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Mechanistic insights into mosquito antennal architecture for auditory adaptations

Adwait A. Trikanad [a], Phani Saketh Dasika [a], Hoover Pantoja-Sánchez [b], Ximena E. Bernal [b,c], Pablo D. Zavattieri [a,*]

[a] Lyles School of Civil and Construction Engineering, Purdue University, West Lafayette, IN, 47907, USA
[b] Department of Biological Sciences, Purdue University, West Lafayette, IN 47907, USA
[c] Smithsonian Tropical Research Institute, Apartado, Balboa, Ancón, Panamá

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ABSTRACT

Unlike organisms equipped with tympanal ears, mosquitoes hear using their antennae, which are lightweight sensory structures capable of detecting sound. Here, we study the antennae of two species — *Aedes aegypti* and *Uranotaenia lowii* — known to use hearing for different functions. Through the use of geometrically comprehensive computational models, we find that architectural features in the mosquito antenna provide mechanisms that promote the detection of species and sex specific acoustic targets amidst the non-target signals produced by their own wingbeats. Structurally, we find that the increased surface area of sensory hairs provides enhanced sensitivity while the tapering effect of intersegmental variation affects the tuning response. These features result in the highest antennal sensitivity through vibration at specific natural frequency modes that correspond to frequencies associated with their acoustic targets.

Statement of Significance: Our study provides valuable insights into the remarkable architectural design of mosquito antennae and its role in auditory adaptations. By dissecting the intricate geometry of antennal architecture in *Aedes aegypti* and *Uranotaenia lowii*, we uncover mechanisms that enhance sensitivity to specific acoustic cues while mitigating interference from wingbeat noise. This research builds upon and extends the existing understanding, providing a deeper comprehension of how mosquitoes navigate their acoustic environment. Our findings have significant implications for understanding sensory adaptations in insects and may inspire the development of bioinspired sensing technologies. We believe our work will interest a broad audience by offering new perspectives on the intersection of biomechanics and sensory biology, which can also find applications in the design of bioinspired architected materials.

1. Introduction

The origin of insect ears, unlike in vertebrates, is not tied to an apparently one-time evolutionary event. In insects, hearing systems have evolved independently >20 times across their body [1]. Since hearing requires acoustic energy transfer from the environment to the receiver, the force exerted on the receiver, which is then available for transmission to the neural cells, is directly proportional to the surface area available for the transfer of energy, making the detection of faint sounds harder. Creative designs have evolved to confront physical constraints imposed by their small size, which complicates acoustic detection due to the smaller surface area available to harness the propagating sound wave [1]. Flying insects such as mosquitoes face additional challenges posed by their beating wings while flying [2–4]. The sounds produced by their wingbeats result in a constant source of antennal acoustic stimulation [3]. Despite these challenges, evolutionary adaptations have resulted in sensitive and specialized ears that allow mosquitoes to accurately detect, localize, and respond to intra- and inter-specific acoustic cues in behaviors such as swarming to copulate [2,5] or host finding [6–8].

Mosquitoes use their antennae as acoustic receivers, which, in contrast to tympanic ears, respond to velocity vectors in an impinging sound field rather than pressure variations [9]. In *Ae. aegypti*, males localize and follow females in swarms by listening to their wingbeats [5, 10–15]. Females, not limited to *Aedes aegypti,* respond to approaching males for mating behavior, and hence acoustic communication plays a

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* Corresponding author.
E-mail address: zavattie@purdue.edu (P.D. Zavattieri).

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crucial role in mediating these interactions across various mosquito species and genera [3,8,16,17]. In other mosquito species, however, audition can be critical in other ecological contexts. In *Uranotaenia lowii*, for instance, mating is not mediated by acoustic signals [6] but females depend on audition to detect, localize and attack their anuran hosts by eavesdropping on their mating calls and, ultimately, feeding on their blood [7,18]. While less widely studied, this eavesdropping behavior on anuran mating calls is widespread among mosquitoes [19]. These two tasks, mating and foraging, require detecting sound sources from different origins and distances. For courtship, *Ae. aegypti* males may need to hear low-power flight tones from female conspecifics swarming with them or females approaching the group, whereas females might only respond behaviorally to the wingbeats of approaching males which are of high-power [3,4,16,20–22]. To feed on frogs, on the other hand, *Ur. lowii* females track distant and high-power calls while, in contrast to many mosquito species, males show no distinctive sound related behavior. These features of *Ur. lowii* offer a unique opportunity to investigate how the hearing system of mosquitoes deals with auditory challenges imposed by these different acoustic contexts. Even though the hearing system of mosquitoes that use acoustic signals for mating has been widely studied [23], no studies have investigated the antennae of mosquito species that use sound only to localize their host.

The mosquito antennal system consists of two functional components: the flagellum (or antennal shaft) and the second antennal segment that corresponds to the sensory organ, called the Johnston's Organ (JO) (See X-Ray Micro-CT in Fig. 1). The flagellum of the mosquito antenna consists of segments of varying dimensions stacked one on top of the other. From each segment, long and thin sensory hairs (fibrillae) extend radially outward from the antenna with a structure vaguely reminiscent of a Christmas tree. These hairs, along with the flagellum, are deflected by an impinging sound field and the system behaves as a simple forced damped harmonic oscillator which is resonantly tuned to specific frequencies [5,24]. Mechanosensory cells in the Johnston's organ convert the flagellar vibrations into electrical signals, which are then processed in the brain. The acoustic response of the antenna is thus governed by both biomechanical and neurophysiological mechanisms. Studies so far, however, have mainly focused on understanding the neurophysiology of mosquito audition [3,25–28] with less attention devoted to examining the biomechanical response of the antennae [5,23,29]. Considering that neural processing is similar across species, with some differences in female JO sensitivity [23], biomechanics are expected to play a critical role in determining interspecific differences in sensitivity and tuning across mosquito species. While some models that explore mosquito auditory systems assume that the antenna is a stiff rod whose primary purpose is to transmit vibrations to the JO [24], we contend that structural variation, as well as material properties in the antennae, are critical to modulating the vibrational response characteristic of the antenna and consequently, to determine hearing traits used for different biological purposes. Due to remarkable differences in the use of hearing of *Ae. aegypti* and *Ur. lowii,* these two species of mosquitoes provide an ideal opportunity to investigate how antennal structure modulates mechanical response to sound (Fig. 2A).

