

Kinematics of Stewart Platform Explains Three-Dimensional Movement of Honeybee's Abdominal Structure

Youjian Liang,* Jieliang Zhao,* Shaoze Yan,¹ Xin Cai, Yibo Xing, and Alexander Schmidt

Division of Intelligent and Biomechanical Systems, State Key Laboratory of Tribology, Department of Mechanical Engineering, Tsinghua University, Beijing, 100084, P. R. China and ¹Corresponding author, e-mail: yansz@mail.tsinghua.edu.cn

*These authors contributed equally to this study.

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Abstract

The Stewart platform is a typical parallel mechanism, used extensively in flight simulators with six degrees of freedom. It is rarely found in animals and has never been reported to regulate and control physiological activities. Now an equivalent Stewart platform structure is found in the honey bee (Hymenoptera: Apidae: *Apis mellifera* L.) abdomen to explain its three-dimensional movements. The stereoscope and scanning electron microscope are used to observe the internal structures of honeybees' abdomens. Experimental observations show that the muscles and intersegmental membranes connect the terga with the sterna and guarantee the honey bee abdominal movements. From the perspective of mechanics, a Stewart platform is evolved from the lateral connection structure of the honey bee abdomen, and the intrasegmental muscles between the sternum and tergum function as actuators between planes of the Stewart platform. The extraordinary structure provides various advantages for a honey bee to complete a variety of physiological activities. This equivalent Stewart platform structure can also be used to illustrate the flexible abdominal movements of other insects with the segmental abdomen.

Key words: Stewart platform, honey bee, abdominal movement, lateral connection

The abdominal attributes for insects, such as honeybees (Slessor et al. 2005, Trhlin and Rajchard 2011), *Parantica sita niponica* (Lepidoptera: Danaidae) (Senda et al. 2012), dragonflies (Miller 1962), and *Drosophila melanogaster* (Diptera: Drosophilidae) (Llopart et al. 2002) must move to gather food, control flight, breathe, and mate. For instance, *Apis mellifera carnica* (Hymenoptera: Apidae) recruit their nestmates by performing the waggle dance to describe the distance and direction to food sources (Riley et al. 2005). Drosophilae can adjust the posture of their caudal bodies to control flight through deflecting their abdomens (Zanker 1987). However, the mechanism underlying the deformable function of the insect abdomen is unclear. Here, we use the honey bee as a representative insect model to analyze the relationship between the movements and abdominal structures.

Recently, research focused on the relationship between abdominal motion and flight behavior. *Apis mellifera* Linnaeus, 1758 (Hymenoptera: Apidae) modulated their abdominal posture based on the speed of the visual pattern (Luu et al. 2011, Dyhr et al. 2013). Abdomen elevation increased as the rate of visual motion

increasing. However, visual information is not the only sense that affects the abdominal position. Taylor et al. (2013) investigated the influence of airflow on the control of the honey bee's streamlining response. A model was established based on the nonlinear combinations of optic flow and air speed to predict the abdomen response. Abdominal posture, such as the waggle dance (Judd 1995, Srinivasan 2010), is also a critical factor for honeybees to communicate. Information about the distance and the direction from the nest to the food source was shared by the waggle dance (Von Frisch 1967). Furthermore, Zhao et al. (2015, 2016) suggested that the folded intersegmental membrane (FIM) played a dominant role in the flexion and extension of honey bee abdomen. In addition, Zhao et al. (2017) found that honeybees swung their abdomens to dissipate residual flying energy when landing on a wall. Afterward, an aerospace vehicle was modified by adding a morphing nose cone (Zhao et al. 2017).

The anatomy of honeybees' physiological structures (Snodgrass 1925, Bharadwaj and Banerjee 1969, Norman et al. 2013) provided a preliminary understanding of the internal lateral connection of the honey bee abdomen. However, a systematic analysis on the structure,

especially from the perspective of mechanics, has not been proposed yet to interpret the abdominal behavior.

