

Insects as Gibsonian Animals

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Research on the visual behavior of insects has uncovered a number of cues that are used for controlling and stabilizing flight and for extracting information about the structure of the environment. Flies monitor their egomotion and maintain a straight course by sensing the patterns of image motion that are induced in the eyes. Bees flying through a tunnel maintain equidistance to the flanking walls by balancing the speeds of the images of the two walls. This enables them to safely negotiate narrow passages or to fly between obstacles. The speed of flight in the tunnel is controlled by holding constant the average image velocity as seen by the 2 eyes. This ensures that the bee slows down to a safer speed when the passage narrows. Bees landing on a horizontal surface hold constant the image velocity of the surface as they approach it, thus automatically ensuring that flight speed is close to 0 at touchdown. Flies and bees distinguish objects from backgrounds by sensing the relative motion between the images of the object and the background. Ranges of objects are gauged in terms of the speeds of motion of the images of the objects. Foraging bees estimate the distance that they have traveled to reach a food source by integrating the optic flow experienced en route—they possess a visually driven odometer.

Insects, being more reliant on image-motion cues than mammals or higher vertebrates, have proven to be excellent organisms on which to test and confirm Gibson's (1958/*this issue*) pioneering concepts about visually guided locomotion.

In 1958, Gibson speculated that an animal could locomote safely in an environment and glean important information about it by monitoring the way in which the image of the surroundings changed as the animal itself moved. Forty years later, most of Gibson's postulates have been confirmed, many through the study of visually mediated behavior in insects.

Unlike vertebrates, insects have immobile eyes with fixed-focus optics. Therefore, they cannot infer the distance of an object 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 possess inferior spatial acuity. Therefore, even if an insect possessed the neural apparatus required for binocular stereopsis, such a mechanism would be relatively imprecise and restricted to ranges of a few centimeters (Collett & Harkness, 1982; Horridge, 1987; Rossell, 1983; Srinivasan, 1993). Not surprisingly, insects have evolved alternative visual strategies for guiding locomotion and for seeing the world in three dimensions. Many of these strategies rely on using image motion as the significant cue. Some of them are outlined here, and references to more complete accounts are provided.

PEERING INSECTS

Over 100 years ago, Exner (1891, pp.130–131), pondering the eyestalk movements of crabs, speculated that invertebrates might use image motion to estimate object range. However, the first clear evidence to support this conjecture did not arrive until the year after Gibson's (1958/this issue) seminal paper, when Wallace (1959) made the astute observation that a locust sways its head from side to side before jumping on to a nearby object (Figure 1a). Wallace hypothesized that this peering

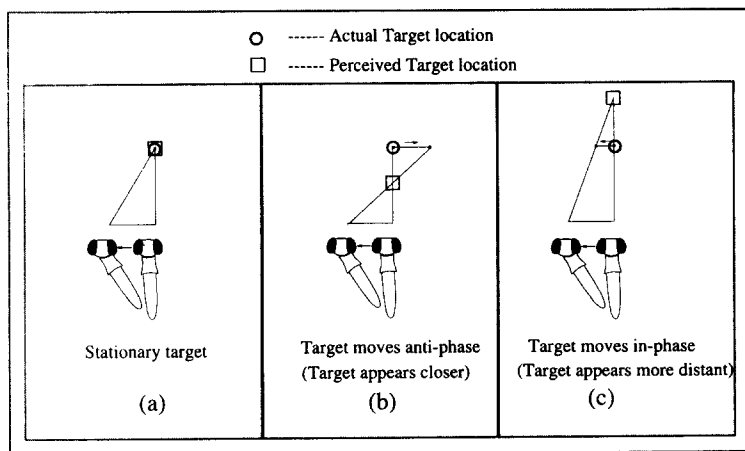


FIGURE 1 Experiments investigating how locusts measure target range by peering. Adapted from Sobel (1990). *Note.* From "The Locust's Use of Motion Parallax to Measure Distance," by E. B. Sobel, 1990, *Journal of Comparative Physiology*, p. 582. Copyright 1990 by Springer-Verlag GmbH & Co. Adapted with permission.

motion, typically 5 to 10 mm in amplitude, was a strategy for measuring object range. To test this hypothesis, he presented a locust with two objects subtending the same visual angle. One object was relatively small in size and was placed close to the locust, whereas the other was larger and situated further away. He found that the locust, after peering, jumped almost invariably to the nearer object. In a further series of elegant experiments, recently confirmed more quantitatively by Sobel (1990), a target was oscillated from side to side, in synchrony with the insect's peering movements. When the target was oscillated out of phase with the movement of the head, thereby increasing the speed and amplitude of the object's image on the retina, the locust consistently underestimated the range of the target (Figure 1b). When the target was oscillated in phase with the head, it consistently overestimated the range (Figure 1c). This showed that the reduced image motion of the target caused the insect to overestimate the target's range, whereas increased motion had the opposite effect. These findings demonstrated convincingly that the peering locust was estimating the range of the target in terms of the speed of the image on the retina. It is now known that certain other insects, such as grasshoppers (Eriksson, 1980) and mantids (Horridge, 1986), also use peering to measure object range.

