

Honeybees as a Model for the Study of Visually Guided Flight, Navigation, and Biologically Inspired Robotics

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Srinivasan MV. Honeybees as a Model for the Study of Visually Guided Flight, Navigation, and Biologically Inspired Robotics. *Physiol Rev* 91: 413–460, 2011; doi:10.1152/physrev.00005.2010.—Research over the past century has revealed the impressive capacities of the honeybee, *Apis mellifera*, in relation to visual perception, flight guidance, navigation, and learning and memory. These observations, coupled with the relative ease with which these creatures can be trained, and the relative simplicity of their nervous systems, have made honeybees an attractive model in which to pursue general principles of sensorimotor function in a variety of contexts, many of which pertain not just to honeybees, but several other animal species, including humans. This review begins by describing the principles

of visual guidance that underlie perception of the world in three dimensions, obstacle avoidance, control of flight speed, and orchestrating smooth landings. We then consider how navigation over long distances is accomplished, with particular reference to how bees use information from the celestial compass to determine their flight bearing, and information from the movement of the environment in their eyes to gauge how far they have flown. Finally, we illustrate how some of the principles gleaned from these studies are now being used to design novel, biologically inspired algorithms for the guidance of unmanned aerial vehicles.

I. GENERAL INTRODUCTION

Anyone with even a cursory knowledge of the *Lebensstil* of a honeybee would marvel at the ability of this insect, carrying a brain weighing less than a milligram, to seek out and find food sources several miles away, return home safely, and then repeat this journey repeatedly and unerringly. Even more amazingly, this so-called “scout” bee will provide navigational instructions to its nestmates about where the food is located so that they, too, can fly there to collect nectar or pollen, and contribute to the foraging requirements of the colony (268). The biology and lifestyle of the honeybee therefore offer us an excellent opportunity to study how these creatures perceive their world and navigate in it, and learn to recognize good sources of food, such as the color, shape, and scent of flowers, and to use landmarks in the environment to help them find their way.

An individual bee can be readily trained to return again and again to an attractive source of food that it has discovered, as often as once every 5 min, throughout the day, for several days at a stretch. This makes it relatively easy to design and conduct experiments, both in the field and in the laboratory, aimed at understanding how bees recognize objects in terms of their color, shape, visual texture or scent, how they learn routes to food sources, and how they communicate this information to their colleagues.

A recent article has reviewed the visual, perceptive and “cognitive” capacities of honeybees, highlighting the perception and learning of the colors and shapes of objects, the learning of complex navigational routes, and the formation of high-level associations (232). Here, we will deal with visually guided flight and navigation in honeybees. We will do this by focussing on a complementary, but equally fascinating, range of questions that deal with how honeybees perceive the world in three dimensions, how they use their vision to guide their flight through it, how they execute smooth landings, how they determine how far and in what direction they have flown to get to a source of food, how they convey this information to their nestmates, and how some of the knowledge gleaned from these studies is being used to design novel, biologically inspired algorithms for the navigation of autonomous aircraft.

We begin with a brief description of the structure of the honeybee’s compound eye and discuss its ability to discriminate color and to resolve spatial and temporal

detail in the visual environment. We then discuss the detection and perception of movement and show how flying bees (and probably most other insects) use the motion of the image of the environment that is created in their eyes to regulate their course, control their flight speed, avoid collisions with obstacles, estimate distance travelled, perform smooth landings, and perceive the world in three dimensions.

We describe how bees extract and use compass information from the sky to aid their navigation and to communicate information about the locations of attractive food sources to their nestmates.

Finally, we show how some of the principles of visual guidance and navigation that these studies have revealed are now being used to design novel, biologically inspired autonomous aircraft.

This review will concentrate on the female (worker) honeybee *Apis mellifera*, about which more is known, in these contexts, compared with the queen or with the male drone. Hence, we will occasionally refer to our subject as “she” rather than “he” or “it.”

II. THE COMPOUND EYE

Most insects, including honeybees, possess two compound eyes. The structure and function of the compound eye have been described in many studies. We provide a brief description here and refer the reader to two recent reviews (88, 232) for further details.

A schematic illustration of the compound eye of a honeybee is given in Figure 1. More detail can be found in Figure 2.5 of Reference 88. In the female (worker) honeybee, each of the compound eyes consists of ~5,500 “little eyes,” or ommatidia (Fig. 1A). An ommatidium consists of a small lens (~15–20 μm in diameter), which focuses light onto a group of nine photoreceptors. A longitudinal cross section through an ommatidium is shown in Figure 1B. Each ommatidium collects light from a small patch of the world; it accepts incoming light from a cone-shaped region subtending about two and a half degrees (142). Neighboring ommatidia view neighboring regions of space, with their optical axes (viewing directions) separated by about two degrees, although this separation varies in different regions of the eye (214, 215). Collectively, the ~11,000 ommatidia in the two eyes capture a near-panoramic view of the environment, with considerable binocular overlap in the frontal (29 degrees),