In this paper, the internal lateral connection structure of the honey bee (*Apis mellifera* L.) abdomen is illustrated and an equivalent Stewart platform is found to explain its three-dimensional movements. The Stewart platform (Stewart 1965) is a typical parallel mechanism with six degrees of freedom (Dasgupta and Mruthyunjaya 2000) which is used extensively in flight simulators. It has not been found among animals and has never been reported to regulate and control physiological activities. Kinematic analysis of the model is accomplished based on abdominal movements. This biological structure provides flexibility to the variety of physiological activities of the honey bee abdomen. It will be of high importance for bionics design.

Materials and Methods

Experimental Animals

This work was performed on adult worker honeybees (*A. mellifera* L.). Hundreds of honeybees were kept in a transparent cage with the size of 120 × 40 × 60 cm. They were fed with honey and sucrose water. To simulate a natural environment, a potted plant was placed in the cage and a fluorescent lamp was used to simulate the sun with a light/dark regime of 16:8 (L:D) h. All specimens were collected from a single hive maintained at the intelligent bio-mechanical laboratory

of Tsinghua University, Beijing, China (40.00 N, 116.33 E). This examination did not involve endangered or protected species, and no specific permissions were required for the locations or activities.

Sample Preparation

Honeybees' abdomens were dissected and fixed in a 2.5% glutaraldehyde solution for more than 4 h. Then the samples were washed with 0.1 mol/liter phosphate buffer (pH 7.2) three times, dehydrated in an ethanol series (50, 70, 85, 90, and 100%, 15 min every time), soaked in tert-butanol, and dried with a critical point dryer. To obtain the FIM implied in the honey bee abdomen, the honey bee was dissected and boiled in 9% sodium hydroxide solution for 3 min before the last step.

Microstructure Observation Experiments

To improve our understanding of the abdominal microstructure, 16 honeybees were used for dissections with the help of a stereoscope (Stemi 508, Carl Zeiss AG, Germany). The viscera and terga in the abdomen were removed. Subsequently, 50 specimens were sputtered with gold after the pretreatment and captured by a scanning electron microscope (FEI Quanta 200, FEI Company, Eindhoven, Netherlands). The motion of the honey bee abdomen was recorded by the high-speed camera (Olympus i-SPEED TR, Tokyo, Japan) (Supp. Movie 1).



Fig. 1. Anatomy of the honeybee abdomen captured by a stereoscope. (a) Connections of terga and sterna; (b) Overall contour of the sterna. The abdomen is unfolded, the sterna are symmetrical; (c) Right half of the abdomen. The apodemes are wrapped in white gelatinous substances.