Here, we characterize the antenna morphology (across four specimens for each species and sex), architecture and vibrational response (across six specimens for each sex of *Ur. lowii,* while data for *Ae. aegypti* measured across five specimens at the antenna tip was adapted from [5]) of the antenna of these two mosquito species. These species represent the use of antennal hearing in different biological and acoustic contexts: *Ae. aegypti* males for close-range mating behavior and *Ur. lowii* females for long-distance foraging behavior (Fig. 2B; see supplementary materials for videos). We construct finite element models of the antennae that are idealized yet with high-fidelity, focusing on exploring the impact of individual structural features on mechanical responses. These models effectively allow us to examine how variations in sex and species-specific structural characteristics influence antennal response to biologically relevant acoustic signals associated with these species. Our study focuses on the effect of structural and material variations in the antennae and as such does not consider the non-linearities associated with the transduction of the mechanical vibrations into neural signals that may occur in the base. Indeed, previous research has found that non-linearities in the antennal hearing system may primarily occur in either the base through the conversion of antennal deflection to rotation in the JO [30], or during the transduction to neural signals [31]. With this foundation, we investigate, for the first time, the challenge of hearing while flying by examining the antennal biomechanical response to target sounds in the presence of their own wingbeats. While background noise (non-target signals) often results in acoustic interference that limits the ability of hearing systems to detect sounds [32–34], we are starting to learn how some organisms have evolved unique adaptations of noise control (e.g. [35]). Our knowledge of such strategies, however, is currently limited. Here, we capitalize on the long evolutionary time over which mosquitos have relied on hearing, despite using a locomotion strategy intrinsically linked to uninterrupted noise production, to broaden our understanding of adaptation to cope with noise and other non-target signals. This is a valuable step towards understanding the mechanisms and evolution of sensory systems under noisy conditions and evaluating potential strategies to confront an increasingly noisier world.

2. Materials and methods: structural and mechanical characterization

While the morphology and vibrational response of the antenna of *Ae. aegypti* are well known, no studies have investigated the antenna of a frog-biting species like *Ur. lowii*. To compare the mechanical design of the antenna between species, we recreated response curves for *Ae. aegypti* antennae from data procured from Gopfert et al. [5] and characterized, by experimentation, the antenna of *Ur. lowii*. Morphology was investigated using microscopy and computer tomography and the vibrational response of *Ur. lowii* was assessed by performing Laser-Doppler Vibrometry [36]. (See supplementary materials for details). The antennae of six males and six females were subjected to pure tone (pure harmonic inputs) stimuli in a frequency range from 50– 10, 000 Hz at 10 Hz intervals, when the mosquitoes were in their immobilized state. Magnitude χ and phase θ of flagellar vibration velocity were measured (see supplementary materials for more details) and recorded at the free end of the antennae as well as along the midpoint. The measurements of flagellar vibration were normalized in reference to the magnitude ($\chi = v_{flagellum}/v_{air}$) and phase ($\theta = \theta_{flagellum} - \theta_{air}$) of air vibration velocity, recorded by a microphone set next to the mosquito during the experiment (experimental setup is same as in [18]).

Sexual dimorphism is common in the antennae of most mosquito species [2,37]. In *Ae. aegypti* such differences in structure have been associated with differences in the vibrational response of the flagellum [5] with the male antenna responding to higher frequencies than the female antenna (male: 383 ± 28 Hz, female: 229 ± 17 Hz). At these frequencies, amplitude peaks are greater than 1, indicating amplification of the signal, with the antenna of males showing higher amplification levels than the antenna of females (male: 3.0 ± 0.3, female: 2.1 ± 0.3). In contrast, the antennae of *Ur. lowii* are not sexually dimorphic (Fig. 2B). Males and females in this species have non-plumose antennae that are structurally similar and comparable in length. Although morphological differences in the flagellum are not evident in *Ur. lowii*, the antenna of males also responds to higher frequencies compared to the antenna of females (male: 518±16 Hz, female: 305±25 Hz). This result suggests that in *Ur. lowii* there are sexual differences in traits

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[1] Videos for Fig. 1 can be seen in the following link: https://youtube.com/playlist?list=PLRa1U7hcuDwpVft61zGjq0Rm1Cx4sphK1&si=3Zdd4WRyUWYX65Kv.

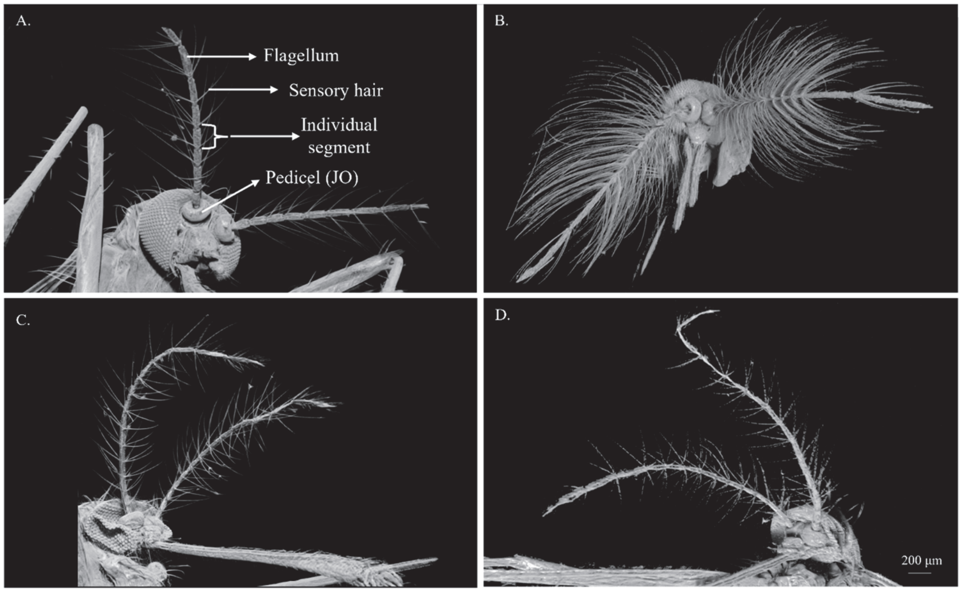

Fig. 1. **μ -CT scan of mosquito species investigated in this study.** **(A)** Female *Ae. aegypti* mosquito highlighting the different structural antennal components, **(B)** male *Ae. aegypti*, **(C)** female *Ur. lowii*, **(D)** male *Ur. lowii*. See supplementary materials for videos.[1] Scale bar: 200 μm.

unrelated to the morphology of the flagellum that determine the mechanical tuning response of the antenna (Fig. 2C). In terms of amplification, contrary to *Ae. aegypti,* the antenna of male *Ur. lowii* shows lower and almost negligible amplification levels compared to the antennae of females (male: 1.07 ± 0.20, female: 1.39 ± 0.23). For comparative purposes, while the resonant frequency ranges for the antennae are between 229 Hz and 518 Hz, the first natural frequencies range between 430 Hz and 921 Hz for wingbeat frequencies and frog calls, as depicted in Fig. 4. Finally, the phase response of *Ae. aegypti* [5] and *Ur. lowii* are similar and show that antennal movement leads the particle velocity at low frequencies, followed by a phase shift at the regions around the best frequency response (Fig. 1C). The phase shift concurrent with the peak in the amplitude indicates the presence of the first resonance mode for each antenna design. Further phase shifts at higher frequencies also indicate the presence of higher-order resonance modes. The midpoint and tip of the antenna move in phase at low frequencies and out of phase at higher frequencies. Thus, the antennae of males and females in both species resemble the movement of a rigid rod in response to low frequencies but a flexible beam in response to high frequencies.

