Landing Strategies in Honeybees, and Possible Applications to Autonomous Airborne Vehicles

MANDYAM V. SRINIVASAN*, SHAOWU ZHANG, AND JAVAAN S. CHAHL
Centre for Visual Science, Research School of Biological Sciences, Australian National University, P.O. Box 475, Canberra, A.C.T. 2601, Australia

Abstract. Insects, being perhaps more reliant on image motion cues than mammals or higher vertebrates, are proving to be an excellent organism in which to investigate how information on optic flow is exploited to guide locomotion and navigation. This paper describes one example, illustrating how bees perform grazing landings on a flat surface. A smooth landing is achieved by a surprisingly simple and elegant strategy: image velocity is held constant as the surface is approached, thus automatically ensuring that flight speed is close to zero at touchdown. No explicit knowledge of flight speed or height above the ground is necessary. The feasibility of this landing strategy is tested by implementation in a robotic gantry, and its applicability to autonomous airborne vehicles is discussed.

Introduction

Unlike vertebrates, insects have immobile eyes with fixed-focus optics. Therefore, they cannot infer the distances to objects or surfaces from the extent to which the directions of gaze must converge to view the object, or by monitoring the refractive power that is required to bring the image of the object into focus on the retina. Furthermore, compared with human eyes, the eyes of insects are positioned much closer together and have inferior spatial acuity (Horridge, 1977). Therefore, the precision with which insects could estimate range through binocular stereopsis would be much poorer and restricted to relatively small distances, even if they possessed the requisite neural apparatus (Srinivasan, 1993). Not surprisingly, then, insects have evolved alternative strategies for dealing with the problems of visually guided flight. Many of these strategies rely on using image motion, generated by the insect’s own motion, to infer the distances to obstacles and to control various maneuvers (Horridge, 1987; Srinivasan, 1993, 1998).

Here we describe how honeybees use image motion cues to perform smooth landings on a flat surface.

How Bees Perform Smooth Landings

The seminal work of Gibson (1950) highlighted the optic-flow cues that can be brought to bear in controlling the landing of an aircraft. Studies of landing behavior in flies have revealed that, as a surface is approached, the expansion of the image of the surface provides strong cues that are used to control deceleration and trigger extension of the legs in preparation for contact (Goodman, 1960; Eckert and Hamdorf, 1980; Wagner, 1982; Borst and Bahde, 1988). There is also evidence that the rate of expansion of the image is used to infer the time to contact the surface, even if the insect does not possess explicit information about the speed of its flight or the distance to the surface (Wagner, 1982).

However, when an insect makes a grazing landing on a flat surface, cues derived from image expansion are relatively weak. This is because the dominant pattern of image motion is then a translatory flow in the front-to-back direction. Given that flying insects often make grazing landings on flat surfaces, what are the processes by which such landings are orchestrated?

Recently, this question was investigated by Srinivasan et al.
al. (2000), who video-filmed trajectories, in three dimensions, of bees landing on a flat, horizontal surface.

Two examples of landing trajectories, reconstructed from the data, are shown in Figure 1a, b. A number of such landing trajectories were analyzed to examine the variation of the instantaneous height above the surface \((h)\), instantaneous horizontal (forward) flight speed \((V_f)\), instantaneous descent speed \((V_d)\) and descent angle \((\alpha)\). These variables are illustrated in Figure 1c.

Analysis of the landing trajectories revealed that the descent angles were indeed quite shallow. The average value measured in 26 trajectories was about 28° (Srinivasan et al., 2000).

Figure 2a, b shows the variation of flight speed with height above the surface, analyzed for two landing trajectories. These data reveal one of the most striking and consistent observations with regard to landing bees: Horizontal speed is roughly proportional to height, as indicated by the linear regression on the data. When a bee flies at a horizontal speed of \(V_f\) cm/s at a height of \(h\) cm, the angular velocity \(\omega\) of the image of the surface directly beneath the eye is given by \(\omega = V_f/h\) rad/s. From this relationship it is clear that, if the bee’s horizontal flight speed is proportional to her height above the surface (as shown by the data), then the angular velocity of the image of the surface, as seen by the eye, must be constant as the bee approaches it. This angular velocity is given by the slope of the regression line. The angular velocity of the image varies from one trajectory to another, but is maintained at an approximately constant value in any given landing. An analysis of 26 landing trajectories revealed a mean image angular velocity of about 500°/s (Srinivasan et al., 2000).

These results reveal two important characteristics. First, bees landing on a horizontal surface tend to approach the
surface at a relatively shallow descent angle. Second, landing bees tend to hold the angular velocity of the image of the ground constant as they approach it.

