

The moment before touchdown: landing manoeuvres of the honeybee *Apis mellifera*

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SUMMARY

Although landing is a crucial part of insect flight, it has attracted relatively little study. Here, we investigate, for the first time, the final moments of a honeybee's (*Apis mellifera*) landing manoeuvre. Using high-speed video recordings, we analyse the behaviour of bees as they approach and land on surfaces of various orientations. The bees enter a stable hover phase, immediately prior to touchdown. We have quantified behaviour during this hover phase and examined whether it changes as the tilt of the landing surface is varied from horizontal (floor), through sloped (uphill) and vertical (wall), to inverted (ceiling). The bees hover at a remarkably constant distance from the surface, irrespective of its tilt. Body inclination increases progressively as the tilt of the surface is increased, and is accompanied by an elevation of the antennae. The tight correlation between the tilt of the surface, and the orientation of the body and the antennae, indicates that the bee's visual system is capable of inferring the tilt of the surface, and pointing the antennae toward it. Touchdown is initiated by extending the appendage closest to the surface, namely, the hind legs when landing on horizontal or sloping surfaces, and the front legs or antennae when landing on vertical surfaces. Touchdown on inverted surfaces is most likely triggered by a mechanosensory signal from the antennae. Evidently, bees use a landing strategy that is flexibly tailored to the varying topography of the terrain.

Key words: honeybee, *Apis mellifera*, landing, flight, hover, vision, mechanoreception, antennae.

INTRODUCTION

The honeybee (*Apis mellifera* L.) is a prime example of an insect that relies on flight for foraging, and hence for survival of the colony. The majority of bees in a hive make dozens of foraging flights per day and cover up to 800 km of foraging distance in their lifetime in order to collect pollen and nectar from the surroundings (Neukirch, 1982; Winston, 1987). The control mechanisms underlying honeybee flight, such as wing stroke control and aerodynamics have been examined in the past [Altshuler (Altshuler, 2005) and references therein]. In addition, parameters such as control of flight speed have also been investigated (Baird et al., 2005; Barron and Srinivasan, 2006). As in most flying insects, honeybee flight appears to be guided predominantly by the visual system (Srinivasan et al., 1996; Srinivasan and Zhang, 1997; Srinivasan and Zhang, 2000). Many strategies employed by bees to control their flight appear to be based on cues derived from optic flow – that is, on the motion of the image of the environment in the eye (Srinivasan et al., 1989; Srinivasan et al., 1990; Srinivasan et al., 1991; Srinivasan et al., 1996; Srinivasan and Zhang 1997; Srinivasan and Zhang, 2000; Baird et al., 2005). For example, a landing bee controls its deceleration by holding constant the velocity of the image of the surface that it approaches. This ensures that the flight speed decreases progressively as the surface is approached, and is close to zero at touchdown (Srinivasan et al., 2000).

While the visual cues that guide the initial phase of landing – namely, the approach to the surface – have been investigated, we know very little about the final moments of landing, and the manoeuvres that occur just prior to touchdown. Wagner (Wagner, 1982) observed that flies decelerate sharply just prior to landing on a target, but that study did not investigate what occurred thereafter.

Pfaff and Varju (Pfaff and Varju, 1991) observed that hawk moths approaching a flower decelerate and hover successively at four distinct distances from it, prior to touching down. How do insects like honeybees, with a relatively simple nervous system, orchestrate smooth landings – especially as they land not only on horizontal surfaces, but also on tilted and vertical surfaces, or even upside down on a ceiling?

We have investigated, for the first time, the final moments of a bee's landing flight before and as she touches down on the surface. Using high-speed video recordings, we conducted a detailed analysis of the landing behaviour of *A. mellifera*, investigating the strategies underlying the hover and touchdown manoeuvres associated with landings on horizontal, vertical, sloping and inverted surfaces. We examine whether these manoeuvres are adapted to the tilt of the surface, and discuss possible underlying sensory mechanisms.

MATERIALS AND METHODS

All experiments were conducted with freely flying honeybees (*Apis mellifera ligustica*) in a temperature- and humidity-controlled indoor flight facility (All-Weather-Bee-Flight-Facility at the Queensland Brain Institute, Brisbane, Australia). Bees were trained to feed from a Perspex platform (10 cm × 15 cm) that was carried by a rotatable arm on a tripod, and positioned 1.5 m above the floor (Fig. 1A). The platform was covered with white paper. Three circles of tissue paper (5 m diameter), soaked in 1 mol l⁻¹ sugar solution, arranged in a horizontal row, were affixed to the white paper. Small circles of yellow paper (1 cm diameter) were affixed in the centre of each tissue circle to provide the bees with a visual aid to assist them in finding and landing on the otherwise uniform platform (Fig. 1B).

Three targets were provided, rather than one, to minimize overcrowding of feeding bees. To eliminate possible interference effects from other bees, data from a bee landing at a target was analysed when it was the only bee at that target.

Once a small number of bees (10–15) were trained to visit the platform and feed from it regularly, we used a high-speed video camera (Red Lake Motion Pro, run at 400 frames per second) to film the landings of individual bees at close range. The camera was mounted at the same height as the platform, approximately 50 cm away, to capture a close up, side view of the landings (Fig. 1A). Landings were initially filmed with the platform oriented horizontally. The platform was then rotated from 0 deg. (horizontal) through 90 deg. (vertical) to 180 deg. (upside down) in 10 deg. steps, and landings were filmed at each tilt. Only landings of bees that were captured in perfect side view were used for the analyses. For each tilt we analysed 16 individual landings. As the intra- and inter-individual variations were in the same range, all data for a given tilt were pooled for calculation of the means and standard errors of the various measurements that were made (described below). Where applicable, a linear regression of the data was performed.

Body position and orientation during the hover phase

For each bee, a single video frame capturing the moment immediately prior to the extension of the legs was selected to determine the body position during the hover phase. (The hover phase is defined below in the results section.) The following angular measurements were taken to analyse the position and orientation of the bee's body in relation to the landing surface (Fig. 2A–D): (A) body–platform angle: the angle between the platform surface and the long axis of the body (a line drawn from the base of the antennae through the thorax and to the tip of the abdomen); (B) body–horizontal angle: the angle between the horizontal plane and the long axis of the body; (C) head–vertical angle: the angle between the horizontal plane and a line drawn from the top of the head through the tip of the mouth (= head tilt); and (D) body–head angle: the angle between the long axis of the body and the head. In addition to the angular data, the following linear measurements were taken to analyse the distance of the bee's body to the landing surface (Fig. 2E–G): (E) antennal base horizontal distance: the distance between the base of the antennae and the landing surface determined by drawing a line parallel to the horizontal plane; (F) head–platform distance: distance between the tip of the mouth and the landing surface following the trajectory of the head tilt; (G) antennal base perpendicular distance: the perpendicular distance between the base of the antennae and the landing surface.

