

Collective mechanical adaptation of honeybee swarms

O. Peleg^{1,4}, J. M. Peters^{2,4}, M. K. Salcedo² and L. Mahadevan^{1,2,3*}

Honeybee *Apis mellifera* swarms form large congested tree-hanging clusters made solely of bees attached to each other¹. How these structures are maintained under the influence of dynamic mechanical forcing is unknown. To address this, we created pendant clusters and subject them to dynamic loads of varying orientation, amplitude, frequency and duration. We find that horizontally shaken clusters adapt by spreading out to form wider, flatter cones that recover their original shape when unloaded. Measuring the response of a cluster to an impulsive pendular excitation shows that flattened cones deform less and relax faster than the elongated ones (that is, they are more stable). Particle-based simulations of a passive assemblage suggest a behavioural hypothesis: individual bees respond to local variations in strain by moving up the strain gradient, which is qualitatively consistent with our observations of individual bee movement during dynamic loading. The simulations also suggest that vertical shaking will not lead to significant differential strains and thus no shape adaptation, which we confirmed experimentally. Together, our findings highlight how a super-organismal structure responds to dynamic loading by actively changing its morphology to improve the collective stability of the cluster at the expense of increasing the average mechanical burden of an individual.

Collective dynamics allow super-organisms to function in ways that a single organism cannot, by virtue of their emergent size, shape, physiology and behaviour². Classic examples include the physiological and behavioural strategies seen in social insects (for example, ants that link their bodies to form rafts to survive floods^{3–6}, assemble pulling chains to move food items⁷, and form bivouacs⁸ and towers⁹, as well as bridges and ladders to traverse rough terrain¹⁰). Similarly, groups of ‘daddy longlegs’ (order Opiliones) huddle together and emperor penguins cluster together for thermoregulation purposes¹¹. While much is known about the static forms that are seen in such situations, the stability of these forms to dynamic perturbation, and their global adaptation to environmental changes is much less understood.

European honeybees, *Apis mellifera* L., show many of these collective behaviours during their life cycle¹. For example, colonies reproduce through colony fission, a process in which a subset of the colony’s workers and a queen leave the hive, separate from the parent colony and form a cluster on a nearby tree branch¹. In these swarm clusters (which we will refer to as clusters), the bees adhere to each other and form a large structure made of ~10,000 individuals and hundreds of times the size of a single organism (Fig. 1a). Generally, this hanging mass of adhered bees takes on the shape of an inverted pendant cone; however, the resultant shape is also influenced by the surface to which the cluster is

clinging to (see two different examples in Fig. 1a). The cluster can stay in place for several days as scout bees search the surrounding area for suitable nest sites¹.

The colony is exposed to the environment during this stage and shows several behaviours to cope with the fluctuating thermal and mechanical environment. For instance, clusters tune their density and surface area to volume ratio to maintain a near constant core temperature despite large fluctuations in the ambient temperature^{12–14}. Furthermore, at high temperatures, the swarm expands and forms channels that are presumed to aid in air circulation¹². Moreover, in response to rain, bees at the surface arrange themselves to form ‘shingles’, shedding moisture efficiently from the surface of the cluster¹⁵. Similarly, the cluster is mechanically stable; while it sways from side to side in the wind (for example, see Supplementary Video 1), it could be catastrophic if the cluster breaks (when a critical load occurs) as the bees would lose the ability to minimize surface area to prevent hypothermia, while still being mechanically stable. However, the mechanism by which a multitude of bees work together to create and maintain a stable structure that handles both static gravity and dynamic shaking stimuli (for example, wind and predators) remains elusive. To understand this, we develop a laboratory experimental set-up, for ease of visualization and manipulation, to quantify the response of a honeybee cluster to mechanical shaking over short and long times.

To prepare a cluster, we attach a caged queen (see Supplementary Section A) to a board and allowed a cluster to form around her (Fig. 1b). The bees at the base grip onto an area that is roughly circular. The board is controlled by a motor that can produce movement in the horizontal direction at different frequencies (0.5–5 Hz) and accelerations (ranged 0–0.1g). We apply both discontinuous shaking in which the acceleration is kept constant and the frequency is modified, and vice versa, continuous shaking in which the frequency is kept constant and the acceleration is modified (see Supplementary Fig. 2).

