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Erection mechanism of glossal hairs during honeybee feeding

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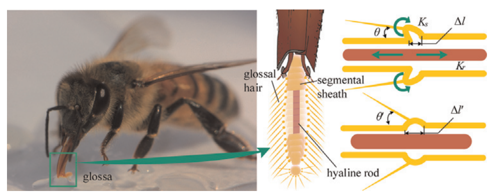
HIGHLIGHTS

- Hair erection is generated by the tension of hyaline rod and elasticity of sheath.
- A physical model is established to reveal the mechanism of hair erection.
- Results indicate that the glossa of honeybee is just like a compression spring.

GRAPHICAL ABSTRACT



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ABSTRACT

Many animals use their mouthparts or tongue to feed themselves rapidly and efficiently. Honeybees have evolved specialized tongues to collect nectar from flowers. Nectar-intake movements consist of rapid protraction and retraction of glossa from a tube formed by the maxillae and labial palps. We establish a physical model to reveal the driving mechanism of hair erection. Results indicate that the glossa of honeybees is similar to a compression spring. Experimental results show that hair erection is generated by the tension of hyaline rod and the elasticity of segmental sheath. The retractor muscle of hyaline rod is contracted at first, which compresses the sheath of pigmented rings and flattens the hairs. While the retractor muscle of hyaline rod relaxes, the elastic energy storage in the compressed glossal sheath will release to change the equivalent stiffness of glossal sheath and erect glossal hairs. These results explain the erection mechanism of glossal hairs during honeybee feeding.

1. Introduction

The drinking mechanisms of many animals have been observed and analyzed (Rico-Guevara and Rubega, 2010; Kim et al., 2012). Some scholars consider animal tongues or tongue-like devices as rigid bodies while drinking, such as the tongue of butterflies (Lee et al., 2014), shorebirds (Prakash et al., 2008), cats (Reis et al., 2010), and dogs (Crompton and Musinsky, 2011). Suction was a main drinking pattern for some insects, which used negative suction pressure generated by the muscular pump located in their head with their tongue protracted and retracted in a tube formed by their mouthparts (Borrell, 2006; Falibene et al., 2009; Kim et al., 2011). However, the dynamic surfaces of some tongues, such as the papillae on the tongue surface of a bat, played an important role in improving the ability of trapping floral nectar (Harper et al., 2013). The papillae on the tongue surface of bats become erect with the action of congestive tongue tip while dipping nectar. Nectar trapped between rows of erected papillae is then carried into the mouth (Wu et al., 2015).

Considering the importance of honeybees in the commercial world, numerous scholars have carefully investigated the proboscis and drinking patterns of honeybees, for instance, their olfactory memory (Wright et al., 2013), gustation preferences (Tan et al., 2014), and nectar-lapping strategies (Yang et al., 2014). The morphology and function of adult mouthparts in flower-visiting insects are adapted for nectar feeding (Krenn et al., 2005). The mouthpart of honeybees, as a versatile tool, is composed of a pair of labial palp, a pair of maxillae (Fig. 2A), and a glossa covered with bushy hairs (Li et al., 2015). To take up the sweet nectar, honeybees erect their tongue hairs at a perfect degree from the base to the tip

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of the tongue. Our previous study indicated that standing up their tongue hairs in this order, and to this degree, may increase drinking efficiency (Wu et al., 2015). Although the kinematics of the hair erection of a honeybee while dipping nectar has been reported (Yang et al., 2014; Li et al., 2015; Wu et al., 2015), the driving mechanism of this behavior has no reasonable elucidation.

In this study, we record a high-speed video of the hair erection of *Apis mellifera ligustica* while dipping nectar to observe a special behavior in nectar drinking. Basing on the segmental microstructure of the glossa, we establish a theoretical model for the driving mechanism of hair erection on honeybee glossa.

2. Materials and methods

2.1. Honeybee specimens

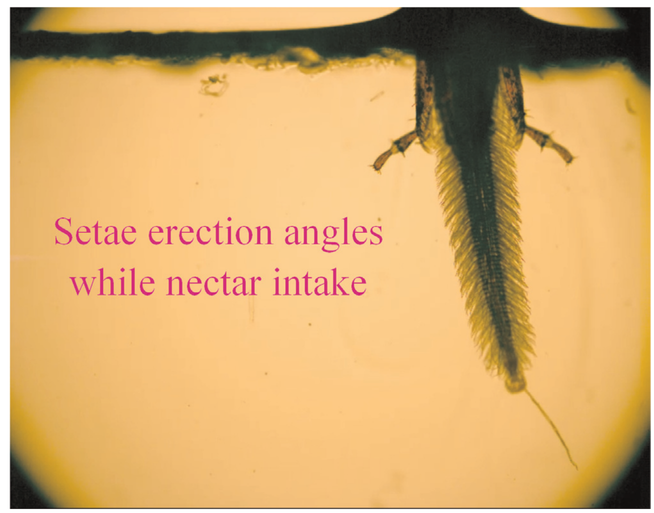
All honeybees were collected in Tsinghua University of Beijing, China (40.000153°N, 116.326414°E) and housed in a wooden beehive where the temperature and humidity were maintained at 25 °C and 50%, respectively. No specific permissions were required for these locations/activities. We confirmed that the field studies did not involve endangered or protected species.