FLYING INSECTS

Peering, however, is practicable only when an insect is not locomoting. Are flying insects capable of gleanng range information from image motion, and if so, how do they accomplish this? Stable flight in a straight line would seem to be a prerequisite for extracting information on range (Horridge, 1987; Srinivasan, 1993). Research over the past 50 years has uncovered a number of different ways in which insects use image motion to control flight and perceive the world in three dimensions.

Stabilizing Flight

For insects, vision provides an important sensory input for the stabilization of flight. If an insect flying along a straight line is blown to the left by a gust of wind, the image on its frontal retina moves to the right. This causes the flight motor system to generate a counteractive yaw torque, which brings the insect back on course (Reichardt, 1969). Similar control mechanisms act to stabilize pitch and roll (e.g., Srinivasan, 1977). This so-called "optomotor response" (Reichardt, 1969) has not only confirmed Gibson's speculation about the existence of "visual kinesthesia" in animals (Gibson, 1958, pp. 185–186/*this issue*), but also provided an excellent experimental paradigm in which to probe the neural mechanisms underlying motion detection. Largely through studies of the optomotor response in flies, we now know that the direction of image movement is sensed by correlating the intensity variations registered by neighboring *ommatidia*, or facets, of the compound eye (Reichardt, 1969). Recent research over the past 30 years has uncovered the existence of a number of

motion-sensitive neurons with large visual fields, each responding preferentially to motion in a specific direction (Hausen, 1993; Hausen & Egelhaaf, 1989) or to rotation of the fly about a specific axis (Krapp & Hengstenberg, 1996). These neurons are likely to play an important role in stabilizing flight and providing the fly with a visually kinesthetic sense.

Hovering

Hoverflies and certain species of bee display an impressive ability to hold a rigid position in midair, compensating almost perfectly for wind gusts and other disturbances. Kelber and Zeil (1997) recently investigated hovering in a species of stingless bee, *Tetragonisca angustula*. Guard bees of this species hover stably in watch near the entrance to their nest, protecting it from intruders. To investigate the visual stabilizing mechanisms, Kelber and Zeil got the bees used to the presence of a spiral pattern mounted on the vertical face of the hive, surrounding the entrance. When the spiral was briefly rotated to simulate expansion, the hovering guard bees darted away from the focus of apparent expansion; when the spiral was rotated to simulate contraction, they moved toward the focus of contraction. These responses were always directed toward or away from the nest entrance, irrespective of the bees' orientation, and therefore irrespective of the region of the eye that experienced the experimentally imposed pattern of image motion. Clearly, then, these creatures were interpreting expansion and contraction of the image as unintended movements toward or away from the nest entrance, and compensating for them. This elegant experiment confirms one of Gibson's (1958/*this issue*) postulates, namely that animals are able to infer approach toward or movement away from objects in the environment by appropriate analysis of the induced pattern of optic flow.

Negotiating Narrow Gaps

When a bee flies through a hole in a window, it tends to fly through its center, balancing the distances to the left and right boundaries of the opening. How does the bee gauge and balance the distances to the two rims?

One possibility is that the bee does not measure distances at all, but simply balances the speeds of image motion on the two eyes as they fly through the opening. To investigate this possibility, Kirchner and Srinivasan (1989) trained bees to enter an apparatus that offered a reward of sugar solution at the end of a 40-cm long tunnel. Each side wall carried a pattern consisting of a vertical black-and-white grating (Figure 2). The grating on one wall could be moved horizontally at any desired speed, either toward the reward or away from it. After the bees had received several rewards with the gratings stationary, they were filmed from above as they flew along the tunnel. When both gratings were stationary, the bees tended to fly

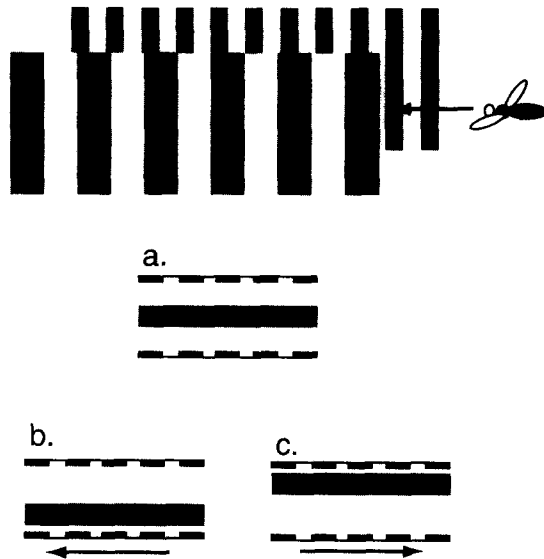


FIGURE 2 Experiment investigating how bees negotiate narrow passages. Bees fly through a tunnel 40 cm long, 12 cm wide, and 20 cm high, in which the flanking walls are lined with black-and-white gratings of period 5 cm. The grey bars in (a) and (c) represent means and standard deviations of the positions of several hundred flight trajectories. *Note.* From "Range Perception Through Apparent Image Speed in Freely-Flying Honeybees," by M. V. Srinivasan, M. Lehrer, W. Kirchner, and S. W. Zhang, 1994, *Visual Neuroscience*, 6, p. 521. Copyright 1994 by Cambridge University Press. Adapted with permission.

along the midline of the tunnel (i.e., equidistant from the two walls; Figure 2a). But when one of the gratings was moved at a constant speed in the direction of the bees' flight—thereby reducing the speed of retinal image motion on that eye relative to the other eye—the bees' trajectories shifted toward the side of the moving grating (Figure 2b). When the grating moved in a direction opposite to that of the bees' flight—thereby increasing the speed of retinal image motion on that eye relative to the other—the bees' trajectories shifted away from the side of the moving grating (Figure 2c). These findings demonstrate that when the walls were stationary, the bees maintained equidistance by balancing the speeds of the retinal images in the two eyes. A lower image speed on one eye was evidently taken to mean that the grating on that side was farther away, and caused the bee to fly along a trajectory closer to it, evidently causing the bee to move closer to the wall seen by that eye. A higher image speed, on the other hand, had the opposite effect.

