Title

Honeybee comb-inspired stiffness gradient-amplified catapult for solid particle repellency

Author list

Wei Zhang[1, 2, #], Wei Jiang[3, #], Chao Zhang[1, 4, #], Xuezhi Qin[1], Huanxi Zheng[2], Wanghuai Xu[2], Miaomiao Cui[2], Bin Wang[1], Jianing Wu[3, 5,*], Zuankai Wang[2,*]

Affiliations

[1]Department of Mechanical Engineering, City University of Hong Kong, Hong Kong SAR 999077, P. R. China.

[2]Department of Mechanical Engineering, The Hong Kong Polytechnic University, Hong Kong SAR 999077, P. R. China.

[3]School of Aeronautics and Astronautics, Sun Yat-sen University, Shenzhen 518107, P. R. China.

[4]MOE Key Lab of Macromolecular Synthesis and Functionalization, Department of Polymer Science and Engineering, Zhejiang University, Hangzhou 310058, China.

[5]School of Advanced Manufacturing, Sun Yat-sen University, Shenzhen 518107, P. R. China.

E-mail address: wujn27@mail.sysu.edu.cn (J. W.) ; zk.wang@polyu.edu.hk (Z. W.).

Abstract

Natural surfaces that repel foreign matter are ubiquitous and crucial for living organisms. Despite remarkable liquid repellency driven by surface energy in many organisms, repelling tiny solid particles from surfaces is rare. The main challenge lies in the unfavourable scaling of inertia versus adhesion in the microscale and the inability of solids to release surface energy. Here, we report a previously unexplored solid repellency on a honeybee's comb: a catapult-like effect to immediately eject pollen after grooming dirty antennae for self-cleaning. Nanoindentation tests revealed the 38-μm long comb features a stiffness gradient spanning nearly two orders of magnitude from ~25 MPa at the tip to ~645 MPa at the base. This significantly augments the elastic energy storage and accelerates the subsequent conversion into kinetic energy. The reinforcement in energy storage and conversion allows the particle's otherwise weak inertia to outweigh its adhesion, thereby suppressing the unfavourable scaling effect and realizing solid repellency that is impossible in conventional uniform designs. We capitalize on this to build an elastomeric bioinspired stiffness-gradient catapult and demonstrate its generality and practicality. Our findings advance the fundamental understanding of natural catapult phenomena with the potential to develop bioinspired stiffness-gradient materials, catapult-based actuators, and robotic cleaners.

Main text

Natural surfaces that repel foreign matter are pivotal for living creatures to survive in surrounding environments with preferential functionalities, ranging from self-cleaning on lotus leaves[1] and prey capturing on pitcher plants[2,3] to fast locomotion of water striders[4,5] and water harvesting of desert beetles[6]. Despite the diversity, the manifestation of matter repellency commonly necessitates a repulsive force sufficient to overcome the adhesive force of the matter on the underlying surfaces. Gravity, for instance, is often used to compete against adhesion, as vividly exemplified by rolling water droplets on lotus leaves[1] and sliding ants on pitcher plants[2]. However, the gravity-based mechanism is only effective for particles with a diameter d_{p} above the millimeter scale, collapsing in the microscale[7,8]. This is because, the gravitational force scales as $F_{\mathrm{g}} \sim d_{\mathrm{p}}^3$. However, the adhesive force scales as $F_{\mathrm{a}} \sim d_{\mathrm{p}}$ for both solid particles and liquid droplets, according to the Johnson-Kendall-Roberts (JKR) contact model[9] and the Young's equation-based derivations[10,11], respectively. As a result, the adhesive force becomes dominant for microscale particles. Interestingly, nature resorts to a surface energy release strategy to repel microscale liquids, as widely found in insect wings, in which the coalescence of droplets into a larger one results in the conversion of surface energy into kinetic energy to propel the jumping of the merged droplet[7,12]. However, such a surface energy-induced jumping mechanism is not applicable to solid particles with definite shapes, which cannot coalesce and release surface energy due to their relatively stronger intermolecular interactions than liquid counterparts[13]. The non-releasable surface energy, coupling with the unfavorable scaling effect, makes it challenging to achieve microscale solid repellency. Although electrodynamic screen technology can generate electrostatic forces to repel particles from surfaces, it usually requires high voltage and consumes substantial energy[14], hindering the practicality and calling for alternative strategies.

In nature, honeybees that frequently shuttle through pollen-rich flowers[15] are a well-known example of manipulating microscale particles. During foraging, honeybees are contaminated by microscale particles such as pollen and dust. These contaminants, if without being timely removed, can lead to the obstruction of sensory organs, the transmission of bacteria and parasites, and even the collapse of a whole colony in the long term[16]. Although removing microscale particles from surfaces has theoretically proven laborious, the ability of honeybees to effectively visit ~100 flowers in a single trip without frequent stops for cleaning[17] implies a potential solution. Despite extensive efforts in studying honeybee behaviors from individual to colony levels[18-23], how honeybees efficiently deal with microparticle contamination has been largely unnoticed, while revealing this could be the key to the development of solid-repellent materials.

In this work, we report a solid repellency phenomenon in the comb of honeybees used for cleaning their antennae. Nanoindentation tests showed that the comb features a stiffness gradient spanning nearly two orders of magnitude from ~25 MPa at the tip to ~645 MPa at the base. This stiffness gradient amplifies the catapult effect, enabling the comb to generate an amplified inertia output that overcomes the originally dominant adhesion and thus repel the adhered pollen and dust. We also develop an elastomeric bioinspired stiffness-gradient catapult and demonstrate its potential in practical applications.

Solid repellency phenomenon

Honeybees forage between flowers on a daily basis, collecting nectar and pollen as food (**Fig. 1**a). At the same time, they are inevitably contaminated by solid particles such as pollen and dust on their body, especially on the antennae used for sensing and probing food[24]. To sustain the antennal function, they use a special antenna cleaner on their forelegs to groom contaminated antennae (**Fig. 1**a and Supplementary Video 1)[25]. The antenna cleaner consists of a comb responsible for grooming and a spur for locking (**Fig. 1**b). The comb is shaped like a semicircle with a diameter $d_{\mathrm{C}} \approx 177\ \mu\mathrm{m}$ and comprises densely arranged hairs, each of which can be modeled as a cylinder with a length $l_0 \approx 38\ \mu\mathrm{m}$ and a diameter $d_0 \approx 6\ \mu\mathrm{m}$ (**Fig. 1**c).