Antennal orientation prior to touchdown

For each bee, a single video frame capturing the moment just before touch down, i.e. immediately prior to the bee making contact with the surface was selected to determine the orientation of the antennae. The following angular measurements were taken (Fig. 2H–J): (H) flagellum–vertical angle: the angle between the vertical plane and a line drawn through the flagellum of the antenna; (I) flagellum–platform angle: the angle between the landing surface and a line drawn through the flagellum of the antenna; and (J) flagellum–head angle: the angle between the directions of the head and the flagellum. For measurement of these angles, the only video frames that were used were those in which the directions of the two antennae in the image differed by 5 deg. or less, and in which the images of the left and right legs (rear and middle) overlapped. This ensured that data were obtained only when the hovering bee was

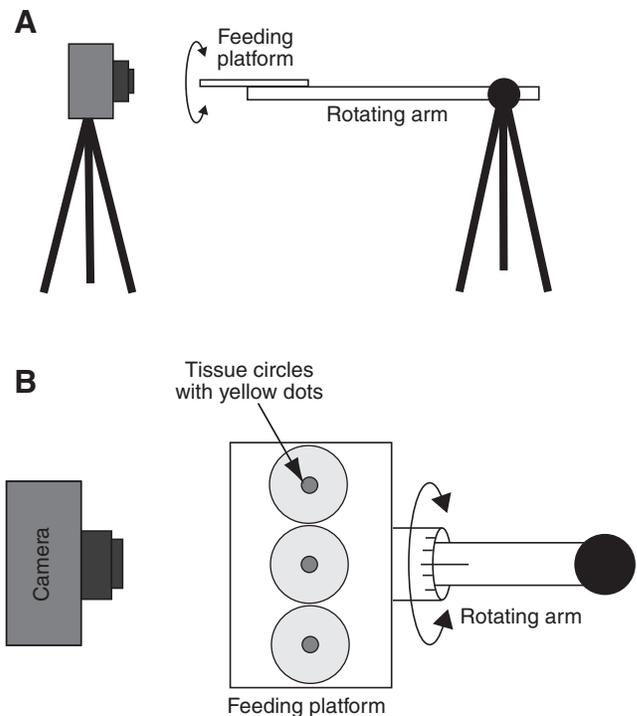


Fig. 1. (A) Side view of the experimental set-up showing the high-speed video camera on a tripod and the feeding platform (15 cm × 10 cm), mounted on the rotatable arm of a second tripod. (B) Top view of the experimental set-up showing the position of the camera with respect to the feeding platform, and the rotatable cylinder at the end of the tripod arm. The feeding platform carries three circles of tissue paper (5 cm in diameter) soaked in sugar syrup, each with a yellow dot (1 cm in diameter) in the centre to provide a visual landing aid. Drawings are not to scale.

oriented perpendicular to the platform, or nearly so. (In the image sequences shown in Fig. 3, this is not always the case.) When the images of the two antennae did not overlap, the mean value of their angles was used. From the quality and resolution of the video images, we estimate that the error in estimating flagellum direction was within ± 5 deg.

In this study the angular and distance measurements of the bee's body relative to the landing surface were all made from the frame captured just before the legs started to extend. The orientations of the bee's antennae were all taken from the frame captured immediately prior to the bee making contact with the surface.

Contact with surface at touchdown

For each landing, the first appendage of the bee's body that made contact with the landing surface was also registered; the hind legs, the middle legs, the front legs, the antennae, or a combination of these. The proportion of landings in which each of these appendages made the first contact with the platform was determined for each orientation of the landing surface.

Antennal ablation

To explore the role of the antenna in mediating the landing process, some tests were conducted with bees in which the antennae were removed. When a bee landed on the platform and commenced feeding, it was caught and gently pushed headfirst into the bottom of an Eppendorf tube, using a piece of tissue paper. The lower 3 mm of the tube had previously been removed to permit access to the

