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Sound reception and radiation in a small insect

N. Mhatre^a, F. Montealgre-Z^a, R. Balakrishnan^b and D. Robert^a

^aUniversity of Bristol, School of Biological Sciences, Woodland road, University of Bristol, BS8 1UG Bristol, UK

^bCentre for Ecological Sciences, Indian Institute of Science, 560012 Bangalore, India
natasha.mhatre@bris.ac.uk

Insects are small; this is a fact of their life. In some contexts this is an advantage, such as insects do not injure themselves through the effects of gravity. In other contexts this is a disadvantage, especially in the context of sound production and reception. The wavelengths of sound that insects such as crickets produce and receive are several times larger than their body size. For sound production, this is particularly challenging and inefficient, as sub-wavelength radiation (size to lambda ratio $> 1:100$) requires great energy expenditure to produce sufficient sound pressure. In receiving sound, they face the reciprocal problem and are inefficient receivers. In addition, because of their size they cannot rely on cues other animals use to detect the direction of sound. Nonetheless, sound is extremely important to these insects as they use it for mate attraction and to evade predators. We investigate this problem by combining the technique of microscanning laser Doppler vibrometry with finite element modelling; and explain some of the biomechanical tricks a tiny tree cricket uses to overcome the disadvantages of size.

1 Introduction

Insects are small in comparison with the better studied mammals. Their small size has been of great advantage to them, allowing them to proliferate and invade nearly every corner of the earth. Yet in some domains, small size remains a challenge because of the physics involved.

The longest known extant insect is a stick insect which has a body length of about 57 cm (1), no longer than a house cat. Most other insects are even smaller and many insects that communicate using sound (crickets, katydids, grasshoppers, locusts, mosquitoes, flies, etc) tend to be smaller still. More importantly they are smaller than the wavelength of sound they produce and receive. In some insects such as flies, this mismatch can be as high as size: λ of 1:1000 (2).

The wavelengths of the sound produced by these insects are under several different constraints, and body size is only one of them. The two primary influences determining communication wavelength seem to be ecological and physiological. Longer wavelengths transmit better than shorter wavelengths along the ground and through vegetation (3). The longer the wavelength, the lower the attenuation of the sound in natural environments and the further sound transmits, the further females can be attracted from. Hence, there is an evolutionary preference for longer wavelengths. The other driving factor for long wavelengths is physiological, shorter wavelength sounds imply higher frequencies, which in turn imply faster muscles. Producing high frequencies is energetically expensive and the oxygen demand of such muscles is limiting in insects who have a diffusion based respiratory system (1). There are, however, competing pressures and the use of long wavelength sounds has consequences for both the sender and the receiver. In this paper, we will examine the challenges posed by long wavelength sound production and reception, each in turn using the example of a small tree cricket, *Oecanthus henryi*.

1.1 Sound production: resonance entrained drives

Crickets including *O. henryi* use their forewings not to fly but to produce sound (Fig. 1A). One of their wings has a structure called a file which consists of a row of microscopic teeth (Fig. 1B). These are rubbed against the plectrum, a hardened margin on the other wing. The force generated by this action sets the wings in vibration and if the frequency of the force matches wing resonance, the sound produced is louder (4).

We examined the force regime produced during singing in *O. henryi* males by recording the motion of one of the two wings in the x direction using a position detector (5) along with simultaneous sound recording (Fig. 1C). Sound

was produced only in the closing wing-stroke and the opening was silent (Fig. 1C). The time series of the wing acceleration was obtained by double differentiating the wing displacement during the closing wing-stroke (Fig. 1D). Based on the acceleration data, and assuming the same effective mass through the wing-stroke, the forces produced by the tooth impacts can be estimated to be periodic but impulsive in nature. The frequency spectra of wing strokes from 3 of 4 individuals showed the presence of a noisy harmonic series which also reflected the periodic and impulsive nature of this drive.