Intuitively, a comb can be contaminated by particles during antennal grooming, and that's why additional maintenance of the comb is required, as also known for other groups of insects[26-28]. Honeybees, however, tend to clean their combs after antennal grooming at an occurrence rate of 25% (Extended Data Fig. 1a), significantly lower than other insects, such as southern green stink bugs (90%)[26], ants (100%)[27], and cockroaches (100%)[28] (Extended Data Fig. 1b). The largely lower occurrence rate of comb maintenance in honeybees implies that their combs may be able to minimize the adverse contamination by repelling adhered particles from comb surfaces. Indeed, only little pollen is found on the surface of a honeybee's comb (Extended Data Fig. 2). Most of the pollen is distributed on the base-to-middle part, leaving the middle-to-tip part almost uncontaminated (Extended Data Fig. 2).

To characterize how the honeybee's comb prevents being contaminated, we digitalize the antennal grooming process using high-speed videography (**Fig. 1** d and e, Supplementary Video 2). We contaminate the honeybee's antennae with 25-μm silica particles, which are similar in size to the pollen we found on the honeybee's comb surface (Extended Data Fig. 2). The honeybee first lowers the contaminated antennae and puts it into the comb, followed by moving the comb downward to groom the antennae from the base to the tip. When reaching the antennal tip, the comb stays there for a while (ranging from a few milliseconds to ~100 ms) and suddenly detaches from the antennae. About 6 ms later, we observe the solid repellency phenomenon as evidenced by many particles being repelled from the comb. Quantitative analysis of the comb surface show that the number of adhered particles only accounts for ~1% of the total, with ~99% being repelled (**Fig. 1** f and g). The average velocity of the repelled particles is ~0.49 m/s, approximately one order of magnitude larger than that generated by gravity (0.06 m/s) (**Fig. 1**h). Thus, we conclude that the solid-repellent phenomenon should originate from a catapult mechanism rather than gravity[29].

To further determine the solid repellency performance, we challenge honeybees with mixed silica particles of sizes from 1 μm to 30 μm, covering the common size of various pollen and dust in the air[30]. Careful inspection shows that a few particles are still adhered to the comb surface, most of which are in the size range below 5 μm (Extended Data Fig. 3 a and b). The sizes of adhered particles gradually increase from the tip to the base of the comb, indicating a location-dependent solid repellency performance (Extended Data Fig. 3c).

Catapult mechanism

The catapult mechanism for solid repellency is distinct from the surface energy-driven liquid repellency. As shown in **Fig. 2**a, upon contact, two liquid droplets initially adhered to a surface will coalesce and convert their surface energy into kinetic energy[7], which generates a force F sharing the same scaling law as the adhesive force and ultimately propels the coalesced droplet to jump with a velocity of $v{\sim}\sqrt{\sigma_P/\rho_\mathrm{p}d_\mathrm{p}}$, where σ_p and ρ_p are the liquid surface tension and mass density[7]. However, two contacting solid particles are unable to merge, and there is no surface energy release for repellency (**Fig. 2**a).

We hypothesize that the insect's comb harnesses elastic energy as an alternative to surface energy to catapult particles into the air, similar to what is known in plants and fungi [31,32]. This hypothesis is based on the potential elastic energy storage of the deformed comb when grooming larger-diameter antennae (Extended Data Fig. 4). Once detaching from the antennae, the deformed comb hair immediately recovers to its initial state, transforming the stored elastic energy into kinetic energy. In this regard, the adhered particle experiences phases of acceleration and deceleration in synchrony with the comb hair, until it is catapulted from the comb (**Fig. 2**b). As a result, the adhered particle is subject to a constant adhesive force F_a and an inertial force F_i that temporally changes in magnitude and direction as the acceleration varies (**Fig. 2**b). Here electrostatic repulsion and gravity are too small and can be neglected. The dynamic competition between F_i and F_a directly determines the onset of the catapult-driven solid repellency. When

$F_i - F_a \geq 0$, particles can be catapulted; otherwise, particles remain adhered (**Fig. 2**b). Satisfying $F_i - F_a \geq 0$ requires that F_i points in the opposite direction to F_a and has a magnitude relatively larger than F_a, which means that the catapult-driven solid repellency only occurs during the deceleration phase (**Fig. 2**b).

To pin down the critical requirements on the acceleration for the onset of catapult-driven solid repellency, we resort to a force analysis on particles of different sizes. Using atomic force microscopy (AFM) equipped with particle-modified probes[33], we measure the adhesive force of silica particles with diameters of 5, 10, 15, and 25 μm (Extended Data Fig. 5a) and demonstrate that the adhesive force is independent of the contact duration in the millisecond timescale (Extended Data Fig. 5b). Fitting the experimental data with $F_a = kd_p$[9], we determine $k = 5.23\ \mathrm{nN/\mu m}$ (**Fig. 2**c). On the other hand, the inertial force of particles can be calculated as $F_i = \pi d_p^3 \rho_p a/6$, where ρ_p and a are the mass density and acceleration of particles, respectively. To better understand the competition between the two forces, we conduct a case analysis in which the curve of F_i with respect to d_p is plotted under $a = 10^4\ \mathrm{m/s^2}$ and compared with that of F_a in **Fig. 2**c. We find that F_i gradually increases from a value smaller than F_a to larger than F_a when d_p increases, indicating a transition from the adhesion-dominant domain to the inertia-dominant domain. This transition involves an intersection point, which determines the lower limit of repellent particle size under a given acceleration (**Fig. 2**c). Equating F_i with F_a, we can derive the critical a required for catapulting a particle of d_p as $a \sim d_p^{-2}$, elucidating the unfavorable scaling effect that makes tiny particles of $d_p < 10\ \mathrm{\mu m}$ more difficult to be repelled (**Fig. 2**d).

Stiffness gradient-amplified catapult effect

We next probe how the honeybee's comb copes with the unfavorable scaling effect. We qualitatively examine the material properties of the comb by using confocal laser scanning microscopy (CLSM), a well-established method that can indicate the presence of elastic resilin, less-sclerotized, and highly sclerotized materials[34]. In the CLSM image, the autofluorescence of elastic resilin, less-sclerotized, and highly sclerotized materials are shown in blue, green, and red, respectively. From the CLSM image of the comb, we find a prominent spatial difference in material compositions (**Fig. 3**a). The tip of each comb hair is resilin-dominated whereas the base is strongly sclerotized, with a gradual transition in between, which suggests a stiffness gradient from the soft tip to the stiff base. To further quantify the stiffness gradient, we measure the Young's modulus along a fresh comb hair via AFM nanoindentation tests. The Young's modulus shows an exponential growth from ~25 MPa at the tip to ~645 MPa at the base, spanning nearly two orders of magnitude in the 38-μm-long comb hair (**Fig. 3**b). The change in Young's modulus along the comb hair can be described by a stiffness gradient coefficient $\delta = 3$, expressed as $\delta = \Delta(\ln E)/\Delta(l/l_0)$ (See Methods).