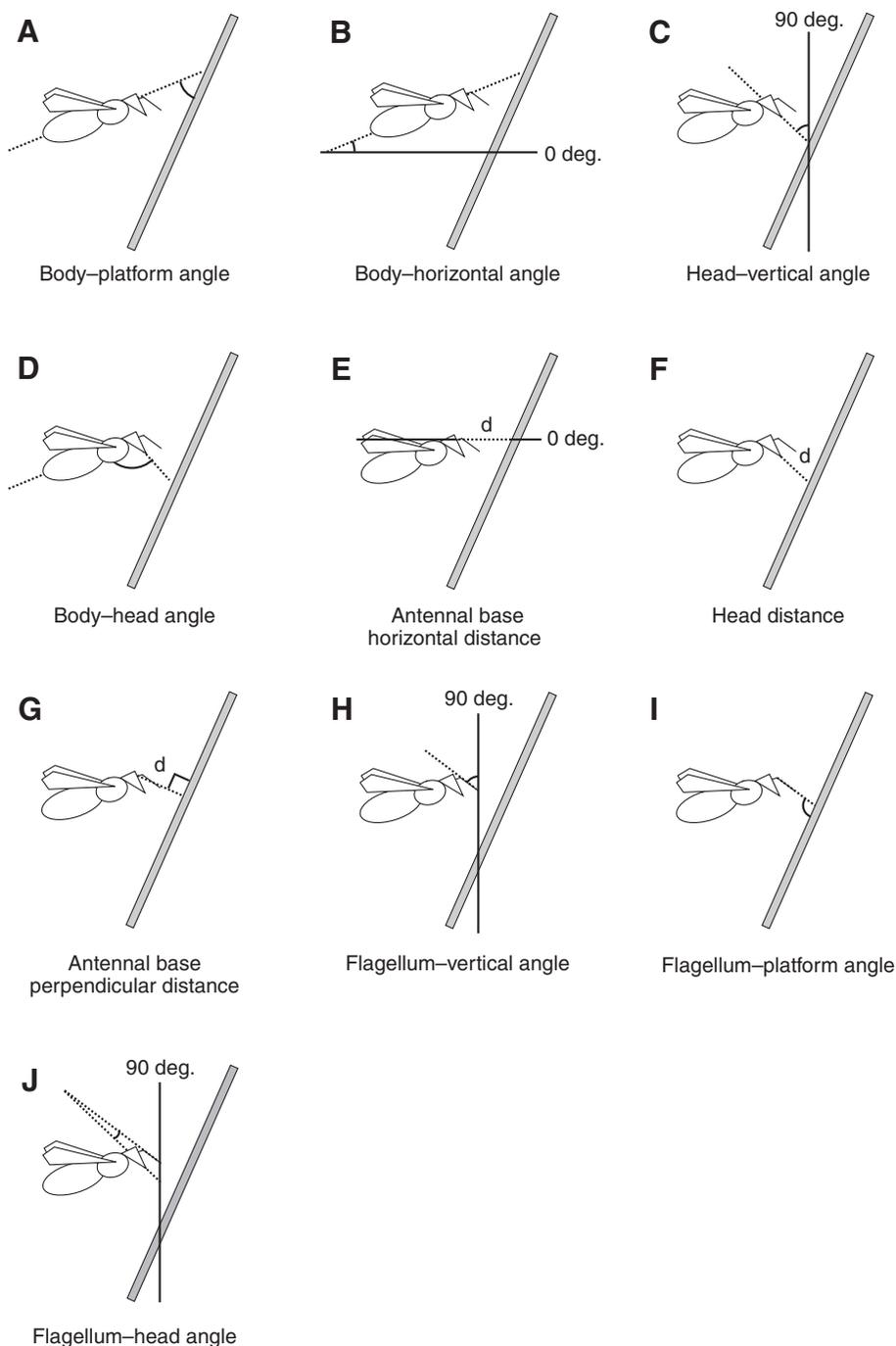


Fig. 2. Diagrams showing the angular and linear measurements that were made to analyse the bee's body orientation and distance in relation to the landing surface during the hover phase (A–D, E–G), the orientation of the bee's antennae in relation to the landing surface immediately prior to touch down (E, F), and the orientation of the antenna in relation to the head (J). In each case, the arc denotes the measured angle and *d* the measured distance. The measurement procedures are described in Materials and methods.

upper part of the head and the antennae of the immobilized bee from the outside. With the bee held in place by the tissue-paper plug, the antennae were amputated close to the base using a pair of fine scissors. The bee was then allowed to escape from the tube by removing the tissue-paper plug. The entire manipulation took less than 5 s. The excised antennae were inspected under the microscope to confirm the position of the amputation. Data from a bee was disregarded if the antennae had not been amputated at the first or second segment from the base. Sham controls, in which bees were inserted into the Eppendorf tube and then released without removing the antennae, behaved completely normally and continued to visit the platform and feed from it. Observations were made with the platform tilted at 0 deg., 90 deg., 135 deg. and 180 deg.

RESULTS

A general overview of the events that occur during approach and touchdown is shown in the film sequences of Fig. 3. This figure illustrates landings on a horizontal surface (Fig. 3A), a sloping surface (Fig. 3B), and an inverted surface (Fig. 3C), showing the positions of the legs and the orientations of the antennae in each case.

Preliminary analysis of the high-speed videos showed that, while approaching the landing surface, honeybees slow down abruptly to enter an initial, quasi-hover phase during which they slowly lowered themselves further toward the platform. They then entered a second, stable hover phase just prior to touchdown during which the bee's body was held comparatively stable. This stable hover phase ended as the bee extended its legs and landed softly on the platform. In

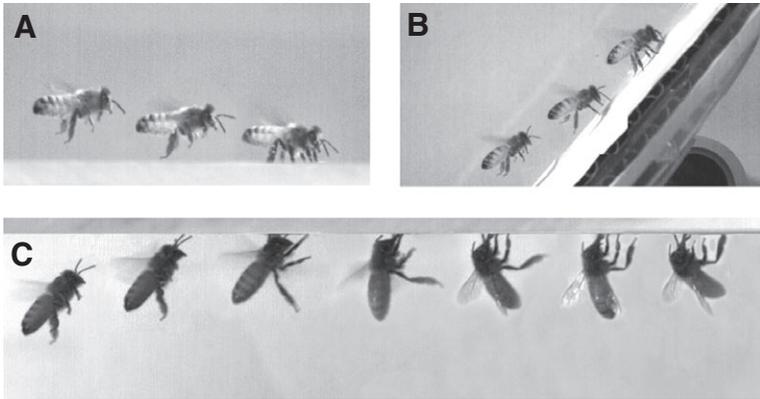


Fig. 3. Superimposed frames from high speed video recordings showing typical landing manoeuvres of a honeybee during the stable hover phase, immediately prior to extension of the legs and touchdown. (A) Horizontal platform (0 deg. tilt), (B) sloping platform (50 deg. tilt), and (C) inverted platform (180 deg. tilt). In each sequence the individual frames are not separated by a constant time interval, but have been selected to depict significant phases in the course of approach and touchdown.

the rest of this paper the term ‘hover’ refers to the final, stable hover phase.

Fig. 4 shows digitized trajectories of the approach to a platform tilted at 40 deg. (Fig. 4A) and at 100 deg. (Fig. 4D). Although the initial quasi-hover phase is quite variable in terms of approach direction and duration, the final, stable hover phase (depicted in red) is much more constant and reproducible. The variation of flight speed during these two approaches is shown in Fig. 4B and E, respectively. In each case, the flight speed decreases progressively

during the quasi-hover phase and drops to a minimum value that characterizes the stable hover phase, depicted by the grey region. During the hover phase the perpendicular distance of the head to the platform (measured as the antennal base perpendicular distance; see Fig. 2G) is held more or less constant, at a value of 10–15 mm, as shown by the examples in Fig. 4C and E. At the end of the stable hover phase the bee briefly increases its speed toward the surface to complete the landing (Fig. 4B,E). The duration of the stable hover phase depends upon the tilt of the platform, ranging from

