Can you hear better if you're lopsided? Tympanal asymmetry may enhance hearing in a parasitoid fly

M. Mikel-Stites[1], A. E. Staples[1], P. Marek[2]

[1]Biomedical Engineering & Mechanics, [2]Entomology

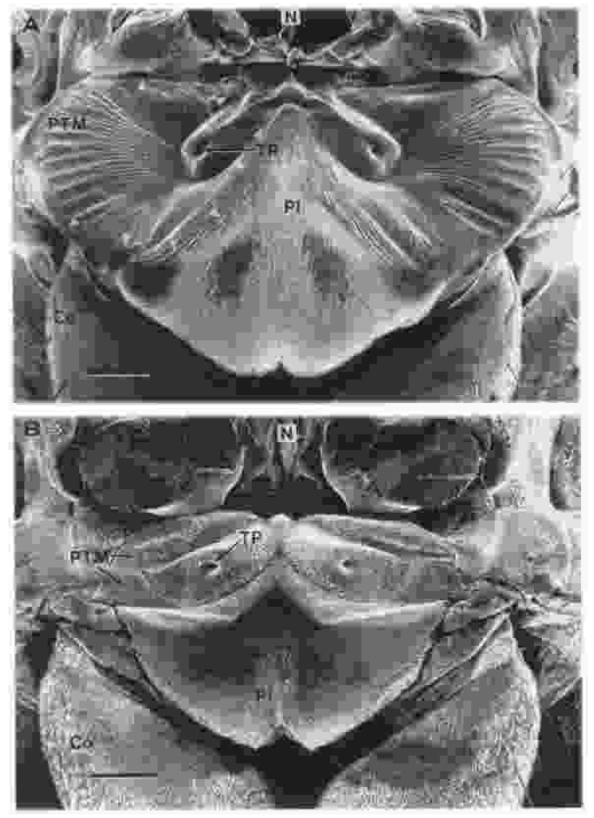
Ormia ochracea is a parasitoid fly endemic to the Americas. Gravid females respond phonotactically to calls of their male *Gryllidae* cricket hosts. Astonishingly, *Ormia* can locate their hosts with an azimuthal precision of 2º – equal to that of humans, in spite of their small size, which should prohibit this level of precision because of fundamental constraints imposed by the physics of sound propagation (Mason *et al., Nature*, 2001). Miles *et al.* demonstrated that *Ormia* is capable of resolving nanosecond time differences due to a direct mechanical coupling of the fly's tympanal membranes (Miles *et al., J. Acoust. Soc. Am.*, 1995). This mechanical coupling increases the interaural time delay (ITD) between the tympana, thus enhancing the fly's sound localization precision. Here, we introduce an asymmetry in tympanal area into the mathematical model provided by Miles *et al*. and demonstrate that an asymmetry of less than 10% between the left and right tympanal areas can increase the ITD 20-fold. We further present initial measurements of 44 *Ormia* tympana that demonstrate an average asymmetry in tympanal area of approximately 5%.

RESEARCH OBJECTIVES

The goals of this work were to:

1. Confirm the existence of tympanal asymmetry in *O. ochracea* via physiological measurements
2. Explore effects of introducing tympanal asymmetry into existing model for *O. ochracea* hearing for low frequency (cricket localization) incident sounds
3. Explore effects of introducing tympanal asymmetry into existing model for *O. ochracea* hearing for high frequency (bat ultrasonic and social call) sounds

Above: *O. Ochracea* samples acquired from the Smithsonian Museum of Natural History and the VT Insect Collection