We resort to an analytical modeling to determine the role of the unique stiffness gradient in the catapult-driven solid repellency. As shown in **Fig. 3**c, the maximum reverse acceleration a generated at the tip of the comb hair exponentially increases with increasing δ, which can be dicpted by $a \sim e^{1.44\delta}$, where e is a mathematical constant following $\ln e = 1$. Specifically, for honeybees (δ =3), the tip of the comb hair can produce a maximum a of $4.2 \times 10^5\ \mathrm{m/s^2}$, approximately two orders of magnitude greater than that of the uniform counterpart (δ =0) (Extended Data Fig. 6). As a consequence, the inertial force boosts and outweighs the adhesive force, successfully triggering the solid repellency (Extended Data Fig. 6). Based on $a \sim d_\mathrm{p}^{-2}$, the corresponding critical d_p can be derived as $d_\mathrm{p} \sim e^{-0.72\delta}$, displaying a rapid decline with linearly increasing δ (**Fig. 3**c). Thus, the presence of stiffness gradient plays an essential role in achieving enhanced catapult performance to suppress the unfavorable scaling effect for solid repellency. The boost in catapult performance through stiffness gradient can be interpreted from the energy perspective. Under the same deformation conditions, the stiffness gradient augments the elastic energy storage of the honeybee's comb hair by ~8 times compared to the uniform counterpart (**Fig. 3**d), providing sufficient energy sources for conversion into kinetic energy. In addition to increasing the energy storage, the stiffness gradient accelerates the energy conversion process through a ~90% reduction of energy conversion duration, defined as the time from the initial release of the comb to the recovery of up to 95% of its deformation (**Fig. 3**d and Extended Data Fig. 7a).

The solid repellency performance is also sensitive to the location of adhered particles on the honeybee's comb hair. Extended Data Fig. 7b plots the maximum acceleration a along the comb hair, which exhibits a strong negative correlation with the normalized distance l/l_0. As shown in **Fig. 3**e, when the normalized distance l/l_0 increases, the acceleration gets smaller and thus the critical d_p gets larger owing to the relationship $d_\mathrm{p} \sim a^{-0.5}$, indicating the location-dependent solid repellency performance. We further build a phase map that reveals the effects of stiffness gradient and spatial location on the onset of solid repellency (**Fig. 3**f). The region of the comb hair that can catapult a certain size range of particles expands as δ increases. Focusing on the region where the honeybee's comb is in direct contact with antennae ($l/l_0 < 0.4$), the stiffness gradient coefficient of $\delta = 3$ in the honeybee's case renders the repellency of particles with a diameter above 5 μm (**Fig. 3**f), a range where most plant pollen and dust in the air are distributed[30]. Further increasing δ would not obtain notable improvement in solid repellency performance (Extended Data Fig. 7c), but generate a larger contact force that may adversely impair the sensory function of honeybees' antennae under repeated grooming (Extended Data Fig. 7d). Consequently, the manifestation of $\delta = 3$ may be an optimal choice for honeybees to attain both flexibility and sufficient solid repellency ability, which endows them an evolutionary advantage for energy-efficient interactions with pollen-rich environments.

Generality and application

To demonstrate the generality of the stiffness gradient-amplified catapult for solid repellency, we design a scaled-up stiffness-gradient catapult (SGC) that mimics the biological counterpart. We fabricate the artificial SGC by leveraging a spontaneous diffusion process to preferentially rearrange the gradient distribution of chemical components such as water, cross-linkers and monomers (**Fig. 4**a). The AFM nanoindentation test shows that the Young's modulus of SGC gradually increases from ~2 MPa at the tip to ~150 MPa at the base (**Fig. 4**a). In contrast, without the presence of stiffness gradient, the Young's modulus along the control sample keeps almost constant at ~2 MPa. The as-fabricated SGC can be further installed onto a motor-driven fixture serving as a self-cleaning cleaning robot for maintaining outdoor infrastructure such as solar panels (**Fig. 4**b). The SGC-based robot generates a maximum a of ~$2 \times 10^3\ \mathrm{m/s^2}$ and shows a ~91% repellent fraction for 25-μm silica particles, which are approximately 10 times and 8 times higher than the control sample (**Fig. 4**c and Extended Data Fig. 8). Owing to the superior solid repellency ability, the SGC-based robot keeps a higher cleaning efficiency under 12-cycle contamination tests, enabling the solar panel system to sustain a higher electric power output even comparable to the uncontaminated state (**Fig. 4**d, Extended Data Fig. 9 and Supplementary Video 3). By contrast, the uniform plate fails to spontaneously remove particles from its surface, and these accumulated particles further cause poor contact between the uniform plate and the solar panel (Extended Data Fig. 10), leading to rapid degradation of the cleaning efficiency over multiple cycles.

In summary, we have shown that the honeybee comb acts like a microscale catapult to repel adhered particles through the stiffness-gradient amplified catapult mechanism. The material gradient from soft tips to stiff bases has been found in adhesive hairs in the attachment systems of insect legs[35]. Such a material gradient has proven to enhance the adhesive force through a mechanism in which stiff bases prevent the clusterization of adhesive hairs, while soft tips improve the contact formation of the attachment system to the substrate[36]. The role of the material gradient in adhesion may also apply to the honeybee comb that needs to adhere to the pollen to clean the antennae: The soft tip adapts to various particle geometries while the stiff base avoids hair clumping. Since the comb needs to repel the attached pollen afterwards, there is a trade-off between enhancing adhesion and enhancing repellency through material gradient, making the honeybee comb an intriguing model for further investigation of optimal material design in bioinspired robotic systems. In addition, catapult mechanism that can modulate power output has been widely manifested by living creatures for specific functions[29], such as the deadly strike of mantis shrimps for preying[37] and the ballistic jaw mechanism of trap-jaw ants for preying and locomotion[38]. Further improving the power output has been reported to require the use of multiple catapults, such as a dual-catapult system inspired by the dragonfly larvae[39]. Our proposed stiffness gradient-amplified catapult mechanism provides an alternative solution that does not require the additional system components. The biological insight of rectifying elastic energy into kinetic energy via the stiffness-gradient catapult also expands the exciting domain of efficient energy conversion in nature, such as the surface energy-driven spore dispersal[40] and the humidity-driven seed drilling[41], and sheds light on developing bioinspired heterogeneous materials and power-modulated systems with promising applications including soft actuators and robotics[39,42-46].