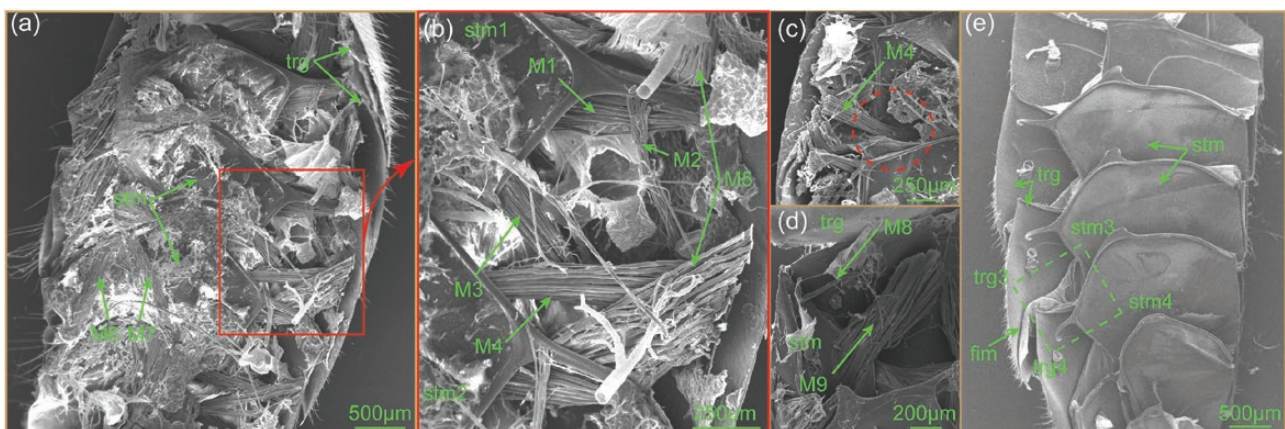


Fig. 2. Internal lateral connection microstructure captured by scanning electron microscope. (a) Lateral connection microstructure of the right part of the abdomen. A multitude of muscles and membranes exist between terga and sterna; (b) Partial enlargement. Muscles on the apodeme and the sides of the sternum are enlarged; (c) Distribution of the muscle M4 on the sternum; (d) The junction between the sternum and the tergum of the first segment; (e) Lateral connection microstructure without muscles of the left part of the abdomen. The folded intersegmental membrane connects terga and sterna together. trg, tergum; stm, sternum; M, muscle; fim, folded intersegmental membrane.