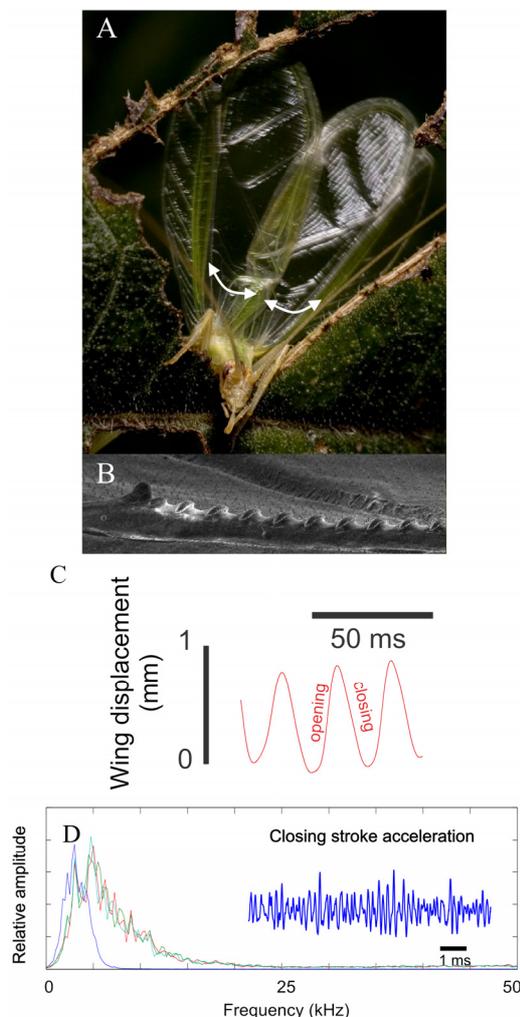


Figure 1: Singing behavior of tree-crickets. (A) A singing tree cricket. (B) SEM of *O. henryi* file teeth. (C) Displacement of wing during singing. (D) Acceleration during a closing stroke and frequency spectra of closing stroke accelerations of 4 individuals.

If the frequency at which the teeth are struck and the eigenfrequency of the wings are matched, then the amplitude of the wing vibration will be greater and hence the insect capable of producing louder sounds (4). Such entrainment would therefore be beneficial and crickets are thought to entrain the driving force to wing resonance using a clockwork like escapement mechanism (6). In this mechanism, the vibration of the wings is oriented such that the plectrum wing engages and disengages the file wing with the period of the vibration (Fig. 2A).

Typically, crickets sing at a single narrow-band frequency (7). Tree crickets, however, sing within a much wider frequency range and *O. henryi* in particular 2.3 to 3.8 kHz (8). In order to examine how variable frequency song is achieved, the resonance of their wings was studied using scanning laser Doppler vibrometry and sound as a driving force.

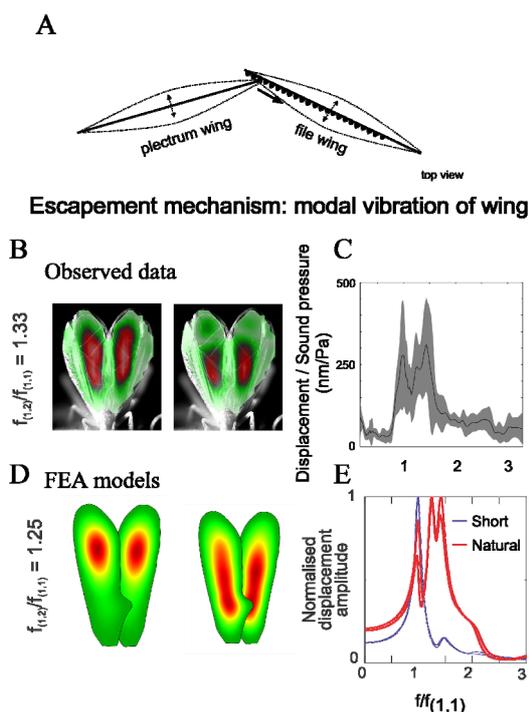


Figure 2: The function of resonance in tree cricket wings. (A) A cartoon of the cricket singing escapement mechanism. (B) A vibrometric map of displacement of tree cricket wings at model (1,1) and mode (1,2). (C) Amplitude spectra of wing displacement, mean and standard deviation as measured at the harp area. (D) FE models of stiff isotropic plates shaped like wings at mode (1,1) and mode (1,2) and (E) the frequency response of these plates with measured damping parameters included.

The response of the wings of *O. henryi* was observed to be greatest near song frequency. The dorsal field which forms the main radiating part of the wing behaved like a plate clamped on all sides with the first resonant frequency showing mode (1,1) and the second, mode (1,2) (Fig.2B). On average, $f_{(1,1)}$ was 3.04 kHz and $f_{(1,2)}$ was 4.32 kHz (N=8). We also found that due to damping, all frequencies lying between mode (1,1) and mode (1,2) showed high amplitudes of vibration. We conclude that this allows the resonance entrained escapement system to function and produce sound within this broader range of frequencies.