Acknowledgments

We acknowledge the financial support from Research Grants Council of Hong Kong (No. C1006-20W, Z. W.; No. SRFS2223-1S01, Z. W.; No. 11215523, Z. W.); Shenzhen Science and Technology Innovation Council (No. JCYJ20170413141208098, Z. W.); Innovation Technology Fund (GHP/021/19SZ, Z. W.); New Cornerstone Science Foundation through the XPLORER PRIZE, Z. W.; the Meituan Green Tech Award, Z. W.; National Natural Science Foundation of China (No. 52005075, Z. W.); National Natural Science Foundation of China (No. 52075528, B. W.); Shenzhen Science and Technology Program (No. 20220817165030002, J. W.).

Author Contributions Statement

Z. W., J. W., and W. Z. conceived the research. W. Z., C. Z., H. Z., and X. Q. designed the experiments. W. Z., W. J., and C. Z. prepared the samples. W. Z., W. J., C. Z., W. X. and M. C. carried out the experiments. W. Z. and W. J. conducted the dynamics simulation. All authors analyzed the data. W.Z., C. Z., Z. W., B. W., and J. W. wrote the manuscript. [#]These authors contributed equally to this manuscript.

Competing Interests Statement

Authors declare that they have no competing interests.

Figure legends

Fig. 1 | Solid repellency phenomenon on the honeybee's comb. a, A honeybee using its foreleg to groom its antennae during foraging. **b,** Scanning electron microscopy (SEM) image of the honeybee's antenna cleaner, consisting of a comb and a spur. **c,** SEM image of the semicircular comb comprised of densely arranged hairs. Here d_{C} denotes the diameter of the comb, l_0 and d_0 denote the length and diameter of the comb hair. The scale bar of the inset is 5 μm. **d, e,** Optical images (**d**) and schematics (**e**) of solid repellency phenomenon on the honeybee's comb during antennal grooming. **f,** The comb surface remains almost uncontaminated after grooming antennae contaminated by 25-μm particles. **g,** The fraction of repelled particles and adhered particles. Data are presented as mean ± standard deviation (s.d.) (n=3). **h,** Comparison of the particle velocity between the measurements and the gravity-based prediction. The gravity-based prediction value is much lower than the measurements, suggesting that the solid repellency may be driven by a catapult mechanism. In the box plot, the box denotes the 25th–75th percentiles, the center line denotes the median, the square point denotes the mean, and the whiskers denote the full data range within 1.5 IQR (interquartile range). The circle points denote the individual measurements (n=19).

Fig. 2 | Critical requirements for catapult-driven solid repellency. a, Comparison analysis between liquid repellency and solid repellency. Here F is the force generated during the coalescence of liquid droplets. And v is the initial velocity of the merged droplet, expressed as $v \sim \sqrt{\sigma_{\mathrm{p}}/\rho_{\mathrm{p}} d_{\mathrm{p}}}$, where σ_{p} and ρ_{p} are the liquid surface tension and mass density, respectively. **b,** Force analysis during the catapult-driven solid repellency process. **c,** The adhesive force F_{a} and the inertial force F_{i} of particles with respect to the diameter d_{P}. In each box plot, the box denotes the 25th–75th percentiles, the center line denotes the median, the square point denotes the mean, and the whiskers denote the full data range within 1.5 IQR. The circle points denote the individual measurements. Here n=28, 29, 31, and 28 for 5-, 10-, 15-, and 25-μm particles, respectively. The dashed, blue line is the fitted curve for the adhesive force. The solid, red line denotes the theoretical prediction of the inertial force. **d,** Critical acceleration a required for solid repellency of particles of d_{P}. The required magnitude of critical a sharply increases as $d_{\mathrm{P}} < 10$ μm, elucidating the unfavorable scaling effect.

Fig. 3 | The stiffness gradient-amplified catapult effect. a, Confocal laser scanning microscope image showing a prominent stiffness gradient from a soft tip to a stiff base in the honeybee's comb.

The blue, green, and red color indicate the autofluorescence of elastic resilin, less-sclerotized, and highly sclerotized materials, respectively. **b,** Measurements of Young's modulus along a fresh comb hair showing a stiffness gradient across approximately two orders of magnitude (n=10). The comb hair has a stiffness gradient coefficient δ of 3, calculated by $\delta = \Delta(\ln E)/\Delta(l/l_0)$. In each box plot, the box denotes the 25th–75th percentiles, the center line denotes the median, the square point denotes the mean, the whiskers denote the full data range within 1.5 IQR, and the diamond points denote outliers. **c,** The maximum acceleration a exhibits a positive exponential relationship with stiffness gradient coefficient δ while the critical diameter d_{P} exhibits a negative one with δ for the tip of the comb hair. **d,** The stiffness gradient coefficient δ augments the elastic energy storage and shortens the energy conversion duration. The values of energy storage and conversion duration are normalized relative to the value for the uniform case ($\delta = 0$). The energy conversion duration is defined as the time from the release of the comb to the recovery of 95% of its deformation. **e,** The location-dependent solid repellency performance of the comb hair. Data are presented as mean ± s.d. (n=3). The inset is the SEM image of the comb surface after grooming antennae covered with 1-30 μm silica particles. **f,** Phase map for the solid repellency under the influences of the stiffness gradient and spatial location.

Fig. 4 | Application of the stiffness gradient-amplified catapult mechanism for solid repellency. a, Young's modulus along the bioinspired stiffness-gradient catapult (SGC) (shown in the inset) and the control sample with a uniform stiffness. Data are presented as mean ± s.d. (n=3). **b,** Optical image of the self-cleaning solar power system that consists of the SGC-based robot and a solar panel. **c,** Comparison analysis on the maximum acceleration and repellency fraction between the SGC-based robot and the control sample. Data are presented as mean ± s.d.. For the measurements of maximum a, n=5 for SGC-based robot and n=4 for the control sample. For the measurements of repellency fraction, n=3 for both SGC-based robot and the control sample. **d,** The system with the SGC-based robot can generate a higher electric power output comparable to the uncontaminated one, much higher than the control sample. Scale bars, 10 mm.

References

1 Barthlott, W. & Neinhuis, C. Purity of the sacred lotus, or escape from contamination in biological surfaces. *Planta* **202**, 1-8 (1997).