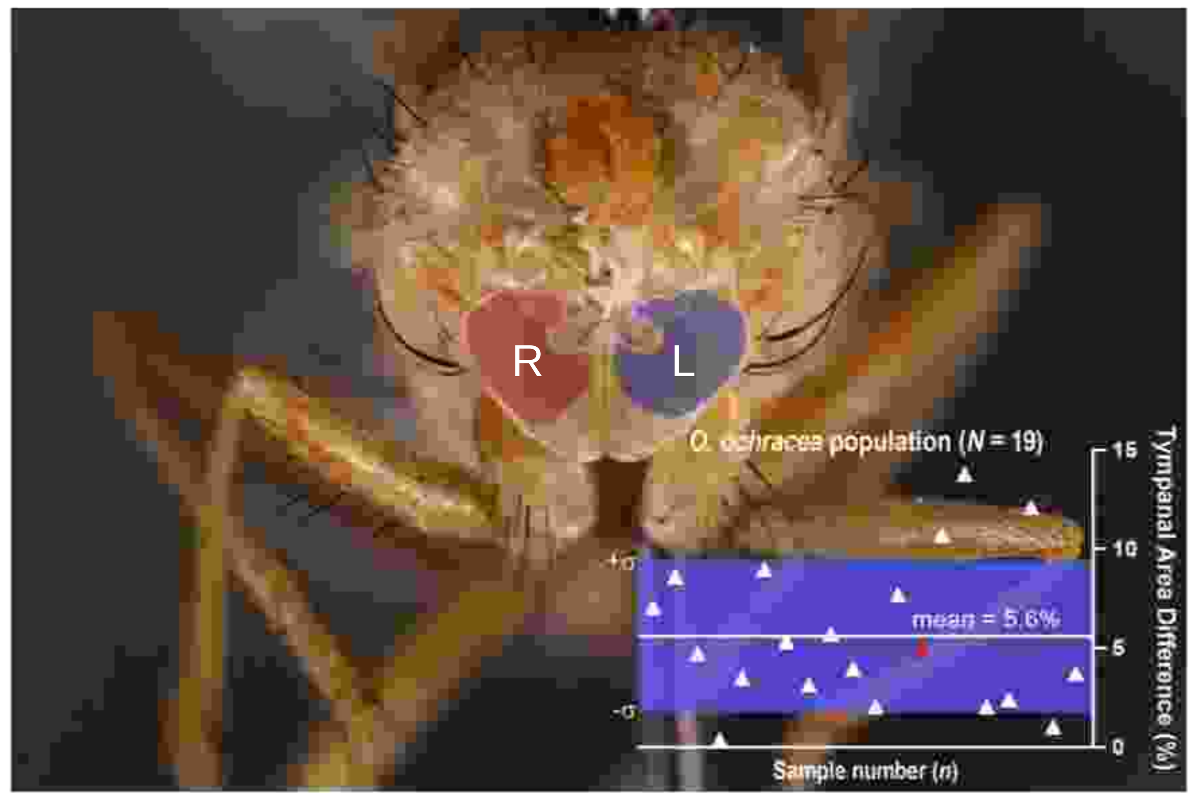


Left top: female *O. ochracea* tympanal membranes

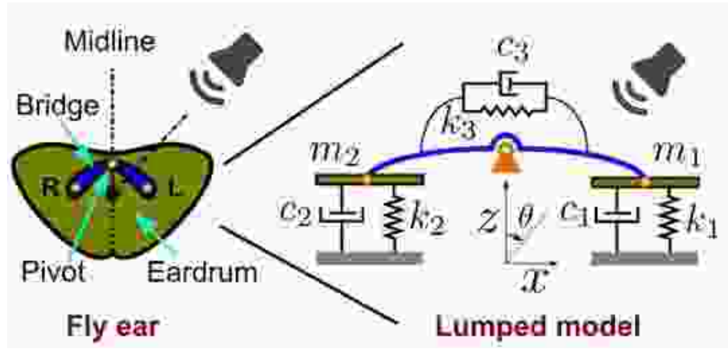
Left bottom: male *O. ochracea* tympanal membranes (note comparatively small membranes and associated structures)

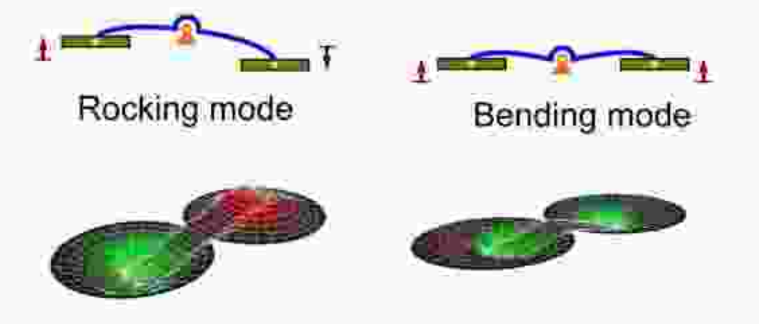
Robert, *et al.*, *Cell Tissue Res.*, 1994

TYMPANAL SYSTEM AND MATHEMATICAL MODEL



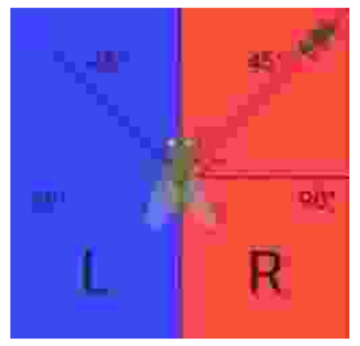
Above: decapitated *O. ochracea* with right tympanal membrane highlighted in red, left highlighted in blue. Inset: Measurements of tympanal asymmetry in sample population.