Experiments using gratings of different periods (Srinivasan, Lehrer, Kirchner, & Zhang, 1991) confirmed that the bees were indeed centering themselves in the tunnel by balancing the image speeds on the two sides and not simply by balancing the temporal frequencies of the intensity fluctuations produced by the succession of dark and light bars of the gratings.

These findings suggest that the bee's visual system is capable of computing the apparent angular speed of a grating independently of its contrast and spatial-frequency content. Indeed, if movement cues are to be exploited to estimate the range of a surface, it is necessary to use a mechanism that measures the speed of the image independently of its geometrical structure. It is this kind of mechanism that would enable an insect to fly through the middle of a gap between, say, two vertical branches of a tree, regardless of the textural properties of the bark on the two sides. We note that this strategy for avoiding obstacles is somewhat different from that suggested by Gibson (1958, p. 188/*this issue*). His proposal was to avoid placing the focus of centrifugal flow on a textured part of the visual scene.

Controlling Flight Speed

Do insects control their flight speed by monitoring the apparent velocity of the surrounding environment? Work by David (1982) and Srinivasan, Zhang, Lehrer, and Collett (1996) suggests that this is indeed the case.

David (1982) observed fruitflies flying upstream in a wind tunnel, attracted by an odor of fermenting banana. The walls of the cylindrical wind tunnel were decorated with a helical black-and-white striped pattern, so that rotation of the cylinder about its axis produced apparent movement of the pattern toward the front or the back. With this setup, the speed of the cylinder (and hence the speed of the backward motion of the pattern) could be adjusted such that the fly was stationary (i.e., did not move along the axis of the tunnel). The apparent backward speed of the pattern then revealed the ground speed that the fly was choosing to maintain, as well as the angular velocity of the image of the pattern on the fly's eyes. In this setup, fruitflies tended to hold the angular velocity of the image constant. Increasing or decreasing the speed of the pattern caused the fly to move backward or forward (respectively) along the tunnel at a rate such that the angular velocity of the image on the eye was always clamped at a fixed value. The flies also compensated for headwind in the tunnel, increasing or decreasing their thrust so as to maintain the same apparent ground speed (as indicated by the angular velocity of image motion on the eye). Experiments in which the angular spacing of the stripes was varied revealed that the flies were measuring (and holding constant) the angular velocity of the image on the eye, irrespective of the spatial structure of the image.

Bees appear to use a similar strategy to regulate flight speed. An experiment illustrating this is shown in Figure 3, where bees are trained to fly through a tapered

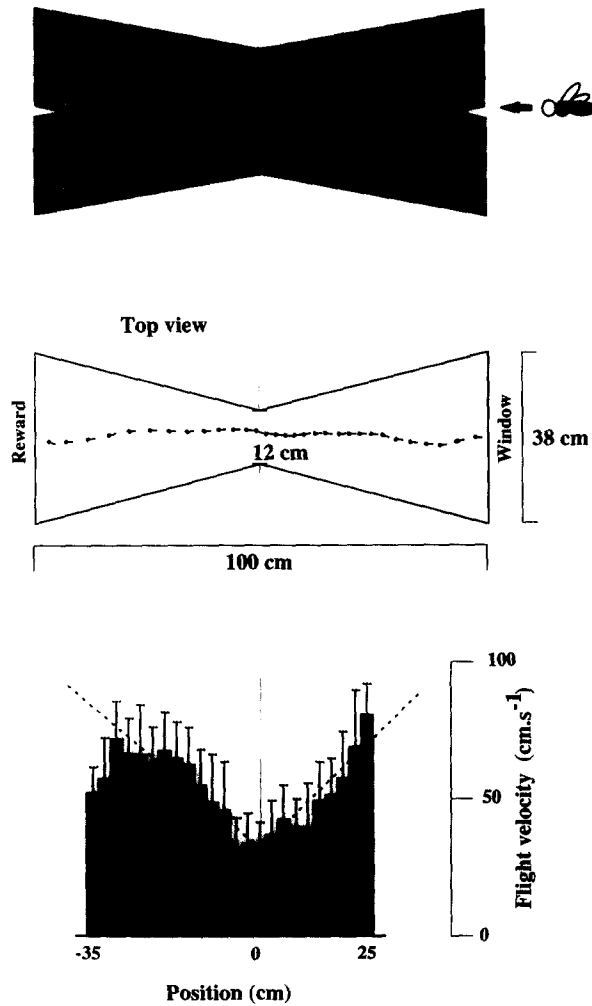


FIGURE 3 Experiment investigating visual control of flight speed. The figure shows flight velocity profiles (bottom panel) of bees flying through a tapered tunnel carrying vertical stripes on either side wall (top and center panels). The dashed line shows the theoretically expected flight velocity profile if the bees were to hold the angular velocity of the image of the walls constant as they fly through the tunnel. *Note.* From "Honeybee Navigation En Route to the Goal: Visual Flight Control and Odometry," by M. V. Srinivasan, S. W. Zhang, M. Lehrer, and T. S. Collett, 1996, *Journal of Experimental Biology*, 199, p. 239. Copyright 1996 by Company of Biologists, Ltd. Adapted with permission.