For the case of horizontal shaking (for both discontinuous and continuous), the tall conical cluster swings to and fro in a pendular mode (one of the lowest energy modes of motion, see Supplementary Section C), with a typical frequency of ~1 Hz. However, over longer durations (that is, minutes), the bees adapt by spreading themselves into a flatter conical form (Fig. 1b–d and Supplementary Video 2), while their total number remains constant (measured by the total weight of the cluster). The final shape flattens as the shaking continues for longer, or as the frequency and acceleration of shaking increases. For the discontinuous shaking, when we plot the relative extent of spreading (scaled by a constant) as measured by $A(t)/A(0)$ for all different frequencies, as a function of number of shakes, the data collapse onto a single curve (Fig. 2a). This suggests that the

¹Paulson School of Engineering and Applied Sciences, Harvard University, Cambridge, MA, USA. ²Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA. ³Department of Physics, Kavli Institute for NanoBio Science and Technology, Harvard University, Cambridge, MA, USA. ⁴These authors contributed equally: O. Peleg, J. M. Peters. *e-mail: lmahadev@g.harvard.edu

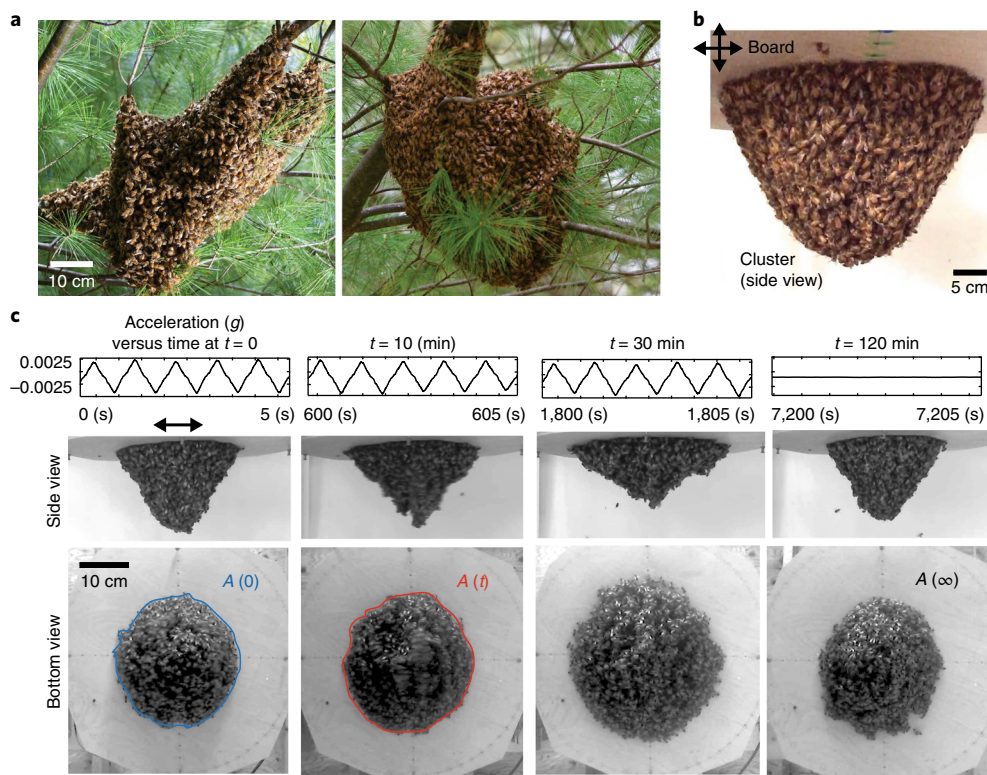


Fig. 1 | A mechanically adaptive honeybee cluster. **a**, Bee clusters on a tree branch. **b**, The experimental set-up consists of a motor driving a wooden board, on which a cluster of bees grips a roughly circular contact area. The motor can produce periodic movement in the horizontal or vertical axis at different frequencies and amplitudes. See Supplementary Fig. 1 for the full set-up. **c**, The top panel shows the acceleration of the board versus time at $t = 0$. The middle and bottom panels show how the bee cluster adapts its shape dynamically: elongated cluster at $t = 0$ (left column), spread-out cluster after horizontal shaking for 10 min and 30 min (middle columns), and elongated cluster after relaxation (right column); side and bottom views. The contact area before and after shaking is highlighted in blue and red, respectively.

cluster response scales with both the number and magnitude of shakes, but over much longer timescales than an individual event. The nature of this response is independent of the type of stimulus: when the shaking signal is continuous, we see a similar response (Fig. 2b). The graded adaptive response that scales with the number of shakes and is a function of applied displacements and frequencies, and the absence of any adaptation to very low frequencies and amplitudes (orange curves in Fig. 2b), suggests that there is a critical relative displacement (that is, a threshold mechanical strain) needed to trigger this adaptation. Once the shaking stops, the cluster returns to its original elongated cone configuration over a period of 30–120 min, a time that is much larger than the time for the cluster to flatten. This reversible cluster shape change in response to dynamic loading might be a functional adaptation that increases the mechanical stability of a flattened cluster relative to an elongated one.