Overall, morphological analyses show sexual and interspecific differences in antennal geometry likely associated with their biomechanical response to incoming sounds. Previous work has also revealed the presence of an endoskeleton, that results in additional stiffening structures, in the antennae of male mosquitos [2,37]. Therefore, when contrasting the response of the antennae of males and females and those between the two species, differences in geometry and materials are involved. Given that in *Ur. lowii,* the antennae of females have slightly higher amplification than the antennae of conspecific males (Fig. 2C), even though there are minimal sexual differences in morphology of the flagellum, suggests differences in antennal materials between the sexes are likely involved in such disparity in biomechanical responses in this species. Within *Ae. aegypti*, however, the plumose (adorned with numerous fine, branching hairs) antennae of males have higher amplification at its resonant frequency than that of females (Fig. 2C), likely due to sexual differences in both morphology and stiffness between their antennae. When comparing the antennal response between species, the plumose antenna of *Ae. aegypti* males have the largest amplification across all antennae studied here, but the antenna of female *Ae. aegypti* also has higher amplification than those of both sexes of *Ur. lowii*. The differences among these natural systems provide an opportunity to examine how geometry and materials promote and shape biomechanical antennal responses to sound. The characterization of these four antenna architectural designs, therefore, was used as a baseline to calibrate computational models and directly investigate how geometry and mechanical properties modulate biomechanical response to further understand the hearing mechanisms underlying antennal systems.

Some previous work has been done in developing computational models to study hearing in mosquitoes. A mathematical framework was developed modeling the antenna as a stiff rod primarily working to transmit vibrations to the JO, mostly ignoring the effects of material and structural variations in the antennal flagellum [24]. Various methodological approaches have been used to examine mosquito antennal hearing, including high fidelity fluid dynamics and aeroacoustic simulations to determine the maximal auditory sensory range of males during phonotactic flight [38] and analysis-by-synthesis approach to address non-linearities in the antennal system that could be produced in the base during the conversion of flagellar deflection into rotation in the JO [30]. Among those, a finite element method modeling analysis of an antenna flagellum concluded that the varying stiffness along the flagellar length could serve to amplify certain frequencies and attenuate others, hence acting as bandpass filters at certain frequencies [29]. However, this approach did not account for structural variations in the flagellum associated with the fibrillae, which are common across mosquito species.

While previous studies have provided valuable insights into the overall functionality of the antennal system, there remains a gap in understanding how distinct structural elements contribute to its complex acoustic behavior. To evaluate the effect of the individual structural features on the vibrational response, finite element modeling (FEM) was performed for the antenna of males and females of both mosquito species, *Ae. aegypti* and *Ur. lowii*, when subject to pure tone stimuli. We measured and characterized the dimensions of individual antenna including hair lengths and distributions (dimensions for hair lengths and distributions for *Ae. aegypti* were also adapted from [39]), segment sizes and the JO. Average values were used to design geometrically accurate computer aided design (CAD) models (Fig. 3A). Three geometric variations or architectures were built for each antenna; geometries with a flagellum of uniform diameter (base architecture), geometries with flagellum including natural intersegmental variation, and finally geometries that included the flagellum, segments and hair lengths and

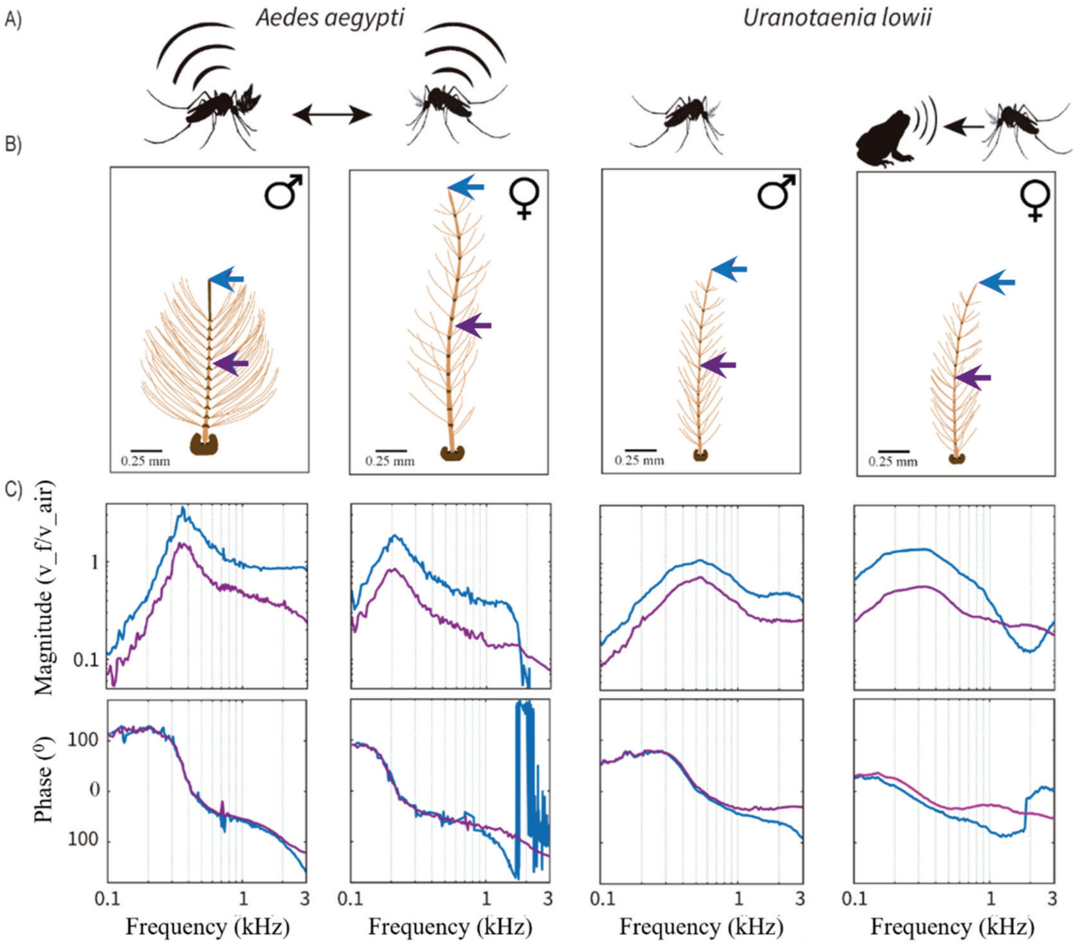

Fig. 2. Sex and species-specific variation in response to sound for mosquito antennae. (**A**) Biologically relevant acoustic cues used by the two focal species of mosquitos in this study. (**B**) Scaled representations of antennae architecture for each species. (**C**) Magnitude and phase of response to pure tone stimuli for vibrations measured at the tip (blue) and middle (violet) for each antenna via LDV. Velocity was measured on the flagellum at the tip and middle following a standard that has been used in similar studies previously [5,12,16]. The data shown here for *Ur. lowii* is averaged over six specimens, with comprehensive details provided in the supplementary materials. Similarly, the *Ae. aegypti* data represents a single measurement, and comprehensive data for *Ae. aegypti* measured at the tip of the antenna across multiple specimens can be found in a previous study [5]. The rationale for using representative data is that the average is very close to the single measurement due to low variation, as shown by the low standard deviation in both the supplementary materials (Appendix F) and the previous study [5].