2 Bohn, H. F. & Federle, W. Insect aquaplaning: Nepenthes pitcher plants capture prey with the peristome, a fully wettable water-lubricated anisotropic surface. *Proc. Natl. Acad. Sci. U.S.A.* **101**, 14138-14143 (2004).

3 Wong, T.-S. *et al.* Bioinspired self-repairing slippery surfaces with pressure-stable omniphobicity. *Nature* **477**, 443-447 (2011).

4 Gao, X. & Jiang, L. Water-repellent legs of water striders. *Nature* **432**, 36-36 (2004).

5 Hu, D. L., Chan, B. & Bush, J. W. The hydrodynamics of water strider locomotion. *Nature* **424**, 663-666 (2003).

6 Parker, A. R. & Lawrence, C. R. Water capture by a desert beetle. *Nature* **414**, 33-34 (2001).

7 Wisdom, K. M. *et al.* Self-cleaning of superhydrophobic surfaces by self-propelled jumping condensate. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 7992-7997 (2013).

8 Bintein, P.-B., Bense, H., Clanet, C. & Quéré, D. Self-propelling droplets on fibres subject to a crosswind. *Nat. Phys.* **15**, 1027-1032 (2019).

9 Johnson, K. L., Kendall, K. & Roberts, a. Surface energy and the contact of elastic solids. *Proceedings of the royal society of London. A. mathematical and physical sciences* **324**, 301-313 (1971).

10 ElSherbini, A. & Jacobi, A. Retention forces and contact angles for critical liquid drops on non-horizontal surfaces. *J. Colloid Interface Sci.* **299**, 841-849 (2006).

11 Extrand, C. & Gent, A. Retention of liquid drops by solid surfaces. *J. Colloid Interface Sci.* **138**, 431-442 (1990).

12 Mukherjee, R., Berrier, A. S., Murphy, K. R., Vieitez, J. R. & Boreyko, J. B. How Surface Orientation Affects Jumping-Droplet Condensation. *Joule* **3**, 1360-1376 (2019).

13 Jespersen, N. D. & Hyslop, A. *Chemistry: The molecular nature of matter*. (John Wiley & Sons, 2021).

14 Sayyah, A., Horenstein, M. N., Mazumder, M. K. & Ahmadi, G. Electrostatic force distribution on an electrodynamic screen. *J. Electrostat.* **81**, 24-36 (2016).

15 Hao, K., Tian, Z. X., Wang, Z. C. & Huang, S. Q. Pollen grain size associated with pollinator feeding strategy. *Proc. Biol. Sci.* **287**, 20201191 (2020).

16 Foose, A., Westwick, R., Vengarai, M. & Rittschof, C. The survival consequences of grooming in the honey bee Apis mellifera. *Insectes Soc* **69**, 279-287 (2022).

17 Free, J. B. *Insect pollination of crops*. (Academic Press, London and New York., 1970).

18 Fard, G. G., Zhang, D., Jimenez, F. L. & Peleg, O. Crystallography of honeycomb formation under geometric frustration. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2205043119 (2022).

19 Mackenzie, D. Proving the Perfection of the Honeycomb. *Science* **285**, 1338-1339 (1999).

20 Esch, H. E., Zhang, S., Srinivasan, M. V. & Tautz, J. Honeybee dances communicate distances measured by optic flow. *Nature* **411**, 581-583 (2001).

21 Seeley, T. D. *et al.* Stop signals provide cross inhibition in collective decision-making by

honeybee swarms. *Science* **335**, 108-111 (2012).

22 Dong, S., Lin, T., Nieh, J. C. & Tan, K. Social signal learning of the waggle dance in honey bees. *Science* **379**, 1015-1018 (2023).

23 Lechantre, A. *et al.* Essential role of papillae flexibility in nectar capture by bees. *Proc. Natl. Acad. Sci. U.S.A.* **118** (2021).

24 Haupt, S. S. Antennal sucrose perception in the honey bee (Apis mellifera L.): behaviour and electrophysiology. *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **190**, 735-745 (2004).

25 Schönitzer, K. & Renner, M. The function of the antenna cleaner of the honeybee (Apis mellifica). *Apidologie* **15**, 23-32 (1984).

26 Rebora, M., Salerno, G., Piersanti, S., Michels, J. & Gorb, S. Structure and biomechanics of the antennal grooming mechanism in the southern green stink bug Nezara viridula. *J. Insect Physiol.* **112**, 57-67 (2019).

27 Hackmann, A., Delacave, H., Robinson, A., Labonte, D. & Federle, W. Functional morphology and efficiency of the antenna cleaner in Camponotus rufifemur ants. *R. Soc. Open Sci.* **2**, 150129 (2015).

28 Robinson, W. & Wildey, K. in *Proceedings of the Second International Conference on Urban Pests.* 361-369 (Exeter Press Exeter, UK).

29 Longo, S. *et al.* Beyond power amplification: latch-mediated spring actuation is an emerging framework for the study of diverse elastic systems. *J. Exp. Biol.* **222**, jeb197889 (2019).

30 Sanz Saiz, C., Polo Martínez, J. & Martín Chivelet, N. Influence of pollen on solar photovoltaic energy: literature review and experimental testing with pollen. *Appl. Sci.* **10**, 4733 (2020).

31 Noblin, X. *et al.* The fern sporangium: a unique catapult. *Science* **335**, 1322 (2012).

32 Edwards, J., Whitaker, D., Klionsky, S. & Laskowski, M. J. A record-breaking pollen catapult. *Nature* **435**, 164-164 (2005).

33 Ito, S. & Gorb, S. N. Attachment-based mechanisms underlying capture and release of pollen grains. *J. R. Soc. Interface* **16**, 20190269 (2019).

34 Michels, J. & Gorb, S. N. Detailed three-dimensional visualization of resilin in the exoskeleton of arthropods using confocal laser scanning microscopy. *J. Microsc.* **245**, 1-16 (2012).

35 Peisker, H., Michels, J. & Gorb, S. N. Evidence for a material gradient in the adhesive tarsal setae of the ladybird beetle Coccinella septempunctata. *Nat. Commun.* **4**, 1661 (2013).

36 Gorb, S. N. & Filippov, A. E. Fibrillar adhesion with no clusterisation: functional significance of material gradient along adhesive setae of insects. *Beilstein J. Nanotechnol.* **5**, 837-845 (2014).

37 Patek, S. N., Korff, W. & Caldwell, R. L. Deadly strike mechanism of a mantis shrimp. *Nature* **428**, 819-820 (2004).