The frequency response of the wing is determined by both its geometry and material properties. However the

elongated shape of *O. henryi* wings suggested that this elongation was the cause of their higher modal density. In order to understand which of these properties determine the observed broad frequency response, we used an FEA approach using the multiphysics software COMSOL. We focussed mainly on wing geometry.

We found that if the normal *O. henryi* wing aspect ratio was used for FE model geometry (Fig. 2D) the ratio between $f_{(1,1)}$ and $f_{(1,2)}$ was close to that observed in the real crickets i.e. FE model: 1.25 to real data: 1.33 (Fig. 2B and D). If the wing aspect ratio was shortened by halving the length, $f_{(1,2)}/f_{(1,1)}$ was significantly larger at 1.47. When damping was incorporated into this model, at natural aspect ratio, the frequencies between the first two modes showed high amplitude displacements (Fig. 2E). This was not true of the shorter wings (Fig. 2E). Hence, we can conclude that wing elongation is responsible for increasing the song frequency range. The reason for elongating the wing is considered in the following section.

1.2 Sound production: critical frequency

The reason for enlargement of wings in tree crickets, we believe is in order to improve the radiated sound power. When wings resonate at their first mode and radiate sound, their behaviour can be approximated by a piston and the sound power produced is a function of the radiation resistance and the average velocity produced over the wing.

$$P_r = R_o \langle |v|^2 \rangle \quad (1)$$

Where, P_r is the power of the radiated sound, R_o the radiation resistance and $\langle |v| \rangle$ the time and space averaged velocity over the wing.

At this point, the principal mechanism determining the efficiency of sound production is the radiation resistance. The radiation resistance is dependent on the match between the wavelength of the sound in air and the size of the piston producing the sound. The critical frequency, for a bipole source, is the frequency at which the sound wavelength in air is the same size as the radiator. Hence, for sub-critical radiators, the larger the radiator size, the higher the power produced at any given velocity.

Part of the mechanism behind this reduction in power is known as acoustic short-circuiting. During singing the wing is raised away from the body of the insect and vibrates in free space acting as a bipolar sound source. When the radiator is smaller than the wavelength of the sound in air, the sound radiated from either side of the wing is out of phase and destructively interferes along the plane of the wing, effectively wasting the sound produced by the insect. If the radiator is the same size as the song frequency this effect is negligible.

The wings of *O. henryi* (Fig. 2B) have an average length of 8.6 mm and a maximum width of 2.3 mm each (N=6). Despite enlargement, both of these dimensions are significantly smaller than the wavelength of sound they produce i.e. 149.1 to 92.7 mm. The radiator produces sound at a frequency significantly lower than critical frequency and we believe *O. henryi* males have enlarged their wings through evolutionary history in order to partially mitigate this effect.

1.3 Sound production: fast, loud and baffling

Another mechanism that the males use, to escape the constraints of size, is simply to produce very large wing velocities and in turn higher amplitude sounds. There are however several challenges even in this solution. There is the obvious energetic challenge for the animal who must expend large amounts of muscular energy to produce sound of sufficiently low frequency. But there is also the challenge of producing sound radiators that are capable of withstanding such high velocities and large deformations. In addition, since these radiators are wings and must be carried by a small insect, they must be light enough not to impede movement or flying.

Another method used in order to improve the efficiency to conversion of wing vibrations into sound, is a well documented behaviour called baffling (9-10). When singing, the insect positions itself in either a self-made or pre-existing hole in a leaf and positions its wings so they are in the same plane as the leaf. This reduces the amount of acoustic short-circuiting experienced by the sound improving the efficiency of the radiator (Fig. 3 A, B).