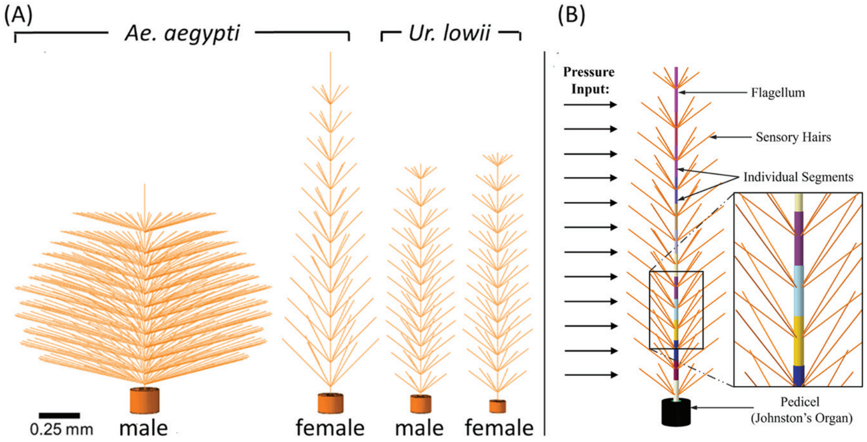

Fig. 3. Computational Setup for simulations (A) Representative CAD models for antennae architectures of all species studied. The measurements were made by averaging optical microscopy measurements across four individuals for each species/sex. (see supplementary materials for more information and list of all measurements) (B) The schematics show the different structural features considered in the CAD models and the boundary conditions for simulations with the bottom of the JO fixed.

distributions (Fig. 5A). Given the complexities involved in modeling fibrillae curvature, our current model represents an optimal balance between accuracy and practicality, making it the most geometrically accurate model to date, though there is room for future improvements. The diameter of the antenna for the base model was chosen such that the mass was held constant between the base model and the segmented model. This approach allowed us to decouple the effect of mass and focus on the geometrical variation due to the segments and its effect on the vibrational response of the antenna.

To our knowledge, no study has comprehensively characterized the mechanical properties of the different materials in the mosquito antennal system. Therefore, for the computational models, we adopted the following approach. The flagellum consists of an external shell of a hard cuticle with an internal soft tissue core. Material properties for the cuticle were obtained from previously published work [40]. Material properties for the other components of the models, including the soft tissue, the JO cuticle, and tissue and the hairs, were assigned using ratios of stiffness variation from the cuticle as observed by Saltin et al. using confocal laser scanning microscopy [29]. A parametric analysis for each material was also performed to evaluate the effect of the material on vibrational response (see SM for details). A rule of mixture approach was used to derive a composite stiffness for the flagellum to ensure computational efficiency. All materials in the model were assumed to have identical densities since no significant variation in densities has been observed despite a range of stiffness values for chitinous structures [40].

We implemented a parametric analysis to determine the effect of each structural feature on the vibrational response. A free vibration analysis was first performed to determine the natural frequencies and associated mode shapes for each geometry. Subsequently, we analyze forced vibration response under steady-state conditions to evaluate the response of each antenna when subjected to harmonic inputs. While differences in the attachment of the flagellum to the JO have been reported between male and female mosquitos [23], our models all use the same attachment. We incorporated the overall dimensions of the JO for each model without modeling the individual prongs in the JO. Because our focus was on the variation in structural features in the flagellum, our choice was to not model individual prongs, since the variations produced by the addition of prongs would not only significantly increase computational complexity but would also make it hard to discern the effect of structural features on the flagellum from the effect of prongs in the JO. This assumption allowed us to maintain computational efficiency while still capturing the effect of the geometrical variations in the flagellum. The models were fixed at the bottom of the JO and to model the incoming sound waves, we applied pressure directly to the antennal surfaces (Fig. 3B) similar to a previous study on computational modeling for mosquito antennae [24]. Since the Reynold's number of the system is very small (<<1), the major driving forces are considered to be friction and damping, which are represented in the model, but as acting directly on the surface of the antenna. This approximation allows us to avoid a computationally expensive fluid-structure interaction model since the focus of this work is on the effect of the individual structural parameters. Further descriptions of the computational models, along with the statistical methods used for experimentation and their results, are provided in the supplementary materials.

To determine the response of these hearing systems to biologically relevant stimuli, the representative antenna models were subject to specific inputs representing the acoustic signals or cues used by these species in their natural environments. The input signals used are the recordings of the wingbeats of *Ae. aegypti* and *Ur. lowii* mosquitoes of both sexes, along with the recording of male barking tree frogs (*Hyla gratiosa*), a species highly attractive to *Ur. lowii* females in their natural environment [7] (Fig. 4). Our approach involved examining equivalent systems focusing on biologically relevant comparisons in which sound is used by each sex in a given context, i.e., *Ae. aegypti* males versus *Ur. lowii* males for mating, and *Ae. aegypti* females versus *Ur. lowii* females for sensing frog calls. The reason for making this decision is that males track females for mating, while there is little evidence for females actively tracking males. On the other hand, in the context of foraging, female mosquitoes often rely on blood meals for egg production, and in some species, they seek anuran hosts for essential nutrients, while males typically depend exclusively on nectar eliminating the need for using host-emitted acoustic cues. Therefore, although simulations were conducted to assess the responses of females to mating calls and males to frog calls, these comparisons are presented in the supplemental materials due to their limited biological relevance.