To explore this suggestion quantitatively, we first define a laboratory-fixed coordinate system with axes as shown in Fig. 2c, with respect to which the board is at $\mathbf{r}_b(t) = [U_b, 0, W_b]$, the position of a bee i is defined as $\mathbf{r}_i(t) = [X_i(t), Y_i(t), Z_i(t)]$ and its displacement is defined as $[U_i(t), 0, W_i(t)] = \mathbf{r}_i(t) - \mathbf{r}_i(0) - \mathbf{r}_b(t)$. This allows us to track individual bees¹⁶ along the surface of the cluster along the centreline $X_i(0) = 0$ (Fig. 2d and Supplementary Video 3), over a period of oscillation. Comparing trajectories of bees in an elongated cluster and a flat cluster (that is, before and after shaking) shows that relative displacement between the bees at the cluster tip and bees at the base is significantly larger for an elongated cluster. Snapshots of tracked bees highlight the decoupling of movement of the tip and base of the cluster; that is, local deformations such as normal and shear strains are reduced in the mechanically adapted state corresponding to a

spread cluster. A similar trend is observed when the cluster is subjected to a single sharp shake (see signal at Supplementary Fig. 2c), as shown in Supplementary Video 4. These measurements confirm that the adapted flattened structure is indeed more mechanically stable in the presence of dynamic horizontal loads.

The spreading of the cluster is a collective process, begging the question of how this collective spreading behaviour is achieved. To study this, we tracked bees on the surface of the cluster during the process of adaptive spreading, particularly at the early stages. In Fig. 2e and Supplementary Video 5, we show how bees move from the tip regions that are subject to large relative displacements towards the base regions that are subject to small relative displacements. This suggests a simple behavioural law wherein the change in relative displacement U_i between neighbouring bees is a driver of shape adaptation: individual bees sense the local deformation relative to their neighbours and move towards regions of lower U_i (illustrated in Fig. 2f). In the continuum limit, this corresponds to their ability to sense strain gradients, and move from regions of lower strain (near the free tip) towards regions of higher strain (near the fixed base). It is worth noting here that this behavioural law is naturally invariant to rigid translation and rotation of the cluster, and thus depends only on the local mechanical environment each bee experiences.

However, what measure of the relative displacements might the bees be responding to? To understand this, we note that the fundamental modes¹⁷ of a pendant elastic cone are similar to those of a pendulum swinging from side to side, and a spring bouncing up and down, and their frequencies monotonically increase as a function of the aspect ratio of the cluster (Supplementary Fig. 3; see Supplementary Section C for details). To quantify the deviations