tunnel lined with black-and-white vertical stripes (top panel in Figure 3). The bees slow down as they approach the narrowest section of the tunnel, and accelerate when the tunnel widens beyond it (Figure 3, middle panel). In fact, the variation of flight speed is very close to that expected if the bees were to hold the angular velocity of the image in the lateral-eye region constant as they fly through the tunnel (dashed line in Figure 3, bottom panel). It is evident that the bees are able to hold the angular velocity of the image on the wall constant, despite the changes in the angular period of the stripes that accompany the narrowing and widening of the tunnel. On the other hand, bees flying through a tunnel of constant width do not change their speed when they encounter an abrupt change in stripe period halfway through the tunnel (Srinivasan et al., 1996). This finding indicates that bees are measuring the angular velocity of the image accurately, irrespective of its spatial structure. Visual control of flight speed is thus achieved by monitoring and regulating the apparent motion of the visual panorama using a movement-sensitive mechanism that is capable of measuring the angular velocity of the image.

An obvious advantage of controlling flight speed by regulating image speed is that the insect would automatically slow down to a safer speed when negotiating a narrow passage. A by-product of this mode of operation is that the speed of flight is significantly higher when the optic-flow cues provided by the environment are weak or absent. Thus, bees flying in a tunnel tend to fly considerably faster when the walls are lined with axial stripes, rather than with cross stripes or a random Julesz texture (Srinivasan, Zhang, & Bidwell, 1997, and unpublished observations). In other words, a tunnel that offers little or no optic-flow cues is interpreted as a very wide tunnel. It is as though the forward thrust exerted by the flying bee is opposed by a kind of visual friction that is created by the induced optic flow, and that the bee flies at a steady-state speed at which the thrust is balanced by this friction. This phenomenon, again, would be predicted by Gibson's notions of visual kinaesthesia and their quantitative formulation by Warren (1988) as the law of ecological optics and the law of specification.

Estimating Distance Flown

Although it is well established that foraging honeybees can gauge the distances to food sources, the mechanisms by which they do so have remained enigmatic (Esch & Burns, 1996). This question was reexamined recently by Esch and Burns (1995, 1996) and by Srinivasan et al. (1996) and Srinivasan et al. (1997) using different approaches.

Esch and Burns (1995) investigated distance measurement by enticing honeybees to find food at a feeder placed 70 m away from a hive in an open field, and recording the distance as signalled by the bees when they danced to recruit other nestmates in the hive. When the feeder was 70 m away, the bees signaled 70 m—the correct distance. But when the feeder was raised above the ground by attaching it to a helium

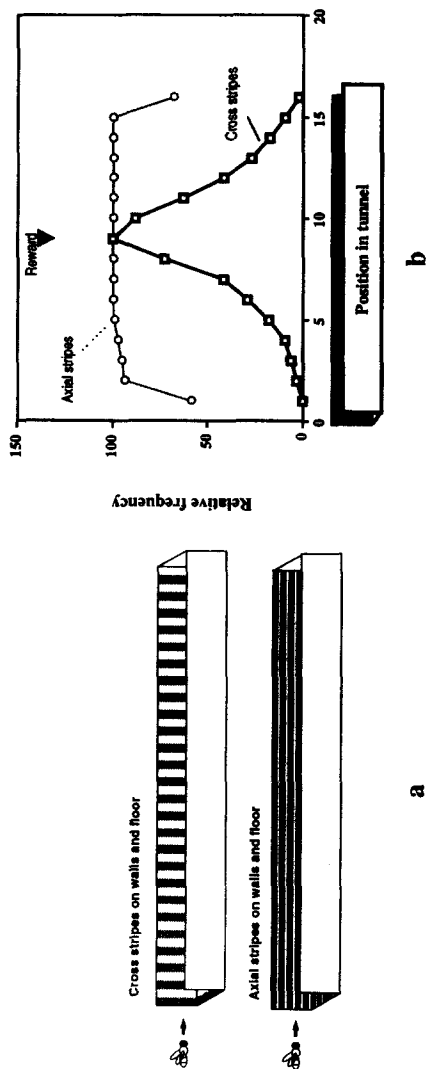


FIGURE 4 (a) Experimental setup for investigating how bees estimate distance flown. Bees are trained to find a feeder placed at a fixed distance from the tunnel entrance. (b) Performance of trained bees in estimating distance traveled in the tunnel, as shown by distributions of searching locations. Note. From "Visually Mediated Odometry in Honeybees," by M. V. Srinivasan, S. W. Zhang, & N. Bidwell, 1997, *Journal of Experimental Biology*, 200, p. 2516. Copyright 1997 by Company of Biologists, Ltd. Adapted with permission.

balloon, the bees signaled a progressively shorter distance as the height of the balloon was increased. This was despite the fact that the balloon was now farther away from the hive! Esch and Burns explained this finding by proposing that the bees were gauging distance flown in terms of the motion of the image of the ground below, rather than, for example, through the energy consumed to reach the feeder. The higher the balloon, the lower was the total amount of image motion that the bee experienced en route to the feeder.