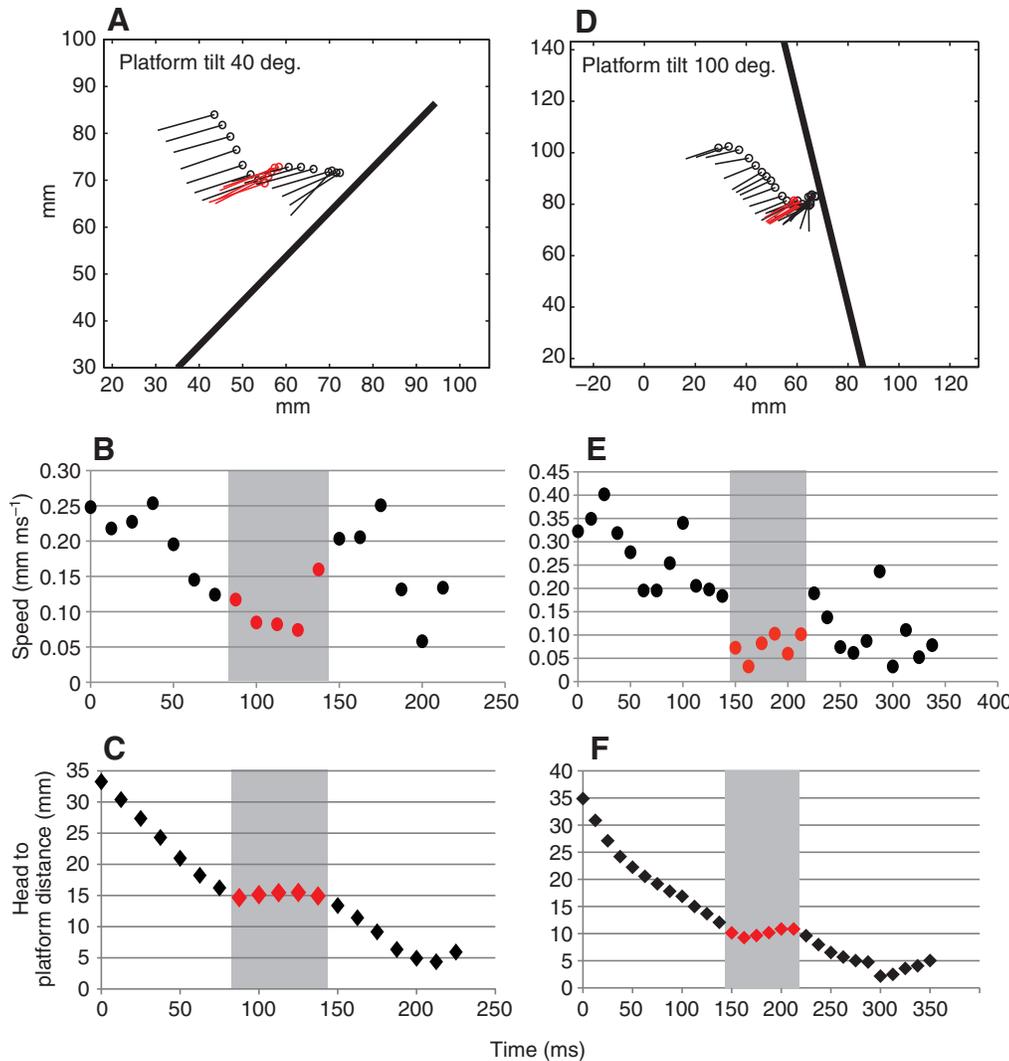


Fig. 4. Example of an approach to a 40 deg. platform (A) and to a 100 deg. platform (D). In each case the circles denote head positions and the lines, body orientations, digitized every 12.5 ms. The red symbols represent the stable hover phase. (B,E) The variation of flight speed with time, as measured by tracking the head. Stable hover is characterized by the period during which the flight speed is lowest, as shown by the grey bars and the red symbols. (C,F) The variation of the head-to-platform distance (measured as shown in Fig. 2G) as a function of time. This distance is held more or less constant during the hover phase, as shown by the grey bars and the red symbols.

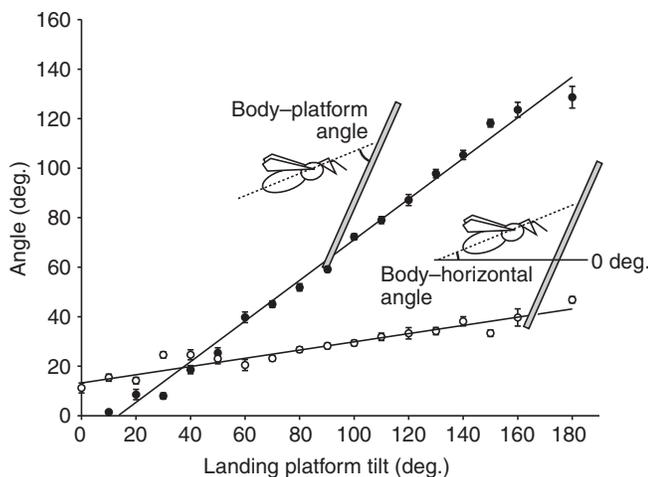


Fig. 5. Honeybee body orientation during landing on platforms of varying tilt. Graphs show the variation of the angle between the body axis and the platform (filled circles), and of the angle between the body axis and the horizontal plane (open circles), with the tilt of the platform. The data are means \pm s.e.m. ($N=16$ landings for each tilt). Data for 170 deg. platform tilt are not shown, because the bee's body was not aligned to provide a perfect side view in any of the landings that were filmed under this condition. The lines are linear regressions on the two data sets. Body angle: slope=0.82, intercept=-11.49, $R^2=0.99$. Body horizontal angle: slope=0.16, intercept=13.74, $R^2=0.92$.

53.6 \pm 23.7 ms (mean \pm s.d., $N=7$) at 40 deg., through 118.5 \pm 66.6 ms at 90 deg. ($N=13$) to over 143.8 \pm 61.7 ms at 150 deg. ($N=10$). (The mean hover duration at 150 deg. is an underestimate, because the duration of the hover exceeded the duration of the filming in four of the 10 cases.) It is clear from this data, however, that the mean hover duration increases with the tilt of the platform. As we shall see later below, this may reflect the progressively greater difficulty of negotiating surfaces of increasing tilt.

Body position during hover phase

The results revealed that almost all of the measured variables pertaining to the bee's body position during the landing manoeuvre varied with the tilt of the landing surface. During hover, the angle between the long axis of the body and the horizontal plane (body-horizontal angle) increases in direct correlation with increasing surface tilt (Fig. 5, open circles). However, the overall change in body orientation is relatively small (ranging from ca. 16 deg. to 45 deg.), compared with the change in platform tilt (which ranges from 0 deg. to 180 deg.). That is, during the hover phase the bee pivots its body upwards only slightly, even when landing on an upside down surface (180 deg.). The body-platform angle increases as the tilt of the platform is increased (Fig. 5, filled circles), although this increase is partially countered by the small increase of body tilt.