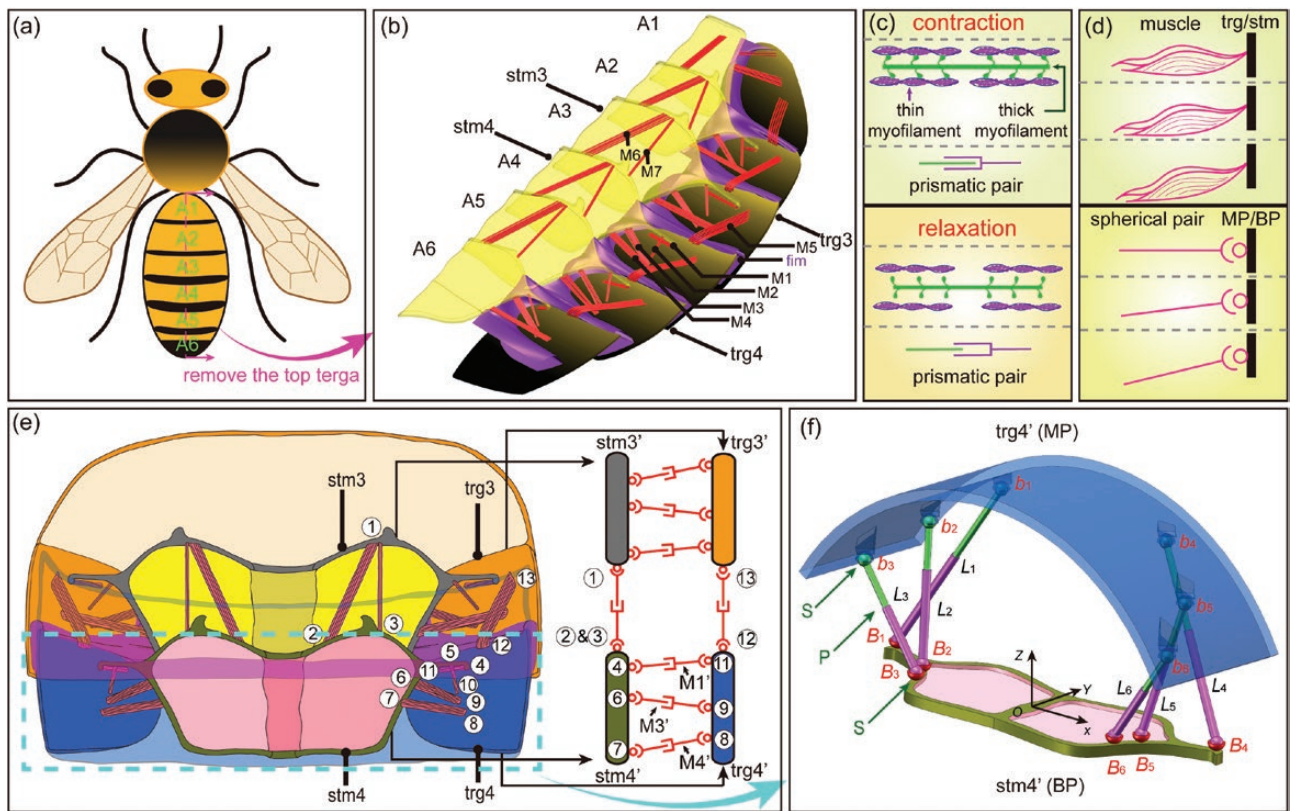


Fig. 3. Equivalent Stewart platform of the lateral connection structure in the honeybee abdomen. (a) Model of a honeybee abdomen; (b) 3D model of the internal lateral connection microstructure of right part of honeybee abdomen; (c) Comparative process of a muscle with a prismatic pair; (d) Comparative process of the junction with a spherical pair; (e) Schematic of the partial adjacent segments; (f) Diagram of the Stewart platform developed from the intrasegmental lateral connection structure of a honeybee abdomen. trg, tergum; stm, sternum; M, muscle; S, spherical pair; P, prismatic pair; MP, moving platform; BP, base platform.

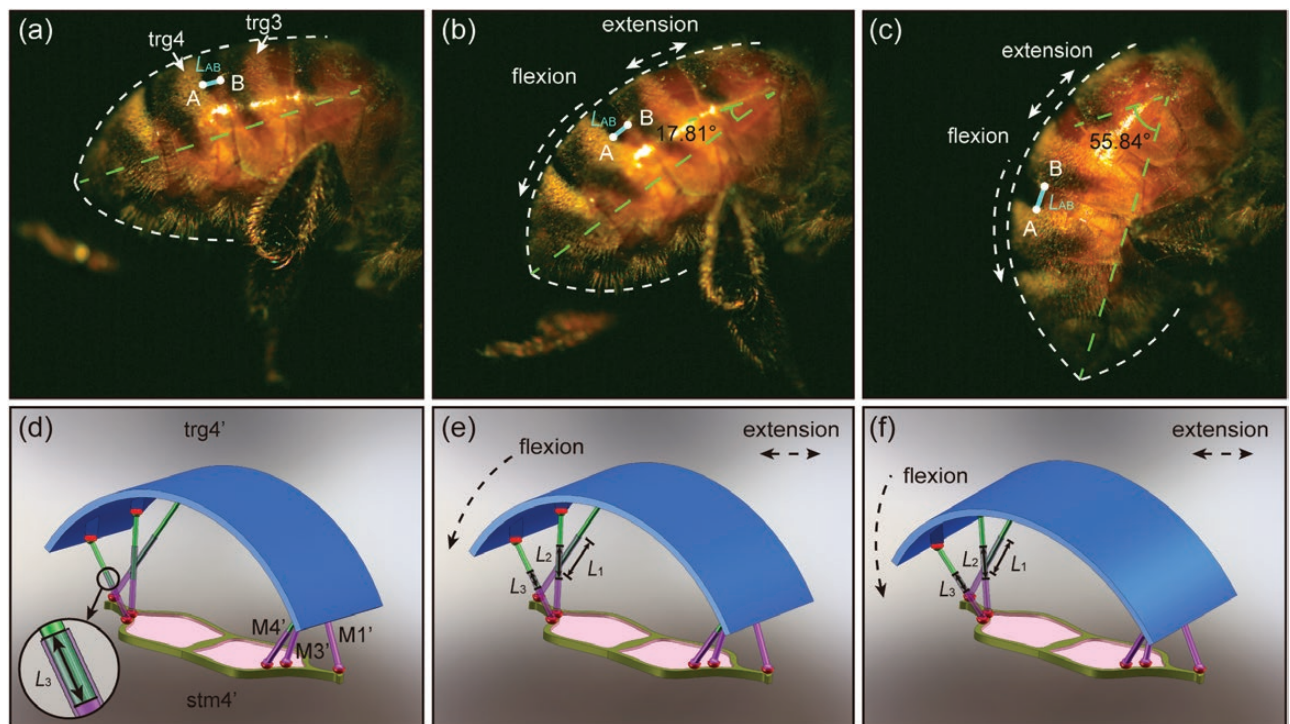


Fig. 4. Flexion of honeybee abdomen. (a-c) Three states of the honeybee abdomen captured by a high-speed camera; (d-f) Corresponding states of the schematic diagrams. trg, tergum; stm, sternum; M, muscle.