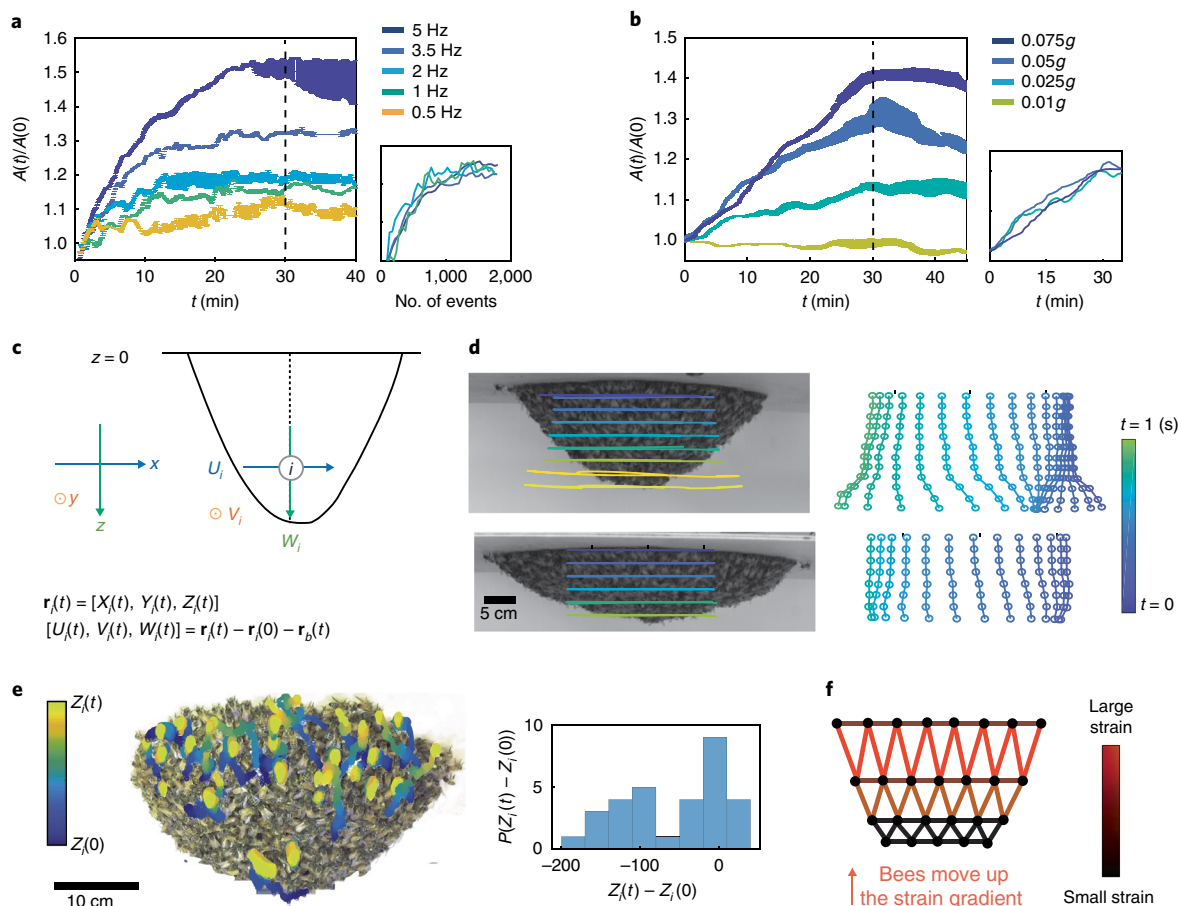


Fig. 2 | Quantifying adaptive response of the cluster to horizontal shaking. For all shaking frequencies, the base contact area of the cluster increases monotonically until a plateau is reached. Once shaking ceases, the cluster responds by gradually reverting to its original shape by increasing its contact area, but at a much slower rate. **a**, Ratio of the contact area of the base of the cluster divided by its original area $A(t)/A(0)$ as a function of time, for the discontinuous case. The colours represent results for different frequencies of periodic shaking. Its inset shows that the scaled base area collapses onto a master curve when plotted versus the number of shaking events. The error bars correspond to the standard deviation of three individual trials (see Supplementary Table 1 for more information about trial repetitions). **b**, $A(t)/A(0)$ for continuous shaking shows the same qualitative behaviour; note that when the acceleration is very small (0.01g), there is no response (that is, there is a critical threshold of forcing below which the bees do not respond). **c**, Coordinate systems of the laboratory frame and the displacement coordinates of the individual bees. **d**, Deformation of an elongated cluster before shaking began ($t=0$, top) and a flattened cluster after shaking ($t=30$ minutes, bottom) shows that displacement at the tip of the cluster is largest. On the right: time snapshots of a string of bees along the centre of the cluster (see Supplementary Video 3). **e**, Trajectories of individual bees during 5 min of horizontal shaking show that when the cluster spreads out, surface bees move upwards. Colour code represents time: the trajectory starts with blue and ends with yellow. Inset: probability distribution function of vertical displacement, showing a net upward trend. **f**, An illustration of the behavioural constitutive law: bees sense the local deformation of connections to their newest neighbours; once the relative deformation reaches a critical value, the bees move up the gradient in relative deformation.

from this simple picture due to the particulate nature of the assemblage, we turn to a computational model of the passive dynamics of a cluster and explore the role of shape on a pendant mechanical assemblage of passive particles used to mimic bees. We model each bee in the cluster as a spherical particle that experiences three forces: a gravitational force, an attractive force between neighbouring particles, and a force that prevents inter-particle penetration (see Supplementary Section C for further details). The bees at the base are assumed to be strongly attached to the supporting board, and those on the surface are assumed to be free. To study the passive response of the entire system, the board is oscillated at different frequencies and amplitudes, while we follow the displacement of individual particles, $U_i(\mathbf{r}_i)$, as well as the relative displacement between neighbouring bees $\mathbf{I}_{ij}(t) = \mathbf{r}_i(t) - \mathbf{r}_j(t)$ (Fig. 3a). Decomposing the vector $\mathbf{I}_{ij}(t)$ into its magnitude and direction allows us to define two local deformation measures associated with the local normal strain and shear strain. The local dynamic normal