This hypothesis was examined by Srinivasan et al. (1996) and Srinivasan et al. (1997), who investigated the cues by which bees estimate and learn distances flown under controlled laboratory conditions. Bees were trained to enter a 3.2-m-long tunnel and collect a reward of sugar solution at a feeder placed in the tunnel at a fixed distance from the entrance. The walls and floor of the tunnel were lined with black-and-white stripes perpendicular to the tunnel's axis (Figure 4a). During training, the position and orientation of the tunnel were changed frequently to prevent the bees from using any external landmarks to gauge their position relative to the tunnel entrance. The bees were then tested by recording their searching behavior in an identical, fresh tunnel that carried no reward and was devoid of any scent cues. In the tests, these bees showed a clear ability to search for the reward at the correct distance, as indicated by the thick curve in Figure 4b.

How were the bees gauging the distance they had flown in the tunnel? Tests were carried out to examine the participation of a variety of potential cues, including energy consumption, time of flight, airspeed integration, and inertial navigation (Srinivasan et al., 1997). It turned out that the bees were estimating distance flown by integrating, over time, the motion of the images of the walls on the eyes as they flew down the tunnel. The crucial experiment was one in which bees were trained and tested in conditions where image motion was eliminated or reduced by using axially oriented stripes on the walls and floor of the tunnel. The bees then showed no ability to gauge distance traveled. In the tests, they searched uniformly over the entire length of the tunnel, showing no tendency to stop or turn at the former location of the reward (thin curve, Figure 4b).

These results, considered together with those of Esch and Burns (1995, 1996) indicate that the bee's odometer is driven by the image motion that is generated in the eyes during translatory flight. Evidently, bees use Gibson's visual kinaesthesia not only to stabilize and regulate the speed of flight, but also to estimate how far they have flown.

Executing Smooth Landings

How does a bee execute a smooth touchdown on a surface? An approach that is perpendicular to the surface would generate strong looming (image expansion) cues that could, in principle, be used to decelerate flight at the appropriate moment. Indeed, work by Wagner (1982) and Borst and Bahde (1988) showed that decelera-

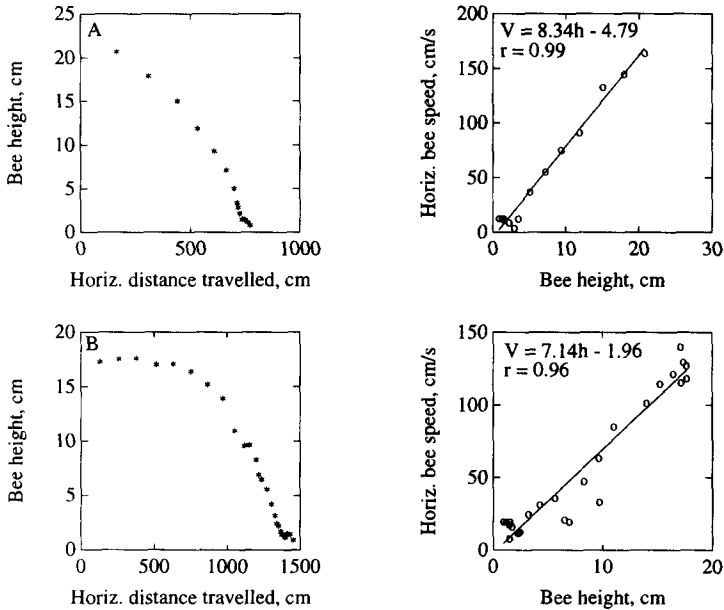


FIGURE 5 Analysis of flight trajectory while landing on a horizontal surface, shown for two bees (A) and (B). In each case, the left-hand panel shows the relation between height (h) and horizontal distance traveled, whereas the right-hand panel shows the relation between horizontal flight speed (V) and height (h). The landing bee holds the angular velocity of the image of the ground constant at $480^\circ/\text{sec}$ in (A), and at $410^\circ/\text{sec}$ in (B), as calculated from the slopes of the linear regression lines. Also shown are the values of the correlation coefficient (r). *Note.* From "Honeybee Navigation En Route to the Goal: Visual Flight Control and Odometry," by M. V. Srinivasan, S. W. Zhang, M. Lehrer, and T. S. Collett, 1996, *Journal of Experimental Biology*, 199, p. 241. Copyright 1996 by Company of Biologists, Ltd. Adapted with permission.

tion and extension of the legs in preparation for landing are triggered by movement-detecting mechanisms that sense expansion of the image (but not contraction), just as Gibson (1958, p. 188/*this issue*) predicted.

Looming cues are weak, however, when a bee performs a grazing landing on a surface. By grazing landings we mean landings whose trajectories are inclined to the surface at an angle that is considerably less than 45° . To investigate how bees execute such landings, Srinivasan et al. (1996) trained bees to collect a reward of sugar water on a textured, horizontal surface. The reward was then removed and the landings that the bees made on the surface in search of the food were filmed on video in three dimensions.

