Changing resonator geometry to boost sound power decouples size and song frequency in a small insect

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AUTHOR SUMMARY

What's In a Song? A memorable feature of warm summer nights is the sound of scores of crickets singing all together. Male crickets put on this impressive auditory display to attract mates. Song provides an acoustic beacon that females can home in on. It also enables other sophisticated functions such as species recognition and the evaluation of mate fitness. Its frequency is generally accepted to be important for species recognition; nonetheless, there is subtle variation in the spectral quality of songs sung by males within a species. This variation is thought to encode information about the quality of the singer. For instance, one important trait coded in song is thought to be the physical size of the singer. The underlying biomechanics is thought to be simple. Male crickets exploit the structural resonance of their wings to produce pure-tone songs; hence, a larger body size would mean a larger wing resonator, which directly leads to lower-frequency songs (1).

This simplicity is found to be deceptive in the case of tree crickets (Fig. P1*A*). In this widespread group of crickets, that also use their resonant wings to produce sound, song frequency changes with temperature, for example from 2.3 to 3.7 kHz over 18 to 29 °C in *Oecanthus henryi*. Such temperature dependence raises questions about the biomechanics of variable-frequency resonators. Frequency variation during sound production by insects is rare and, therefore, studying its basis contributes to our knowledge of the evolution and biophysics of acoustic communication.

Defining the Resonator. The geometry and structure of the wings of tree crickets are different from those of previously studied field crickets. Using a noncontact vibration measurement technique called microscanning laser Doppler vibrometry, we characterized the frequency response of the wings of the tree cricket *O. henryi*. Measurements revealed that the entire wing vibrated near the song frequency range (Fig. P1 *B* and *C*). In addition, the frequency response did not change with temperature. The first two resonant modes of vibration were observed near the song frequency range and had similar displacement amplitudes (Fig. P1*C*). This broad frequency response and nonlocalized vibration pattern is quite different from observations made on field crickets where only a small portion of their wing vibrates at a single and sharply defined frequency (2).

Resonator Geometry. This differential use of the wing along with existing geometric differences means that tree and field crickets have very different resonators; the former have long resonators with a high aspect ratio; whereas, the latter have rounded ones with a low aspect ratio. In order to understand the effect of resonator geometry, we used finite element modelling (FEM) conventionally used in engineering to model structures with complicated geometries. The typically irregular geometries of biological structures could thus be incorporated into more realistic biophysical models. Model geometries were then manipulated borrowing from the classical biology method of comparative analysis. In effect, the FEM approach allowed us to generate and study virtual cricket wings and compare them with real cricket wings.

A broad-range frequency response similar to that of real wings was observed in FE models of resonators shaped like

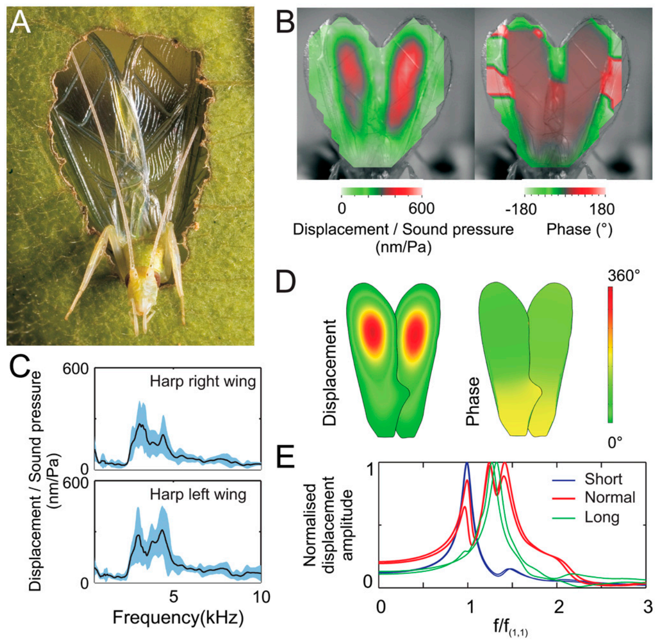

Fig. P1. Modeling the resonant behavior of tree cricket wings. (*A*) Male tree crickets sing by rubbing their wings together. (*B*) The whole dorsal field of the wing was found to move near the song frequency range when measured by laser Doppler vibrometry. The first mode of vibration of a male wing is depicted. (*C*) The frequency response of the wings (measured at the harp) clearly showed multiple frequency peaks merging into each other and corresponding to modes of vibration ($N = 8$, mean ± SD). (*D*) Finite element models of the wings show a similar spatial response in producing similar modes of vibration when the natural aspect ratio of the wings is maintained. (*E*) The frequency response of the model with natural-aspect-ratio wings closely matches that of real wings (as measured at the harp on both wings). Changing the wings' aspect ratios clearly altered their frequency response. Shorter wings, like those of field crickets, resulted in a second vibrational mode with a much smaller amplitude and higher frequency.

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tree cricket wings (Fig. P1 *D* and *E*). At the natural aspect ratio, the first two resonant modes were similar in frequency and displacement amplitude and were comparable to the modes observed in real wings (Fig. P1*E*). This effect was enhanced when the model geometry was further elongated. Interestingly, a shortened low-aspect-ratio model geometry mimicking a field cricket resonator led to a field-cricket-like single-mode sharp frequency response. This model-based analysis validated by vibrometric data revealed that geometry alone (aspect ratio) could broaden the range of frequencies produced by the resonating wing (Fig. P1*E*).

The Escapement Mechanism. The frequency response of the resonator affects the force delivered to the wings in keeping with the escapement mechanism, an integral part of sound production (3). It is through this mechanism that the frequency at which a driving force is applied to the wings is regulated by the wing resonances; hence, if the wing is capable of vibrating at a range of frequencies, then the driving force can also be applied in that range. We found that as the temperature increased, singing tree crickets were able to produce higher wing stroke rates and drive the wing resonators at higher frequencies near the second resonant mode. As a result, song frequency increased with temperature without losing the benefits of resonant sound radiation.

Variable Frequency Song: Adaptation or By-Product? The evolution of songs with variable frequency remains an interesting question. Producing such a song does not appear to present any obvious advantages at first. The scenario that emerges from our analysis relates to physical size. Tree crickets are among the smallest known singing crickets; thus, they encounter quite severe biophysical constraints related to size and song frequency (4). Given their song frequencies, the ratio of wing size to sound wavelength is most unfavorable for sound radiation; therefore, an increase in wing area constitutes an improvement. Results of analytical calculations based on FEM revealed that using the entire wing as a resonator caused a 2.5-fold increase in radiated sound power compared to using part of the wing, as in the case of a field cricket. Using the entire wing also provided the ability to keep the song frequency as low as 2.3 kHz. Because low frequencies transmit further in tree cricket habitat, using the entire wing provides an elegant-two part biophysical adaptation to achieve effective sound radiation.

Outcomes. An immediate outcome of this study is that the low-frequency radiators that tree crickets have evolved can now be seen as being optimized for effective sound radiation with variable frequency being a by-product rather than an adaptation. The trade off that they have had to make in allowing variable song frequency is its potentially deleterious effect on other functions of acoustic communication such as species recognition and sexual selection. This study also shows how song frequency can be decoupled from body size by a small change in morphology, belying the common assumption that insects are obliged to signal honestly their size through song. Enticingly, the techniques of analysis applied here open up ways to investigate acoustic communication systems in terms of not only sound production but also sound reception. In terms of technology, these miniature sound radiators are beginning to reveal unique ways to use evolutionarily honed geometries to design actuators many times smaller than the sound waves they broadcast.

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