2.2. Microstructure of glossa

To investigate the microstructure of glossa, we examined the tongue of honeybees via scanning electron microscopy (SEM; FEI Quanta 200, Netherlands) and transmission electron microscopy (TEM; Hitachi H7650, Japan). Specimens for the SEM and TEM experiments were completely dehydrated with ethanol (100%) over several stages, dried using hexamethyldisilazane, sputter-coated with gold (Emitech K500, Ashford, Kent, UK), and fixed on a rotatable specimen holder. Specimens were embedded in methacrylate to investigate the ultrastructure of glossa. Methacrylate was then dissolved using xylol. Xylol was gradually replaced by acetone, and specimens were dried at the critical point and subsequently examined using the SEM and TEM.

2.3. Observation of nectar feeding of honeybees

The experimental setup for observing the nectar feeding of honeybees was composed of a positioner and a microscope (Axiostar Plus, Zeiss, Germany) equipped with a positioner, a height adjuster, a glass feeder filled with artificial nectar (35 % wt/wt sucrose solution), a light source, and a high-speed camera (Olympus, i-Speed TR, Japan) (Fig. 1A and B). High-speed video of



Video S1. Setae erection of honeybee's glossa in the process of nectar-intake. Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.jtbi.2015.09.002.

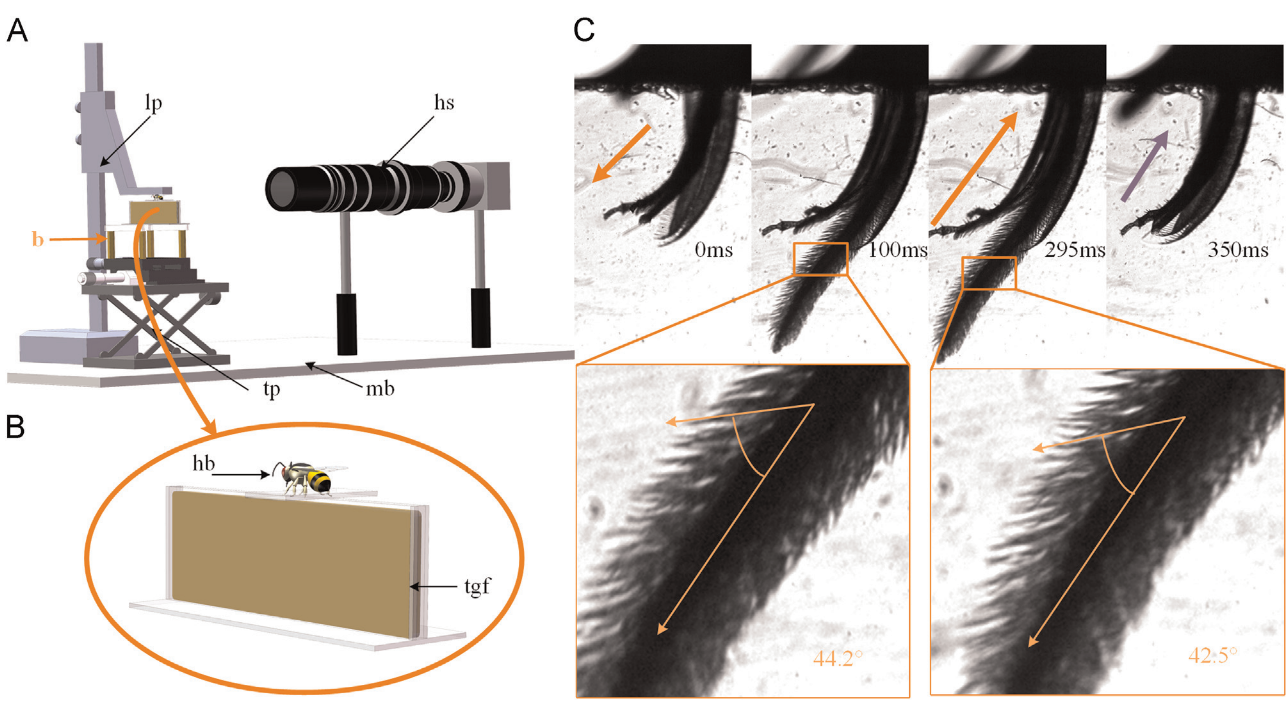


Fig. 1. Rhythmical erection of glossal hairs when dipping nectar. (A, B) Experimental observations of nectar intake with the role of glossa. We filmed three samples feeding from a transparent glass tank and captured the position of glossa at 1000 frames per second. lp, lifting platform; tp, three-axis precision positioner; hs, high-speed image acquisition system; mb, mounting base; hb, honeybee; tgf, transparent glass feeder. (C) Selected frames from a high-speed video (Movie S1) of a honeybee dipping nectar, with direction of movement in each video frame. The timing of each figure relative to the first outline within the sequence is provided in milliseconds (ms).