

Structural resonance and kinematic tuning in the pure-tone song of the bell cricket *Meloimorpha japonicus*

Norihiko Saga

saga@kwansei.ac.jp

Kwansei Gakuin University

Takuma Saga

University of Shiga Prefecture

Naoki Saito

Akita Prefectural University

Toshiyuki Satoh

Akita Prefectural University

Article

Keywords: Stridulation, Structural resonance, Bioacoustics, *Meloimorpha japonicus*, Experimental modal analysis, Kinematics

Posted Date: June 5th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-9751662/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Title: Structural resonance and kinematic tuning in the pure-tone song of the bell cricket *Meloimorpha japonicus*

Authors: Norihiko Saga*[1], Takuma Saga[2], Naoki Saito[3], Toshiyuki Satoh[3]

Affiliations:

1. Artificial Intelligent and Mechanical Engineering Course, School of Engineering, Kwansei Gakuin University, Sanda, Hyogo, Japan.
2. Department of Mechanical Systems Engineering, School of Engineering, The University of Shiga Prefecture, Hikone, Shiga, Japan.
3. Department of Machine Intelligence and Systems Engineering, Faculty of Systems Science and Technology, Akita Prefectural University, Yurihonjo, Akita, Japan.

Corresponding author:

*Correspondence and requests for materials should be addressed to N.S. (email: saga@kwansei.ac.jp)

Key Words: Stridulation, Structural resonance, Bioacoustics, *Meloimorpha japonicus*, Experimental modal analysis, Kinematics

Abstract

Cricket calling songs are produced through stridulation, where a scraper rhythmically engages a serrated forewing file. While song carrier frequency is typically attributed to wing membrane resonance, the contributions of file morphology and tooth engagement dynamics remain poorly understood. We integrated high-speed videography, 3D microscopic file profiling, and laser Doppler vibrometry (LDV) modal analysis to investigate sound production in the Japanese bell cricket (*Meloimorpha japonicus*).

We identified two previously unrecognized file features: (1) directionally asymmetric teeth with a steep angle promoting mechanical catch during wing closing, and a shallow angle facilitating sliding during opening; and (2) a progressive decrease in tooth spacing along the file. This pitch gradient compensates for decreasing wing-closing velocity, maintaining a constant tooth-strike rate.

Crucially, LDV reveals that this kinematically determined tooth-strike rate perfectly matches the intrinsic resonant frequency of the forewing (approx. 4.6 kHz), with the expanded apical area vibrating synchronously to enhance acoustic radiation. Our findings reveal that the pure-tone song of *M. japonicus* emerges from precise kinematic tuning governed by file micro-geometry

seamlessly coupled with whole-wing structural resonance, providing new insights into the evolution of insect bioacoustics.

Introduction

Acoustic communication in crickets and their relatives (Orthoptera: Ensifera) has long served as a model system for understanding how neural control, biomechanics, and morphological specialization interact to generate species-specific signals [1–4]. The Japanese bell cricket (*Meloimorpha japonicus*), commonly known as “suzumushi,” produces tonal calling songs through stridulation, a process in which the scraper of one forewing engages the serrated file of the other. Although the temporal pattern of chirps and pulses is strictly governed by central pattern generators (CPGs) in the thoracic and abdominal ganglia [5–9], the spectral properties of the sound have traditionally been attributed to the resonant characteristics of the forewing [10, 11].

Classic biomechanical studies established that the “harp” and “mirror” regions of the forewing act as finely tuned acoustic resonators that amplify specific frequencies [12–14]. Subsequent work has robustly shown that the dominant carrier frequency of the calling song corresponds to the intrinsic vibrational modes of these wing structures [15–20]. Furthermore, recent non-destructive techniques such as laser Doppler vibrometry (LDV) have highlighted how wing material properties and desiccation affect these resonant modes [21]. Collectively, these studies emphasize the role of wing resonance in shaping the spectral envelope of the song, suggesting that the carrier frequency is heavily constrained by passive biomechanical properties rather than being actively tuned solely by the nervous system.

However, stridulation is not simply a passive resonance phenomenon. Sound is generated through repeated tooth–scraper interactions during wing closure, and the tooth-strike rate—determined by wing kinematics and file morphology—directly dictates the fundamental frequency of the mechanical input [22–26]. If this input frequency does not match the wing's resonant frequency, the efficiency of energy conversion from muscular contraction to acoustic radiation drops significantly [14, 27]. Despite the critical role of the mechanical input, the stridulatory file has often been modeled as a uniform structure, and the detailed three-dimensional geometry of the teeth has rarely been incorporated into mechanistic models of sound production or evolutionary phylogenies [28–30].

Recent advances in micro-imaging (such as micro-CT and laser confocal microscopy) and high-speed videography have revealed that file morphology is far more complex than previously assumed, exhibiting species-specific variations in tooth spacing, curvature, and stiffness that

govern acoustic purity and harmonic generation [31–35]. Yet, the functional consequences of these micro-structures remain poorly understood, particularly in non-*Gryllus* species such as *M. japonicus*, which is renowned for its high-Q pure tone.