Left: Coupled beam model for *O. ochracea* tympanal hearing organ; fundamental modes of model

Figures adapted from Liu *et al.*, *Scientific Reports*, 2013



Created with BioRender

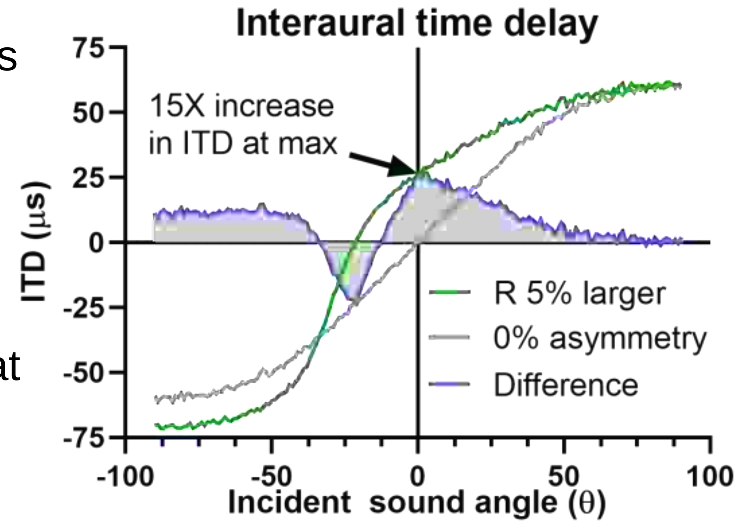
Definition of incident sound angle and left and right sides

$$\begin{bmatrix} k_1+k_3 & k_3 \\ k_3 & k_2+k_3 \end{bmatrix}\mathbf{x} + \begin{bmatrix} c_1+c_3 & c_3 \\ c_3 & c_2+c_3 \end{bmatrix}\dot{\mathbf{x}} + \begin{bmatrix} m & 0 \\ 0 & m \end{bmatrix}\ddot{\mathbf{x}} = \mathbf{f}$$

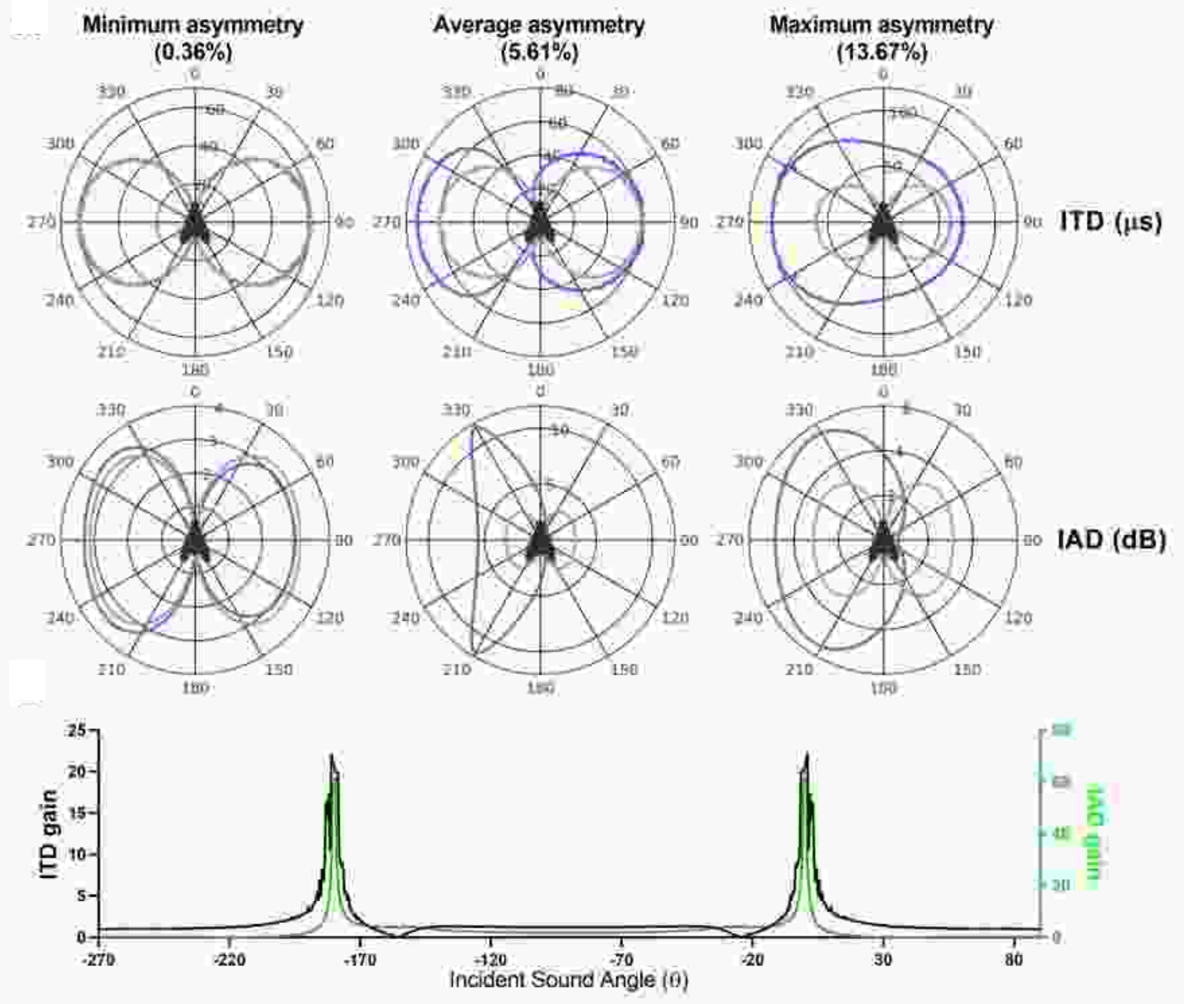
$$\mathbf{f} = p_{\text{inc}} \cdot A_{\text{surface}} \cdot a_{\text{asymm}}$$