strain associated with a particle (bee) i relative to its extension at $t=0$ is defined as $\delta l_i = \langle \max_{0 \leq t \leq T} \|\mathbf{I}_{ij}(t)\| - \|\mathbf{I}_{ij}(0)\| \rangle$, where T is the duration from the onset of the applied mechanical shaking until the swarm recovers its steady-state configuration, and the angle brackets represent the average over all bees j that are connected to bee i . The local shear strain is calculated from the changes in the angle $|\angle(\mathbf{I}_{ij}(t), \mathbf{I}_{ik}(t))|$ between $\mathbf{I}_{ij}(t)$ and $\mathbf{I}_{ik}(t)$, connecting bees i and j , and bees i and k , respectively, with the shear strain, $\delta\theta_i$ defined as $\delta\theta_i = \langle \max_{0 \leq t \leq T} |\angle(\mathbf{I}_{ij}(t), \mathbf{I}_{ik}(t)) - \angle(\mathbf{I}_{ij}(0), \mathbf{I}_{ik}(0))| \rangle$, where the angle brackets represent the average over all pair of bees $j-k$ that are connected to bee i .

As expected, we see that for the same forcing, the maximum amplitude of the local strains increases as the cluster becomes more elongated (Fig. 3a,b and Supplementary Video 6). Therefore, these local strains can serve as a signal for the bees to move, and a natural hypothesis is that once the signal is above a certain critical value, the bees move. However, how might they chose a direction? While