38 Patek, S., Baio, J., Fisher, B. & Suarez, A. Multifunctionality and mechanical origins: ballistic jaw propulsion in trap-jaw ants. *Proc. Natl. Acad. Sci. U.S.A.* **103**, 12787-12792 (2006).

39 Büsse, S., Koehnsen, A., Rajabi, H. & Gorb, S. N. A controllable dual-catapult system inspired by the biomechanics of the dragonfly larvae's predatory strike. *Sci. Robot.* **6**, eabc8170 (2021).

40 Noblin, X., Yang, S. & Dumais, J. Surface tension propulsion of fungal spores. *J. Exp. Biol.* **212**, 2835-2843 (2009).

41 Luo, D. *et al.* Autonomous self-burying seed carriers for aerial seeding. *Nature* **614**, 463-470 (2023).

42 Ilton, M. *et al.* The principles of cascading power limits in small, fast biological and engineered systems. *Science* **360** (2018).

43 Hawkes, E. W. *et al.* Engineered jumpers overcome biological limits via work multiplication. *Nature* **604**, 657-661 (2022).

44 Son, K., Guasto, J. S. & Stocker, R. Bacteria can exploit a flagellar buckling instability to change direction. *Nat. Phys.* **9**, 494-498 (2013).

45 Majidi, C. Soft robotics: a perspective—current trends and prospects for the future. *Soft Robot.* **1**, 5-11 (2014).

46 Feldmann, D., Das, R. & Pinchasik, B. E. How can interfacial phenomena in nature inspire smaller robots. *Adv. Mater. Interfaces* **8**, 2001300 (2021).

Methods

Sample collection

The *Apis mellifera ligustica* honeybees were collected from Guangzhou, Guangdong, China (23.13° N, 113.27° E) and housed in outdoor beehives. The honeybees were fed a 1500-g mixture of water, sugar, and pollen with a mass ratio of 6:4:3 once a week. All experiments were performed on randomly selected worker honeybees. We verified that no permissions were required to access these locations and that no endangered or protected species were involved in the experiments.

Scanning electron microscopy

The honeybee foreleg and antenna samples were soaked in 2.5% glutaraldehyde for 3 hours at 25 °C. Subsequently, they were cleaned with 0.1 mol L^{-1} phosphate buffer (pH=7) and dehydrated with 70% to 100% ethanol (concentration increment: 10%). Next, the samples were processed with tert-butyl alcohol for permutation, oven-dried for 10 min, and coated with gold palladium for 60 s. Finally, the samples were observed using a scanning electron microscope (SEM) (FEI Quanta 200, Czech Republic) in the high-vacuum mode at 15 kV.

High-speed video of the solid repellency phenomenon in honeybees

We put a honeybee into a 5-ml microcentrifuge tube (Nantonghairui, China) to restrict its locomotion during the experiments. The honeybee's forelegs were carefully adjusted to ensure that it could freely groom its antennae. Then we used a cotton bud covered by 25-μm silica particles to contaminate the honeybee's antennae to stimulate the antennal grooming process. At the same time, the grooming behavior was filmed using a high-speed camera (Phantom, Micro LC310, USA) equipped with a macro lens (Canon, EF100mmf/2.8LISUSM, Japan) from a front view. The frame rate was set as 1000 frames per second (fps).

Characterization of adhesive force of particles

We resorted to atomic force microscopy (AFM) equipped with particle-modified probes to determine the relationship between the size and adhesion of particles on the honeybee's comb surface based on a previously established method[33]. Conducting quantitative characterization of size effects on natural pollen is challenging due to the irregular and incontrollable geometry. By contrast, silica particles that feature regular spheres with controllable diameter make them an ideal candidate for quantitative examination. Together with that dust is another major contamination source for insects, most of which contain silica, we therefore chose silica particles for further investigation. As a preliminary, we modified commercial cantilever tipless probes with silica particles of different sizes, including 5, 10, 15, and 25 μm. For example, we adhered a 5-μm particle upon the tip of a probe using epoxy glue under AFM and immediately placed the probe upside down to avoid particle shedding during 16 hours of glue curing. Additionally, we prepared six fresh forelegs, glued them on a glass slide, and placed them under a scanning probe microscope (SPM) (Dimension Fast scan Bio, Bruker, USA) to measure the adhesive force of particles on the comb surface. We preloaded the particle-modified probe to enable the silica particle to be firmly in contact with the comb surface. After 50 ms of contact duration, the probe was actuated to retract from the comb surface. The adhesive force, defined as the minimum value of pull-off force during the retraction of the probe, was measured simultaneously[33]. The data were processed and analyzed in Nanoscope Analysis software (2.0, Bruker, USA).

Confocal laser scanning microscopy

To characterize the material composition and distribution of the honeybees' comb, we employed a previously established method based on confocal laser scanning microscopy (CLSM)[34,47]. A fresh honeybee comb sample was placed into a test petri dish (diameter=35.00 mm, height=9.90 mm) filled with glycerol (99%, Macklin, China). Then the presence and distribution of the materials in the comb sample were visualized with the confocal laser scanning microscope (TCS-SP5, Leica, Germany) equipped with four solid-state lasers (wavelengths: 405, 488, 561, and 633 nm). To visualize the autofluorescence of the elastic resilin, the excitation 405 nm laser line and a bandpass emission filter transmitting 420-480 nm were used. To visualize the autofluorescence of less-sclerotized cuticle, the excitation 488 nm laser line and a bandpass emission filter transmitting 495-560 nm were used. To visualize the autofluorescence of the highly sclerotized cuticle, the excitation of 561 nm and a bandpass emission filter transmitting 570-630 nm as well as the excitation of 633 nm and a bandpass emission filter transmitting 640-700 nm were used. We then created maximum intensity projections by means of the Leica Application Suite Advanced Fluorescence (LAS AF) software (Leica Microsystems). In the obtained RGB CLSM images, the resilin autofluorescence was shown in blue, the less-sclerotized cuticle autofluorescence was shown in green, and the highly sclerotized cuticle autofluorescence was shown in red.

Nanoindentation tests for materials property characterization

To quantify the Young's modulus of the comb, we performed nanoindentation tests on the fresh comb samples using AFM. Samples were examined in water (liquid phase) at a temperature of 21 °C immediately to prevent the onset of dehydration. We conducted the nanoindentation operations using a scanning probe microscope (SPM) (Dimension Fast scan Bio, Bruker, USA) equipped with a probe (PFQNM-SMPKIT-12 M, Bruker, USA) for liquid phase examination. We set the indentation depth at 50 nm, only about 0.81% of the thickness of the indented comb hair to avoid any potential influence of the underneath substrate on the measurements of Young's modulus[35]. We used NanoScope Analysis software 2.0 (Bruker, USA) to visualize and process the experiment data.