In the present study, we integrate high-speed video analysis, three-dimensional imaging of the file teeth, and experimental modal analysis using LDV to investigate the biomechanical basis of sound production in the bell cricket. We identify two previously unrecognized morphological features of the file: (1) directionally asymmetric triangular teeth, with a steep, sharp angle that promotes mechanical catch during wing closing and a shallow, rounded angle that facilitates sliding during wing opening; and (2) a progressive decrease in tooth spacing toward the distal end of the file, creating a spatial gradient in strike density.

By combining these morphological data with measured wing vibrational modes, we demonstrate that the calculated effective tooth-strike rate closely matches the wing's intrinsic resonant frequency. This finding provides a new mechanistic explanation for how crickets achieve stable and species-specific acoustic frequencies: the song emerges from the precise synchronization between the mechanical input driven by the file's graded geometry and the natural resonance of the wing membranes. Our results refine existing models of stridulatory sound production and highlight the importance of integrating morphology, kinematics, and vibrational mechanics in the study of acoustic communication in Gryllidae.

Results

Morphology of the stridulatory file

To investigate the mechanical input system, we examined the three-dimensional structure of the stridulatory file on the right forewing using a laser scanning confocal microscope (Fig. 1a). Measurements of wing thickness revealed that the left mirror region was approximately 14–15 μm thick, while the right mirror was slightly thinner at 12 μm . High-resolution profiling of the file teeth revealed a distinct and dramatic spatial gradient in both tooth pitch and height along the file (Fig. 1b). At the medial end, where the scraper begins its engagement during wing closure, the tooth pitch was widest (21.56 μm) and the teeth were highest (6.56 μm). Moving along the file, these dimensions progressively decreased through the central region (pitch: 18.06 μm , height: 6.38 μm) and dropped significantly towards the basal end, reaching a minimum pitch of 6.84 μm and a height of 3.96 μm . Furthermore, the 2D surface profiles of individual teeth exhibited a pronounced directional asymmetry (Fig. 1b): the face engaged during the closing phase was steep and sharp, whereas the opposite face, engaged during the opening phase, was shallow and rounded.