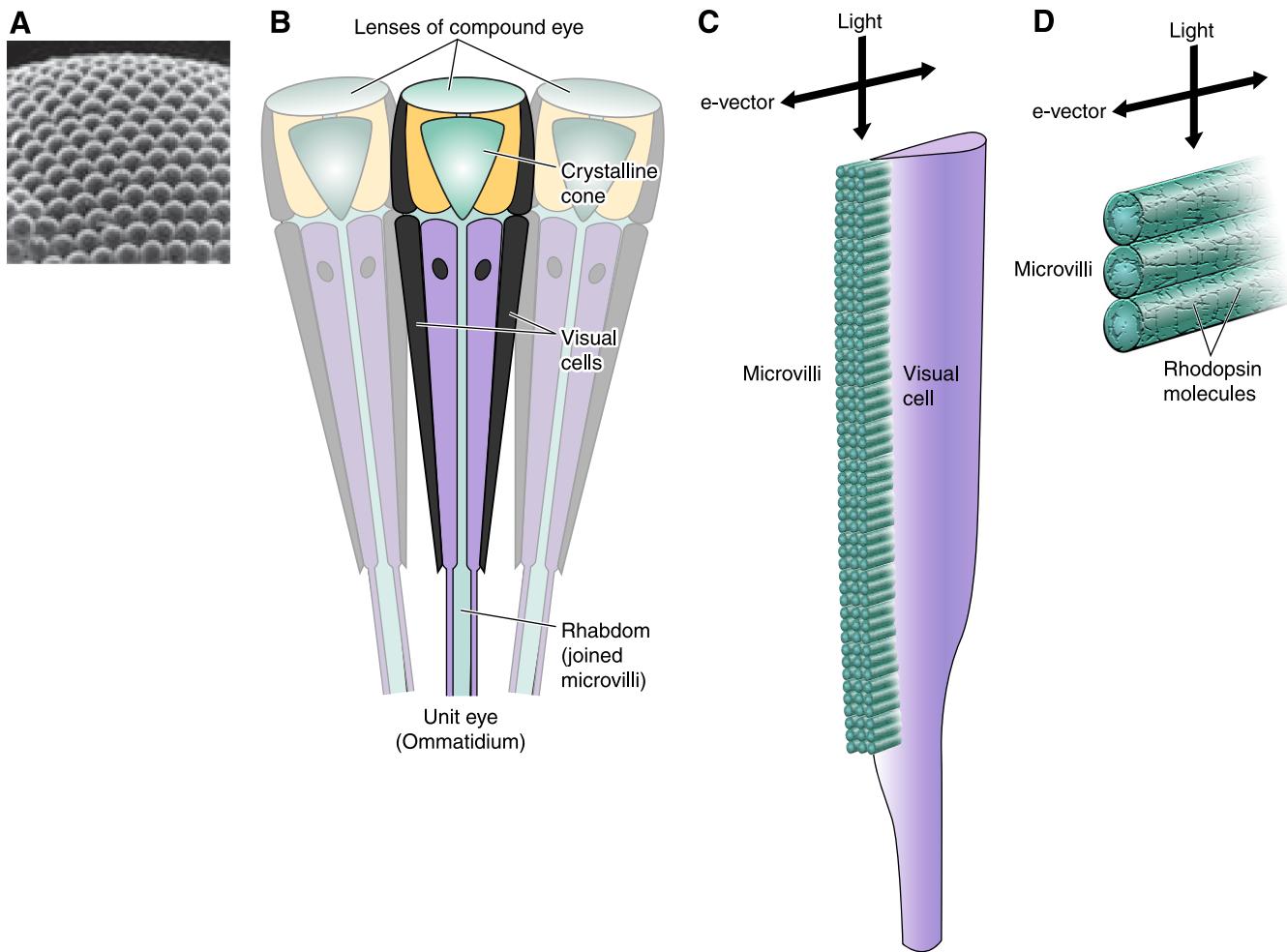


FIG. 1. Schematic illustration of the compound eye of an insect. *A*: surface of compound eye, showing the facet lenses. *B*: longitudinal cross section of an ommatidium. *C*: structure of one of the photoreceptor cells within an ommatidium, showing the microvilli, containing the photopigment, that contribute to the structure of the rhabdom. *D*: detail of microvillar structure, illustrating the location and inferred alignment of the photopigment (rhodopsin) molecules.

dorsal (42 degrees), and ventral (31 degrees) fields of view, and a small blind zone in the rear where the body occludes vision (214–216).

The nine photoreceptor cells within each ommatidium can be grouped into three classes, according to the spectral sensitivity of the light-sensitive pigment (photopigment) that they contain: ultraviolet sensitive, blue sensitive, and green sensitive. Within each cell, the photopigment is packed into an array of slender tubular structures, called microvilli. Each cell is elongated in shape, aligned radially, and carries a set of slender tubular structures, called microvilli, which contain the photopigment. The microvilli are present throughout the length of the cell body of each photoreceptor and are oriented at right angles to the optical axis of the ommatidium (Fig. 1C). Absorption of light by the photopigment causes a chain of events (the so-called phototransduction cascade), which produces a change in the electrical potential across the cell membrane (a so-called depolarization). It is this

change in potential that is signaled to the brain, and which ultimately leads to the perception of light. The microvillar regions of the nine different cells are closely juxtaposed to form a cylindrical, central column that runs along the length of the ommatidium. This cylindrical column, known as the rhabdom, is surrounded by the photoreceptors. The rhabdom possesses a higher optical refractive index than the surrounding photoreceptors and functions as an optical waveguide, thus confining the incoming light to the rhabdom, and encouraging its absorption by the photopigment. As light travels down the rhabdom, it is absorbed (to different extents) by the three different spectral classes of photoreceptors, depending on its intensity and spectral composition. The axons of the nine photoreceptors within each ommatidium project to the next neuropil, the lamina, which performs further processing. Visual information is then conveyed to the next ganglion, the medulla, for further processing, and eventually to the lobula, where complex analysis of the image

takes place, leading to the perception of color, shape, and motion (for a recent review, see Ref. 86). Different regions of the compound eye are specialized to serve different functions. For example, the frontal region is specialized for high visual acuity (216), the fronto-ventral region of the eye is specialized for color and spatial vision, and the region at the dorsal rim area (DRA) of each eye is specialized for the perception of the polarized light patterns in the sky (134, 137). The perception of color and spatial detail by honeybees is reviewed in Reference 232.

III. COLOR VISION

As was explained above, the nine photoreceptor cells within each ommatidium can be grouped into three classes, according to the spectral sensitivity of the light-sensitive pigment (photopigment) that they contain: ultraviolet sensitive (with a peak sensitivity at 340 nm), blue sensitive (peaking at 463 nm), and green sensitive (peaking at 530 nm) (6, 88, 120, 161, 162). These three spectral classes of photoreceptors endow the honeybee with excellent trichromatic color vision, which plays an important role in flower recognition (54, 55, 160, 268, 270). Compared with human color vision, the visible spectrum of honeybees is shifted toward shorter wavelengths: contrary to humans, bees can see ultraviolet, but not red. And, contrary to humans, where the three classes of photoreceptors are unequally spaced along the wavelength spectrum, with the “red” and the “green” receptors set very close together spectrally and relatively remote from the “blue” receptors, the three spectral classes of photoreceptors in the honeybee are spaced more or less equally (6, 162) and sample the honeybee’s visual spectrum in a more uniform fashion. Presumably, this facilitates uniformly good discrimination of a large range of flower colors (35, 272).

The honeybee has figured prominently in the history of the study of color vision. After humans, the honeybee was the second nonhuman organism in which the existence of color vision was demonstrated, only a year after the discovery of color vision in fish. Both of these discoveries were made by the Nobel Laureate Karl von Frisch nearly a hundred years ago (266, 267). The classical experiments demonstrating color vision in honeybees are described, for example, in References 54, 55, and 268, and are reviewed in many articles and books (e.g., Refs. 88, 91, 161, 232). They are not discussed here.

IV. SPATIAL RESOLUTION OF HONEYBEE VISION

How much detail does the compound eye resolve? The spatial resolving power of the compound eye is determined primarily by two parameters: The acceptance

angle of the ommatidium (symbolized by $\Delta\rho$), and the interommatidial angle (symbolized by $\Delta\phi$). $\Delta\rho$ determines the extent to which the image of the world is smeared, or blurred, by the optics of the compound eye, the larger the value of $\Delta\rho$, the greater the blur, or the lower the amount of spatial detail that is captured by the optics. $\Delta\phi$ determines the fineness of the visual mosaic of the compound eye: the smaller the value of $\Delta\phi$, the greater the capacity of the eye to sample the detail in the image that is transmitted by the optics. In most compound eyes, including that of the honeybee, these two parameters are closely matched; that is, the optics transmits only as much detail as the mosaic can sample (or represent) accurately. Given the values of $\Delta\rho$ and $\Delta\phi$, one can theoretically predict how much spatial detail the insect’s visual system can resolve (90, 126, 219). In the honeybee, this theoretical prediction has been confirmed by behavioral experiments that involve training the bee to distinguish between vertically and horizontally oriented striped patterns, and examining how fine the stripes have to be before the orientations can no longer be discriminated (232, 238). This experiment shows that bees cannot resolve black-and-white stripes that are thinner than 1.4 degrees, a figure that agrees very well with the theoretical expectations based on the optical structure of the compound eye (219, 238). This implies that the visual nervous pathway registers and transmits to the brain most of the spatial detail that is captured by the compound eye.

V. TEMPORAL RESOLUTION OF HONEYBEE VISION

There is substantial evidence that the visual systems of flying insects are able to detect rapidly changing images, as when flying past a bush at close range. This allows the moving image to be transmitted to the brain without excessive smear.