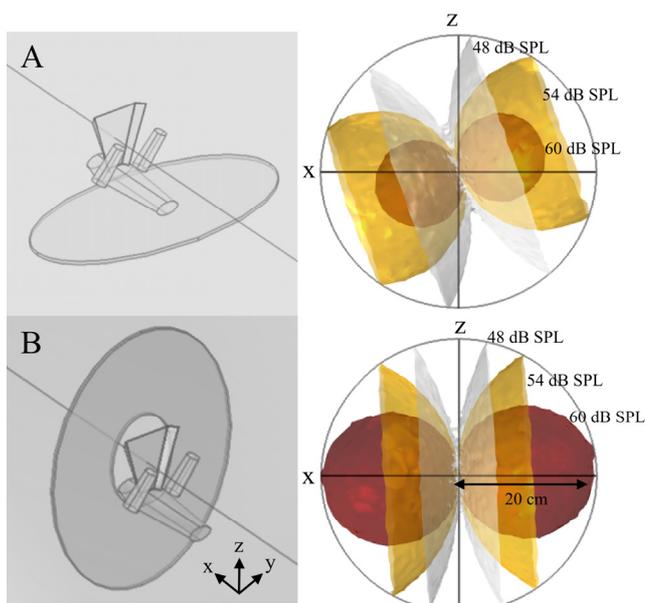


Figure 3: The effect of a baffle on sound radiation.

Sound radiation from the moving wings of an animal singing from (A) a leaf and (B) from a baffle when the velocity of the radiator is the same ($\langle |v|^2 \rangle = 0.22 \text{ m/s}$). The 3D plots show isosurface plots at indicated dB SPL.

Using laser Doppler vibrometry, we measured the wing motion of live *O. henryi* males singing from a baffle provided by us. We also simultaneously monitored the sound produced by the male.

In preliminary analysis, we find that singing *O. henryi* males in baffles, on average, during each pulse of sound, reach peak velocities of $1.78 \pm 0.24 \text{ m/s}$. By numerically integrating the data we find that this corresponds to peak displacements of $99 \pm 14 \mu\text{m}$ and by finding the numerical derivatives, peak accelerations were estimated to be $33.41 \pm 6.17 \text{ km/s}^2$ (mean \pm SE, $N=5$). They produce peak sound pressures of $70.96 \pm 3.6 \text{ dB SPL}$ as measured at a distance 20 cm in front of the singing insect (Fig. 4). These measurements indicate that *O. henryi* males have to expend a very large amount of effort during singing. In addition,

their wings also have to withstand large accelerations and undergo large deformations several times the width of the wing itself in order to produce sound at ecologically reasonable SPLs.

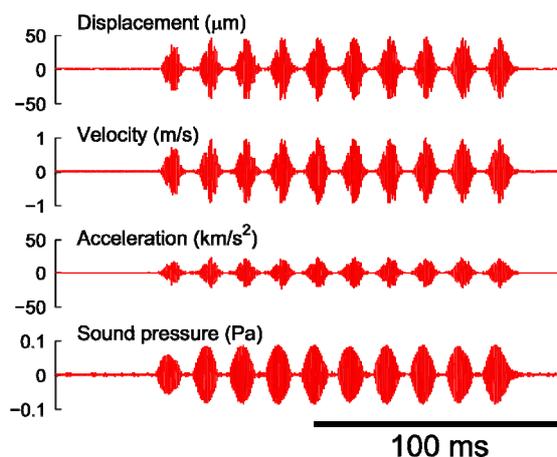


Figure 4: Wing motion and song of an *O. henryi* male singing from a baffle. Wing displacement, velocity and acceleration at point of maximum amplitude on the wing and simultaneous sound recording at 20 cms from animal.

1.4 Sound production: corrugation effects

Several questions are raised by the results of these experiments. One question is how do the wings withstand these repeated large deformations without being damaged? The other question relates to the stiffness of the wings. *O. henryi* and other tree cricket have wings that are very thin and transparent (Fig. 1A, 5A). Yet, the first resonant mode observed is at the relatively high frequency of 3 kHz (Sec. 1.1). This indicates that these wings must be stiffened in some way, either structurally or through the incorporation of metals as seen in other insects (11).

On closer observation, the wings are seen to be corrugated which might be a possible answer to these questions (Fig. 5A, B). Corrugation is a simple structural technique used to make a structure stiff in one direction (along the corrugation axis) and compliant in the other direction (perpendicular to the corrugation axis) and is hence an excellent solution to the two contrasting demands made on the *O. henryi* wing. We use a combination of analytical and FE models to investigate the expected effects of the corrugation observed on the wings. We investigate the expected increase in stiffness and the shift in $f_{(1,1)}$ and $f_{(1,2)}$ due to the corrugation. We also investigate whether the deformation experienced by a corrugated wing will be greater per unit force compared to an uncorrugated wing.