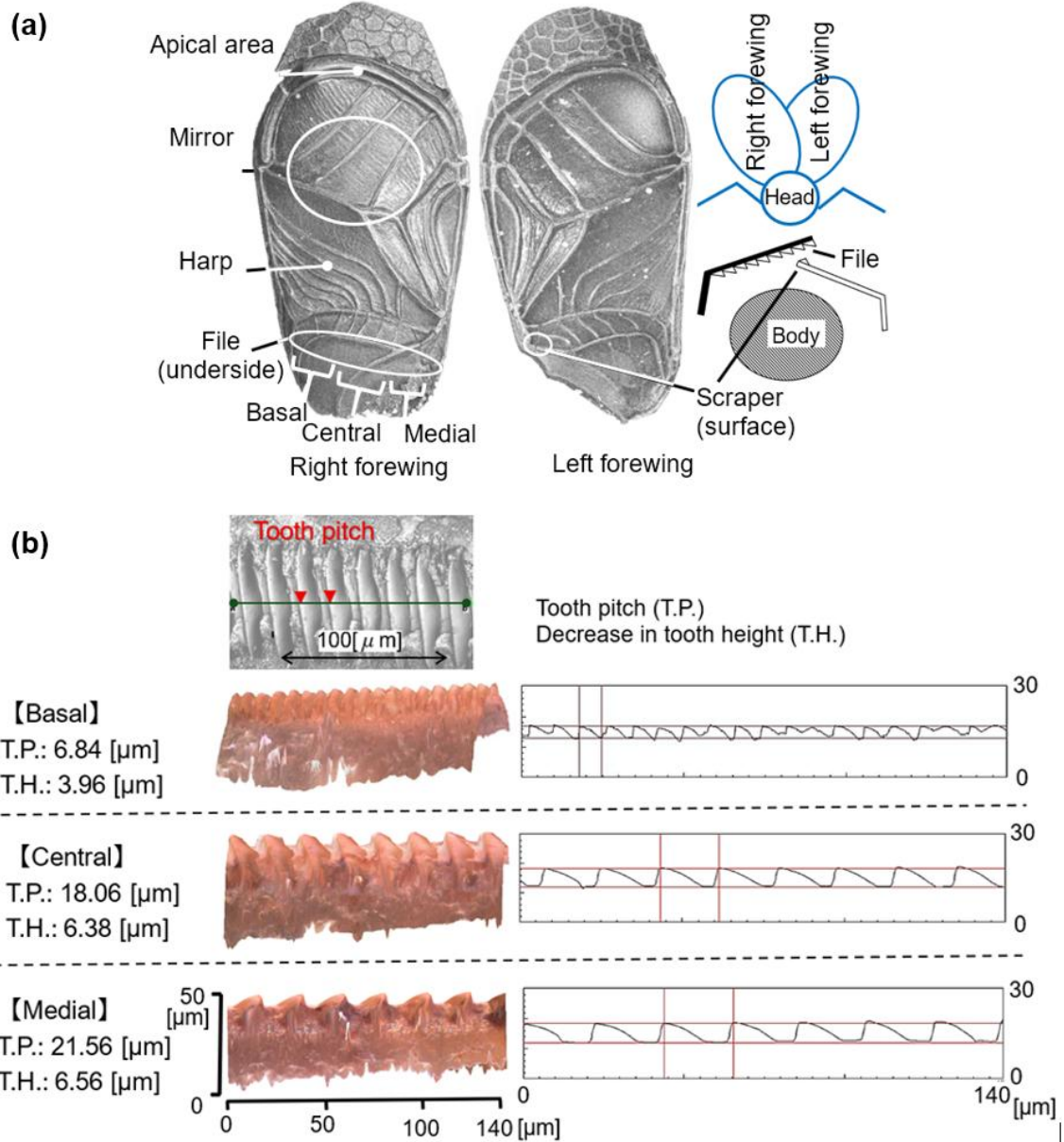


Figure 1: Morphological analysis of the forewings and the stridulatory file. (a) Overview of the excised right and left forewings. Key acoustic and stridulatory structures are annotated, including the apical area, mirror, harp, file (on the underside of the right forewing), and scraper (on the surface of the left forewing). The inset schematic illustrates the typical right-over-left forewing overlap and the mechanical interaction between the file and scraper during stridulation. (b) Three-dimensional micro-geometry and surface profiles of the stridulatory file acquired via laser scanning confocal microscopy. The panels display the spatial gradient in tooth pitch (T.P.) and tooth height (T.H.) at three distinct locations along the file: basal, central, and medial. Both pitch and height progressively decrease from the medial end (initial engagement point; T.P. = 21.56 μm , T.H. = 6.56 μm) through the central region (T.P. = 18.06 μm , T.H. = 6.38 μm) to the basal end

(T.P. = 6.84 μm , T.H. = 3.96 μm). The accompanying 2D profiles highlight the directional asymmetry of the teeth, characterized by a steep closing face and a shallow opening face.

Kinematics and acoustic characteristics

The kinematic relationship between wing motion and sound generation was quantified using synchronized high-speed videography (4,500 frames per second) and acoustic recording (Fig. 2a). The calling song of *Meloimorpha japonicus* exhibited a dominant fundamental frequency (carrier frequency) of 4.65 kHz. Time-domain analysis of the acoustic waveform synchronized with the high-speed video revealed that sound is predominantly generated during the wing-closing phase (Fig. 2b). Interestingly, a brief and weaker acoustic signal was also recorded during the significantly shorter wing-opening phase.

To validate the mechanical origin of the acoustic signal and investigate the bi-directional sound generation, we calculated the predicted mechanical input frequencies based on wing kinematics for both the closing and opening phases separately.

According to the synchronized data, the primary sound-producing closing phase initiated at 3.789 ms and terminated at 17.148 ms, yielding a closing duration (T_{close}) of 13.359 ms. The equivalent motion frequency (f_{motion_close}) is approximately 74.87 Hz. During this stroke, the acoustic waveform indicates that the scraper engaged exactly 62 teeth ($N_{close} = 62$). The predicted mechanical input frequency ($f_{predicted_close}$) is the product of the motion frequency and the number of engaged teeth:

$$f_{predicted_close} = f_{motion_close} \times N_{close} = 74.87 \text{ Hz} \times 62 \approx 4641 \text{ Hz}$$

This theoretically calculated frequency for the closing phase perfectly aligns with the measured acoustic carrier frequency of 4.65 kHz.

Subsequently, the rapid opening phase occurred between 17.148 ms and 23.008 ms. This resulted in a much shorter duration ($T_{open} = 5.860$ ms) and a correspondingly higher motion frequency ($f_{motion_open} \approx 170.65 \text{ Hz}$). The acoustic data revealed that only 29 teeth were engaged during this fast recovery phase ($N_{open} = 29$). Following the identical kinematic relationship:

$$f_{predicted_open} = f_{motion_open} \times N_{open} = 170.65 \text{ Hz} \times 29 \approx 4949 \text{ Hz}$$

