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# Influence of hydrodynamic pressure and vein strength on the super-elasticity of honeybee wings

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## ABSTRACT

The wings of honeybees (*Apis mellifera* L.) usually produce bending and torsional deformations during flapping wing movement. These deformations endow honeybees with perfect aerodynamic control to escape predators and exploit scattered resources. However, the mechanisms by which honeybee wings recover from large deformations are unclear. This study demonstrates that honeybee wings are super-elastic that they can recover rapidly from one extreme contorted state to their original position. A comparative experiment is conducted to evaluate the difference in super-elastic recovery between attached and detached wings. Results show that the structural stiffness of wings is affected by the reticulate vein and the haemolymph pressure generated by the blood circulation. Further analysis indicates that the haemolymph pressure can increase the stiffness of honeybee wings, especially that of the subcostal veins. This phenomenon shortens the recovery time of wing deflection behaviour.

## 1. Introduction

Insect wings are extremely thin and exhibit a hierarchical structure that is vital to the flight and foraging of insects (Young et al., 2009; Kang & Shyy, 2013, Mountcastle & Combes, 2013, 2014). When foraging in bushes or moving in beehives, honeybee wings frequently bump into obstacles, causing deformations or rotations. In addition, high flapping frequency, particularly at 230 Hz (Dudley, 2002; Altshuler et al., 2005; Ma et al., 2015), may cause wing deformations. Honeybee wings can offset the strain through their flexibility, which allows them to conserve kinetic energy at the end of each stroke and avoid fractures during flight. Honeybees maintain their flight through their wings' elasticity to facilitate recovery after deformation.

Materials embedded in the wings, particularly resilin, are essential to their flexibility. Resilin is highly flexible and resilient under natural conditions and capable of storing energy (Haas et al., 2000a,b; Vincent & Wegst, 2004; Ma et al., 2015; Rajabi et al., 2016). In addition, resilin protects the wings against permanent damage (Ma et al., 2015; Michels et al., 2016; Mountcastle & Combes. 2014). Meanwhile, various spikes in the vein joints can adjust the flexural stiffness of insect wings (Donoughe et al., 2011). Blood circulation is another factor that considerably affects the inertia, mass centre and natural frequency of wings (Arnold, 1964; Wootton, 1992) and enhances their stability. Notwithstanding, the effects of blood circulation on wing flexibility are rarely analysed. Previous studies have proposed several simplified physical models of insect wings, such as a whole inextensible Euler–Bernoulli beam (Michelin et al., 2008) and several beams connected by veins (Donoughe et al., 2011). A physical model reflecting the function of resilin joints and cuticular spikes is important to reveal the basic principles of insect wings (Donoughe et al., 2011).

In the present study, we conducted a comparative experiment between attached and detached wings to evaluate the super-elastic recovery of chordwise wing bending. Differences in recovery times can indicate differences in structural stiffness between attached and detached wings. Such information can be used to verify the effect of the haemolymph pressure generated by the blood circulation on wing stiffness. We also observed the morphology, especially the reticulate vein ultrastructure, of honeybees via scanning and transmission electron microscopy (SEM and TEM). We further analysed the synergistic effect of resilin and blood circulation on the quick recovery of honeybee wings and established a numerical model of the relationship between recovery time and contorted degree. This study can serve as a reference for elucidating the super-elastic mechanism of other insect wings.

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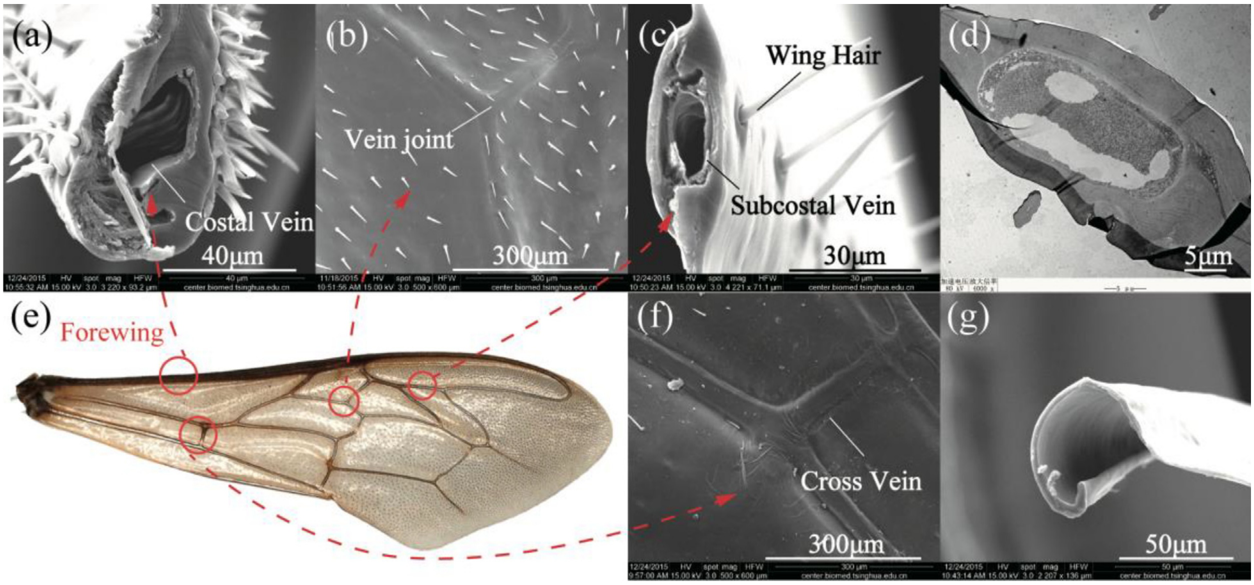