Results

As shown in Fig. 1a, the viscera and top terga of the honey bee abdomen are removed. Terga and sterna overlap one another, each rear edge overlapping the front margin of the segment next behind. The abdomen is unfolded and we obtain the arrangement of the terga and sterna (Fig. 1b). There are some white gelatinous substances adhering to the terga and sterna (Fig. 1c). In fact, these white gelatinous substances represent muscles.

In order to capture the intuitionistic internal structures of honey bee abdomen, the scanning electron microscope experiment is carried out (Fig. 2a). We eliminate the top terga and obtain the right internal lateral connection structure of the honey bee abdomen. There are groups of muscles and membranes distributing between the terga and sterna. The muscle M1 is protractor muscle and M2 is opercular muscle (Fig. 2b). M2 is responsible for opening and closing the spiracle. The muscles M3 to M7 stand for the retractor muscles (Dade 1962, Norman et al. 2013). On the other hand, muscles can be divided into two categories: M1 to M4 are intrasegmental muscles, whereas M5 to M7 represent intersegmental muscles. Notably, muscle M4 is located on stm1 (Fig. 2c) instead of stm2. As demonstrated in Fig. 2d, there are only two beams of muscles M8 and M9 locating between the sternum and tergum of the first segment. The distribution of muscles differs from other segments. As shown in Fig. 2e, muscles are removed and it is the FIM that connects trg3, trg4, stm3, and stm4 together.

Table 1. Length changes of the three limbs and the distance variations between reference points A and B

	Values (mm)					
	1st state		2nd state		3rd state	
L_{AB}	Fig. 4a	2.4	Fig. 4b	2.8	Fig. 4c	3.6
L_1	Fig. 4d	31.4	Fig. 4e	30.0	Fig. 4f	27.5
L_2		21.1		20.5		20.2
L_3		9.5		10.5		11.0

Discussion

The abdomen of a worker honey bee consists of six well-defined, visible segments (except for the propodeum) (Fig. 3a). The 3D model of the lateral connection structure is drawn by using SolidWorks based on the above results (Fig. 3b). The muscles can be generalized to actuators. As shown in Fig. 3c, the muscle is comparable to a prismatic pair on the basis of myofibril sliding theory (Dragomir 1970). Relative movements between the thin and thick myofibrils in the processes of contraction and relaxation are analogous to the motions of prismatic pairs in mechanisms. As manifested in Fig. 3d, the relative motion of the muscle and tergum (trg)/sternum (stm) is congruent with the rotating of a spherical pair around the moving platform (MP)/base platform (BP). We focus on two consecutive segments A3 and A4 because the connective structures between terga and sterna are homologous (Fig. 3e). Intersegmental muscles combine the adjacent segments together and play a dominant role in the physiological activities of honey bee abdomen especially in extension and contraction. From the perspective of mechanics, a Stewart platform is developed from the intrasegmental lateral connection structure of honey bee abdomen (Fig. 3f). The trg4 is equivalent to the MP, whereas the stm4 is equivalent to the BP. The blue board represents the trg of the whole segment, whereas the green one represents the stm. Moreover, the coordinate system is established on the BP. Points B_1-B_6 and b_1-b_6 stand for the coordinates of the spherical pairs' centers. The parameters L_1-L_6 represent the distances between the spherical pairs located on the BP and MP. In addition, this model may also be available to elucidate the abdominal deformation mechanism of butterflies, dragonflies, and drosophilae, since the abdomens of these three insects have similar physiological structures (Mill 1964, Wasserthal et al. 1980, Currie and Bate 1991). For example, there are many bundles of muscles at the lateral connection of the drosophilae. This structure is a redundant input mechanism in mechanics which indicates that the number of muscles can be reduced appropriately.