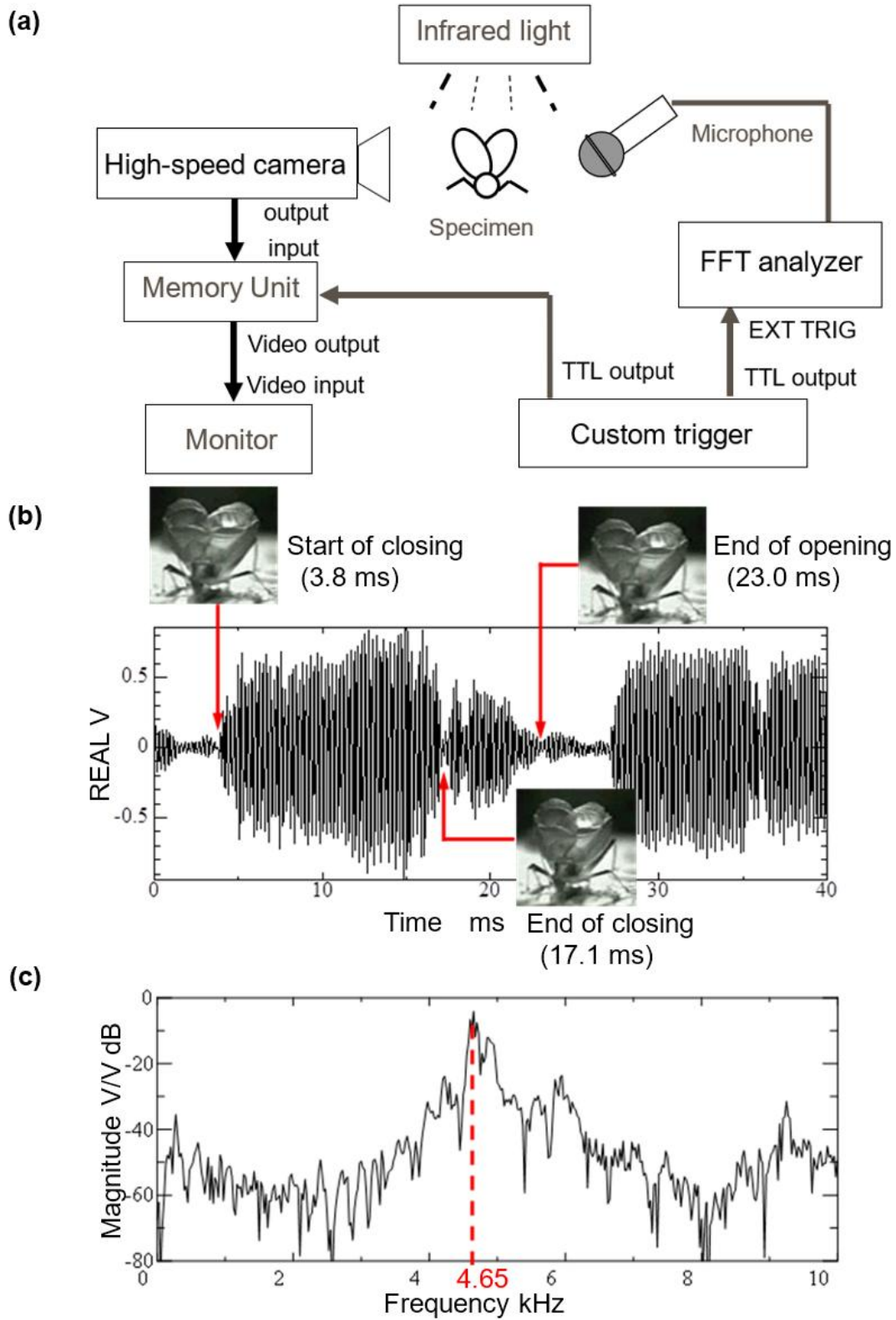


Figure 2: Experimental setup and synchronized stridulation dynamics. (a) Schematic block diagram of the synchronized measurement system, illustrating the signal flow

between the high-speed camera, the sound level meter, and the FFT analyzer triggered simultaneously. (b) Time-domain acoustic waveform (oscillogram) synchronized with high-speed video frames (4,500 fps). The annotated inset images correspond to the start of wing closing, the end of closing, and the end of opening, revealing that the primary acoustic signal is generated during the longer closing phase. (c) The corresponding acoustic power spectrum highlighting the dominant carrier frequency peak at approximately 4.65 kHz.

These calculations robustly demonstrate a striking biomechanical feature: although the wing opens more than twice as fast as it closes (170.65 Hz vs. 74.87 Hz), the number of mechanically engaged teeth drops significantly (from 62 to 29). Consequently, the mechanical input frequency during the opening phase (4,949 Hz) remains remarkably close to the primary 4.65 kHz resonance band, explaining the consistent tonal quality throughout the entire stridulatory cycle.

Experimental modal analysis of the forewing

To determine whether the forewing acts as a structural resonator tuned to the mechanical input, we performed experimental modal analysis using a laser Doppler vibrometer (LDV) (**Fig. 3a**). This technique has been increasingly and effectively applied in studies of insect wing mechanics and resonant sound production [12–14, 18, 31]. Frequency response functions (FRFs) acquired from multiple points on both the left and right forewings revealed a prominent primary bending mode at approximately 200 Hz, followed by higher-order modes near 700 Hz and 1.2 kHz (**Fig. 3b**). These modal patterns are consistent with previous reports describing low-frequency structural modes in cricket and katydid wings [15, 18, 30].

Crucially, distinct and sharp resonance peaks were observed in the 4.0–4.6 kHz range, corresponding to the carrier frequency of the calling song. Three-dimensional reconstruction of the mode shapes at approximately 4.56 kHz (11th and 12th modes) demonstrated that the harp and mirror regions exhibited large-amplitude, in-phase vibrations, consistent with their established role as the primary acoustic radiators in *Ensifera* [12–14, 18] (**Fig. 3c**). Notably, the modal analysis also revealed that the apical area (the distal reticulated network of the wing), which has often been overlooked in previous models, vibrated significantly and synchronously with the mirror region at this specific frequency. This finding aligns with recent work showing that additional wing regions can structurally contribute to high-frequency radiation and spectral purity [18, 30, 33].