Early studies measured the temporal resolving ability of the honeybee’s compound eye by recording the response of the electroretinogram (ERG) to a flickering light source (5). The ERG represents the mass extracellular (current) response of the photoreceptor cells (and, to some extent, the higher-order neurons) to the visual stimulus (e.g., Refs. 2–4, 257). The ERG was recorded while the light was either turned on and off regularly, or was modulated sinusoidally, at a range of frequencies. At low frequencies, the ERG exhibited an oscillatory response at the same frequency as the visual stimulus, indicating that the photoreceptors in the eye were able to register the fluctuations of intensity to which they were exposed. As the frequency of the stimulus was increased, the oscillatory amplitude of the ERG response decreased steadily until a certain frequency, termed the “critical fusion frequency” (CFF), beyond which there was no

detectable response. For honeybees, the CFF measured using this technique was in the range 165–300 Hz (5), suggesting that the photoreceptors can resolve temporal fluctuations of intensity at frequencies up to a maximum of 300 Hz. The CFF for humans (measured via the ERG, or through psychophysical measurements of flicker perception) is in the range of 20–70 Hz, depending on the mean intensity of the stimulus, its spatial extent, and the level of ambient illumination (207), indicating that, speaking broadly and approximately, honeybee vision is about five to six times as fast as ours. It should be noted that the CCF increases with the mean intensity of the light source, as well as with the intensity of the surrounding ambient light, for most animals and humans (207). In other words, visual systems are generally faster when they operate in bright light. It is important to bear this in mind when one attempts to compare CFFs across various studies, and across various species.

Behavioral studies have attempted to measure the CFF of honeybees by attempting to train them to distinguish between a steady light source and flickering light source (of the same mean intensity), with a view to determining the highest frequency at which the bees can distinguish between the two sources (225, 239). Curiously, bees could never be trained on such a discrimination task, regardless of the frequency or the contrast of the flickering light! Although many neurons at each stage of the visual pathway, from the photoreceptors to the higher reaches of the optic lobe, would undoubtedly show strong responses to such a flickering stimulus, it appears

that the brains of bees are not wired to learn or recognize flicker. Presumably, this is because flicker is not a stimulus that is biologically relevant to bees. (Of course, this explanation begs the question as to why humans have no difficulty in learning the same task, even though flicker is equally irrelevant to them).

However, bees are able to learn to distinguish between flickering and steady stimuli when the flicker is presented in the context of a moving stimulus. Srinivasan and Lehrer (240) exposed bees to two stimuli, each comprising a sectored, black-and-white disc (Fig. 2). One disc was rotated at a speed that was high enough that the alternating black and white sectors produced a flicker frequency (temporal frequency) of 300 Hz, which was well beyond the CFF of the photoreceptors. Consequently, this disc would have appeared uniformly gray to the bees, as it did to humans. The other disc rotated at a slower speed to produce a flicker that was well within the temporal resolving ability of the photoreceptors (30 Hz). Srinivasan and Lehrer found that bees could easily be trained to distinguish between the two stimuli by rewarding the bees on the “gray” stimulus. By varying the speed of the other stimulus (the test stimulus) systematically, they found that the trained bees could distinguish between the two stimuli as long as the temporal frequency produced by the test stimulus was lower than 200 Hz. When the contrast frequency of the test stimulus exceeded 200 Hz, the trained bees were no longer able to distinguish it from the gray stimulus. The results are displayed in Figure 3, which shows the variation of the choice frequency of the trained

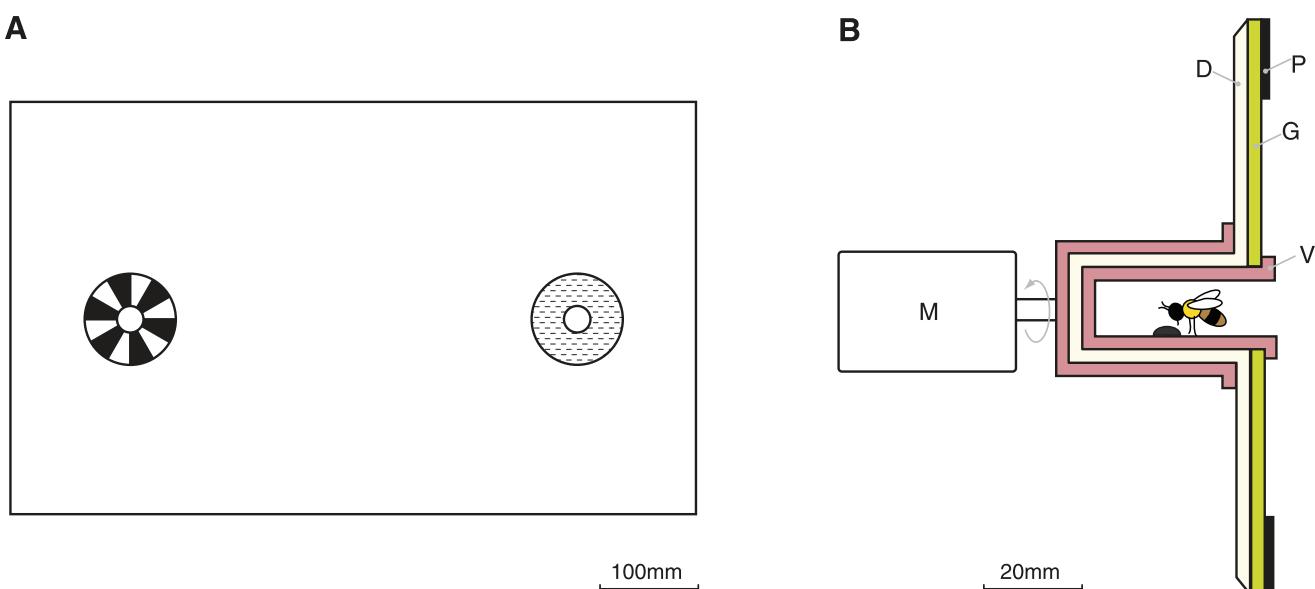


FIG. 2. Experimental apparatus for measuring temporal resolution of honeybees using moving stimuli. *A*: front view, showing the two visual stimuli. The “gray” stimulus is produced by a radial sector pattern identical to that on the left, but rotating at a high speed. *B*: vertical cross section through one of the two pattern-bearing discs. The metal disc *D*, carrying the visual pattern on its front face, is rotated by a variable-speed motor *M*. The stimulus is presented behind a transparent glass window *G*, with a central hole carrying a cylindrical vial *V* that offers a reward of sugar solution. The stimuli are visible through circular apertures cut in a sheet of black cardboard *P* that covers the entire front panel of the apparatus. [Redrawn from Srinivasan and Lehrer (240), with permission from Springer-Verlag.]

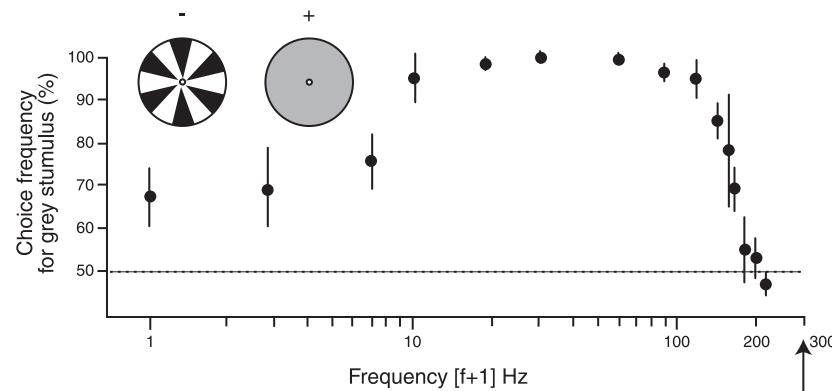


FIG. 3. Typical result obtained from the apparatus illustrated in Figure 2. Bees were trained to distinguish between a rapidly rotating black-white disc that produced a temporal frequency of 300 Hz and appeared uniformly gray, and a slowly rotating black-and-white sectored disc (as in Fig. 2A) by rewarding them with food at the gray stimulus. The trained bees were able to distinguish between the gray stimulus and a test stimulus that rotated at various speeds, as long as the test stimulus presented a contrast frequency lower than 200 Hz. The figure shows the variation of the choice frequency of the trained bees for the gray stimulus, as a function of the temporal frequency f generated by the test stimulus. Note that frequency is plotted on a logarithmic scale that displays $[f+1]$ rather than f , to include the condition in which the test stimulus was stationary [$f = 0$]. The arrow indicates the temporal frequency produced by the gray stimulus (300 Hz). This experiment reveals that the visual system of the bee (as a whole) can resolve fluctuations of intensity at frequencies of up to 200 Hz, when tested with moving stimuli. [Redrawn from Srinivasan and Lehrer (240), with permission from Springer-Verlag.]

bees for the gray stimulus, as a function of the temporal frequency f generated by the test stimulus. This experiment reveals that the visual system of the bee (as a whole) can resolve fluctuations of intensity at frequencies of up to 200 Hz, when tested with moving stimuli.