Derivation of the stiffness gradient coefficient

From the logarithmic plot (**Fig. 3**b), we found a linear relationship between the Young's modulus in logarithmic form ($\ln E$) and the normalized distance l/l_0. It means that $\ln E$ is proportional to l/l_0, and the proportion solely depends on the slope of the linear curve. As a result, the Young's modulus change can be described by the value of the slope, also known as the stiffness gradient coefficient δ. By denoting the change in l/l_0 as $\Delta(l/l_0)$ and the corresponding change in $\ln E$ as $\Delta(\ln E)$, we can derive the equation of the stiffness gradient coefficient δ as

$$\delta = \frac{\Delta(\ln E)}{\Delta(l/l_0)} \tag{1}$$

After that, we can determine Young's modulus in logarithmic form along the beam as:

$$\ln E = \delta\left(\frac{l}{l_0}\right) + \ln E_0 \tag{2}$$

Here E_0 is 25 MPa, the value of Young's modulus of the tip of the comb hair ($l = 0$). Based on Eq. (2), we can obtain the exponential distribution of Young's modulus along the beam

$$E = E_0 e^{\delta(l/l_0)} \tag{3}$$

Here the lower case e is a mathematical constant that follows $\ln e = 1$. By fitting experimental data with Eq. 3, we can determine the value of δ for the honeybee comb.

According to Eq. (3), we can control the stiffness gradient of the beam through the value of δ to explore the stiffness influence. For example, when $\delta = 0$, the term of $e^{\delta(l/l_0)}$ is a constant value of 1 regardless of the change in l, which means that there is no stiffness gradient along the beam (i.e., uniform case). Otherwise, the beam has stiffness gradient and the gradient extent is dependent on the magnitude of δ.

Analytical model

Before conducting dynamic simulations, we need to determine the initial deformation of the comb hair based on a static force analysis. We modeled the comb hair as a non-uniform cantilever beam with a length l_0, second moment of inertia I and gradient stiffness (Young's modulus E). For simplicity, we considered the most conservative case in which the comb hair directly comes into contact with the antennae, corresponding to an amount of elastic energy storage in the comb hair smaller than in other cases involving particles. When grooming the antennae, the comb hair would deform to shorten its total length by 16 μm in the longitudinal direction owing to the size mismatch with the antennae. At the deformed state, the part of the comb hair that is in direct contact with the antennae should maintain straight because of the smooth surface of the antennae, and have an angular deformation of 90° relative to the undeformed position. The rest part should gradually deform from the fixed end and smoothly coordinate with the straight part. Such a deformation behavior, including a curved part and a straight part, can be achieved by perpendicularly inserting a concentrated force *P* on the beam.

Next, we determined the settings of the force *P*, including its magnitude and place of application. We first built a global coordinate *OXY* to describe the deformation behavior, in which the origin locates at *O*, the *x*-axis aligns with the comb hair, and the *y*-axis is perpendicular to the *x*-axis. Also, we built a local coordinate *Ol* fixed to the comb hair, featuring a shared origin *O* with the global one and an *l*-axis always aligning with the centroidal axis of the comb hair. The deformation behavior at *l* of the comb hair can be described by $\phi(l)$, $x(l)$ and $y(l)$, denoting the angular deformation of the centroidal axis, the length in the *x*-direction, and the deflection in the *y*-direction, respectively. Since the deflection of the comb hair was comparable to its dimensions, we adopted the large-deflection theory of the Euler–Bernoulli beam[48] and got a nonlinear differential equation governing the deformation behavior of the comb hair as [49]

$$\frac{d}{dl}\left(EI\frac{d\phi}{dl}\right)+P\sin\left(\phi+\frac{\pi}{2}-\phi(0)\right)=0 \tag{4}$$

which is subject to the boundary conditions as

$$\begin{cases}\phi(0)=0\\ \dfrac{d\phi}{dl}(l)=0\end{cases} \tag{5}$$

We considered the length of the curved part as the effective length of the modeled beam in the calculations. Using the above equations, we can determine the slope of the whole deformed comb hair. After determining the slope, we can calculate $x(l)$ and $y(l)$ from the relations below

$$\begin{cases}x(l)=\displaystyle\int_0^l \cos(\phi)dl\\ y(l)=\displaystyle\int_0^l \sin(\phi)dl\end{cases} \tag{6}$$

The derived formulations belong to the nonlinear two-point boundary-value problems and are usually solved with complex iterative methods. To simplify the solution, we adopted a commutation method by introducing a new variable $z(l)=\phi(l)+\alpha-\phi(l_P)$ to replace $\phi(l)$, which reduces the boundary-value problem to the initial-value problem as [50]

$$\frac{d}{dl}\left(EI\frac{dz}{dl}\right) + P\sin(z) = 0 \tag{7}$$

with initial and supplementary conditions as

$$\begin{gathered} z(l_P) = \alpha \\ \frac{dz}{dl}(0) = \frac{d\phi}{dl}(0) = 0 \\ z(0) = \phi(0) + \frac{\pi}{2} - \phi(l_P) = \frac{\pi}{2} - \phi(l_P) \end{gathered} \tag{8}$$

Here l_P denotes the application place of the force *P*. Using the fourth-order Runge-Kutta method to solve the initial-value problem, the settings of the force *P* can be obtained, which allows us to further determine the initial deformation behavior of the comb hair.