Discussion

Our results demonstrate that the pure-tone calling song of *Meloimorpha japonicus* emerges from a precise biomechanical synchronization between the mechanical input—governed by the specialized geometry of the stridulatory file—and the intrinsic structural resonance of the forewing. By visualizing the active vibration modes of the wing using LDV and coupling these with high-speed kinematic data, we reveal the intricate evolutionary adaptations that allow crickets to achieve highly efficient, species-specific acoustic communication.

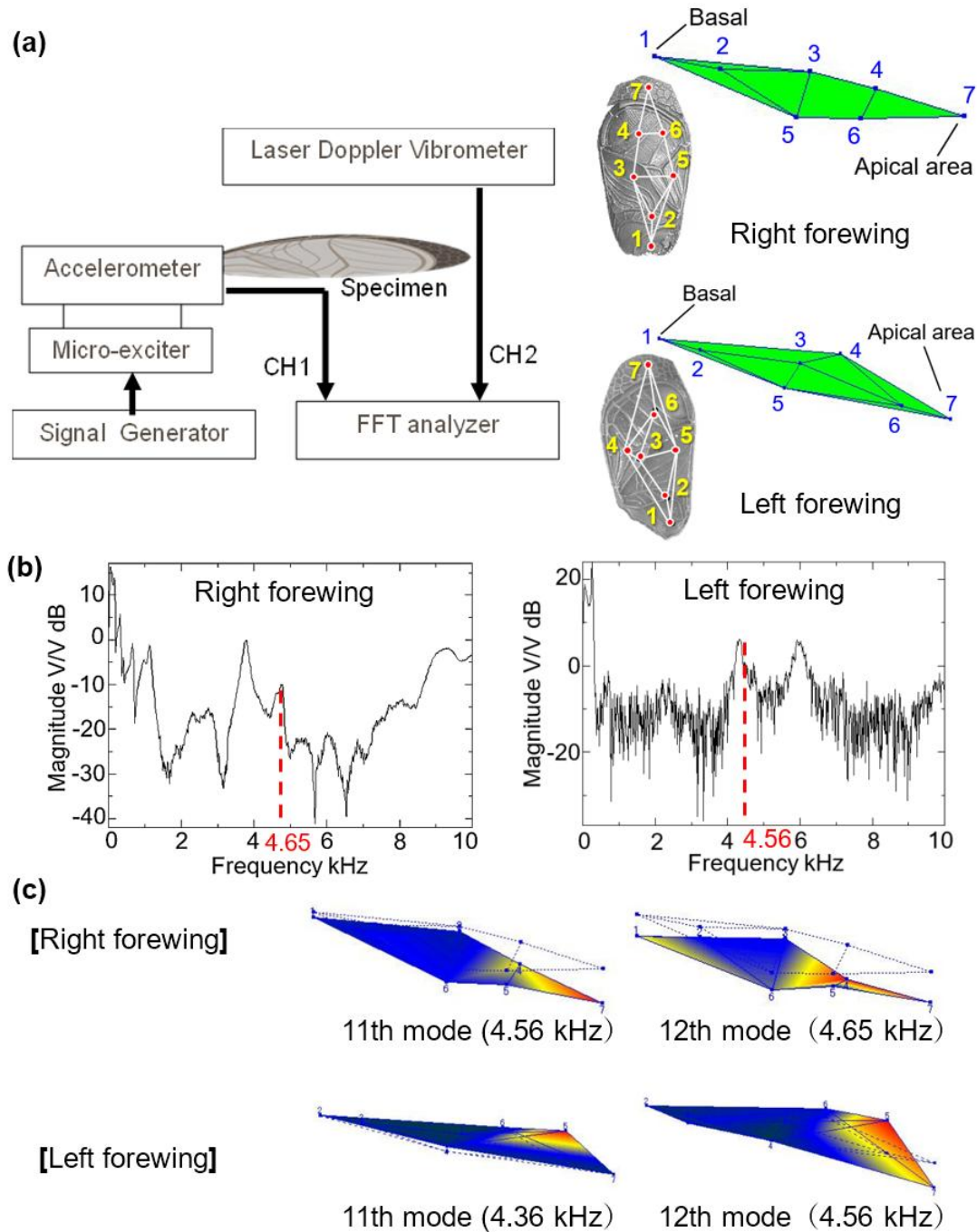


Figure 3: Experimental modal analysis of the forewing.

(a) Schematic representation of the experimental setup using a laser Doppler vibrometer (LDV) and the predefined measurement grid on the wing surface. ((b) Representative frequency response functions (FRFs) measured at the mirror region of the right forewing (left panel) and the harp region of the left forewing (right panel). Distinct structural resonance peaks are visible in the 4.4–4.7 kHz range, tightly corresponding to the carrier frequency of the song. Additional FRF data from other measurement points are provided in the Supplementary Information. (c) Reconstructed 3D vibrational mode shapes near 4.6 kHz. The color gradient indicates displacement amplitude. At this critical frequency band (11th and 12th modes), not only the mirror and harp regions but also the distal apical area vibrate synchronously with large amplitudes, acting as an extended acoustic radiator to enhance sound emission.