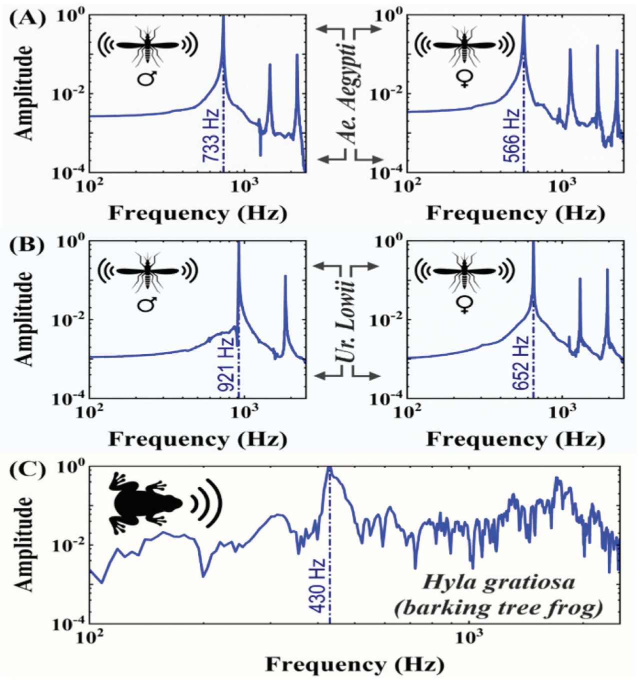

Fig. 4. Recorded Input Signals. Wing beat tones for (A) *Ae. aegypti* male and female mosquitoes (B) *Ur. lowii* male and female mosquitoes. (C) Recordings of frog calls. Frequency values at the location of the peak amplitude for each plot are marked using a vertical dash-dot line. All measurements are individually normalized, ensuring comparability in terms of signal intensity. Different background colors in panels (A), (B), and (C) differentiate between the wing-beats of the two mosquito species and the frog call recordings.

3. Results and discussion

3.1. Quantification of the effect of individual structural features

Antennal hairs represent about 32 % of the total mass of the *Ae. aegypti* male, and about 6 % of the total mass for the other three antenna models. Free vibration analysis showed that the first mode of natural frequencies consisting of bending at the base of the antenna showed an excellent match (± 10 Hz) with the experimentally observed first resonance peaks (see Figs. S5 and S6). These models were then subjected to pure tone stimuli ranging from 100 to 3000 Hz, which included all the auditory frequencies that were relevant to these mosquito species. Velocities were extracted at points along the tip of the antennae to determine the effect of individual structural parameters on the steady-state vibrational response (Fig. 5B). First, natural frequency modes for all models matched those observed experimentally (Fig. 5B, dashed line). In highlighting the effect of the structural parameters, the most apparent is the effect that the sensory hairs have on the sensitivity of these antennae. All models displayed a significant increase in sensitivity due to the presence of hair. The highly plumose male *Ae. aegypti* antenna, showed a remarkable 90 times increased sensitivity (9000 % / gain of 39.1 dB) as compared to the base model, with the female showing a 7 times increased sensitivity (700 % / gain of 16.9 dB). For the *Ur. lowii*

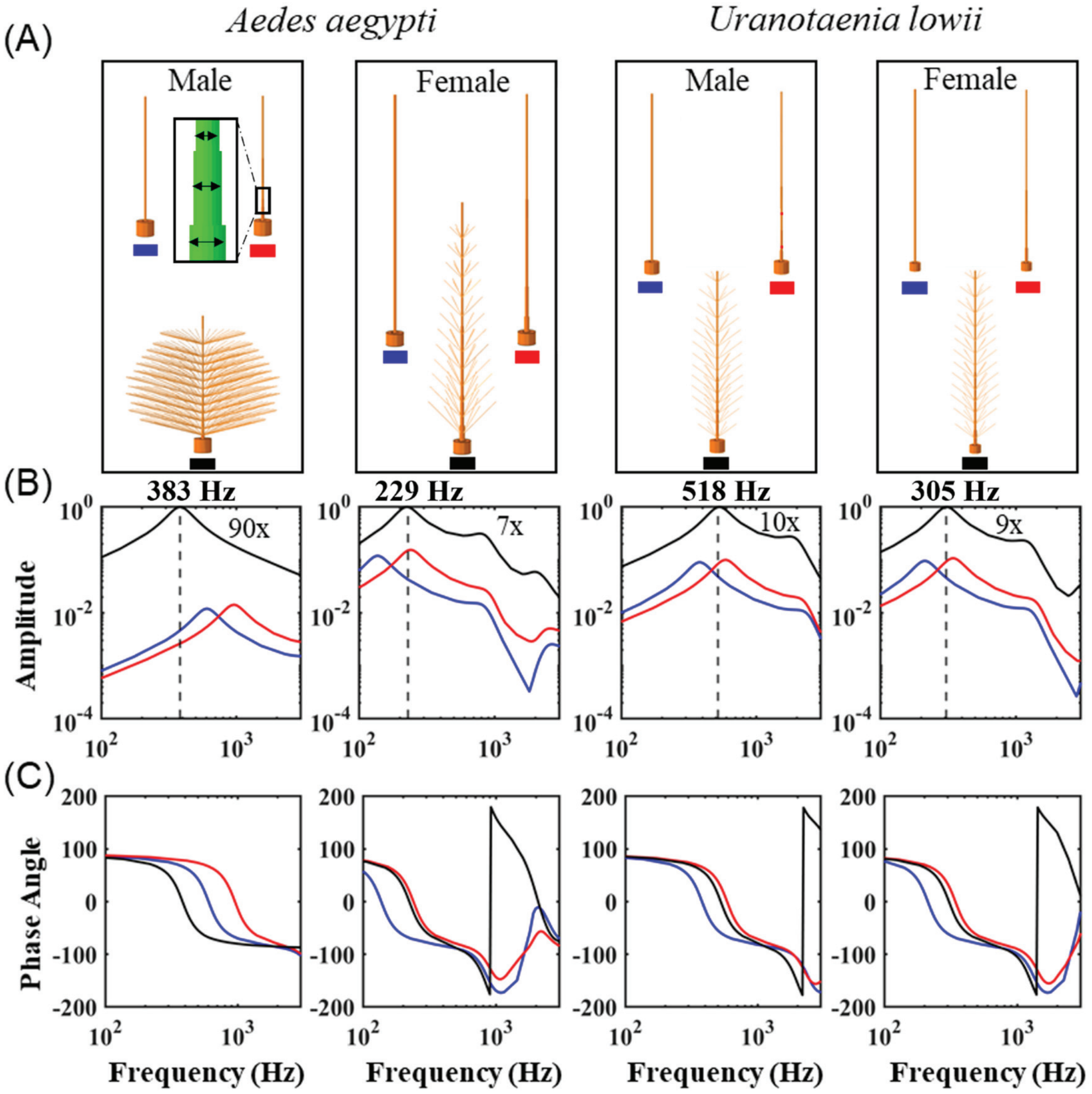

Fig. 5. Effect of sensory hair and intersegmental variation on mechanical response of antennae to pure tones. (**A**) Three models for each antenna consisting of a base model with a rod of constant diameter (blue), a rod with varied diameters leading to a tapering cross-section to mimic intersegmental variation (red), a rod with varied diameter as well as sensory hairs (black). Inset in black box shows one such segment. (**B**) Magnitude of velocity response to pure tone stimuli for all 3 variations for both sexes of both species extracted from the tip of the antenna. The dashed line indicates the mean value of experimentally observed first natural frequency (see Fig. S6 for a full comparison of experimental versus simulation data). Amplitudes are normalized by the largest amplitude observed in each model. Peak values are labelled. (**C**) Phase response for all 3 variations for both sexes of both species extracted at the tip of the antenna.