Analysis of the landing trajectories revealed that the forward speed of the bee decreases steadily as the bee approaches the surface (Figure 5). In fact, the speed of

flight is approximately proportional to the height above the surface, indicating that the bee is holding the angular velocity of the image of the surface approximately constant as the surface is approached. This may be a simple way of controlling flight speed during landing, ensuring that its value is close to zero at touchdown. The advantage of such a strategy is that the control is achieved by a very simple process, and without explicit knowledge of the distance from the surface.

Distinguishing Objects at Different Distances

The aforementioned experiments show that bees stabilize flight, negotiate narrow passages, and orchestrate smooth landings by using what seem to be a series of simple, low-level visual reflexes. But they do not tell us whether flying bees see the world in three dimensions in the way we do. Do bees perceive the world as being composed of objects and surfaces at various ranges? Although this is a difficult question—one that a philosopher might declare unanswerable—one can at least ask whether bees can be trained to distinguish between objects at different distances. Lehrer, Srinivasan, Zhang, and Horridge (1988) trained bees to fly over an artificial meadow and distinguish between artificial flowers at various heights. The training was carried out by associating a reward with a flower at a particular height. The sizes and positions of the flowers were varied randomly and frequently during the training. This ensured that the bees were trained to associate only the height of the flower (or, more accurately, the distance from the eye), and not its position, or angular subtense, with the reward. Using this approach—details of which are described in Srinivasan, Lehrer, Zhang, and Horridge (1989)—it was possible to train bees to choose either the highest flower, the lowest flower, or even one at intermediate height. Clearly, then, the bees were able to distinguish flowers at different heights. Under the experimental conditions, the only cue that a bee could have used to gauge the height of each flower would be the speed of the flower's image as she flew over it: The taller the flower, the faster the motion of its image. To test if the bees were really using image motion to infer flower height, the same experiment was repeated with the flowers presented inside a drum whose inside was lined with vertical stripes (Lehrer & Srinivasan, 1992). Bees trained in this apparatus lost the ability to discriminate height when the drum was rotated. Evidently, the optomotor response evoked by the rotating drum caused the bees to turn with the drum, and therefore disrupted the relation between the range of each object and the speed of its image on the retina. This experiment demonstrates that optic flow cues are crucial to discriminating range. Rotation of the drum does not affect the bee's capacity to perform other kinds of visual tasks, such as color discrimination (Lehrer & Srinivasan, 1992). Therefore, the stimulus created by the rotating drum does not confuse the bees in a nonspecific way—it only disrupts cues that rely on image motion.

In summary, these experiments suggest that bees indeed use cues based on image motion to distinguish between objects at different distances.

Kirchner and Lengler (1994) extended the basic meadow experiment by training bees to distinguish the heights of artificial flowers that carried spiral patterns. Six flowers were presented at the same height, while a seventh was either higher (in one training experiment) or lower (in another experiment). Bees trained in this way were tested with a constellation of three identical spiral-bearing flowers of the same height. One test flower was stationary, one was rotated to simulate expansion, and the other rotated to simulate contraction. Bees that had learned to find the higher flower in the training chose the expanding flower in the test, whereas bees that had learned to choose the lower flower in the training chose the contracting flower. For a bee flying above the flowers and approaching the edge of one of them, the expanding flower produced a higher image motion at its boundary than did the stationary one, and was evidently interpreted to be the higher flower. The contracting flower, on the other hand, produced a lower image motion and was therefore taken to be the lower one. This experiment confirms the notion that image motion is an important cue in establishing the relative distances of objects.

Discriminating Objects From Backgrounds

In all of the work described earlier, the objects that were being viewed were readily visible to the insects, because they presented a strong contrast—in luminance or color—against a structureless background. What happens if the luminance or color contrast is removed and replaced by motion contrast? To the human eye, a textured figure is invisible when it is presented motionless against a similarly textured background. However, the figure pops out as soon as it is moved relative to the background. This type of relative motion, termed *motion parallax*, can be used to distinguish a nearby object from a remote background. Is an insect capable of distinguishing a textured figure from a similarly textured background purely on the basis of motion parallax?

In a series of pioneering experiments, Reichardt and his colleagues in Tübingen showed that a fly is indeed capable of such figure-ground discrimination (Egelhaaf, Hausen, Reichardt, & Wehrhahn, 1988; Reichardt & Poggio, 1979). A tethered, flying fly will show no sign of detecting a textured figure when the figure oscillates in synchrony with a similarly textured background, but will react to the figure by turning toward it when the figure moves incoherently with respect to the background.

In antipodean Canberra, this question was approached in a different way. Srinivasan, Lehrer, and Horridge (1990) examined whether freely flying bees could be trained to find a textured figure when it was presented raised over a background of the same texture. The figure was a disc, bearing a random black-and-white texture, carried on the underside of a transparent perspex sheet that could be placed

