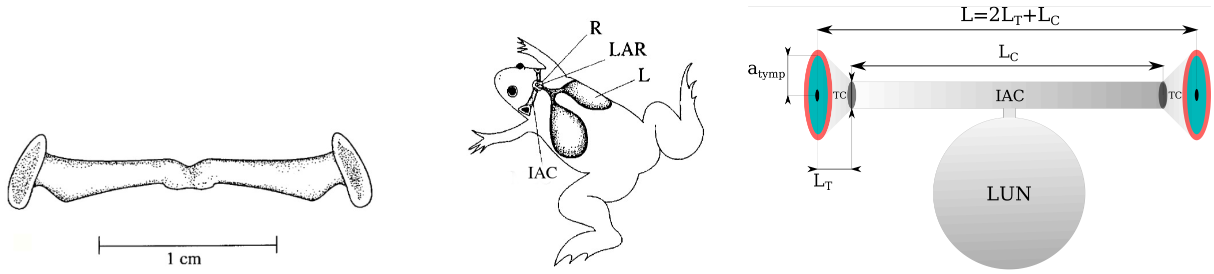

Figure 1: (Left) Middle ear cavity in *Xenopus*, which is the interaural canal (IAC) plus left and right tympanic cavities (TC). (Middle) Schematic diagram of air filled cavities in a submerged *Xenopus*. The two tympanic cavities taper into a shared Eustachian tube or IAC, which is medially connected to the lungs (L) through a recess (R) in the roof of the mouth. LAR denotes the larynx and is not relevant to our present discussion. Plots adapted from Christensen-Dalsgaard and Elepfandt [7] (Springer-Verlag, by permission). (Right) ICE model schematic for the air-filled cavities in *Xenopus* based on the left two figures. The rigid, circular, cartilaginous tympanic plates (dark/blue) at far left and right are suspended in a flexible annular outer membrane (red). The shallow TC have a distinct taper in a direction away from the tympanic plates and are connected through a narrow IAC. The lungs (LUN) are represented by a single volume connected medially to the interaural canal (IAC) and function as a Helmholtz resonator []. Both the tympanic plates (instead of ear*drums*) and the lungs as Helmholtz resonator are the keys to understanding *Xenopus*' underwater hearing while exploiting ICE.

2. RESULTS

Male calls attract females and their localization is through amplitude differences. That is, through determining iLD generated by ICE. It is known that the calls have two frequency centers, around 1.0 and 1.7 kHz. Figure 2 shows the effect of ICE

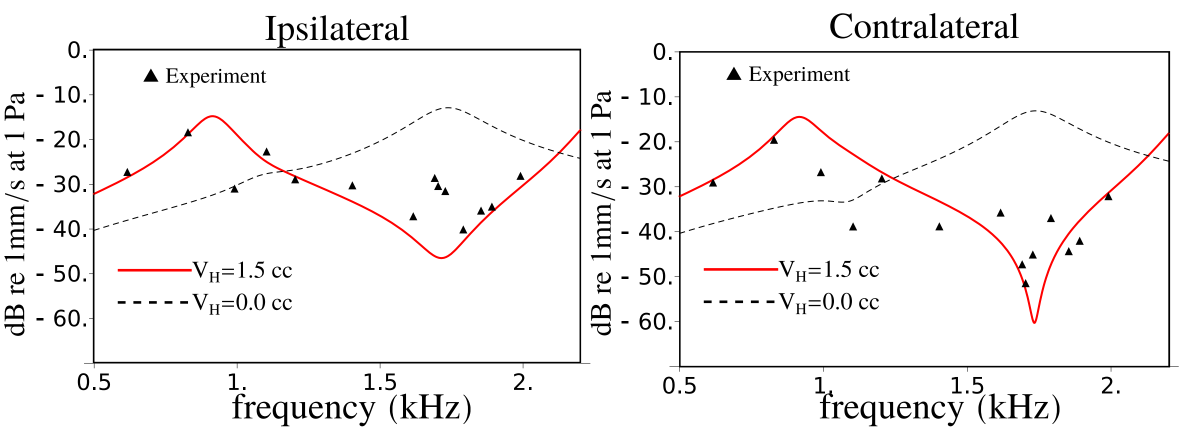

Figure 2: Experimentally measured (filled triangles) and model vibration velocities (solid and dashed lines) of the *Xenopus* ipsilateral (left) and contralateral (right) eardrum underwater. The eardrum vibration velocities have been measured [7] by using laser vibrometry and have been normalized w.r.t. the input pressure. The solid (red) line corresponds to inflated lungs with a total

volume V_H = 1.5 cc and the dashed (black) line corresponds to the case V_H = 0 cc, i.e., absent or fully deflated lungs. The sound-source direction is ±90°. There is a maximum at about 1 kHz and an outspoken difference between ipsi- and contralateral only at 1.7 kHz, which is needed for sound localization. As both plots show, the experimental results can be explained only with inflated lungs that perform a Helmholtz-resonator function.

3. CONCLUSIONS

Figure 2 actually shows three things. First, without inflated lungs one cannot explain the experimental data. Second, clawed frogs exhibit an outspoken auditory sensitivity around 1.0 kHz, which facilitates noticing a sexual partner. Third, only around 1.7 kHz do we see a clear difference between ipsi- and contralateral response; that is, an outspoken iLD (of about 18 dB), which allows decently precise localization of a sound source by turning the head. After all, mating needs no narrow time window.

Finally, why does *Xenopus* use a rigid plate as eardrum? A rigid plate absorbs [6] more power than a flexible eardrum near 1 kHz both *in water* and in air (for rare peregrinations from one pond to another one), whereas the flexible membrane only peaks [6] below 400 Hz. This suggests that the Xenopus eardrum is adapted to improve hearing around 1 kHz in both media; cf. the fictitious frog *Xenopus2* [6].

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