antennae, the male showed a 10-times increase in sensitivity with hair (1000 % / gain of 20 dB), while the female showed a 9-times increased sensitivity (900 % / gain of 19.1 dB) when compared with the base model. The natural frequency of such a system is dependent on the stiffness and the mass as indicated by the following relationship:

$$f_n = \frac{\alpha_n}{2\pi}\sqrt{\frac{\Sigma}{m}}$$

where f_n is the natural frequency, Σ is the stiffness, m is the mass and α_n is a parameter dependent on the natural frequency mode and the boundary conditions. Mechanically, the addition of sensory hairs causes an increase in mass and stiffness of the system while, at the same time, increasing the surface area available to capture the applied pressure. In general, an increase in mass for such a system is expected to cause a negative shift in the tuning response, resulting in a lower resonant frequency. In contrast, the increased surface area can result in an increased sensitivity, with the increased stiffness also potentially increasing the resonant frequency. For the *Ae. aegypti* male model, we see an interplay between these competing mechanisms where the stiffness and surface area effects dominate the vibration amplitude response, leading to a large increase in sensitivity, while the tuning response seems dominated by the mass, resulting in a lower first natural frequency peak.

All models showed a characteristic 180-degrees phase shift concurrently with a peak in amplitude indicating the presence of the first natural frequency mode, similar to the experiments (Fig. 5C). The addition of hair in all models, except for the *Ae. aegypti* male resulted in a secondary 180-degree phase shift at a higher frequency, indicating the presence of a second mode of natural frequency within the frequency range studied, characterized by a bending of the antenna. The absence of a secondary natural frequency mode for the *Ae. aegypti* male and the presence of the second mode in the *Ae. aegypti* female within the 100–3000 Hz frequency range is, again, consistent with the experimental data. The *Ur. lowii* computational models also showed the secondary mode, albeit at the high end of the range studied. The secondary mode is, in fact, also present for these antennae in the experimental data but at frequencies slightly outside the range studied here (see Figs. S3 and S4 in SM for vibrational data up to 10,000 Hz).

The effect of the intersegmental variation was also quantified as part of the architecture of the antenna, with the addition of the segment geometry leading to a relatively smaller increase in sensitivity (20 % / gain of 1.6 dB increased sensitivity for *Ae. aegypti* male, 30 % for females / gain of 2.3 dB, and about 10 % / gain of 0.8 dB increased sensitivity for both *Ur. lowii* models), but with a larger effect on the tuning of the resonant frequencies. The addition of the segment geometries led to an increase in the first resonant frequency for all models. The segmented antenna shows a tapered cross-section from base to tip with mechanical behavior similar to a tapered cantilevered beam. Since the mass is maintained between the base model and the segmented model, the geometrical effect of tapering leads to an increased stiffness and, consequently, an increase in the natural frequency. The effect of this tapering led to an increase in the first natural frequency of 350 Hz for the *Ae. aegypti* male, and an increase of 100 Hz for the *Ae. aegypti* female. In the *Ur. lowii* models, the addition of segment geometries led to an increase in natural frequency of 200 Hz for the male and about 150 Hz for the female. Interestingly, while the vibrational response for the *Ae. aegypti* male seems dominated by the hairs (likely due to their abundance), the effect of the segmental variation for the other three models on tuning is more impactful, allowing for a shift in the natural frequency modes in the simulations that more closely align with those observed via experiments. Overall, these results indicate that the sensory hairs play a large role in increasing the sensitivity of these antennae, while the intersegmental variation is integral in tuning the natural frequencies of these resonantly tuned antennal systems (see Fig. S5 for visualizations of the first / natural modes of vibration).

3.2. Mechanical vibration response to real world stimuli

First, representative CAD models for antennae architectures of male mosquitoes of the *Ae. aegypti* and *Ur. lowii* species were subjected to the wingbeats of the opposite sex within their respective conspecific groups. Additionally, to account for potential acoustic interference caused by their own wingbeats while flying, the models were also subjected to their own wingbeats (non-target signal) alongside the signals from the opposite sex (target signal). To account for the proximity of non-target signals, four different scenarios of antennal responses to the input signal intensities were examined, varying the amplification value of the wingbeat signal of the opposite sex from 0.25 times, 0.5 times, 1 time (originally recorded scale), and 2 times. The objective of this analysis was to examine differences among mosquito species in their capacity to detect the wingbeat signal of the opposite sex under varying intensities of the target signal, ranging from very low to high. In our study, very low signal intensity refers to input levels below typical environmental conditions, where the signal might be undetectable. Conversely, high signal intensity refers to levels that can be more easily detected by mosquitoes in natural settings. All velocities were extracted from the base of the antenna on the basal plate to identify the information reaching the JO more accurately. We define successful sensing of the target signal as instances where the antennal response exhibits a peak amplitude at the frequency corresponding to the target signal (e.g., frog calls or conspecific flight tones), with a search interval of ±10 Hz around the target signal frequency. Peak detection was performed using a search algorithm that verifies the robustness and distinctiveness of the identified peak. To ensure the validity of the detected peak, the algorithm evaluates its surrounding data points to confirm that it is part of a smooth response profile rather than an isolated noise artifact. Additionally, the algorithm applies a threshold criterion, requiring the maximum peak to exceed the next highest peak in the evaluated range by at least a few standard deviations. Sampling density near the target frequency was enhanced using an adaptive algorithm incorporating a bias parameter [41] to densely sample points closer to natural frequencies and peaks. This rigorous approach ensures that the detected peak is both reliable and distinct. To standardize results and improve visualization, all amplitude data were normalized by dividing each value by the maximum amplitude observed in the evaluated range. In the normalized plots (see Fig. 6), the separation threshold is evident as a minimum difference of ±0.01 between the detected peak and nearby peaks, clearly distinguishing the target signal. This match indicates that the mosquito's antennae resonated at the frequency of the target signal achieving the first step necessary for hearing. In contrast, failure to detect the target signal occurs when the antennal response shows peak amplitude at the mosquito's own wingbeat frequency rather than at the frequency of the target signal.

Both male models of the *Ae. aegypti* and *Ur. lowii* antennae exhibited peak sensitivity at the wingbeat frequency of the opposite sex under both low and high signal intensities. However, at very low signal intensities of the opposite sex, only the antenna of the *Ae. aegypti* male model displayed peak sensitivity at the opposing sex's wingbeat frequency, while that of the *Ur. lowii* showed peak sensitivity at its own wingbeat frequency (Fig. 6 and Table 1). This finding conforms to the biological behavior of *Ae. aegypti* male mosquitoes, which have undergone strong selection over evolutionary time to have highly sensitive antennae for tracking the wingbeats of conspecifics of the opposite sex in a swarm for courtship purposes. Furthermore, although our simulations suggest that *Ur. lowii* males may have the capability to sense or resonate when exposed to conspecific female wingbeats, this ability seems biologically unnecessary as they do not rely on acoustic signals for courtship or mating [18]. Further work that investigates the neural responses of *Ur. lowii* males to conspecific wingbeats are necessary to determine whether this information is processed at higher sensory levels.