Detailed investigation revealed that, in this experiment, the bees were not actually “learning” to distinguish between the two stimuli. Rather, they were choosing the rewarded stimulus (gray stimulus) because they were being “repelled” by the motion generated by the other stimulus (the test stimulus) as long as they could sense its motion. As we shall see later below, this “movement avoidance response” may be a mechanism that prevents collisions with obstacles during flight, by causing the bee to steer away from regions of the visual field that experience rapid image motion (227, 253). The value of the CFF obtained with this method agrees with early measurements of the honeybee’s optomotor response in which the speed of a rotating striped drum was varied systematically to determine the highest flicker frequency at which a turning response could still be elicited (5).

Let us return briefly to the experiments that used flickering stimuli. In a subsequent study, Srinivasan and Lehrer (225) found that bees could indeed be trained to discriminate flicker if the flicker was presented in the domain of color (as heterochromatic flicker), rather than intensity. Here, one stimulus presented a periodic alternation between two colors (say, blue and green), while the other presented a steady mixture of the two colors (turquoise). Bees could be easily trained to distinguish between the two stimuli, regardless of whether they were trained on the flickering stimulus or the steady one. Thus bees can learn to distinguish changes in color, but not changes in intensity. By systematically varying the fre-

quency of the heterochromatic flicker, Srinivasan and Lehrer found that the fusion frequency for heterochromatic flicker was ~ 100 Hz, which is about half the CFF for intensity flicker (as revealed by the ERG and the rotating disc experiments described above). Thus one can infer that the honeybee’s visual system requires ~ 10 ms to compute color, which is about twice as long as it requires for computing intensity. Interestingly, for humans, the CFF for heterochromatic flicker is in the range 10–30 Hz, depending on stimulus intensity (57, 58), suggesting that, for humans as well, this critical frequency is about half that for intensity flicker (which is in the range of 20–70 Hz; see above).

VI. MOVEMENT PERCEPTION

Research over the past 50 years has uncovered a number of different ways in which insects (including honeybees) use image motion to stabilize and guide flight through the environment, and to extract useful information about the structure of the environment. Indeed, it is probably fair to say that many of the fundamental principles that underlie the detection and perception of movement were first unearthed in insects, probably because of their exquisite sensitivity to motion of the image of the world in their eyes and their heavy reliance on motion cues to guide their behavior (224).

We begin by considering strategies for visual control and stabilization of flight and then proceed to examine the ways in which image motion is used to glean information about the structure of the environment, and about the insect’s movement within it.

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 corrective yaw torque, which brings the insect back on course (188). Similar control mechanisms act to stabilize pitch and roll (e.g., Ref. 229). This so-called "optomotor response" (188) has provided an excellent experimental paradigm with which to probe the neural mechanisms underlying motion detection.

An insect, flying tethered inside a striped drum (Fig. 4), will tend to turn in the direction in which the drum is rotated (188). If the drum rotates clockwise, the insect will generate a yaw torque in the clockwise direction, and vice versa. This reaction helps the insect maintain a straight course by compensating for undesired deviations: a gust of wind that causes the insect to veer to the left, for example, causes the image in the eyes to move toward the right, and the insect to generate a compensatory yaw to the right. Investigation of this so-called optomotor re-

sponse over several decades has provided valuable information on some of the characteristics of motion perception by the insect visual system (19, 23, 188). If the angular period of the stripes is kept constant and the angular velocity (rotational speed, in degrees/s) of the drum is varied, the strength of the optomotor response varies in a bell-shaped curve as shown by the green curve of Figure 4D. If the stripes are made finer (angular period decreased, Fig. 4A), one obtains a similar bell-shaped curve, but with the peak shifted toward the left, to a lower angular velocity (red curve, Fig. 4D). Making the stripes coarser (increasing the angular period, Fig. 4C) has the opposite effect (blue curve, Fig. 4D). An interesting insight appears, however, if these curves are replotted to show the variation of the response as a function of the temporal frequency of optical stimulation that the moving striped pattern elicits