There are specific challenges associated with modelling corrugations of the size observed in the wings (Fig. 5A, B). The size of the corrugations is orders of magnitude smaller than the dimensions of the wings (Table 1). This makes modelling the geometry of the corrugation explicitly extremely time consuming. Hence, we use orthotropic equivalents of a corrugated sheet developed by Liew *et al* (12), Briassoulis (13) and benchmarked by Wennberg *et al* (14) and also verified by us.

The corrugation parameter values used for the models are based on an SEM through a section of the wing (Fig. 5B) and measurements from whole wing images (Fig. 5A). We ignore for these models the observed periodic increase

in thickness. Instead we use an average thickness across the corrugation. The terminology used by us is as in Wennberg *et al* (14). The density of insect cuticle as measured so far falls within very small limits (11) and hence the mean value of 1200 kg/m³ is used. Similarly, unlike other softer biological materials, a μ of 0.3 is reasonable for insect cuticle and is used (15-16). The only free parameter is the Young's modulus, which is known to be quite variable depending on the species and the function of the cuticle (11). Hence, we test the models at a range of values for E.

Table 1: Wing and membrane geometry.

Property	Wings	ATM
Length (m)	8.60E-03	9.80E-04
Width (m)	2.30E-03	3.48E-04
t (m)	2.00E-06	1.00E-06
c (m)	1.25E-04	5.00E-05
f (m)	1.50E-06	5.00E-06
theta (degrees)	14	38
l (m)	1.25E-04	5.34E-06
d (m)	6.02E-06	6.40E-06
b (m)	1.13E-04	3.72E-06

Using eigenmode studies, for flexural analysis, we find that uncorrugated wings with E of 91 GPa are expected to have an $f_{(1,1)}$ at 3.06 kHz and $f_{(1,2)}$ at 3.86 kHz. Equivalent corrugated wings will have a $f_{(1,1)}$ at 3.11 kHz and $f_{(1,2)}$ of 4.09 kHz at 71 GPa (Fig. 5C). The ratio between $f_{(1,1)}$ of the corrugated and uncorrugated wings is 1.15 and between their $f_{(1,2)}$ is 1.19. Similar analysis based on the extensional mode approximations in Briassoulis (13), the wings undergo a 15% higher extension under the same force regime when they are corrugated as against when they are not.

Both these estimates suggest that wing corrugations contribute only a little to the stiffness and compliance of sound radiating wings. The complete answers to those questions probably lie within the versatile molecular structure of insect cuticle. However, the models suggest that the Young's modulus of these wings is at the higher end of the scale known for insects (11) and would be interesting to investigate further.

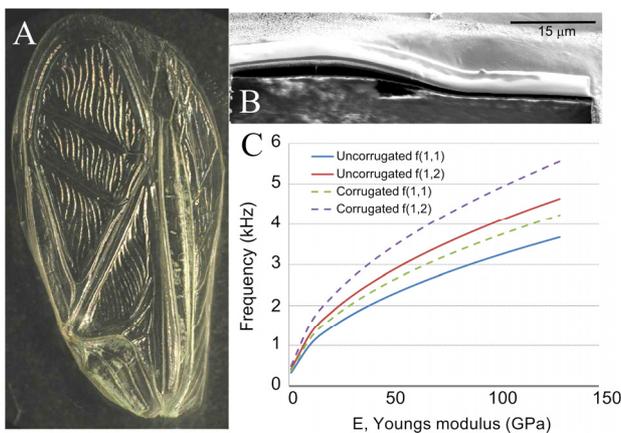


Figure 5: Effects of wing corrugation (A) Wing of *O. henryi* male. Corrugations are clearly visible on flat wing areas. (B) SEM through a corrugation on the harp. (C) Eigenfrequencies, $f_{(1,1)}$ and $f_{(1,2)}$ in corrugated and uncorrugated wings their relationship with the wings bulk Young's modulus.

1.5 Sound reception: convergent structure

In order to listen to mate attraction songs produced by males, females must be able to perceive it. Female crickets use simple ears with tympana (eardrums) exposed on the surface of their bodies to perceive sound. The tympana of *O. henryi* are near the joint on their fore-legs. *O. henryi* like other crickets have two tympana on each leg, one in the anterior position called the anterior tympanal membrane (ATM) and another in the posterior position called the posterior tympanal membrane (PTM).

Interestingly, similar to male wings, the tympanal membranes of *O. henryi* are also corrugated (Fig. 6A). Recent work on several systems has shown that tympanal membranes are rarely simple membranes and often have interesting structural properties (17-19). These properties have been shown to allow these membranes to carry out a certain degree of signal analysis even before the sound signal is transduced to the nervous system.