In the next set of simulations, representative CAD models for antennae architectures of female mosquitoes of the *Ae. aegypti* and *Ur. lowii* species were subjected to the inputs gathered from the recording of male barking tree frogs (*Hyla gratiosa*). Similar to the approach used for male mosquitoes in previous simulations, the models included potential interference from their own wingbeats as a non-target signal, in addition to the frog calls as the target signal. The *Ur. lowii* female model displayed peak sensitivity at the frog call frequency across both very low and high input signal intensities. This finding is in contrast with the model representing the antenna of *Ae. aegypti* females, which only demonstrated peak sensitivity to the frog call frequency at higher input signal intensities (Fig. 6 and Table 1). Conversely, it showed peak sensitivity at the frequency of its own wingbeats, which is not the target signal. This finding aligns with the biological behavior of *Ur. lowii* females, which have evolved a heightened sensitivity to auditory cues, enabling them to localize frog calls to obtain a blood meal necessary for egg production. Moreover, *Ae. aegypti* females do not require this sensing feature, as they rely instead on chemical cues like carbon dioxide (CO_2) and use heat maps to track humans and other mammals to feed on their blood [42].

While there is a close match between the antenna structure and the response to biologically relevant sounds, some features of antenna structure may generally improve sound detection. The response of *Ae. aegypti* and *Ur. lowii* males to frog calls, for instance, exhibited peak sensitivity at the frequency of the frog call, irrespective of very low or high input signal intensities (see Fig. S7 and Table S2 in supplementary materials). These findings suggest the antennal structure of male mosquitoes has features that make them efficient at detecting diverse sounds, which is probably a side effect of strong selection for refined sensitivity to conspecific signals earlier in this family (Culicidae). Furthermore, theoretical observations from FEM indicate that the female models of *Ae. aegypti* and *Ur. lowii* display peak sensitivity at the wingbeat frequency of conspecific individuals from the opposite sex under normal to high signal intensities but failed to do so under lower signal intensities (see Fig. S7 and Table S2 in supplementary materials). However, these findings require further research investigating the neural responses of females to conspecific wingbeats to establish whether this information is processed at higher sensory levels.

The simulations presented in this study help us deepen our

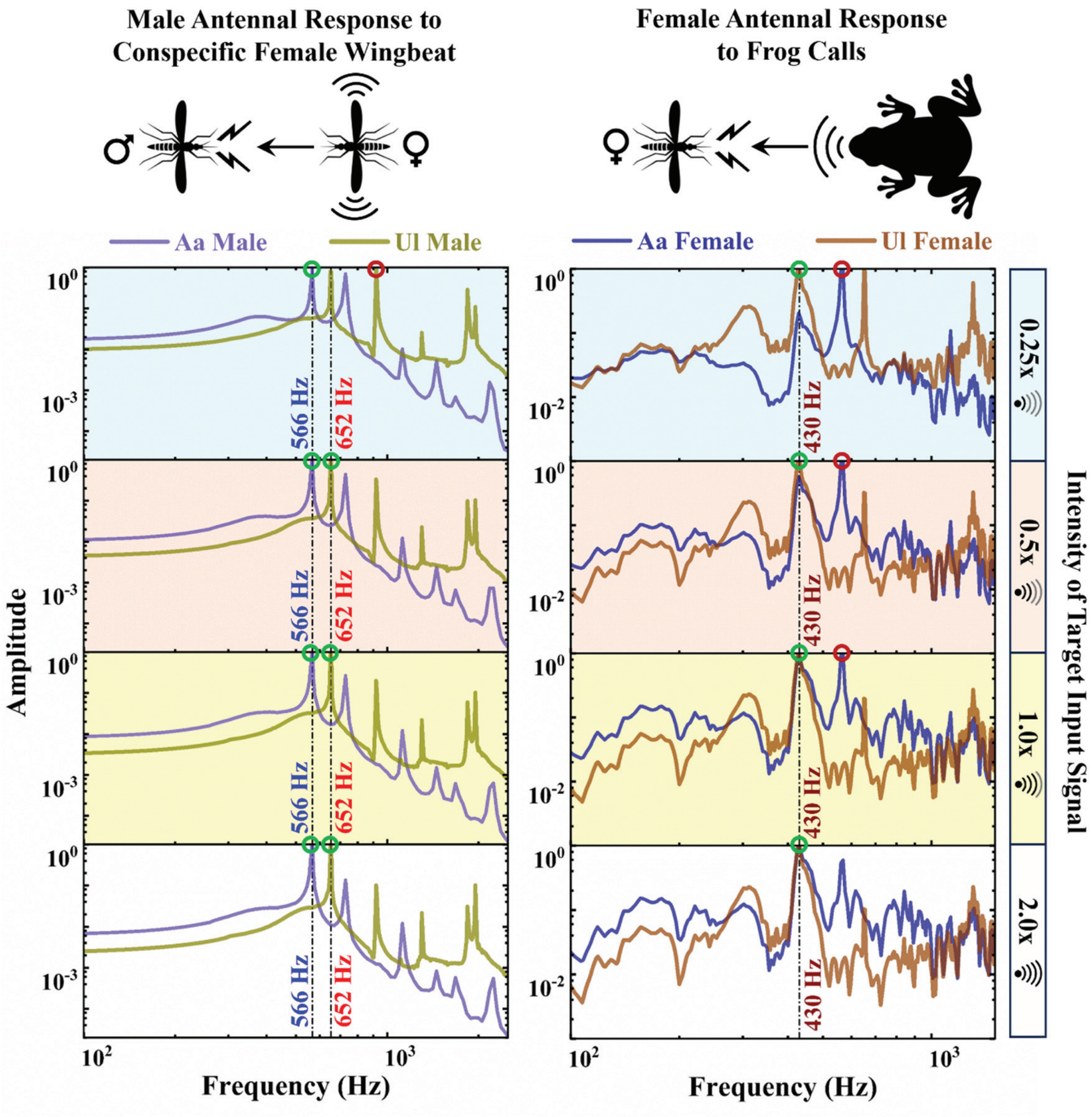

Fig. 6. Antennal Response of Mosquitoes. Response of the antenna for *Ae. aegypti (Aa)* and *Ur. lowii (Ul)* male mosquitoes to input tones of their own wingbeats and conspecific female flight tones on the left, and female mosquitoes to input tones of their own wingbeats and frog calls on the right. All antennal responses were simulated and recorded for varying intensity levels of the input target signal, with the intensity scale bar shown on the right. The frequencies of the acoustic targets are marked using a vertical dash-dot black line. The circles highlight the frequency values at which peak amplitude was recorded for each curve. Green circles indicate that the mosquito species detected the target signal, as the peak amplitude matched the resonance frequency of the target signal. Red circles indicate that the target signal was not detected, with peak amplitude observed at the frequency of its own wingbeat instead. All plots are locally normalized by the largest amplitude in each curve, as the main objective is to identify the frequency location at peak amplitude.