During hover, the orientation of the head changes, but not dramatically, as the tilt of the platform is increased. The angle between the head and the vertical plane (head-vertical angle) increases by approximately 50 deg. over the 180 deg. change in platform tilt (Fig. 6, filled circles). This means that the bee tilts its head backwards with increasing platform tilt. As a result of the increase in the body-horizontal angle (Figs 5 and 6, open circles), and the simultaneous increase in the head-vertical angle (Fig. 6, filled circles), the angle between the long axis of the body and the head (body-head angle, Fig. 6, filled squares) shows only a very

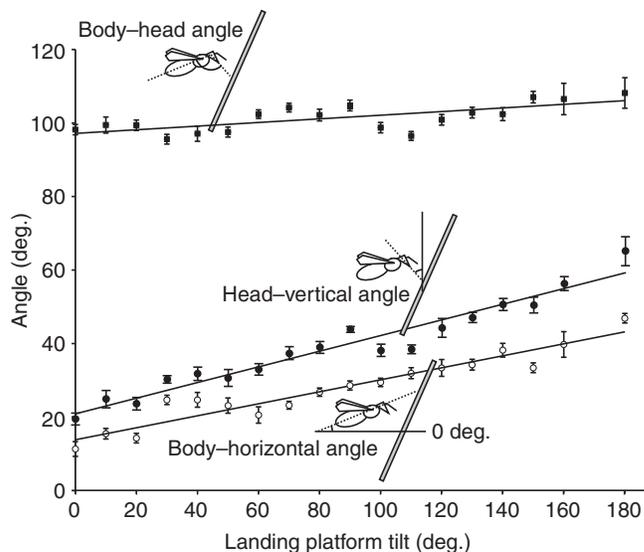


Fig. 6. Honeybee body orientation during landing on platforms of varying tilt. Graphs show the variation of the angle between the body axis and the horizontal plane (open circles), of the angle between the head and the vertical plane (filled circles), and of the angle between the body axis and the head (filled squares), with the tilt of the platform. The data are means \pm s.e.m. ($N=16$ landings for each tilt). Data for 170 deg. platform tilt are not shown, for the same reason as in Fig. 5. The lines are linear regressions on the three data sets. Body-horizontal angle: slope=0.16, intercept=13.74, $R^2=0.92$. Head-vertical angle: slope=0.21, intercept=20.90, $R^2=0.94$. Body-head angle: slope=0.05, intercept=96.96, $R^2=0.52$.

slight increase as the tilt of the platform is increased. Thus, during hover, as the tilt of the landing platform is increased the bee increases the pitch of its body slightly, and tilts its head back by a small amount, keeping the angle between its body and head fairly stable.

Fig. 7 shows the distance of the head from the platform, measured along the head axis, during hover (open circles). This distance remains fairly constant at 17–18 mm until a platform tilt of 70 deg., beyond which it increases rapidly. These changes can be explained by the fact that the bee tilts its head only slightly with respect to the horizontal plane (Fig. 6, filled circles), leading to a large increase in the head distance, for platform tilts beyond the vertical plane.

During hover, the horizontal distance between the base of the antennae and the landing platform (Fig. 7, filled circles) also changes considerably with surface tilt. This distance is some 90 mm for a horizontal platform, but decreases rapidly with increasing platform tilt. It then remains constant, at approximately 20 mm, for platform tilts ranging from 60 deg. to 120 deg., beyond which the distance increases again as the platform is tilted towards 180 deg.

The reason for this behaviour becomes apparent in Fig. 8, which shows the variation, with platform tilt, of the perpendicular distance from the base of the antennae to the platform, during hover. This distance is remarkably constant, at 15.7 \pm 1.5 mm (mean \pm s.e.m., $N=266$ landings), as the tilt of the landing platform is varied from 0 deg. to 180 deg. It is the only measured variable that remains constant, irrespective of the orientation of the landing platform. This means that landing bees hover at a fixed distance from the platform, irrespective of the tilt of the platform and therefore irrespective of the region of the eye that views it. Thus, hovering bees are capable of evaluating and adjusting the distance to the platform, irrespective of whether the platform is horizontal, vertical or inverted.

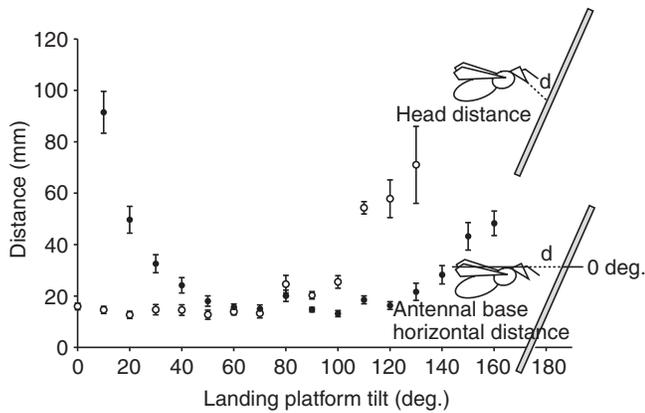


Fig. 7. Honeybee body orientation during landing on platforms of varying tilt. Graphs show the variation of the head distance from the landing surface (open circles), and of the horizontal distance of the antennal base from the landing surface (filled circles), with the tilt of the platform. The data are means \pm s.e.m. ($N=16$ landings for each tilt). Data for head distance were only collected up to 130 deg. platform tilt, and data for antennal base horizontal distance were only collected up to 160 deg. platform tilt, as the distance measurements beyond these tilts were very large or infinite.

Antennal orientation prior to touchdown

Measurements of the orientation of the antennal flagella, just prior to touchdown, reveal that an increase in platform tilt leads to elevation of the antennae (Fig. 9A, open circles). This behaviour can be split into three categories. As the tilt of the platform is increased from 0 deg. to 40 deg., the flagella are raised progressively, at about the same rate. As a consequence, the flagellum–platform angle remains more or less constant, at about 50 deg. As the platform tilt is increased from 50 deg. to 80 deg. the orientation of the flagellum is held more or less constant at about 65 deg., which causes the flagellum–platform angle to increase steadily from 50 deg. to 100 deg. Finally, as the platform tilt is increased from 80 deg. to 180 deg., the flagella are raised steadily, but at a lower rate than the platform, so that the flagellum–platform angle increases steadily (but slowly) to a maximum value of about 130 deg. when the bee lands on the inverted platform. As the tilt of the platform is varied, the angle between the head and the flagella (Fig. 2J) changes, as shown in Fig. 9B. The head–flagellum angle increases with increasing platform tilt. This demonstrates, importantly, that the antennae are moved independently of the head during the landing manoeuvre.