What is the significance of holding the angular velocity of the image constant during landing? One important consequence is that the horizontal speed of flight is automatically reduced as the height decreases. In fact, by holding the image velocity constant, the horizontal speed is regulated to be proportional to the height above the ground, so that when the bee finally touches down (at zero height), her horizontal speed is zero, thus ensuring a smooth landing. The attractive feature of this simple strategy is that it does not require explicit measurement or knowledge of the speed of flight, or the height above the ground. Thus, stereoscopic methods of measuring the distance of the surface (which many insects probably do not possess) are not required. What is required, however, is that the insect be constantly in motion, because the image motion resulting from the insect’s own motion is crucial in controlling the landing.

The above strategy ensures that the bee’s horizontal speed is zero at touchdown, but it does not regulate the descent speed. How is the descent speed controlled? Plots of descent speed versus height reveal a linear relationship between these two variables, as well. Two examples are shown in Figure 2c, d. This finding implies that landing bees (a) control their forward flight speed to hold the image velocity of the ground constant and (b) control the descent speed to be proportional to the forward speed, so that the descent speed decreases with the forward speed and also becomes zero at touchdown. (In flying Drosophila, for example, there is good evidence that lift and thrust co-vary [Götz and Wandel, 1984].) The ratio of descent speed to forward speed, $V_d/V_f$, determines the descent angle. The two rules described above, operating together, ensure a smooth landing.

**Tests on a Robotic Gantry**

The feasibility of the landing strategy described above has been tested by implementation in a computer-controlled gantry robot carrying a visual system (Srinivasan et al., 2000). Vision is provided by a video camera mounted on the

---

**Figure 2.** (a, b) Variation of horizontal flight speed ($V_f$) with height ($h$) above the surface, for two landing trajectories. (c, d) Variation of descent speed ($V_d$) with height ($h$) above the surface, for two landing trajectories. The straight lines are linear regressions through the data, as represented by the equations; $r$ denotes the regression coefficient. Adapted from Srinivasan et al. (2000).
gantry head, which can be translated in three dimensions \((x, y, \text{ and } z)\). For the purpose of implementing the landing strategy, translatory motion of the camera is restricted to the forward \((x)\) and downward \((-z)\) directions. There is no rotary motion about the \(z\) axis.

The system is placed under closed-loop control by using a computer to analyze the motion in the image sequence captured by the camera, and to control the motion of the gantry. A view of the gantry and camera is shown in Figure 3. The floor, defined to be the landing surface, is covered with a spatially random, black-and-white visual texture. The camera faces downwards and views the floor. The velocity of image motion is measured by using an image interpolation algorithm, details of which are given in Srinivasan (1994).

Landing is controlled as follows. The system is required to maintain a constant descent angle \((\tan^{-1}(V_d/V_f))\) and a constant image angular velocity, \(\omega_{\text{set}}\), as it descends. In the first time step, the gantry moves the camera head along the direction of descent at an arbitrarily chosen initial speed. The image velocity is measured during this step, using the image interpolation algorithm. Let us denote the measured image velocity by \(\omega_{\text{meas}}\). In the next step, the speed of motion of the head is increased or decreased, depending upon whether the measured image velocity is lower or higher than the set image velocity. Specifically, the forward speed \(V_f(i + 1)\) of the camera during the next step is related to the current speed \(V_f(i)\) by

\[
V_f(i + 1) = V_f(i) \cdot \frac{\omega_{\text{set}}}{\omega_{\text{meas}}} \tag{1}
\]

The speed of descent is also corrected by the same factor, since the forward and descent speeds are proportional to each other and linked by the desired angle of descent. This speed correction ensures that the image velocity during the next step will have the desired value \(\omega_{\text{set}}\), provided the camera maintains its present altitude. However, since the camera continues to descend during the new step, the forward speed in the following step would have to be reduced further. Thus, both the forward and descent speeds decrease continuously as the camera descends, reaching very low values when the camera is close to the ground.

Landing trajectories generated, using this procedure, by the gantry are shown in Figure 4a for three descent angles. The image velocities maintained during these three landings are shown in Figure 4b. It is clear that the image velocity, though somewhat noisy, is held approximately constant. The height of the camera decreases exponentially with time (Fig. 4c), as do the forward speed and the speed of descent. These behaviors are as expected: a quantitative model of the landing strategy predicts and verifies that these variables do indeed vary exponentially with time (Srinivasan et al., 2000).