understanding of the mechanical response of the mosquito antenna and highlight fertile venues for future experimental research. This approach, however, has limitations, particularly regarding how mosquitoes hear and locate sound sources while flying. The models, for instance, did not replicate the deflections and vibrations produced by motion during flight. Additionally, in our models, we applied pressure directly to the antenna, but complex air dynamics can also influence the mechanical response of the antenna. Finally, we did not consider the impact of the neural mechanisms on the mechanical response of the flagellum. Overall, this work is a first stepping stone for future models that further incorporate the complexity of the phenomenon at hand and address these limitations to ultimate further our understanding about how the mechanical response of the antenna shape hearing in mosquitoes.

Overall, these results reveal the importance of structural features and geometrical variation in the antennal system to detect specific acoustic targets associated with their biological function. These findings suggest that the non-target signal produced by flying does not interfere with hearing conspecific wingbeats despite the acoustic similarity of such stimuli. Furthermore, these findings indicate that the antennal hearing system can effectively detect target signals amidst the non-target signals generated by their own wingbeats, suggesting robustness despite acoustic similarities that could result in acoustic interference. The biomechanical response of the flagellum, however, is the first step in the auditory process. The detected vibrational information from the acoustic target is transmitted via the basal plate at the base of the antenna to the JO which performs the transduction of mechanical vibrations to electrical signals, and then through the antennal nerve to the brain where information is processed. Electrophysiological recordings at the antennal nerve show that in some species the JO works like a low-pass filter of frequencies below 1000 Hz and relies on a non-linear transduction process [31]. That is, there is a non-linear relationship between flagellar displacement and electric current recorded at the antennal

Table 1

Antennal responses of all mosquito species and sexes to varying intensities of the target input signal. (A) Antennal responses of male mosquitoes to wingbeat signals of the conspecific opposite sex. (B) Antennal responses of female mosquitoes to frog call signals.

(A) Mosquito Species	Intensity of Target Input Signal *(Wingbeats of Conspecific Opposite Sex)*			
	0.25x [21.93 dB SPL (re 20 μPa)]	0.5x [27.96 dB SPL (re 20 μPa)]	1x [33.97 dB SPL (re 20 μPa)]	2x [40 dB SPL (re 20 μPa)]
Ae. aegypti Male	✔	✔	✔	✔
Ur. lowii Male	✖	✔	✔	✔

(B) Mosquito Species	Intensity of Target Input Signal *(Frog Call)*			
	0.25x [21.93 dB SPL (re 20 μPa)]	0.5x [27.96 dB SPL (re 20 μPa)]	1x [33.97 dB SPL (re 20 μPa)]	2x [40 dB SPL (re 20 μPa)]
Ae. aegypti Female	✖	✖	✖	✔
Ur. lowii Female	✔	✔	✔	✔

nerve. The proximity of the peaks seen in our models when *Ae. aegypti* antennae are subjected to wingbeats of both sexes, combined with previous findings that describe the ability of these mosquitos to use intermodulation distortion to distinguish their acoustic targets [3,26], suggests the antennal systems in mosquitos may have evolved to take advantage of the non-target signals they produce when flying. Other strategies to regulate such self-generated sensory information, such as corollary discharges, which have been identified across diverse organisms, [43] may act in conjunction with the biomechanical response described here. Our results are the foundation for the development of more complex mechanical-electrical models to provide a more complete understanding of hearing in mosquito species while considering the role of the non-target signals imposed by their locomotory strategy.

4. Conclusion

Our study shows that mosquito antennae are minuscule, sensitive, and specialized acoustic detectors tuned to biologically relevant acoustic stimuli. Using finite element analysis, we investigated how geometrical features in the morphology of mosquito antennae contribute towards their sensitivity and tuning. We show how sensory hairs, a structural feature assumed to be relevant but previously formally unexplored in mosquito antennae may play a key role in hearing sensitivity. The addition of hairs produces an interplay between structural and inertial mechanisms with the increased surface area to capture the propagating sound wave leading to an order of magnitude increase in sensitivity. At the same time, the increased mass due to the presence of hair causes a negative shift in the resonant frequency. We also quantified the effect of the geometrical variation of the individual antennal segments. The tapering of the antenna due to the segmental variation produces a stiffening effect which serves to increase the resonant frequency of the antenna and leads to some increased sensitivity. Our analysis of these antennae when subject to real-world stimuli unveiled their remarkable abilities to accurately capture their acoustic targets despite the acoustic interference generated by the non-target signals of their own wingbeats, which are in close proximity to their antennae. We showed the importance of structural variations in capturing only the signals of interest for each mosquito species and sex. In male *Ae. aegypti*, their antennae exhibited peak sensitivity to the wingbeat frequency of conspecific female mosquitoes, regardless of signal intensity (in the ranges that we studied, i.e. from 0.25x to 2x of input target signal), which aligns with their courtship behavior. Conversely, in male *Ur. lowii*, their antennae were limited in responding to the target signal at low signal intensities from conspecific female flight-tones. Thus, the *Ae. aegypti* male antenna exhibits a clear advantage at detecting female flight-tones compared to the *Ur. lowii* male antenna. In female *Ur. lowii*, their antennae displayed peak sensitivity to frog call frequencies across both low and high signal intensities, aiding in locating their anuran host. In contrast, female *Ae. aegypti* antennae only exhibited peak sensitivity to frog call frequencies at higher signal intensities, while otherwise being sensitive to their own wingbeat frequency. These results strengthen the claim that *Ae. aegypti* males, with their plumose antennae, are more adept for courtship purposes, while *Ur. lowii* females have evolved antennae with heightened sensitivity specifically for detecting frog calls. Ultimately, these findings reveal a uniquely engaging method of acoustic communication relying on both material as well as structural mechanisms to act as sensitive and specialized acoustic detectors. Taken together, these results can provide new avenues of exploration in sensing technologies [44], acoustic metamaterials [45,46], metasurfaces, smart skins, microarchitected materials and MEMS systems where slight modifications in structure and geometry can be used to access a new design space that is not overly dependent on material composition. With recent innovations in additive manufacturing [47], such structures are not limited to manufacturing challenges and these design strategies can be implemented to produce smarter and more efficient solutions inspired by nature.

CRediT authorship contribution statement

Adwait A. Trikanad: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Phani Saketh Dasika:** Writing – review & editing, Visualization, Validation, Software, Investigation. **Hoover Pantoja-Sánchez:** Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Ximena E. Bernal:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Pablo D. Zavattieri:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.actbio.2024.12.031.

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