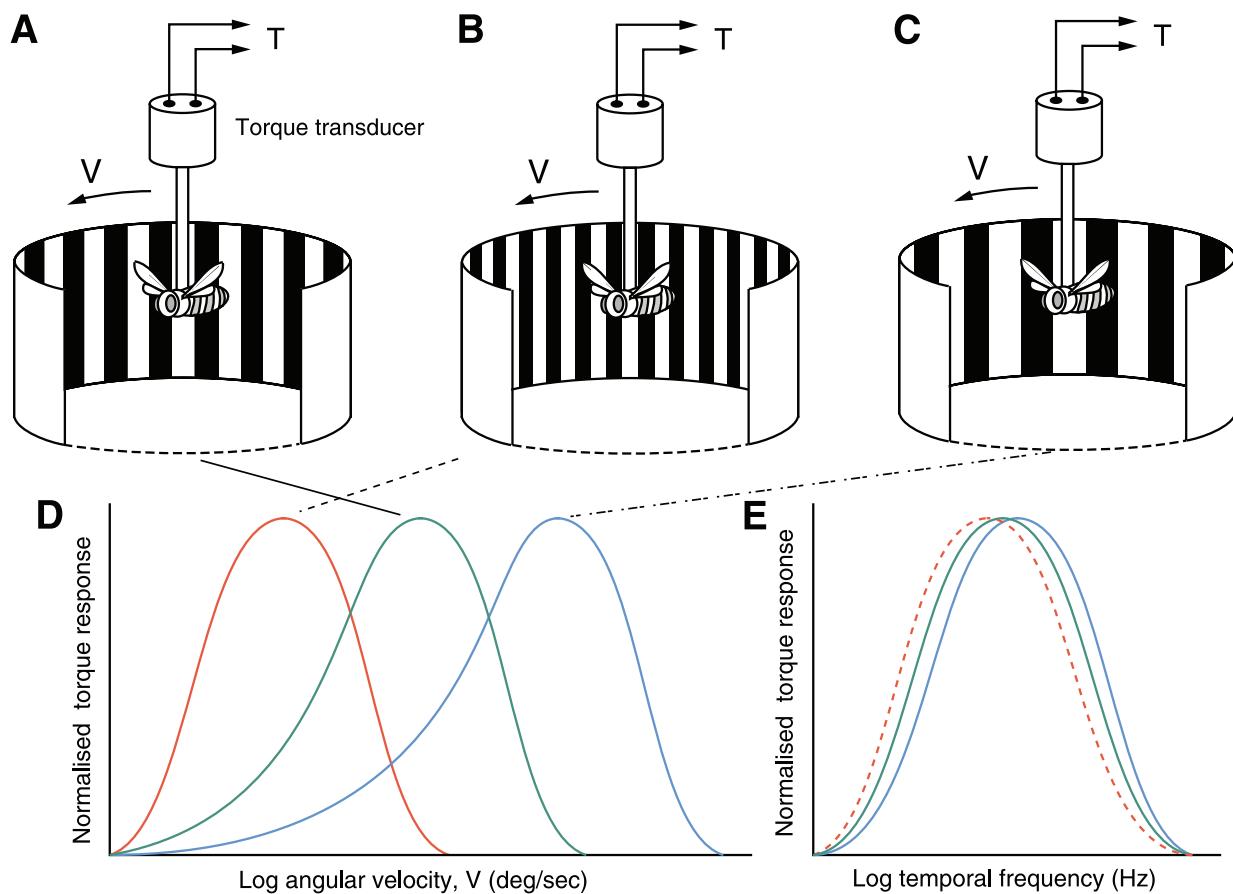


FIG. 4. Properties of the optomotor response of insects. If a flying insect is suspended in a rotating striped drum, it will attempt to turn in the direction of rotation of the drum. The resulting yaw torque, as registered by a torque transducer, is a measure of the strength of the optomotor response. For stripes of a given angular period (as in B), the normalized strength of the optomotor response is a bell-shaped function of the rotational speed of the drum, peaking at a specific angular velocity of rotation (green curve, D). If the stripes are made finer (as in A), one obtains a similar bell-shaped curve, but with the peak shifted toward a lower angular velocity (red curve, D). If they are made coarser (as in C), the peak response occurs at higher angular velocities (blue curve, D). However, the normalized response curves coincide with each other if they are replotted to show the variation of response strength with the temporal frequency of optical stimulation that the moving striped pattern elicits in the photoreceptors, as illustrated in Figure 1E. Thus the optomotor response that is elicited by moving striped patterns is tuned to temporal frequency, rather than to angular velocity. [Modified from Srinivasan et al. (244), with permission from Elsevier.]

its in the photoreceptors. This temporal frequency is given by the number of dark (or bright) stripes passing the receptive field of a given photoreceptor per second. The curves then all peak at the same temporal frequency and exhibit similar widths (Fig. 4E). This implies that the movement-detecting system underlying the optomotor response is not sensitive to the angular velocity of rotation of the drum per se: the angular velocity at which the response is strongest depends on the angular period of the stripes. The optomotor response thus depends on the temporal frequency of optical simulation that is induced by the stripes, and not by the angular velocity of the stripes. This property is true for a number of insect species (e.g., *Chlorophanus* beetle, Ref. 93; housefly *Musca*, Refs. 64, 77, 291; fruit fly *Drosophila*, Refs. 89, 90), as well as honeybees (132).

The structure and connectivity of a neural circuit that would exhibit such properties has been modeled quantitatively (93, 188) and is shown in Figure 5. Consider two neighboring photoreceptors, A and B, situated in neighboring ommatidia of the compound eye, viewing adjacent regions of a moving scene. Since the two photoreceptors are viewing the same scene, they will register the same signal (i.e., the same temporal waveform of intensity vari-

ation). However, the signal from one receptor will lead or lag behind that from the other receptor, depending on the direction in which the scene is moving. If the scene is moving from A to B (left to right), the signal from A will lead that from B. On the other hand, if the scene is moving from B to A (right to left), that from A will lag behind that of B. A simple way to determine the direction of movement, then, would be to 1) delay the signal from A and multiply it with the signal from B; and 2) delay the signal from B and multiply it by that from A. If the delayed signal from A is more strongly correlated with the signal from B than the delayed signal from B is with A, we can conclude that the scene is moving from A to B; and if the opposite is true, the scene is moving from B to A. The correlations are performed by the “multiplication” boxes, and the “average” box, which computes the time average of the multiplied signals. The response of the circuit is positive (excitatory) if the scene moves to the right, and negative (inhibitory) if the scene moves to the left. A neural circuit of this nature, that uses delay followed by multiplication, can provide a reliable indication of the direction of motion of the scene along one axis (left or right) within a small patch of the insect's visual field. Conceptually, it is known as an “elementary movement detector (EMD)”.

Given the hexagonal arrangement of the ommatidia in the compound eye, one can configure EMDs that are directionally sensitive to motion along any of six different axes, by comparing the signals from adjacent ommatidia that are appropriately aligned (94). Thus, by comparing the responses across a group of six EMDs with different preferred directions, it would be possible to compute the direction of the motion that is occurring within a small patch of the image in two dimensions.

The EMDs that are actually believed to be present in the insect eye do not perform a simple delay-and-correlate. Rather, they incorporate temporal filters with different dynamics in the two arms, as shown in Figure 5. The photoreceptor signals are initially filtered in time by the temporal filters labeled R, which represent the dynamics of the front end of the visual system. This includes the dynamics of phototransduction, as well as the dynamics of other processes occurring at early stages of the visual pathway. The output of the R filter associated with one receptor passes through a further temporal filter, G, and is multiplied with the output of the R filter associated with the neighboring receptor, after that signal has been further processed by another temporal filter, H. The G and H filters represent the temporal dynamics of processing at higher levels of the motion-detecting pathway, for example, in the lamina and the medulla. Such a scheme will detect the direction of movement in a manner that is qualitatively similar to the simple delay-and-multiply scheme discussed above. But it is biologically more realistic, because pure time delays are not commonly found in nervous systems. For example, the H filter could repre-

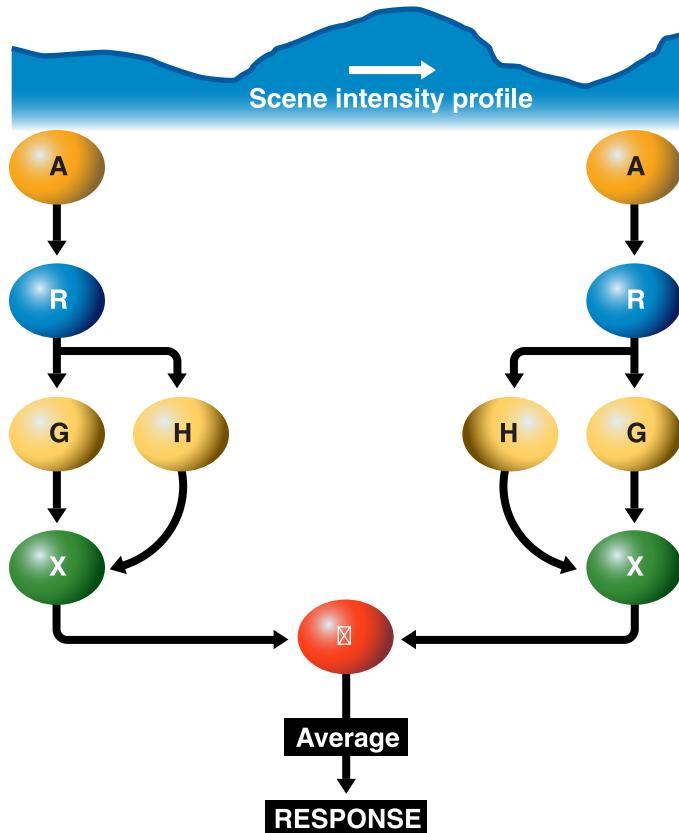


FIG. 5. Hassenstein-Reichardt correlation model of directionally selective motion detection. See the description in text.

sent a temporal low-pass filter (which produces a phase lag, approximating a time delay), and the G filter could represent a temporal high-pass filter (which produces a phase lead, approximating a time advance). The model is excellent at predicting the variation of the strength of the steady-state optomotor response as a function of the speed, spatial structure, and contrast of a motion stimulus consisting of a moving sinusoidal grating (93, 188).

The correlation-based structure of the Hassenstein-Reichardt model of movement detection predicts a high sensitivity to coherent motion in the image and a strong immunity (low sensitivity) to random spatiotemporal noise (as in television "snow"). Indeed, it had been shown that flies can detect coherent motion when it is buried in random spatiotemporal noise whose contrast eight times that of the motion signal (236). This impressive ability to reject noise should make such systems robust to photon noise, which becomes significant at low levels of ambient light, and promote detection of weakly coherent background motion, as when flying amidst foliage that is fluttering in the breeze.