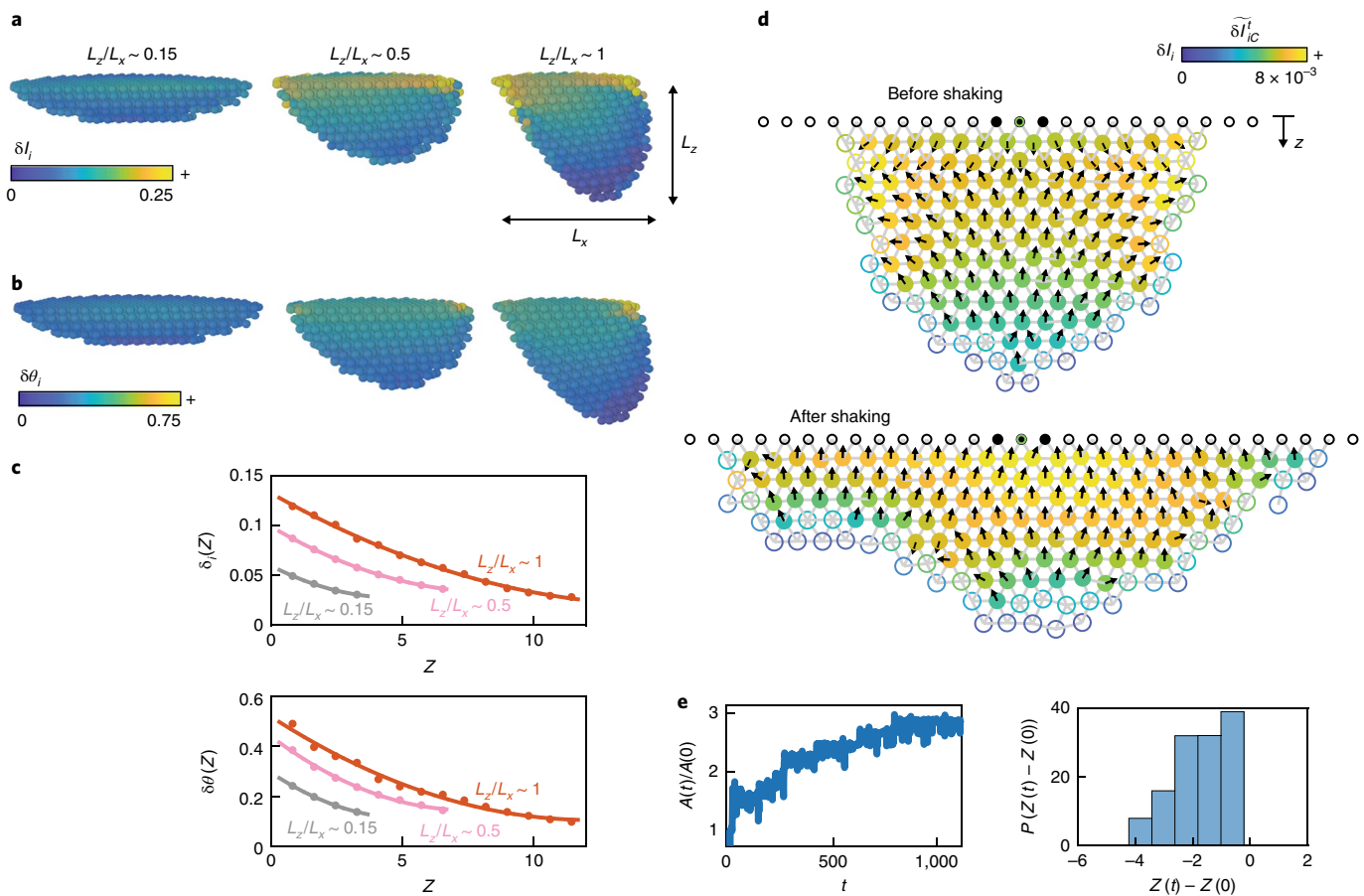


Fig. 3 | Computational model of mechanical adaptation. A cluster is modelled using particles that are linked via springs in a simple triangular lattice. **a**, Passive simulations: clusters of different aspect ratios (L_z/L_x), shown at the extreme of a period of horizontal oscillation. The colours represent the local normal strain of each honeybee δl_i , as defined in the text. Elongated clusters (on the right) experience a larger deformation at the tip of the cluster, while flattened clusters (on the left) experience much less deformation. **b**, For the same state as in **a**, we also show the maximum shear strain, $\delta\theta$. **c**, Plots of the mean normal and shear strain ($\delta l(Z)$ and $\delta\theta(Z)$) as a function of the distance from the base, Z , and aspect ratio L_z/L_x . We see that the maximum magnitude of the strains decreases as the cluster becomes flattened. **d**, Active stochastic simulations: when we impose a behavioural rule that allows the bees to sense the strains around them and move in the direction of increasing strain when the magnitude crosses a threshold (δl_i^t), this leads to spreading. The colours represent the local integrated signal, δl_i^t , and the arrows point towards higher local signal. **e**, The scaled base contact area $A(t)/A(0)$ as a function of time, with the probability distribution function of vertical displacement, shows a net negative response (that is, bees move upwards on average), similar to experimental observations (see Fig. 2e).

it may be plausible for the bees to simply move upwards against gravity, it is probably difficult to sense a static force (that is, gravity) when experiencing large dynamic forcing (that is, shaking) in a tightly packed assemblage. Instead, we turn to ask whether there are any local signals that would give honeybees a sense of direction. For all clusters, the strains are largest near the base (Fig. 3a,b and Supplementary Video 6) and decrease away from it, but in addition, as the cluster becomes more elongated, there are large local strains along the contact line where $x = \pm L_x/2$, where the bees are in contact with the baseboard. This is due to the effect of the pendular mode of deformation that leads to rotation-induced stretching in these regions. To quantify how the normal and shear strain vary as a function of the distance from the base, Z , we average δl_i and $\delta\theta_i$ over all bees that were at a certain Z position at $t=0$ and define the following mean quantities: $\delta l(Z) = \langle \delta l_i \rangle$, and $\delta\theta(Z) = \langle \delta\theta_i \rangle$, where the angle brackets indicate the average overall spring connection at the vertical position $r_z^i(0) = Z$. Similar to the experimental data, the simulations show that the displacements U_i for horizontal shaking of elongated clusters are larger in comparison to flattened clusters. As both strains $\delta l(Z)$ and $\delta\theta(Z)$ are largest near the base, $z=0$ (Fig. 3c and Supplementary Video 6), and decrease away from the

supporting baseboard, they may serve as local signals that bees at the tip of the cluster respond to by moving up the strain gradient (Supplementary Figs. 3–5 and Supplementary Videos 7 and 8).

This passive signature of a horizontally shaken assemblage suggests a simple behavioural hypothesis: bees can sense the local variations in the normal strain above a critical threshold, and move slowly up gradients collectively. We note that mechanical strain is invariant to translation and rotation of the whole assemblage; that is, it is independent of the origin and orientation of the frame of reference, and thus a natural choice (similar to how cells and bacteria respond to mechanical stresses¹⁸). This behaviour will naturally lead to spreading of the cluster and thence smaller strains on the cluster. Noting that the timescale of the response of the bees is of the order of minutes while the duration of a single period is seconds, it is natural to consider the integrated local normal strain signal: $\widetilde{\delta l}_i^t = \sum_{\tau=t-T_w}^t \delta l_i^\tau \times dt$, where T_w is chosen to be the period of the shaking (see detailed description in Supplementary Section C). Then our behavioural hypothesis is that when $\widetilde{\delta l}_i^t > \delta l_i^t$ the bee becomes active, and moves in the direction of the time-integrated negative normal strain gradient (that is, the active force is directed