Kinematic tuning via file pitch gradient

The tooth-strike rate directly dictates the mechanical excitation frequency transferred to the wing resonators. Assuming the closing muscle acts as an elastic actuator, the kinetic energy and wing-closing velocity (v) naturally decrease as the stroke progresses towards the basal end. To maintain a constant fundamental frequency (f), the tooth pitch (P) must satisfy the relationship $f = v/P$. Our 3D morphological analysis confirms this kinematic tuning: the tooth pitch decreases progressively from the medial end (approx. 21.56 μm) to the basal end (approx. 6.84 μm). This steep spatial gradient—where the pitch narrows to approximately one-third of its initial width—ensures that even as the wing significantly decelerates toward the end of the stroke, the scraper engages the teeth at a constant temporal rate (approx. 4.6 kHz), precisely matching the wing’s resonant frequency. This structural compensation prevents frequency modulation (chirping effect) and preserves the high-Q pure-tone quality characteristic of *M. japonicus*.

Mechanical asymmetry and bi-directional sound generation

While it is generally assumed that crickets stridulate silently during the wing-opening phase, our synchronized acoustic recordings detected brief, distinct acoustic signals during opening. However, the opening phase is significantly shorter (approx. 5.9 ms) than the closing phase (approx. 13.4 ms). This temporal and acoustic asymmetry can be elegantly explained by the directional geometry of the file teeth. We propose a non-linear mechanical diode model where the interaction force (F_{int}) is highly dependent on the tooth angle (θ). The fundamental frequency of mechanical excitation (f_{strike}) is governed by the general kinematic equation:

$$f_{strike} = \frac{v}{P_{eff}}$$

where v represents the instantaneous wing velocity (the relative sliding speed of the scraper across the file), and P_{eff} is the effective tooth pitch, defined as the actual distance the scraper

travels between consecutive acoustic impacts. During closure, the steep tooth angle (θ_{close}) acts as a high-friction ratchet, temporarily catching the scraper, storing elastic strain energy in the wing, and releasing it as a powerful mechanical impulse. This high resistance forces the scraper to engage nearly every physical tooth on the file. Consequently, the effective pitch during the closing phase (P_{eff_close}) is roughly equal to the actual anatomical tooth spacing measured along the file ($P_{anatomical}$), such that $P_{eff_close} \approx P_{anatomical}$. This strong interaction naturally slows down the closing stroke, resulting in a low closing velocity (v_{close}), a longer duration, and highly efficient acoustic conversion. Conversely, during the rapid opening phase, the wing velocity is significantly higher ($v_{open} \gg v_{close}$). If the scraper engaged every physical tooth at this high speed, the resulting frequency would far exceed the wing's resonant frequency. However, the shallow angle (θ_{open}) during opening minimizes friction, causing the scraper to glide or skip over multiple teeth. This skipping behavior effectively increases the engagement distance during opening (P_{eff_open}), making it much larger than the physical spacing ($P_{eff_open} > P_{anatomical}$). Thus, the system maintains a consistent acoustic frequency that matches the intrinsic wing resonance (f_{res}) by perfectly balancing the kinematic and morphological asymmetries. This relationship can be expressed as:

$$f_{res} \approx \frac{v_{close}}{P_{eff_close}} \approx \frac{v_{open}}{P_{eff_open}}$$

This generalized model demonstrates that the brief sound produced during wing opening is not an arbitrary noise, but a frequency-matched signal resulting from the scraper rapidly skipping over the shallow faces of the file teeth.

Coupled resonance and methodological considerations

It is noteworthy that the modal analysis revealed a slight asymmetry in the resonant frequencies of the two wings: the 12th mode of the right forewing (file side) aligned perfectly with the 4.65 kHz calling song, while the corresponding mode of the left forewing (scraper side) was slightly lower at 4.56 kHz. We propose that this reflects a highly specialized functional division. The right forewing, driven directly by the file-scraper interaction, acts as the primary mechanical resonator precisely tuned to the final carrier frequency. The overlapping left forewing—which possesses a slightly thicker mirror membrane (14–15 μm vs. 12 μm)—exhibits a slightly shifted resonance but

strongly couples with the right wing, likely to broaden the overall resonant response and enhance acoustic radiation.

Furthermore, minor discrepancies between the absolute maximum peaks in the individual FRFs and the in vivo calling song frequency are expected in experimental modal analysis. These small deviations likely arise from the altered boundary conditions of excised wings (in vitro) compared to the intact, frictionally coupled wings of a singing cricket. Despite these inherent methodological limitations, the presence of distinct, large-amplitude modes near 4.6 kHz in both wings robustly supports our conclusion of structural resonance.

The functional role of the apical area in acoustic radiation

Classic models of cricket sound production, the "clockwork cricket" hypothesis, emphasize the harp and mirror as the primary resonant structures. However, our experimental modal analysis reveals that the apical area—the distal reticulated region of the wing—vibrates significantly and synchronously with the mirror region at the 4.56 kHz resonance mode. In *M. japonicus*, the wings are exceptionally large relative to their body size, primarily due to the expanded apical network. We suggest that this apical area functions as a vital extension of the acoustic radiator. By vibrating in phase with the mirror, it increases the effective radiating surface area, thereby improving the acoustic impedance matching with the surrounding air for wavelengths corresponding to 4 kHz. This indicates that the entire wing structure, not just isolated membranes, has been evolutionarily optimized to maximize sound radiation efficiency.