Movement-sensitive neurons with large visual fields have been discovered and characterized in the lobula plate of the fly, that display many of the characteristics of the behaviorally measured optomotor response, and of the Hassenstein-Reichardt correlation model (e.g., Refs. 17, 20, 67–69, 94–97, 100 129, 131). It is believed that these neurons are in the visual pathway that mediates the optomotor (yaw) response, and in the pathways that mediate the detection and stabilization of pitch and roll. Some of these neurons appear to be exquisitely tuned to respond to rotation of the head about a specific axis, e.g., yaw, pitch, roll, or some other axis (129–131). The tuning of each of these neurons to a specific pattern of image motion, known as "optic flow," appears to be achieved by selective pooling of signals from a large array of EMDs, with the appropriate preferred directions. For example, a large-field neuron that senses a clockwise roll of the head would be wired to collect signals from EMDs with a preferred direction of motion that is downward in the left lateral visual field and upward in the right lateral visual field; a neuron that senses a counterclockwise roll would be organized in a complementary fashion (130). Any unintended roll of the head would then be detected and corrected by comparing the outputs of the two neurons, and using the difference between the outputs to obtain the appropriate corrective command to the motor systems controlling the head and the flight musculature. These highly tuned motion-sensitive neurons can thus be regarded as "matched filters" for sensing specific patterns of optic flow, and issuing appropriate compensatory commands to the motor system (129). Directionally selective motion detecting neurons with large visual fields have also been studied in the honeybee (59, 118, 159, 180), although not as extensively as in flies.

VII. VISION IN THREE DIMENSIONS

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 measuring ranges of only a few centimeters (47, 107, 193, 224, 255). 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 cues derived from the image motion that the animal experiences when it moves in its environment. Some of these cues are outlined below, and references to more complete accounts are provided.

A. Avoiding Obstacles and 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 she gauge and balance the distances to the two rims?

One possibility is that she does not measure distances at all, but simply balances the speeds of image motion on the two eyes, as she flies through the opening. To investigate this possibility, Kirchner and Srinivasan (124) trained bees to enter an apparatus that offered a reward of sugar solution at the end of a tunnel. Each side wall carried a pattern consisting of a vertical black-and-white grating (Fig. 6). The grating on one wall could be moved horizontally at any desired speed, either towards 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 along the midline of the tunnel, i.e., equidistant from the two walls (Fig. 6A). 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 towards the side of the moving grating (Fig. 6B). 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 (Fig. 6C). These findings demonstrate that when the walls were stationary, the bees maintained equidis-

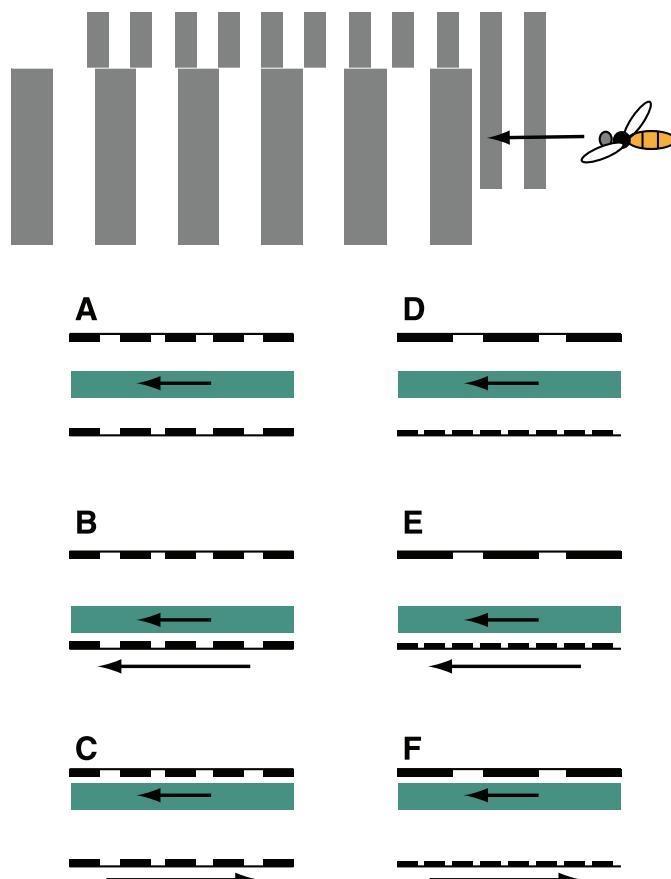


FIG. 6. Illustration of an experiment demonstrating that flying honeybees negotiate narrow gaps safely by balancing the speeds of image motion that are experienced by the two eyes. The shaded areas represent the positions of the flight trajectories, analyzed from video recordings of several hundred flights. The position of the long axis of the bar represents the mean flight position, and the width of the bar denotes the standard deviation. [Adapted from Srinivasan and Zhang (227), with permission from Birkhauser Verlag.]

tance by balancing the speeds of the retinal images in the two eyes. A lower image speed on one eye evidently caused the bee to move closer to the wall seen by that eye. A higher image speed, on the other hand, had the opposite effect.

When the gratings on the two walls were stationary, but differed in their spatial periods, the bees continued to fly through the middle of the tunnel (Fig. 6D). This was the case even when the gratings possessed square-wave intensity profiles (with abrupt changes of intensity) or sinusoidal profiles (with gradual intensity changes), and irrespective of whether the contrasts of the gratings on the two sides were equal, or considerably different (242).

Further experiments revealed that, knowing the velocities of the bee and the pattern, it was possible to predict the position of a bee's flight trajectory along the width of the tunnel, on the assumption that the bee balances the apparent angular velocities on either side of the

tunnel (242). An example is illustrated in Fig. 7, where one wall (the upper wall in the illustration) is stationary and the other wall (the lower wall in the illustration) moves at a constant velocity of $V_1 = -38 \text{ cm/s}$ (toward the left). Each wall carries a vertically oriented square-wave grating. The figure shows the mean measured positions of bees flying along the tunnel at various flight velocities V_0 , in the direction of movement of the wall (negative V_0) as well as against it (positive V_0) compared with the theoretically expected position (D) of the bee across the width of the tunnel as a function of the flight velocity (V_0), assuming that the bee is positioning itself so as to balance the angular velocities of the images in the two eyes. The good agreement between the data and the theory indicates that this assumption is indeed true.

These observations indicate that bees steer collision-free paths through narrow gaps by balancing the speeds of the motion of the images in the two eyes, and that the bee's visual system is capable of computing the speed of the image in each eye accurately, largely independently of