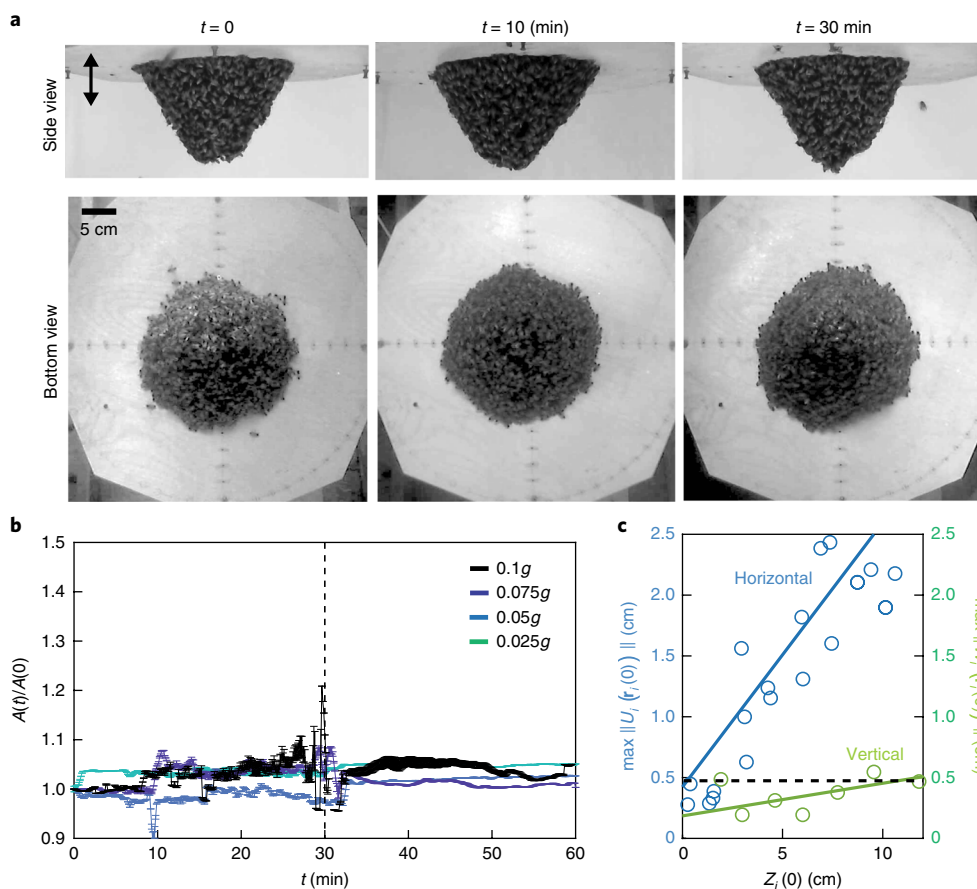


Fig. 4 | Response to vertical shaking. **a**, Vertical shaking (maximum acceleration 0.05g) of the bee cluster leads to a very small displacement. This is consistent with our simulations (see Supplementary Fig. 4 and Supplementary Section D) that vertical shakes do not destabilize the bees differentially. **b**, Contact area of the base of the cluster relative to its initial area $A(t)/A(0)$ versus time. Areas are defined as in Fig. 1d. The colours represent results for different accelerations of continuous shaking. **c**, Maximum displacement at the tip of a tall cluster as a result of a single horizontal and vertical shake. Bees do not respond or change the shape of the cluster when subjected to vertical shaking (green), but do respond substantially when shaken horizontally (blue). The black dotted line represents the experimentally observed threshold value to initiate active behaviour.

toward a higher local normal strain) according to the simple proportional rule $F^{\text{active}} = -f^{\text{active}} \delta l_i^t$. We note that moving up a gradient in time-integrated normal strain would also suffice to explain the observed mechanical adaptation.

We carry out our simulations of the active cluster in two dimensions for simplicity and speed (we do not expect any changes in three dimensions), allowing bonds to break and reform on the basis of proximity, similar to how bees form connections, and follow the shape of the cluster while it is shaken horizontally. We find that over time, the cluster spreads out to form a flattened cone (Fig. 3d,e and Supplementary Video 7), confirming that the local behavioural rule that integrates relative displacements that arise due to long-range passive coupling in the mechanical assemblage wherein bees actively move up the local gradient in normal strain δl_i is consistent with our observations.