The general observation that the orientation of the flagella varies with the tilt of the platform, reveals that the hovering bee is able to sense the tilt of the platform before any mechanical contact is made with it.

Contact with the platform at touchdown

At touchdown, the tilt of the platform, and the orientations of the body and the antennae together determine which appendage of the bee's body makes initial contact with the landing surface (Fig. 10). Depending on the tilt of the platform, this can be a single appendage, or a combination of appendages that make contact simultaneously. For surfaces that are close to horizontal (0–30 deg. tilt) the hind legs, often in conjunction with the middle legs, are the first to make contact. As the platform tilt increases towards the vertical plane, the middle legs and front legs are also incorporated into the touchdown. Once the platform tilt exceeds 120 deg., the first contact with the landing surface is made predominantly with the antennae.

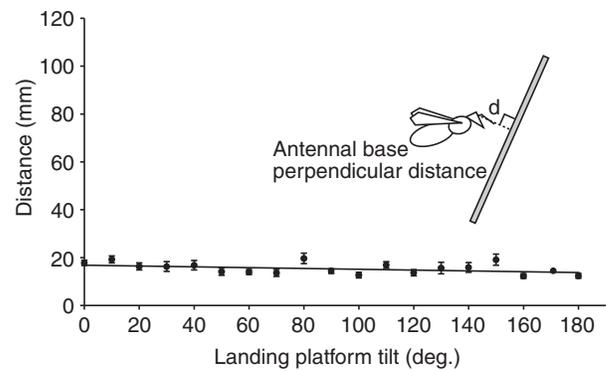


Fig. 8. Honeybee head position during landing on platforms of varying tilt. The graph shows the variation, with the tilt of the landing platform, of the perpendicular distance between the base of the antennae and the platform. The data are means \pm s.e.m. ($N=16$ landings for each tilt). The line is a linear regression on the data: slope = -0.02 , intercept = 17.16 , $R^2 = 0.17$.

It should also be noted that in most cases it is the antenna on one side that initially makes contact with the surface, e.g. the right antenna alone, rather than both antennae simultaneously. This is because the approach is not always exactly perpendicular to the surface, although it usually deviates from the normal direction by less than 10 deg. in yaw (C.E., P.K., M.D., J.R. and M.V.S., unpublished data).

The role of the antennae

To further investigate the role of the bee's antennae in the landing process, we made observations on bees that had their antennae amputated. The landing behaviour of these bees was examined on platforms of 0 deg., 90 deg., 135 deg. and 180 deg. tilt. In each case we observed 10 antenna-amputated bees, as well as 10 intact (sham control) bees. Interestingly, approximately 60% of the antenna-amputated bees landed successfully on the 0 deg. and 90 deg. platforms, but only 30% of them were successful in landing on the 135 deg. platform, a couple of individuals bumping the platform with their heads prior to landing. None of the amputated bees were successful in landing on the upside-down platform, although two of them returned to investigate the platform without making any attempts to land on it. This is noteworthy, because the antennae are always the first appendages to make contact when landing on an inverted surface. Thus, the behaviour of the amputated bees might have been the consequence of not receiving the appropriate inputs that are expected from the visual system and the antennae when approaching a ceiling. The control bees continued to visit and land on the platform, at all of the tilts. These observations suggest that bees indeed use their antennae during the landing process, albeit with varying significance depending on the tilt of the landing surface.

It was difficult to film and perform quantitative analyses of the approaches and landings of the antenna-amputated bees. This was because these bees made fewer landings, especially at the increased platform tilts. Furthermore, their approaches and landings (when they occurred) were much more variable than in the case of bees with intact antennae.

DISCUSSION

When observed with the unaided eye, the landing manoeuvre of a honeybee appears to be a simple, smooth movement. However, our high-speed camera analysis reveals that the manoeuvre consists of several distinct phases. When a bee approaches a surface to land on it, it commences its deceleration from as much as a metre away

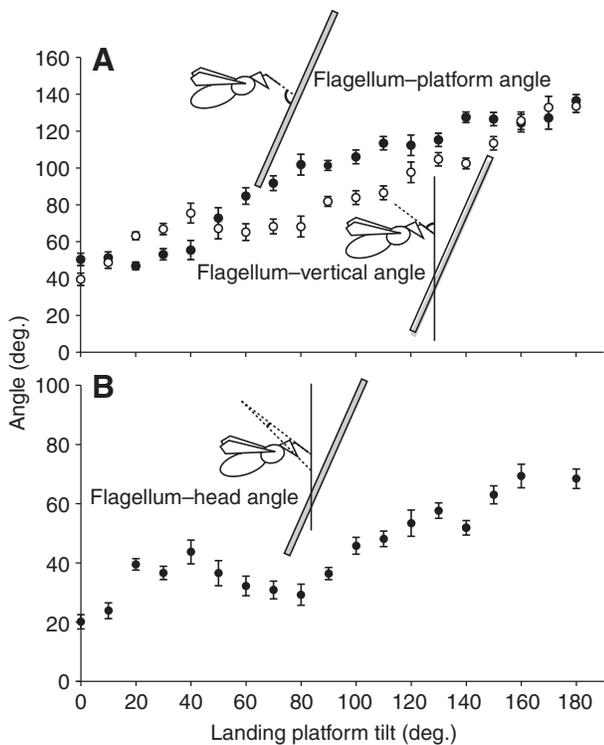


Fig. 9. (A) Antennal orientation of hovering bees, and its variation with the tilt of the landing platform. The graphs show the variation, with the tilt of the landing platform, of the angle between the antennal flagella and the vertical plane (open circles), and of the angle between the antennal flagella and the platform (filled circles). The data show means \pm s.e.m. ($N=16$ landings for each tilt). (B) Variation of head–flagellum angle with platform tilt, estimated from the data in Fig. 6 (head orientation) and A (antennal orientation).