The results with the robotic gantry suggest that the strategy proposed is a feasible one for landing on flat surfaces, provided the surface carries visual texture that will enable the measurement of image motion. In undulating terrain, the system reduces the forward and descent speeds when the ground rises toward the camera, and increases them when the ground falls away. This is obviously a desirable feature, but has limitations in that the system cannot cope with a situation in which the ground in front rises abruptly to a level above the camera’s current height.

A little reflection will reveal that the landing strategy described here can be used by an aerial vehicle to dock with any flat surface, regardless of its orientation: horizontal, vertical, or oblique. All that is required is that the vehicle approach the surface in a straight line and hold the image velocity constant during the approach. This will automatically ensure that the vehicle’s speed decreases as the surface is approached, ensuring smooth docking. In the special case in which the surface is approached perpendicularly, the image velocity will be zero in the “straight ahead” direction: the flow field has a pole there. However, the strategy can still be implemented by holding constant the image speed in an annular region surrounding the pole, or in a large region.

**Figure 3.** View of robotic gantry, showing camera head and visual texture on the floor. Adapted from Srinivasan et al. (2000).
centered on the pole. Although the present study does not reveal whether bees are actually “aware” of the orientation of the surface in relation to the direction of their approach, it is clear from the above discussion that this information is not necessary for executing the landing process.

**Conclusions**

Analysis of vision in simple natural systems, such as those found in insects, can often point to novel ways of tackling tenacious problems in autonomous navigation. This is probably because insects, with their “stripped down” nervous systems, have been forced to evolve ingenious strategies to cope with visual challenges within their environment. This article has outlined a surprisingly simple way in which insects use motion cues to perform smooth landings on flat surfaces. The next step is to investigate whether this principle can be used to advantage in the design of visually based control systems for autonomously flying vehicles.

**Acknowledgments**

We thank the anonymous referees for their assistance in improving the manuscript. This research was supported partly by a grant from the Australian Defence Science and Technology Organisation, Salisbury, Grant RG 84/97 from the Human Frontiers in Science Program, and Grant N00014-99-1-0506 from the U.S. Defense Advanced Research Projects Agency and the Office of Naval Research.

**Literature Cited**

Borst, A., and S. Bahde. 1988. Visual information processing in the fly’s landing system. J. Comp. Physiol. A 163: 167–173.

Eckert, H., and K. Hamdorf. 1980. Excitatory and inhibitory response components in the landing response of the blowfly, Calliphora erythrocephala. J. Comp. Physiol. 138: 253–264.

Gibson, J. J. 1950. The Perception of the Visual World. Houghton Mifflin, Boston.

Goodman, L. J. 1960. The landing responses of insects. I. The landing response of the fly, Lucilia sericata, and other Calliphoridae. J. Exp. Biol. 37: 854–878.

---

**Figure 4.** Landing trajectories generated by the robotic gantry. (a) Height versus distance traveled for three descent angles: −26.5° (circles), −45° (squares), and −63.5° (triangles). (b) Variation of image angular velocity as a function of time. The symbols in this and other panels refer to the three different descent angles, as in (a). (c) Variation of height with time. (d) Variation of forward speed with time. The line curves in (c) and (d) depict least-squares fits of exponential functions to the data. Descent speed also declines exponentially (data not shown). Adapted from Srinivasan et al. (2000).
Götz, K. G., and U. Wandel. 1984. Optomotor control of the force of flight in Drosophila and Musca. II. Covariance of lift and thrust in still air. Biol. Cybern. 51: 135–139.

Horridge, G. A. 1977. Insects which turn and look. Endeavour 1: 7–17.

Horridge, G. A. 1987. The evolution of visual processing and the construction of seeing systems. Proc. R. Soc. Lond. B 230: 279–292.

Srinivasan, M. V. 1993. How insects infer range from visual motion. Pp. 139–156 in Visual Motion and Its Role in the Stabilization of Gaze, F. A. Miles and J. Wallman, eds. Elsevier, Amsterdam.

Srinivasan, M. V. 1994. An image-interpolation technique for the computation of optic flow and egomotion. Biol. Cybern. 71: 401–416.

Srinivasan, M. V. 1998. Insects as Gibsonian animals. Ecol. Psychol. 10: 251–270.

Srinivasan, M. V., S. W. Zhang, J. S. Chahl, E. Barth, and S. Venkatesh. 2000. How honeybees make grazing landings on flat surfaces. Biol. Cybern. 83: 171–183.

Wagner, H. 1982. Flow-field variables trigger landing flies. Nature 297: 147–148.