Conclusion

The stridulatory apparatus of *M. japonicus* is not merely a passive serrated edge but a finely tuned mechanical interface. The asymmetric, graded file geometry acts as an active controller that regulates both the impulse efficiency and the temporal frequency of the input. When this regulated input precisely strikes the natural frequency of the wing structure—which utilizes the apical area for enhanced radiation, it results in a highly amplified, pure-tone song. Integrating these detailed morphological and kinematic parameters into future biomechanical models will be crucial for fully understanding the evolutionary mechanics of insect acoustic communication.

Methods

Insects and sample preparation

Adult male Japanese bell crickets (*Meloimorpha japonicus*) were used for the experiments. To perform experimental modal analysis on the forewings while maintaining their natural mechanical

properties, live crickets were briefly placed in a freezer for 3 minutes to induce a state of cold anesthesia. The forewings were then carefully excised at the base using micro-scissors (**Fig. 1a**). To prevent changes in stiffness and mass due to desiccation or the loss of hemolymph from the wing veins, all vibration measurements were completed within one hour of excision. As this study exclusively involved non-cephalopod invertebrates (the insect *Meloimorpha japonicus*), formal approval from an institutional animal care and use committee was not required under national and institutional guidelines.

Measurement of file morphology

The three-dimensional micro-geometry of the stridulatory file and the thickness of the wing membranes were measured using a 3D laser scanning confocal microscope (VK-8550, Keyence, Japan). Surface profiles were extracted at the basal, central, and medial sections of the file to quantify the spatial gradients in tooth pitch and height, as well as the directional asymmetry of the teeth (**Fig. 1b, c**).

High-speed videography and acoustic recording

To correlate wing kinematics with sound production, the stridulatory behavior of intact, singing crickets was recorded using a high-speed video camera (FASTCAM-Ultima, Photron, Japan) operating at 4,500 frames per second (**Fig. 2a**). To minimize behavioral artifacts caused by thermal stress, an infrared light source was used for illumination during filming. Acoustic signals were recorded simultaneously using a precision sound level meter (LA-5120, Ono Sokki, Japan). The audio and video recordings were hardware-synchronized using a custom trigger switch. The acoustic data were subsequently processed using a portable FFT analyzer (CF-3400, Ono Sokki, Japan) to extract the time-domain waveform and power spectrum (**Fig. 2b**).

Experimental modal analysis

The structural dynamic properties of the excised forewings were determined through experimental modal analysis, a well-established engineering framework for identifying structural dynamics [36] (**Fig. 3a**). The basal end of the wing was fixed to a micro-exciter (MES251, Akashi, Japan) driven by a signal generator providing broadband white noise or a swept-sine signal. An accelerometer (3105A, Aero-Brown) was mounted on the exciter to measure the input acceleration. The vibrational velocity at predefined points across the wing surface (including the harp, mirror, and apical area) was measured using a highly precise laser displacement sensor/laser Doppler vibrometer (LC-2420, Keyence, Japan). The input and output signals were fed into the FFT analyzer (CF-3400) to compute the Frequency Response Functions (FRFs). Based on standard modal testing theory [36], the FRF data were then imported into ME'scopeVES software

(Vibrant Technology, USA) to perform curve fitting, extract the natural frequencies, and reconstruct the 3D vibrational mode shapes of the wing (**Fig. 3c**).

Data availability

All data generated or analysed during this study are included in this published article and its supplementary information files.

References

1. Alexander, R. D. Evolutionary change in cricket acoustical communication. *Evolution*. **16**, 443–467 (1962).
2. Huber, F., Moore, T. E. & Loher, W. Cricket Behavior and Neurobiology. (Cornell Univ. Press, 1989).
3. Greenfield, M. D. Signalers and Receivers: Mechanisms and Evolution of Arthropod Communication. (Oxford Univ. Press, 2002).
4. Song, H. et al. Phylogenomic analysis sheds light on the evolutionary pathways towards acoustic communication in Orthoptera. *Nat. Commun.* **11**, 4939 (2020).
5. Huber, F. Untersuchungen über die Funktion des Zentralnervensystems und insbesondere des Gehirns bei der Fortbewegung und Lauterzeugung der Grillen. *Z. Vergl. Physiol.* **44**, 60–132 (1960).
6. Hedwig, B. Control of cricket stridulation by a command neuron: efficacy depends on the behavioral state. *J. Neurophysiol.* **83**, 712–722 (2000).
7. Schöneich, S. & Hedwig, B. Cellular basis for singing motor pattern generation in the field cricket. *Brain Behav.* **5**, e00371 (2015).
8. Jacob, P. F. & Hedwig, B. Structure, activity and function of a singing CPG interneuron. *J. Neurosci.* **39**, 96–111 (2019).
9. Jacob, P. F. & Hedwig, B. Modular timer networks: abdominal interneurons controlling the chirp and pulse pattern in a cricket calling song. *J. Comp. Physiol. A*. **206**, 1–14 (2020).
10. Nocke, H. Biophysics of sound production in the field cricket *Gryllus campestris* L. *J. Comp. Physiol.* **80**, 81–105 (1971).
11. Michelsen, A. The tuned cricket. *News Physiol. Sci.* **13**, 32–38 (1998).
12. Elliott, C. J. H. & Koch, U. T. The clockwork cricket: the role of the escapement mechanism in the cricket *Gryllus campestris*. *J. Exp. Biol.* **115**, 359–372 (1985).
13. Bennet-Clark, H. C. The mechanism and efficiency of sound production in mole crickets. *J. Exp. Biol.* **52**, 619–652 (1970).
14. Bennet-Clark, H. C. Resonators in insect sound production: how insects produce loud pure-tone songs. *J. Exp. Biol.* **202**, 3347–3357 (1999).