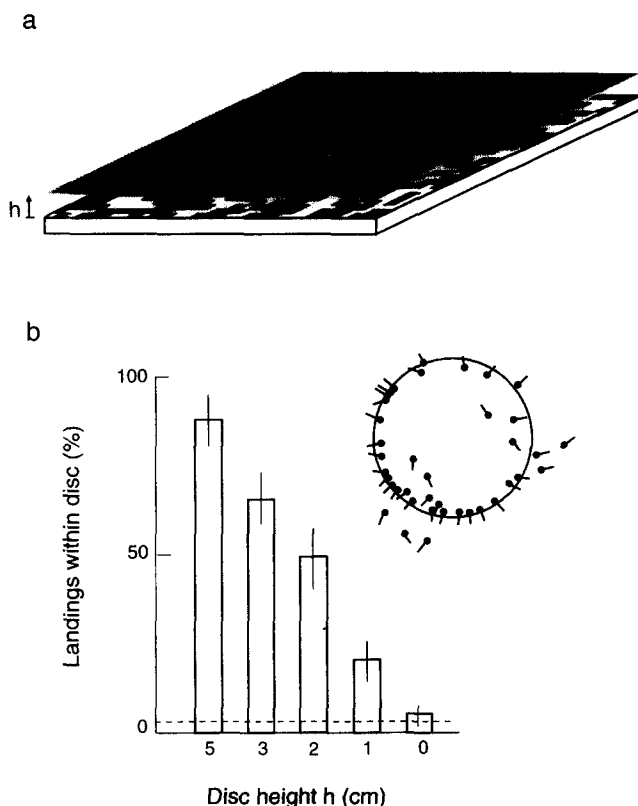


FIGURE 6 Experiment investigating the ability of bees to use motion parallax cues to distinguish a figure from its background. (a) Apparatus presents a textured disc, 6 cm in diameter, positioned under a sheet of clear perspex at a height h cm above a similarly textured background (42 cm \times 30 cm, pixel size 5 mm \times 5 mm). The disc is shown as being brighter than the background only for clarity. (b) Bars show percentage of landings occurring within the disc, for various heights (h) of the disc above the background. A total of 1,121 landings were analyzed. Detectability of the disc reduces as h decreases, reaching the random-hit level (dashed line) when $h = 0$, that is, when there is no motion parallax. Inset shows a sample of the distribution of landings of trained bees on the perspex sheet when $h = 5$ cm. *Note.* From "Visual Figure-Ground Discrimination in the Honeybee: The Role of Motion Parallax at Boundaries," by M. V. Srinivasan, M. Lehrer, and G. A. Horridge, 1990, *Proceedings of the Royal Society of London B*, 238, p. 333, 336, and 338. Copyright 1990 by the Royal Society of London. Adapted with permission.

at any desired height above the background (Figure 6a). It was found that bees could indeed be trained to locate the figure and land on it, provided the figure was raised at least 1 cm above the background (Figure 6b). When the figure was placed directly on the background, the bees failed to find it (Srinivasan et al., 1990), demonstrating that the cue used to locate the figure is the apparent relative motion between figure and background, caused by the bees' own flight above the setup. Video films of the landings of the bees showed that, when the disc was visible to the bees, they did not land at random on it. Rather, they landed primarily near the boundary of the disc, facing the visual cliff (Figure 6b). These experiments showed that the boundary has special visual significance and that bees are capable of detecting it reliably. Further investigation is needed to determine whether such boundaries are detected in terms of the differences in image speeds on the two sides, or in terms of the progressive occlusion of the background as the bee flies against a more remote background. In the language of Gibson (1979/1986), occlusion at the boundary may provide the affordance of where to land. The landing studies conducted so far do not reveal whether the apparent relative motion between the figure and the background causes the figure to pop out perceptually for the bee, as it does for humans, or whether it simply provides a low-level cue that ensures touchdown at a suitable spot.

The ability to detect objects through the discontinuities in motion that occur at the boundaries is likely to be important when an insect attempts to land on a leaf or a shrub. This is a situation where it may be difficult to distinguish individual leaves or establish which leaf is nearest, because cues based on contrast in luminance or color are weak. Visual problems of this nature are not restricted to insects. Over 130 years ago, Helmholtz (1866/1962) speculated that humans might use motion-based cues in a similar way to distinguish individual trees in a dense forest.

Can insects discriminate the shapes of camouflaged objects that are visible only through motion parallax? It turns out that bees cannot directly be trained to distinguish between two such camouflaged shapes (Zhang & Srinivasan, 1994). However, they can learn to do so when they are initially primed with solid versions of these shapes, presented, for example, as black figures on a white background. Evidently, the luminance contours in the priming stimuli facilitate the detection of the motion-parallax contours in the subsequently presented, camouflaged stimuli (Zhang & Srinivasan, 1994; Zhang, Srinivasan, & Collett, 1995). Furthermore, bees that have been trained to discriminate camouflaged shapes in this way can quickly learn to distinguish novel camouflaged shapes without being primed on the new shapes. Because these experiments were conducted with the stimuli presented in the vertical plane in a Y-maze, and because the bees had to choose between alternate shapes from a distance (Zhang & Srinivasan, 1994), it seems very likely that relative motion did indeed cause these shapes to, clearly, then, pop out perceptually against their backgrounds. These experiments demonstrate that pattern

recognition in bees embodies some form of top-down processing in which prior experience not only facilitates the detection and recognition of poorly visible objects, but also changes the nature of the cues that the visual system extracts to carry out the stipulated task. In other words, bees can learn to look at their world in new ways.