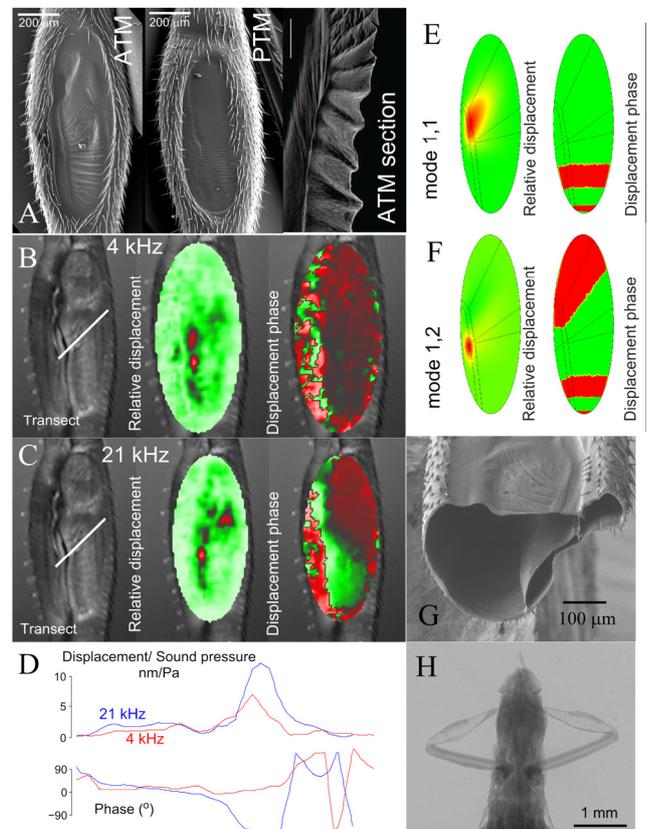


Figure 6: *O. henryi* auditory system. (A) The tympanal membranes, ATM and PTM of *O. henryi*. ATM response to sound at (B) 4 kHz and at (C) 21 kHz. (D) The amplitude and displacement of the ATM along the transect shown on (C) at these two frequencies. (E, F) First two eigenmodes of the FE models of the *O. henryi* ATM (G) A section through an *O. henryi* leg near the tympanal membranes. (H) X-ray micrograph of *O. henryi* auditory trachea.

The ATM of *O. henryi* appears to have a few distinct signal analysis properties. One of its properties is the ability to localise the membrane displacement produced by sound to a small section of the membrane over a large range of frequencies (20) (Fig. 6B, C). The part of the membrane that is corrugated seems to behave like a hinged plate and a much higher displacement is seen at the edge of this

structure where a blood vessel runs underneath the ATM (Fig. 6D). This behaviour can allow efficient sound transduction even with a small number of mechanoreceptors if they are localised in the area of high displacement.

We attempt to model this behaviour of the membrane using an FE approach. The corrugations are modelled as before with parameters measured from FIB and SEM images (Table 1). The section of the membrane above the blood vessel is expected to be thinner than the membrane and best results are obtained for a membrane that is 5 times thinner. The eigenmodes of the preliminary models of the *O. henryi* ATM show similarities to the behaviour of the real membranes in that they localise displacement at the edge of the membrane corrugations. The corrugated part of the membrane also shows hinged plate like behaviour and has lower displacements than the edge of the corrugated plate (Fig. 6E, F).

However, there are subtle differences in the phase of the membrane behaviour (Fig. 6E, F), suggesting that there are additional structural mechanisms affecting the behaviour of the ATM. FIB and micro CT investigations of the *O. henryi* auditory system show that the tympanal membranes are attached to complicated structures on their interior surface (Fig 6 G, H). The ATM and PTM are bridged by a membrane which is under tension in an intact animal (Fig. 6G). The ATM and PTM are also not simply backed by a large hollow volume, but by an intricate series of tracheal tubes (Fig. 6H). These structures will need further investigation to gain a more complete understanding of the behaviour of this intricate auditory system.

The work presented here, however, shows that there are a range of problems in bioacoustics which are best approached not only by using powerful experimental tools such as laser Doppler vibrometry but also powerful FE modelling techniques which allow the incorporation of complex biological geometries. In combination, these techniques allow us to examine the relative contributions of different anatomical morphology in understanding the behaviour of insect auditory systems which have been honed over millions of years of evolution.

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