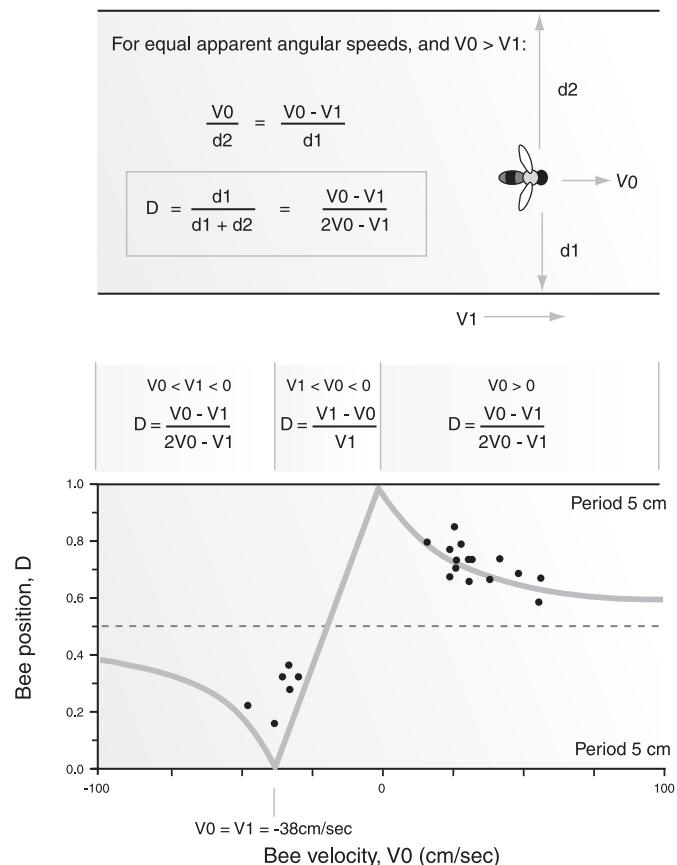


FIG. 7. Measurement of centering response for bees flying at different speeds in either direction in a tunnel in which the upper wall is stationary and the lower wall moves at a constant speed of $V_1 = -38 \text{ cm/s}$ towards the left. The dots show the experimentally measured mean positions of bees flying at various velocities V_0 (in either direction), and the curve shows the theoretically predicted bee position (D) as a function of its flight velocity (V_0). [Adapted from Srinivasan et al. (242), with permission from Cambridge University Press.]

its contrast or spatial texture. The capacity to measure and compare image speeds in this robust way is obviously important when flying through the middle of a gap between the trunks of two trees whose barks may carry different textures.

The strategy for steering through corridors can also be used to avoid obstacles. Consider, for example, an insect flying along a straight line toward a goal. If an object on the left is dangerously close to the intended trajectory, it will generate a high image velocity in the left eye, causing the insect to veer to the right (provided there is not an equally close object on the other side, repelling it back). Indeed, it has been shown that flying bees strongly avoid stimuli that present rapid movement (227, 240, 253).

Subsequent studies (227, 253) have investigated this "centering" response further by comparing its properties with those of the well-known optomotor response, in an experimental setup that allows the two responses to be compared in one and the same individual, under the same conditions. The results indicate that the centering response differs from the optomotor response in three respects. First, the centering response is sensitive primarily to the angular speed of the stimulus, regardless of its spatial structure. The optomotor response, on the other hand, is sensitive primarily to the temporal frequency of the stimulus; therefore, it confounds the angular velocity of a striped pattern with its spatial period. Second, the centering response is nondirectional, whilst the optomotor response is directionally selective. Third, the centering response is sensitive to higher temporal frequencies than is the optomotor response. Whereas the optomotor response exhibits a relatively low bandwidth (with half-magnitude points at 6 and 75 Hz), the centering response exhibits a relatively high bandwidth (with half-magnitude points at 3 Hz and well beyond 100 Hz). Thus the motion-detecting processes underlying the centering response exhibit properties that are substantially different from those that drive the well-known optomotor response (227, 253). Models of movement-detecting mechanisms that may underlie the centering response are described in Reference 244.

Given that the role of the centering response is to ensure that the insect flies through the middle of a gap irrespective of the texture of the side walls, it is easy to see why this response is mediated by a movement-detecting system which measures the angular speed of the image independently of its spatial structure. The movement-detecting system that drives the optomotor response, on the other hand, does not need to measure image speed accurately: it merely needs to signal the direction of image motion reliably so that a corrective yaw of the appropriate polarity may be generated.

B. Controlling Flight Speed

Do insects control the speed of their flight, and if so, how do they achieve this control? Experiments on fruit flies and bees suggest that flight speed is controlled by monitoring the speed at which the image of the environment moves across the visual field of the eye.

David (56) observed fruit flies flying upstream in a horizontally oriented, cylindrical wind tunnel, attracted by an odor of fermenting banana. The cylindrical walls of the 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 towards the front or the back. With this setup, the rotational 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 flies' eyes. In this setup, fruit flies 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 angular velocity of image motion in the eye. Experiments in which the angular period of the stripes was varied revealed that the flies were measuring (and holding constant) the angular velocity of the image irrespective of the spatial structure of the image. Similar results have been obtained by Fry et al. (80–82), also for fruit flies, using more accurate and sophisticated equipment for visual stimulation and response measurement.

Bees appear to use a similar strategy to regulate flight speed (254). When a bee flies through a tapered tunnel, it decreases its flight speed when the tunnel narrows, and increases it when the tunnel widens, in such a way that velocity of the image of the walls, as seen by the eye, always remains constant at about 320 degrees/s (254). This observation suggests that the speed of flight is adjusted by monitoring and regulating the angular velocity of the image of the environment, as seen by the eye. (If the width of the tunnel is doubled, the bee flies twice as fast.) On the other hand, bees will fly through a uniform-width at a constant speed, which does not change when the spatial period of the stripes lining the walls is abruptly changed (254). When both walls of the tunnel are moved, the speed of flight increases or decreases, depending on whether the walls are moved in or against the direction of the bees' flight (7, 8). These observations indicate that flight speed is regulated by a visual motion-detecting mechanism that measures the velocity of the image on the

eye in a robust way, largely independently of its spatial texture. However, it is not yet known whether the regulation of flight speed in bees is mediated by a directionally selective movement-detecting mechanism, or a nondirectional one.

An obvious advantage of controlling flight speed by regulating image speed is that the insect will automatically slow down to a safer speed when negotiating a narrow passage. Thus the speed of flight is automatically tailored to the structure of the environment. The act of maintaining a constant velocity in the eye (at ~320 degrees/s) will automatically cause the bee to fly fast in an open environment, and slow in a cluttered environment.

Another advantage of using image speed to regulate flight speed is that headwinds can be compensated for. Bees flying in a headwind strive to maintain the same flight speed as in still air, by increasing their thrust to maintain the target image velocity (9).

C. 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 (273) and Borst and Bahde (18) has shown that deceleration and

extension of the legs in preparation for landing are triggered by movement-detecting mechanisms that sense the expansion of the image. 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 <45 degrees. In such landings, the motion of the image of the surface would be dominated by a strong translatory component in the front-to-back direction in the ventral visual field of the eye.

To investigate how bees execute grazing landings, Srinivasan and co-workers (250, 254) 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 video-filmed in three dimensions.

Analysis of the landing trajectories revealed that the flight speed of the bee decreases steadily as she approaches the surface. In fact, both the forward speed and the descent speed are approximately proportional to the height above the surface (Fig. 8), indicating that the bee is holding the angular velocity of the image of the surface approximately constant as the surface is approached. This strategy automatically ensures that both the forward and the descent speeds are close to zero at touchdown. Thus a smooth landing is achieved by an elegant and surprisingly simple process that does not require explicit