Linear ODE model for coupled beam system used in numerical simulations (Miles, 1995). We introduce tympanal asymmetry into the model via the force term to model the asymmetric acoustic pressure forces that result from the asymmetric tympanal surface areas

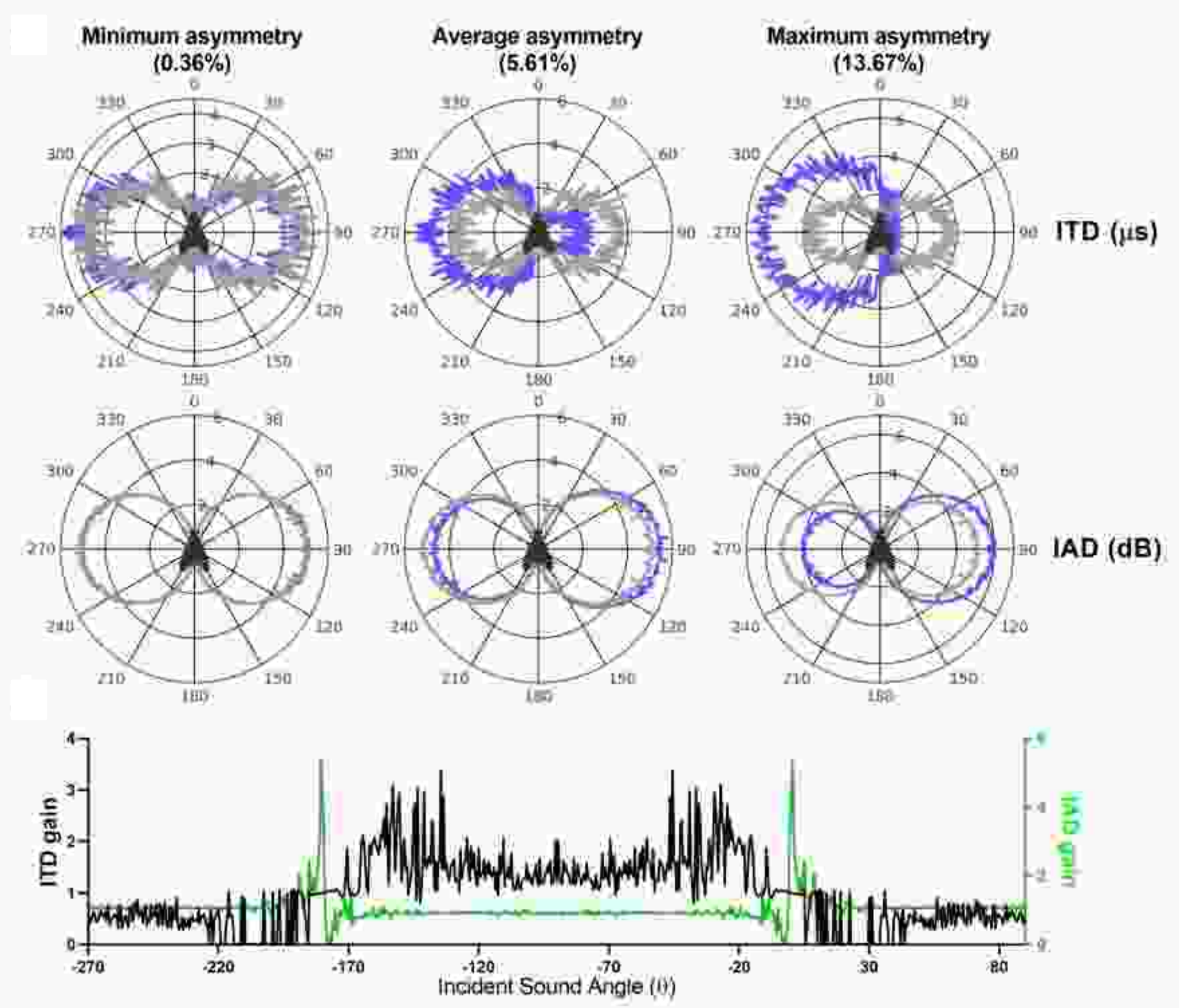
Symmetric model results (grey) compared to model results using average population asymmetry of 5% (green). Maximum gain (15-fold) in ITD occurs at 2º incident sound angle