(C.E., P.K., M.D., J.R. and M.V.S., unpublished observations). When it is within a few centimetres of the surface, a rapid deceleration occurs, resulting in an initial quasi-hover phase in which the bee drifts toward the surface slowly. The bee then enters a second, stable hover phase, about 16 mm from the surface. This second hover phase has been the subject of the present study. At the end of this hover phase, the legs are extended to contact the surface and complete the touchdown process.

Influence of surface orientation on the landing manoeuvre

In nature, bees rarely land on perfectly horizontal surfaces. More often than not, they have to negotiate landings on variously oriented surfaces, including inverted surfaces when foraging at flowers with hanging blossoms. Our findings suggest that the bee's body attitude during the final hover phase is tuned, to some extent, to the tilt of the landing surface. With increasing surface tilt the bee lifts its body and head, but never beyond a certain angle from the horizontal plane, even when landing on vertical or inverted surfaces. Considering that the ratio of body weight to wing area (the so-called 'wing loading') is relatively high in honeybees, and especially in *Apis mellifera* (Hepburn et al., 1999; Goodman, 2003), it is possible that these insects need to keep the orientation of their body with respect to the horizontal plane within a restricted range to maintain a stable hovering position. Should the bees tilt their body further towards the vertical (which would make touchdown on a vertical surface certainly easier), they would most likely lose lift and/or stability. Dacke and Srinivasan (Dacke and Srinivasan, 2007) observe that,

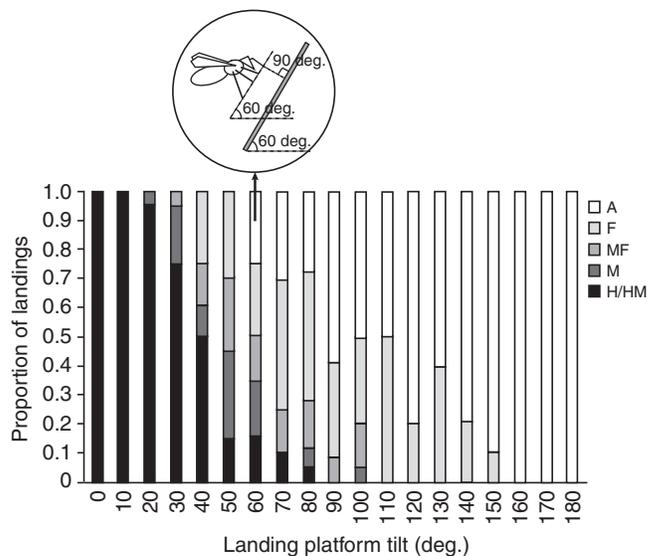


Fig. 10. Proportion of landings in which a given appendage makes the first contact with the platform at touchdown, for platforms of varying tilt ($N=16$ landings for each tilt). H/HM, hind legs or hind and middle legs together; M: middle legs; MF, middle and front legs together; F, front legs; A, antennae. The drawing illustrates that, when landing on a 60 deg. platform, all of the six legs and the two antennae contact the surface more or less simultaneously, and the antennae are oriented perpendicular to the surface. Details in the text.

even when flying a vertical trajectory, bees keep their body axis oriented close to the horizontal. Such constraints may be less stringent for flying insects that are more manoeuvrable, e.g. flies or dragonflies.

Hover distance

The most interesting finding of the present study is that, during the final hover phase, bees keep the distance from their head to the landing surface amazingly constant at a value of about 16 mm, irrespective of the tilt of the surface. Presumably, this is the perfect distance from which to initiate the final landing manoeuvre, namely, extending the legs for touchdown. From about 16 mm away a bee can just reach the surface with one or more of its appendages, be it merely extending the hind legs onto a horizontal surface, or grabbing an overhead surface by extending the forelegs over its head.

Sensory cues mediating hover distance and perception of surface inclination

How do bees achieve this constant distance, what are the sensory mechanisms by which the hover distance is computed and controlled? Given that visual cues such as optic flow are known to play a crucial role in control of flight speed during landing, it seems plausible that the visual sense might provide the key input required to calculate this distance (Srinivasan and Zhang, 2004). The honeybee maintains a constant rate of image flow over the eye as it nears its landing target, namely $\sim 320 \text{ deg. s}^{-1}$ mean image angular velocity, which results in automatic deceleration, the closer the bee gets to the surface (Srinivasan and Zhang, 1997; Srinivasan and Zhang, 2004; Srinivasan et al., 2000; Srinivasan et al., 2001). However, it seems that this strategy of automatic deceleration based on optic flow can only be used to reach the initial, quasi-hover phase (see above). From there the bee lowers itself slowly until it is 16 mm away from the surface, where it enters the second, stable hover phase.

It is well known that when an observer approaches or moves across a plane surface, the pattern of optic flow will display gradients that depend systematically on how the surface is oriented relative to the observer (e.g. Koenderink, 1986). In principle, the magnitudes and gradients of the optic flow pattern could be sensed by the visual system to determine the distance and tilt of the surface. Although the movements are slow, the distance to the surface is small, and so the resulting optic flow signals may be strong enough to provide reliable estimates of the distance and tilt.

Stereo-based distance cues are another possibility: despite the small interocular separation (*ca.* 2–3 mm), disparity cues can be large at such close ranges (Srinivasan, 1993). Further work, for example investigating landing and hover behaviour when one eye is occluded, may shed light on this possibility. Pfaff and Varju (Pfaff and Varju, 1991) reported that hawk moths approaching a flower decelerate rapidly four times, and thus hover successively at four distinct distances from the flower before landing on it. Although they suggested that stereo cues might play a role in setting these hover distances, the evidence for this was circumstantial.

Apart from visual cues, one has to consider the possibility that bees use other sensory modalities to determine surface distance. Plausible candidates are the extremely sensitive mechanoreceptive sensilla on the antennae, and/or the Johnston's organ, located at the base of the antennae. Both the mechanoreceptors and the Johnston's organ are known to play a role in detecting airflow (Gewecke, 1974; Winston, 1987; Towne, 1995). Hover close to a surface could produce a characteristic pattern of airflow arising from the interaction of the surface with the downwash generated by the flapping wings. In principle, bees could detect this pattern of airflow with their antennal mechanoreceptors and/or the Johnston's organ, and use the information to judge the distance and orientation of the surface before touchdown. However, this possibility is unlikely because such interactions would occur primarily when the surface is below the hovering bee (i.e. when the surface is nearly horizontal) and would be weak or absent when the surface is vertical or inverted. Therefore, it is difficult to imagine how such a cue, on its own, could enable bees to hover at the same distance from the landing surface, irrespective of its orientation.