If sufficiently large dynamic normal strain gradients drive shape adaptation, different shaking protocols that result in lower local strains should limit adaptation. One way is to shake the cluster gently, and this indeed leads to no adaptation (Fig. 2b responding to 0.01g). Another way to test our hypothesis is to shake the cluster vertically, exciting the spring-like mode of the assemblage. For the same range of amplitudes and frequencies as used for horizontal shaking, our simulations of a passive assemblage show that vertical shaking results in particles being collectively displaced up and down, with little variations in normal

strain. As expected, even in active clusters with the behavioural rule implemented, little or no adaptation occurs as the threshold normal strain gradient is not achieved (Supplementary Figs. 5 and 6 and Supplementary Video 8). To test this experimentally, we shake the cluster vertically. We see that, in this case, the cluster shape remains approximately constant (Fig. 4a,b) until a critical acceleration is reached, at which time a propagating crack results in the detachment of the cluster from the board (Supplementary Video 9). The resulting displacements at the tip for vertical shaking and horizontal shaking are in agreement with our hypothesis that differential normal strain gradients drive adaptation (Fig. 4c and Supplementary Video 10).

Our study has shown how dynamic loading of honeybee swarm clusters leads to mechanical adaptation wherein the cluster spreads out in response to repeated shaking that induced sufficiently large gradients in the relative displacements between individuals. We show that this adaptive morphological response increases the mechanical stability of the cluster. A computational model of the bee cluster treated as an active mechanical assemblage suggests that the active behavioural response of bees to local strain gradients can drive bee movement from regions of low strain to those of high strain and cause the cluster to flatten. This behavioural response improves the collective stability of the cluster as a whole via a reversible shape change, at the expense of increasing the time-averaged mechanical burden experienced by the individual.

Reporting Summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this article.

Data availability. The data that support the plots within this paper and other findings of this study are available from the corresponding author upon request.

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Author contributions

O.P., J.M.P. and L.M. conceived of the research study; O.P., J.M.P., M.K.S. and L.M. designed the experiments, O.P., J.M.P. and M.K.S. performed the experiments; O.P. analysed the data with the help of J.M.P.; O.P. and L.M. conceived of the behavioural rule and designed the simulations; O.P. carried out the simulations; O.P., J.M.P. and L.M. wrote the paper; L.M. supervised the project.

Competing interests

The authors declare no competing interests.

Additional information

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▶ Experimental design

1. Sample size

Describe how sample size was determined.

Each swarm consisted of about 10,000 honeybees. The number of bees was estimated using the weight of the swarm and the mean weight of individual bees. A size of 10,000 is the standard for artificial clusters prepared by commercial beekeepers.

2. Data exclusions

Describe any data exclusions.

There was no data exclusion.

3. Replication

Describe whether the experimental findings were reliably reproduced.

We performed three replications for each mechanical shaking condition (set by the board's movement direction, frequency, amplitude, and wave-form). All attempts for replication were successful.

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

The order in which mechanical shaking of different conditions was randomly chosen.

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

Investigators were not blinded during the experiments and the analysis.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a Confirmed

- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
- A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- A statement indicating how many times each experiment was replicated
- The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
- A description of any assumptions or corrections, such as an adjustment for multiple comparisons
- The test results (e.g. P values) given as exact values whenever possible and with confidence intervals noted
- A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
- Clearly defined error bars

See the web collection on [statistics for biologists](#) for further resources and guidance.

► Software

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7. Software

Describe the software used to analyze the data in this study.

The shape of the cluster was extracted using the image analysis tool box of MATLAB 2016a. Individual honeybee positions were digitized using a freely available MATLAB application, DLTdv5 (ref. 18 in the main text).

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* [guidance for providing algorithms and software for publication](#) provides further information on this topic.

► Materials and reagents

Policy information about [availability of materials](#)

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

There are no restrictions on availability of unique materials.

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

No antibodies were used.

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

No eukaryotic cell lines were used.

b. Describe the method of cell line authentication used.

No eukaryotic cell lines were used.

c. Report whether the cell lines were tested for mycoplasma contamination.

No eukaryotic cell lines were used.

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by [ICLAC](#), provide a scientific rationale for their use.

No commonly misidentified cell lines were used.

► Animals and human research participants

Policy information about [studies involving animals](#); when reporting animal research, follow the [ARRIVE guidelines](#)

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.

All of the honeybee swarm clusters studied were artificial clusters bought from honeybee suppliers (New England Beekeeping LTD, and Gold Star bees LTD). Bees were a mix of Russian, Italian, and Carniolan bees.

Policy information about [studies involving human research participants](#)

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

This study did not involved human research participants.