RESULTS FOR 5 kHz AND 20 kHz INCIDENT SOUND



Polar plots show the absolute interaural time difference (ITD) and interaural amplitude difference (IAD) (blue) as functions of the incident sound angle, with radial distance from the center indicating magnitude. The grey curves show the symmetric case. The bottom figure is 'unrolled' and displays the gain in ITD and IAD for the average 5.61% asymmetry case relative to the symmetric case, with 0º aligned along the midline of the fly. In each figure, the incident sound was a 5 kHz sinusoid at 72 dB, consistent with host cricket mating calls, and the right membrane is chosen as the larger membrane. The response is mirrored and symmetric for a larger left membrane (not shown).



Absolute interaural time difference (ITD) and interaural amplitude difference (IAD) with incident sound at 20 kHz and 72 dB, within the range for bat social calls and some low ultrasonic chirps. While the degree of asymmetry in the response is increased, especially in ITD, the gains compared the symmetric case are less substantial than for 5 kHz incident sound.

CONCLUSIONS

- A population of 19 *O. ochracea* specimens was found to have an average left-right asymmetry in tympanal surface area of 5.61%.
- A surface area asymmetry of as little as 5% significantly increased both the interaural time delay (ITD) and the interaural amplitude difference (IAD) for a given incident sound, by factors up to approximately 15 and 60, respectively. ITD and IAD are two quantities used commonly by binaural organisms to localize the source of incident sounds in the plane.
- The gain depended heavily on the incident sound angle. The greatest gains occurred near the midline of the fly (2º) and were consistent with the maximum azimuthal sound localization precision of 2º observed in *O. ochracea* specimens in laboratory settings. In addition, a 5% or larger asymmetry introduced large left-right asymmetries in IAD.
- The model results suggest that in low-frequency fly-cricket interactions, when O. *ochracea* acts as a predator, a small tympanal asymmetry could give the fly a dramatic increase in the precision of its sound localization abilities at small incident sound angles, and could improve her lateralization abilities.
- In higher-frequency fly-bat interactions, model results suggest that small tympanal asymmetries could create pronounced asymmetries in IAD and ITD. These asymmetries could be related to observed aerial startle responses exhibited by the flies when exposed to ultrasonic and near ultrasonic acoustic stimuli (Rosen, 2009).
- Live animal experiments demonstrating that flies with pronounced tympanal asymmetries display improved sound localization abilities are needed to support the hypothesis that a slight tympanal asymmetry provides a fitness advantage for *Ormia ochracea*.

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ACKNOWELDGEMENTS & CONTACT INFORMATION

Thanks to Maddie Hellier for *O. ochracea* tympanal measurements and to the Virginia Tech Engineering Mechanics Student Travel Fund for enabling travel

Max Mikel-Stites: mmikelst@vt.edu, @i_max
Anne Staples: aestaples@vt.edu, @StaplesLabFluid
Paul Marek: pmarek@vt.edu, @apheloria