The deformable honey bee abdomen has diverse motion forms, such as extension, contraction, flexion, and waggle (Supp. Movie 1). As shown in Fig. 4a, it is the initial state of honey bee abdomen. As illustrated in Fig. 4b and c, the relative rotation angles compared with the initial state are 17.81 degrees and 55.84 degrees, respectively.

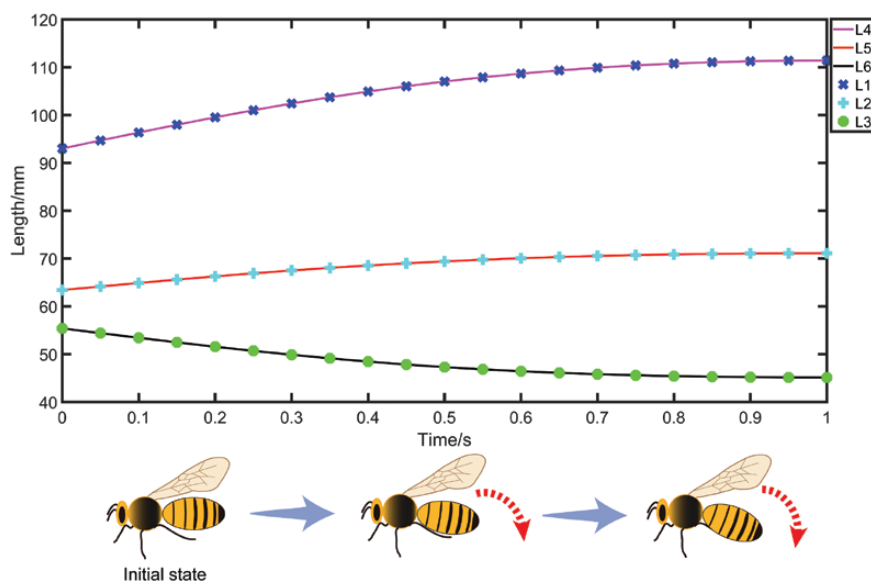


Fig. 5. Length changes of the six limbs of the Stewart platform in the process of honeybee abdominal flexion.

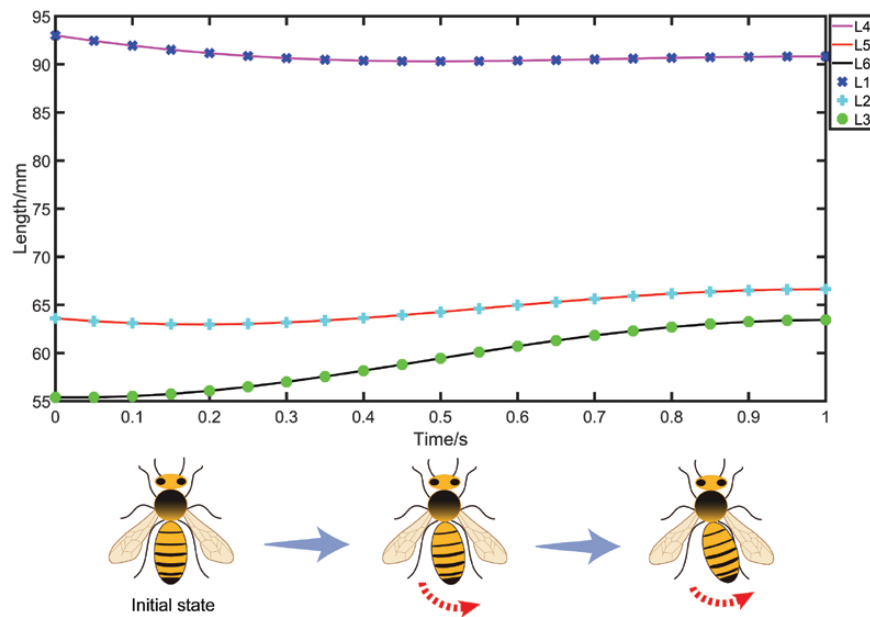


Fig. 6. Length changes of the six limbs of the Stewart platform in the process of honeybee abdominal waggle.