The finding that both the body orientation (Fig. 5) and the antennal orientation (Fig. 9) are tightly coupled to the tilt of the landing surface, must mean that the hovering bee is able to determine the tilt of the surface before making any contact with it. From the above discussion, it appears that this assessment of surface tilt is accomplished through visual cues.

The role of the antennae

Fig. 9 reveals a clear tendency of the antennae to point toward the surface at which the landing is directed. Presumably, this is useful not only for sensing olfactory cues emanating from the surface, but also for making mechanical contact with the surface when it is tilted at angles greater than 150 deg. This mechanical contact appears to be important when landing on an inverted surface, as it is then the antennae that make first contact with the surface. Antennal contact, in the presence of a characteristic pattern of optic flow in the dorsal eye region, could then trigger elevation of the front legs, which hook on to the surface and pull the body up and around, as described later below.

For a given surface tilt the antennae are held at a constant orientation, irrespective of where along the surface a bee is hovering. (The same is true for head orientation and body orientation.) This suggests that, in our experiments, the antennae were not directed specifically at any of the three discs that decorated the platform.

Rather, antennal orientation was determined by the tilt of the platform. This has been confirmed in control experiments in which the platform carried a checkerboard pattern or a random texture, rather than distinct visual targets. The mean flagellum–vertical angle of bees hovering in front of the 90 deg. platform (Fig. 9) was 80.2 ± 2.7 deg. (\pm s.e.m.), which is not significantly different from that measured when they hovered in front of a vertical platform that carried a checkerboard pattern (84.0 ± 4.7 deg.; $P=0.48$, *t*-test), or a random texture (76.6 ± 3.4 deg.; $P=0.40$, *t*-test).

It is very unlikely that the antennal direction during hover was determined by any olfactory signals emanating from the landing platform. The reasons are (a) the food reward consisted of sugar solution, which does not carry any scent; and (b) since the reward was provided in several locations over the surface of the platform, scents from any marking pheromones deposited by the feeding bees would have been diffusely distributed over the entire surface. Consequently, at the close range of hover, the bees would have been totally immersed in the marking scent (if it was indeed present), and the antennae could not have been directed at any single, local olfactory target.

Moreover, the variability in the measured antennal orientations is very small at each platform tilt (see the standard errors in Fig. 8), despite the fact that the bees hovered at arbitrary locations along the surface of the platform (and not necessarily near a drop of sugar water). This fact argues against the possibility that the antennae were directed at any local target on the platform, be it visual or olfactory, and supports our contention that the orientation of the antennae is determined by the general surface tilt. Unfortunately, it is extremely difficult to conduct control experiments without food on the platform, to categorically exclude the possibility that the antennae are directed at local targets. Although trained bees approach unrewarded platforms and display similar antennal orientations, they are less motivated to land and do not hover for periods long enough to permit collection of sufficient data. This is probably because unrewarded platforms (1) present no visual evidence of the presence of food and (2) carry no previously deposited pheromones that label them as a food-bearing target.

The tendency of bees to point their antennae toward the surface that they are approaching lends credence to the notion that the antennae are sensitive indicators of where an insect is directing its 'attention'. It is known that crickets use their visual system to point their antennae at moving targets and track them (Honegger, 1981). Photographs of bees that are about to alight on a flower reveal that the antennae are usually directed toward the flower, and are oriented nearly orthogonal to the plane of the petals (C.E., P.K., M.D., J.R. and M.V.S., unpublished observations). Such pointing may optimize the detection of olfactory signals, as well as ensure that the tip of the antennae make early mechanical contact with the flower to facilitate a well-controlled touchdown.

The crucial role of the antennae in the honeybee's landing manoeuvre also becomes apparent during the final touchdown phase. When the tilt of the landing surface exceeds 90 deg., bees appear to rely increasingly on mechanosensory signals from the antennae to sense contact with the surface, and to execute a successful landing (see Fig. 9). This notion is reinforced by the experiments with the antenna-amputated bees, which reveal that such bees rarely land on surfaces with tilts that exceed 135 deg.

Landing on an inverted surface

When an intact bee lands on an inverted surface, it hovers at the chosen landing point until the upward-pointing antennal flagella make contact with the surface. This contact appears to initiate the

touchdown process, which then begins with the front legs being raised and hooked onto the surface. The front legs in turn pull the body around and cause the remaining legs to hook to the surface, completing the inverted landing (Fig. 3C). Flies appear to use a different strategy for landing on a ceiling. They approach the surface at a comparatively high speed, with their front legs extended over their head. When the front legs make contact with the ceiling, the momentum of the body causes the body to pivot about this point of contact, and to finish in the upside-down position (Hyzer, 1962; Nachtigall, 1968). In other words, the fly performs an inverted 'somersault', relying primarily on its large forward momentum to execute the manoeuvre. Bees, on the other hand, approach a ceiling at a comparatively slow speed, and cannot use this technique. They have to hook their front legs on to the surface, and then hoist themselves up and around.

Flexibility in the touchdown process

In summary, bees use a combination of visual and antennae-derived cues to guide and initiate the touchdown process. Visual cues (based on optic flow or stereo) seem sufficient for bees to touch down on surfaces that are oriented from horizontal through to vertical, whereas antenna-based cues, presumably mechanosensory in nature, are important for triggering touchdowns on inverted surfaces.

During the actual touchdown, bees simply use the appendage closest to the landing surface to make first contact – that is, the hind legs in the case of horizontal surfaces, and the front legs or antennae in the case of vertical or inverted surfaces (Fig. 10). Inspection of Fig. 10 reveals that when the platform is tilted at 60 deg., all of the legs, as well as the antennae, are likely to touch the surface at about the same time. Thus, when a landing bee approaches a platform that is tilted at 60 deg., the tips of the legs and the tips of the antennae all lie approximately in a plane that is oriented parallel to the platform, as illustrated in the drawing of Fig. 10. Interestingly, it is at this very platform tilt (60 deg.) that the antennae are also exactly perpendicular to the plane of the platform (Fig. 9, filled circles), and are hence optimally oriented to make early contact. Thus, 60 deg. may well be the orientation of the surface upon which bees are best adapted to land. It would be of interest to examine whether 60 deg. is indeed the most frequently encountered orientation of flowers that rely on honeybees for pollination.

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