Motion Camouflage

As an animal moves, the images of the objects in the environment move on the retina, even if the objects are physically stationary in the environment. Nevertheless, a number of animals (Cott, 1966, pp. 141–143), including insects (Lehrer & Srinivasan, 1992), are adept at distinguishing between stationary and moving objects, even when they themselves are in motion. Usually, the optic flow produced on the retina by a self-moving object is different from that produced by a stationary one (Gibson, 1950). Evidently, the visual systems of many animals are capable of detecting this inconsistency. Given this, can one animal (or agent) track, or shadow, another without giving itself away by its own motion? A lioness approaching her prey (Cott, 1966; Curio, 1976, pp. 136–152) or an amorous male praying mantis approaching a potential mate (Roeder, 1967, pp. 160–164) uses a simple but effective ploy—that of moving very slowly. But stealth is feasible only when the prey or mate is stationary; it is not an option when the prey is moving rapidly away from the predator. Do rapidly moving animals attempt to hide their own motion, and if so, how do they accomplish this?

Hoverflies may provide an answer to this question, at least in instances where the shadower is far enough away that he appears as a dot on the shadowee's retina, and therefore generates negligible expansional or contractional cues. The male hoverfly, *Syritta pipiens*, sometimes shadows females in flight. When a male spots a female he tracks the female (Collett & Land, 1975), maintaining a roughly constant distance from her by ensuring that her image subtends a constant vertical angle, à la Gibson (1958, pp. 188–189/*this issue*). When the female eventually lands, say, on a flower, the male darts rapidly toward her to mate. This behavior has been filmed and characterized elegantly by Collett and Land (1975, 1978) but primarily with the object of understanding the mechanisms subserving the visual control of tracking. These trajectories can, however, be re-examined from a different point of view—that of motion camouflage. An example, adapted from Figure 28a of Collett and Land (1975), is shown in Figure 7. Here, the shadowing male (A) moves in such a way as to emulate a stationary object behind him, located approximately at the circle. As the female (B) moves forward, the male yaws and moves laterally in such a way that he always stays on a line connecting the shadowee to the circle. Thus, to the female, the male appears as a stationary object located at the position of the circle. Other examples are given in Srinivasan and Davey (1995).

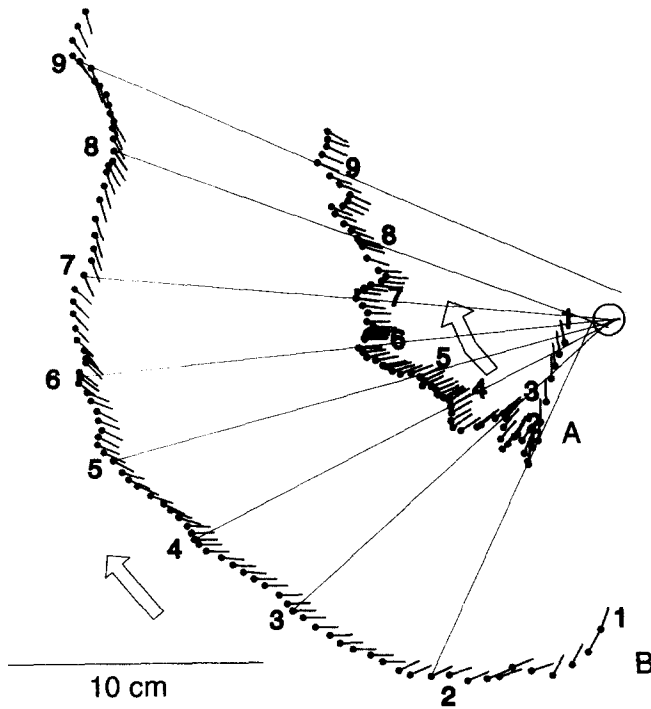


FIGURE 7 Shadowing behavior in hoverflies. Numbers denote 200-msec time intervals. Adapted from Collett and Land (1975) and Srinivasan and Davey (1995). *Note.* From "Strategies for Active Camouflage of Motion," by M. V. Srinivasan and M. Davey, 1995, *Proceedings of the Royal Society of London B*, 259, p. 24. Copyright 1995 by the Royal Society of London. Adapted with permission.

Although we do not yet know precisely how the male computes and executes such shadowing trajectories, there are two simple possibilities (Srinivasan & Davey, 1995). In one, the shadower picks a stationary landmark in the environment and moves in such a way that he always stays on the line connecting this landmark to the shadowee. The shadower thus emulates a stationary object situated at the position of the landmark. Alternatively, if no convenient landmark is available, the shadower can emulate a stationary object at a virtual landmark by measuring his egomotion relative to this landmark (by using some form of odometry, as described, for example, in Srinivasan et al., 1997) and moving in such a way that the ratio of his lateral translation to his yaw is proportional to his distance from the virtual landmark.

Motion camouflage of this sort may represent one instance in which the motives of one Gibsonian animal, highly reliant on motion cues to detect other creatures in

the environment, are thwarted by another animal that adopts what seems to be a very appropriate counter-measure.

CONCLUDING REMARKS

Forty years ago, Gibson postulated a number of visual cues that an organism could use to guide locomotion and to extract information about the surrounding environment. We can now say that insects have confirmed many of his hypotheses convincingly. We now know that flying insects exploit cues derived from image motion to stabilize flight, regulate flight speed, orchestrate smooth landings, distinguish objects from their backgrounds, avoid obstacles. These creatures are prime subjects for testing the ideas that Gibson proposed 40 years ago because, possessing poor or no stereopsis, they literally need to move in order to see. In this sense, insects may be regarded as the quintessential Gibsonian animals.

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