15. Montealegre-Z, F. & Mason, A. C. The mechanics of sound production in *Panoploscelis*. *J. Exp. Biol.* **208**, 1219–1237 (2005).
16. Bennet-Clark, H. C. Wing resonances in the Australian field cricket *Teleogryllus oceanicus*. *J. Exp. Biol.* **206**, 1479–1496 (2003).
17. Prestwich, K. N. & O'Sullivan, K. Simultaneous measurement of metabolic and acoustic power and the efficiency of sound production in two species of crickets. *J. Exp. Biol.* **208**, 1495–1512 (2005).
18. Montealegre-Z, F., Jonsson, T. & Robert, D. Sound radiation and wing mechanics in stridulating field crickets (Orthoptera: Gryllidae). *J. Exp. Biol.* **214**, 2105–2117 (2011).
19. Chivers, B. D., Jonsson, T., Welsh, R. J. & Montealegre-Z, F. Wing biomechanics and the scaling of singing range in field crickets. *J. Exp. Biol.* **220**, 1303–1311 (2017).
20. Mhatre, N. et al. Changing resonator geometry to boost sound power decouples size and song frequency in a small insect. *Proc. Natl. Acad. Sci. USA.* **109**, E1444–E1452 (2012).
21. Laskri, H. et al. Changes in wing resonance in dried preserved crickets. *R. Soc. Open Sci.* **11**, 241147 (2024).
22. Koch, U. T., Elliott, C. J. H. & Schaffner, K. H. Tooth impact rate and song frequency in crickets. *J. Comp. Physiol. A.* **162**, 213–223 (1988).
23. Simmons, L. W. & Ritchie, M. G. Symmetry in the song of crickets. *Proc. R. Soc. B.* **263**, 1305–1311 (1996).
24. Ritchie, M. G., Townhill, R. M. & Hoikkala, A. The role of wing morphology in cricket song. *Anim. Behav.* **49**, 249–256 (1995).
25. Bennet-Clark, H. C. & Bailey, W. J. Ticking of the clockwork cricket: the role of the file and scraper in stridulation. *J. Exp. Biol.* **205**, 613–625 (2002).
26. Jonsson, T. et al. Convergent evolution of harmonic hopping: multiple origins of high-frequency calls in crickets. *J. Exp. Biol.* **227**, jeb251734 (2024).
27. Prestwich, K. N. The energetics of acoustic signaling in anurans and insects. *Am. Zool.* **34**, 625–643 (1994).
28. Robillard, T. & Desutter-Grandcolas, L. Phylogeny and evolution of acoustic communication in crickets. *Zool. Scr.* **33**, 471–493 (2004).
29. Desutter-Grandcolas, L. Functional morphology and evolution of acoustic communication in crickets. *Ann. Soc. Entomol. Fr.* **39**, 3–20 (2003).
30. Montealegre-Z, F., Morris, G. K. & Mason, A. C. Generation of extreme ultrasonics in rainforest katydids. *J. Exp. Biol.* **209**, 4923–4937 (2006).
31. Montealegre-Z, F. et al. Scale effects and constraints in insect production and perception of high-frequency sound. *Curr. Biol.* **27**, 3363–3370 (2017).
32. Nishino, H. et al. Monitoring the stridulatory movement of the cricket wings. *J. Comp.*

- Physiol. A.* **202**, 393–404 (2016).
33. Baker, E. et al. Structural biomechanics determine spectral purity of bush-cricket calls. *Biol. Lett.* **13**, 20170573 (2017).
 34. Woodrow, C. et al. Reviving the sound of a 150-year-old insect: The bioacoustics of *Prophalangopsis obscura*. *PLoS One.* **17**, e0270498 (2022).
 35. Gu, J. et al. Morphological comparison of the forewing stridulatory file between two mole crickets. *Zootaxa.* **5357**, 101–114 (2023).
 36. Ewins, D. J. *Modal Testing: Theory, Practice and Application*. 2nd edn. (Research Studies Press, 2000).

Acknowledgements

We thank Mr. Toru Kuriyama of Akita Prefectural University for his valuable assistance with the experiments and data analysis.

Funding

This research did not receive funding.

Author contributions

Norihiko Saga conceived the study, supervised the project, contributed to the experimental design and the interpretation of the modal analysis, and drafted the initial manuscript. Takuma Saga conducted the experiments, analyzed the data, and revised the manuscript. Naoki Saito and Toshiyuki Satoh contributed to the experimental design and revised the manuscript. All authors reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryInformation.pdf](#)