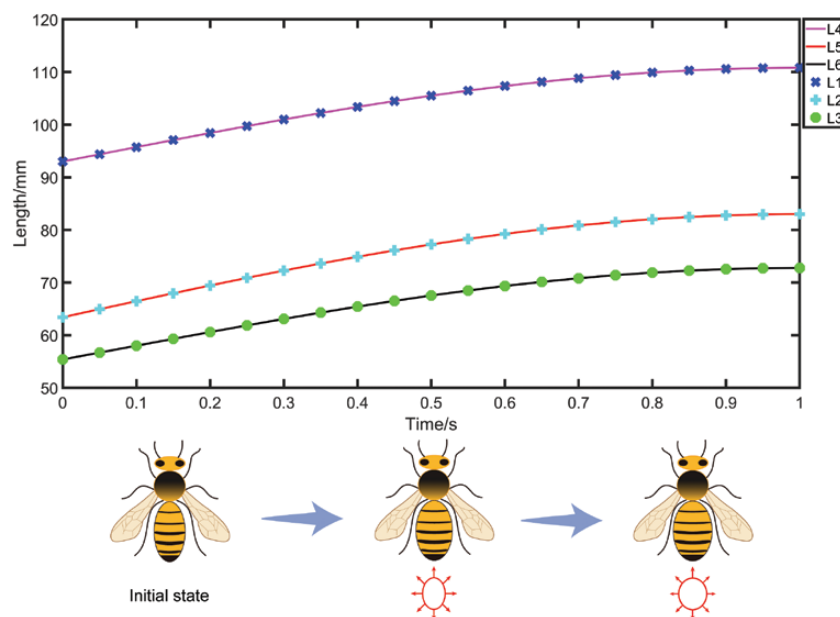


Fig. 7. Length changes of the six limbs of the Stewart platform in the process of honeybee abdominal breath.

The extensions of the distance between reference points A and B are 0.4 mm and 1.2 mm, respectively. The entire abdomen moves together through the connection of the intersegmental muscles in the process of flexing. Similarly, gradient changes of the branch chains result in the flexion movement (Figs. 4d–f) of the Stewart platform (Supp. Movie 2). Changes in the limbs' lengths, which can be seen from Table 1, are synchronous to the flexion of the honey bee abdomen. It means that the variation in the Stewart platform is consistent with the actual motion of the honey bee abdomen.

Furthermore, the relationship between the model and the physiological activities of the honey bee abdomen is elucidated by the kinematic analysis. As shown in Fig. 3f, the coordinate system is established on the BP. The flexion of honey bee abdomen is the same

as the rotating of MP around X-axis in this model. Here, the MP rotates 55.84 degrees around X-axis and the length changes of the six limbs are shown in Fig. 5. In this process, the lengths of L_1 , L_4 , L_2 and L_5 increase, whereas the lengths of L_3 and L_6 decrease. In addition, the waggle of honey bee abdomen is congruent with the rotating of MP around Z-axis. Likewise, assuming that the rotation angle is 25 degrees. In this motion, the lengths of L_1 , L_4 , L_2 and L_5 initially decrease and then increase while the lengths of L_3 and L_6 increase throughout the entire process (Fig. 6). Besides, the respiration of honey bee abdomen is analogous to the moving of MP along Z-axis. As shown in Fig. 7, all lengths of the limbs increase gradually. The kinematic analysis of the Stewart platform can be seen from the Supp. Information.

Differences, such as size and configuration, may exist between the model and the honey bee abdominal structures. However, this work aims to reveal the deformation mechanism of honey bee abdomen based on the theoretical analysis of the Stewart platform. This parallel mechanism can be adjusted appropriately according to actual needs. Although this work only shows movements of a single abdominal segment, variations of the other abdominal segments are analogous because the distribution pattern of the muscles for each segment is homologous. Thus, the Stewart platform properly illustrates the physiological activities of honey bee abdomen through the interaction with intersegmental structures.

Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

Acknowledgments

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