Based on the obtained initial deformation, we simulated the vibration of the comb hair using the finite element method (COMSOL Multiphysics 5.6). Because the hair's deformation is in-plane, we selected a two-dimensional analysis rather than a three-dimensional one for calculation simplification. We used stationary and time-dependent studies to compute initial deformation and transient vibration. We chose the beam interface in structural mechanics to build a 1D Euler-Bernoulli cantilever beam model of the comb hair. The geometry and materials properties of the model, including linear elasticity and gradient stiffness, are assigned based on the experimental data. As the experimental data of Young's modulus can be fitted as $E = 25e^{\delta l/l_0}$ MPa, we can readily change the stiffness gradient through the stiffness gradient coefficient δ, for example, $\delta = 0$ corresponding to uniform stiffness and $\delta = 3$ for honeybee's comb. Note that the properties of the uniform beam are the same as those of the stiffness gradient beam except for Young's modulus. Owing to the difficulty in examining the damping of this tiny biological structure, a widely adopted Rayleigh damping method[51-53], in which the damping matrix is proportional to a linear combination of the mass and stiffness matrices, is assigned to the comb hair model. Then we set up the boundary conditions, including the free and fixed ends, and apply the force conditions obtained from the above section to the model. To save the calculation time, we discretized the 1D hair model with a line segment mesh of coarse element size. To obtain the dynamics of the whole comb hair, we selected 11 nodes uniformly distributed along the comb hair. The time-varying displacements of these nodes can be simulated and fitted to calculate the time-varying accelerations in MATLAB software (R2021b). We then determined the value of the maximum reverse acceleration for each node during the vibration process as well as the corresponding critical size of particles that can be catapulted. Moreover, the elastic energy storage and the energy conversion duration for various δ were also calculated through the finite element method and compared to reveal the influence of stiffness gradient.

Fabrication of the bioinspired stiffness-gradient catapult

Materials: Acrylic acid (AAc), choline chloride (CCl), poly (ethylene glycol) diacrylate (PEGDA, Mn = 700), 2-Hydroxyethyl methacrylate (HEMA), 2-hydroxy-4′-(2-hydroxyethyl)-2-methylpropiophenone (photoinitiator 2959), and Rhodamine 6G were purchased from Sigma-Aldrich (China) and used without further process. Deionized water (18.2 MΩ·cm) was used in all experiments.

Preparation: The basic formulation for fabricating an elastomer comb comprises ionic monomer (mixture of AAc and CCl), resin monomer (HEMA), cross-linker (PEGDA 700), photoinitiator (2959), and a specific amount of deionized water. Generally, the stiffness of a fabricated elastomer comb is positively correlated to the concentration of cross-linker and polymer in the cured solution, and one type of homogenous solution corresponds to one stiffness. When solutions of different concentrations are put together, the chemical elements spontaneously diffuse from high to low concentrations and gradually form a spatial gradient distribution. We chose three different concentrations of the solution, named solutions A, B, and C, which correspond to stiff, medium, and soft parts, respectively. We started with synthesizing a homogenous ionic monomer solution by mixing 14.5 g of AAc and 14 g of CCl and heating the mixture at 80 °C for 2 hours. For solution A, the ionic monomer solution was blended with 66.7 wt% (referred to as the amount of ionic monomer) of HEMA, 1 wt% of PEGDA, 1 wt% of 2959 under ultrasonication for forming a homogenous solution at room temperature. For solution B, the ionic monomer solution was mixed with 66.7 wt% of HEMA, 1 wt% of PEGDA, 2 wt% of 2959, and 66.7 wt% deionized water. For solution C, the ionic monomer solution was mixed with 66.7 wt% of HEMA, 1 wt% of PEGDA, 2 wt% of 2959, and 166.7 wt% deionized water. We subsequently added solutions A, B, and C to a customized mold at a volume ratio of 1:1:1 in turn and cured the solution in the mold under a UV lamp (purchased from Alibaba.com) for 40 minutes. The cured samples were washed with water to remove potential residual monomers and dried with airflow. After that, the stiffness gradient catapult (SGC) was obtained. To visualize the gradient stiffness, we colored solutions A, B, and C red, yellow, and blue by adding a very small amount of Rhodamine 6G, yellow, and blue dye (purchased from Alibaba.com), respectively. We also manufactured the control sample with uniform stiffness cured from solution C. The total volumes of solution used to fabricate the SGC and the control sample were the same.

Construction and characterization of the SGC-based cleaning robot

To test the solid repellency performance, we first developed a SGC-based cleaning robot by mounting the SGC on a motor-driven customized 3D-printed fixture. We then actuated the robot to sweep a surface covered with 25-μm silica particles and recorded the whole process using a high-speed camera (PhotronFASTCAM SA4) at 2000 frames per second. We analyzed the videos in the Tracker software for acceleration determination. To obtain the amount of the particles repelled, we measured the amount of the repelled particles by calculating the total area of particles departing from the SGC-based robot using an image processing program (ImageJ). We also measured the total area of the residual particles on the surface of the SGC-based robot, which allowed us to calculate the repellent fraction.

To demonstrate the practical potential, we engineered a self-cleaning solar panel system by integrating the SGC-based cleaning robot with a commercial solar panel. We tested an area of $4 \times 4\ \mathrm{cm}^2$ on the solar panel owing to the limited motion range of the motor. We conducted multiple consecutive cycles of contamination tests on the tested area by simulating the severe soiling conditions in arid/semiarid regions with frequent sandstorms. In each cycle, we contaminated the solar panel system with excess dust and actuated the SGC-based cleaning robot to sweep the solar panel surface. A digital sourcemeter (Keithley 2400) was used to measure the power generation performance of the tested area on the solar panel before and after cleaning with the rest area covered by an opaque patch. There was no additional manual maintenance on the cleaning robot between cycles. The same experiment procedures and conditions were applied to the control sample.

Statistics & Reproducibility

We carried out the statistical analyses using Origin software. The sample sizes and experiment repetitions are stated under each graph.

Data availability

Source data are provided with this paper.

Code availability

The custom-made code is publicly available in https://github.com/WinnJiang/Bee-code.

Methods only references

47 Li, C., Gorb, S. N. & Rajabi, H. Cuticle sclerotization determines the difference between the elastic moduli of locust tibiae. *Acta Biomater.* **103**, 189-195 (2020).

48 Vassiliadis, S., Kallivretaki, A. & Provatidis, C. Mechanical modelling of multifilament twisted yarns. *Fibers Polym.* **11**, 89-96 (2010).

49 Rao, B. N. & Rao, G. V. Large deflections of a nonuniform cantilever beam with end rotational load. *Forschung im Ingenieurwesen A* **54**, 24-26 (1988).

50 Shvartsman, B. Large deflections of a cantilever beam subjected to a follower force. *J. Sound Vib.* **304**, 969-973 (2007).

51 Kaliske, M. & Rothert, H. Damping characterization of unidirectional fibre reinforced polymer composites. *Composites Engineering* **5**, 551-567 (1995).

52 Rajabi, H. *et al.* Both stiff and compliant: morphological and biomechanical adaptations of stick insect antennae for tactile exploration. *J. R. Soc. Interface* **15**, 20180246 (2018).

53 Zabaras, N. & Pervez, T. Viscous damping approximation of laminated anisotropic composite plates using the finite element method. *Comput. Methods Appl. Mech. Eng.* **81**, 291-316 (1990).