**Fig. 1.** Wing structure observed through SEM and TEM. (a) SEM images of the forewing costal vein section. (b) Mobile vein joint on the dorsal side. (c) SEM image of the forewing subcostal vein section. (d) TEM image of the transverse cross section of the forewing costal vein. All the vein walls exhibited regular closed texture, indicating a layered vein structure. (e) Image of the forewing structures. (f) Immobile vein joint on the ventral side. (g) SEM image of the wing membrane section.

## 2. Materials and methods

### 2.1. Experimental animals

The morphological data of this study dealt with adult foraging worker honeybees (*Apis mellifera* L.). All specimens were collected from a single wooden hive at the Intelligent & Bio-mimetic Machinery Laboratory of Tsinghua University, Beijing, China. The hive was maintained under an artificial light cycle, a constant temperature of 25 °C ± 2 °C and a constant environmental humidity of 50%. No specific permissions were required for these locations or activities. Moreover, the field studies did not involve endangered or protected species.

### 2.2. Macro- and microstructure of honeybee wings

The wing has a complex network structure, including resilin, the membrane, veins, joints and cuticular hairs. Resilin stripes and pitches are detected near the areas connecting the veins and membrane. These areas are located in a single side or in both sides of the wings (Ma et al., 2015). Six pieces of honeybee wings were fixed on a rotating specimen holder, and the wing microstructure was observed through SEM (Philips XL30 ESEM) and TEM (Hitachi H7650, Japan), respectively.

### 2.3. Observational experiments of elasticity recovery for honeybee wings

The elasticity recovery of 33 detached and 33 attached bee wings was observed with a high-speed camera (Olympus i-SPEED TR). The root of the wing was fixed at the centre of a goniometer stage, and the tip of the wing was clamped by a pair of tweezers controlled by an electro-holding magnet. At the initial state, the ventral side of the right wings faced up. Then, the goniometer stage was rotated clockwise, whereas the left wing was rotated counterclockwise. The tweezers were released after rotating the goniometer stage from 60° to 360° in a 30° pace. The rotation angle of the wings is defined as the rotation angle of the goniometer stage. A detailed description of the experiment setup can be found in Supplementary Material.

Force measurements with a tailored device were implemented on two pieces of honeybee wings to determine the bending stiffness. A smooth glass substrate was attached to the end of the wing fixed on a Mettler-Toledo Analytical Balance (Mettler-Toledo, XPE205, Switzerland). The contact area of the wing was observed under a microscope (Motic, PSM 1000, China) and was recorded at 100 Hz by a high-speed video camera (Artray, Artcam 424KY, Japan). Details are listed in Supplementary Material. The active manipulation of honeybees was eliminated because the hinge of the wing was clipped using two magnets.

## 3. Results

### 3.1. The morphology of honeybee wings

Fig. 1 shows the macroscopic and microscopic structures of honeybee wings. The tubular structures (Fig. 1a,b,d) are the pathways for the blood, the tracheae and the nerves. The blood in the veins also affects the vibration characteristics by increasing the mass and the moments of inertia (Wootton, 1992). The joints where the veins merge also have various functions (Ma et al., 2015). Assuming that cuticular hairs on the veins and the membrane are evenly distributed on the dorsal side of the wings, we did not consider the effect of the hairs on the recovery process. Newman (1982) regarded joint-associated spikes in the odonate wings as ‘joint-stoppers’. These spikes inhibit the rotation of the cross veins around the longitudinal wings. To the best of our knowledge, no study has previously demonstrated these results in honeybee wings. Notably, the spikes exhibit various morphologies (Donoughe et al., 2011).

Basing on the structure of honeybee wings, we can determine the average parameters of three honeybee wings. Viewing the section as a hollow rectangle, we measured the length ($l$), width ($b$) and thickness ($h$) of the membrane as 8.4, 2.6 and 2.9 μm, respectively. The inner height ($h_{v,1}$) was 18.83 μm, the length ($b_{v,1}$) was 35.43 μm, the outer height ($h_{v,2}$) was 28.38 μm and the length ($b_{v,2}$) was 57.64 μm. The cross section of the subcostal veins was rectangular, whereas that of the costal veins was cylindrical. For the subcostal veins, the thickness of the side vein wall was approximately 2.3 times than that of the dorsal (or ventral) side.