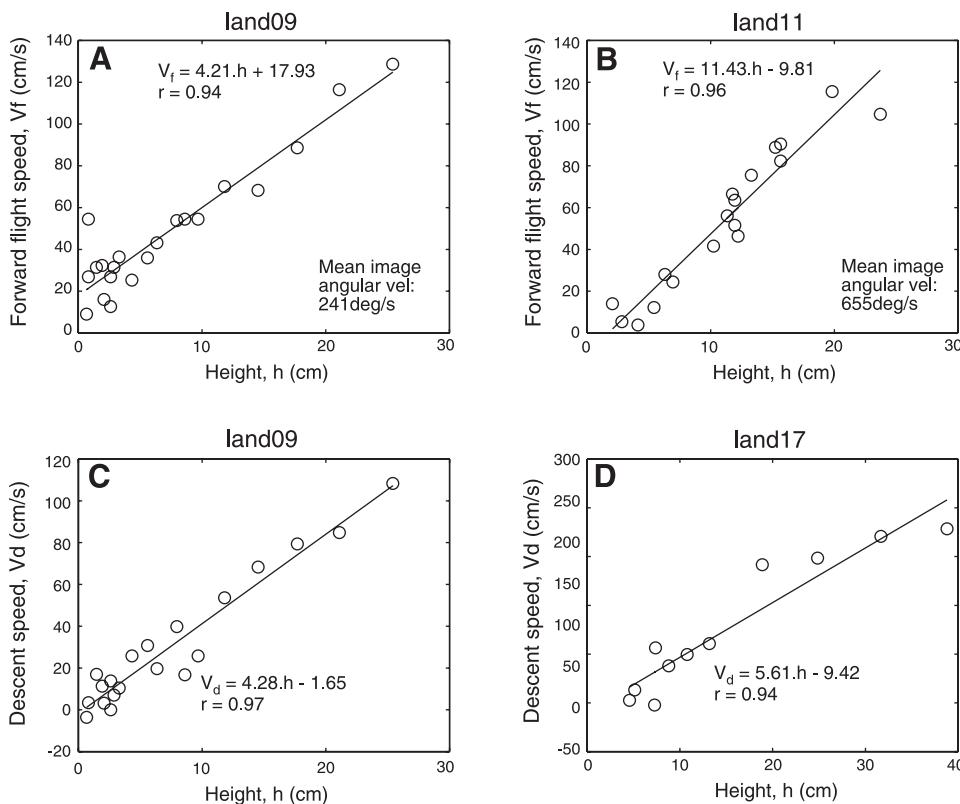


FIG. 8. Typical results of an experiment investigating how bees make a grazing landing on a horizontal surface. *A* and *B*: variation of forward flight speed (V_f) with height (h) above the surface, for two landing trajectories. *C* and *D*: variation of descent speed (V_d) with height (h) above the surface, for two landing trajectories. The landing bee holds the angular velocity of the image of the ground constant at 241 degrees/s in *A* and at 655 degrees/s in *B*, as calculated from the slopes of the linear regression lines. Also shown are the values of the correlation coefficient (r). Holding the image velocity of the ground constant during the approach automatically ensures that the landing speed is zero at touchdown. [Adapted from Srinivasan et al. (252), with permission from Professional Engineering Publishing.]

knowledge of the bee's instantaneous speed or height (250).

Interestingly, landing bees hold the image velocity of the ground constant at ~ 300 degrees/s (250), a figure that is very similar to the image speed that they strive to maintain whilst cruising (see sect. VIIB). Thus cruising and landing may be guided by the same movement-detecting system. During cruise the bee flies horizontally (i.e., aims at the horizon), keeps its thrust constant, and holds the image speed of the ground constant, thus ensuring flight at a constant height above the ground. During landing, on the other hand, the bee aims at a specific point on the ground and adjusts the speed of its flight so as to keep the image velocity of the ground constant, thus ensuring a smooth landing.

Just prior to landing, bees come to a hover $\sim 14\text{--}15$ mm from the surface, a distance just barely outside the reach of the extended legs when the surface is beneath them, and then make the final touchdown (76). The distance from the surface at which this hover occurs is remarkably constant regardless of whether the surface is oriented horizontally (as in the ground) or vertically (as in a wall) or is inverted (as in a ceiling). The hover appears to be controlled visually, although it is not clear what visual cues are used to gauge the distance to the surface. Prior to touchdown, the antennae tend to be oriented nearly perpendicular to the surface, for a large range of surface orientations. This again appears to be achieved through vision, although it is not clear what visual cues are used to assess the tilt of the surface. On steep surfaces (vertical through inverted), the final touchdown maneuver appears to be initiated when the tips of the antennae make mechanical contact with the surface. Early contact with the surface is ensured by pointing the antennae perpendicular to the surface, under visual control (76). Thus touchdown, in general, is mediated by visual as well as tactile cues. Bees approaching flowers also use vision to direct their antennae toward biologically important parts of the flower, such as the anthers or the nectar guides, presumably to optimize antennal contact as well as olfactory sensing (e.g., Ref. 155).

D. Distinguishing Objects at Different Distances

The experiments described above 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? While this is a difficult question, one that a philosopher might even declare unanswerable, one can at least ask whether bees can be trained to distinguish between ob-

jects at different distances. Lehrer et al. (147) and Srinivasan et al. (243) 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 Reference 243, 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 higher the flower, the faster the motion of its image.

Kirchner and Lengler (123) extended this "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 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.

E. Discriminating Objects From Backgrounds

In all of the work described above, the objects that were being viewed were readily visible to the insects, since 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. But 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. Are bees capable of distinguishing a textured figure from a similarly textured background purely on the basis of motion parallax?

Srinivasan et al. (241) 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 Julesz texture, carried on the underside of a transparent perspex sheet that could be placed at any desired height above the background (Fig. 9A). It was found that bees could indeed be trained to find the figure and land on it, provided the figure was raised at least 1 cm above the background (Fig. 9B). When the figure was placed directly on the background, the bees failed to find it, demonstrating that the cue used to locate the figure is the relative motion between the images of the figure and the background, caused by the bees' own flight above the setup. Video films of the bees' landings 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" (Fig. 9B). These experiments showed that the boundary has special visual significance and that bees are capable of detecting it reliably. Kern et al. (121) have shown, through behavioral experiments and modeling, that the detectability of such boundaries can be well accounted for by a neural network which compares image motion in spatially adjacent receptive fields.

The ability to discriminate individual objects through the discontinuities in image motion that occur at their boundaries is likely to be important when an insect attempts to land on a leaf or a shrub. This is a situation where it is 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 140 years ago, von Helmholtz (269) speculated that humans might use cues derived from image motion in a similar way to distinguish individual trees in a dense forest.

VIII. "COLOR-BLIND" BEHAVIORS IN A COLOR-PERCEIVING ANIMAL

Although the honeybee as a whole possesses excellent trichromatic color vision (as described above), some of its behaviors, including many that depend on the perception of motion, appear to be mediated by visual pathways that are "color-blind" (144). This is intriguing, because many organisms endowed with good color vision (including primates and humans) display this characteristic.

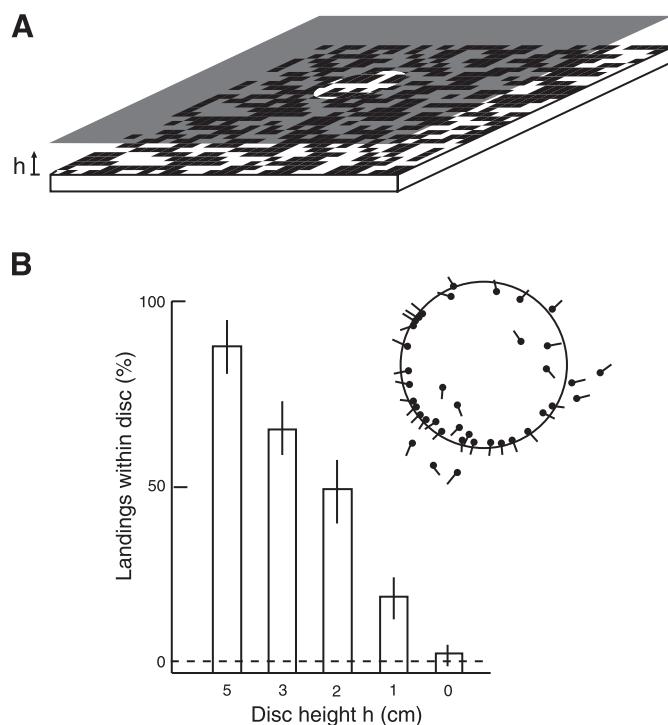


FIG. 9. Experiment investigating the ability of bees to use motion parallax cues to distinguish a figure from a similarly textured background. A: the apparatus presents a textured disc, 6 cm in diameter, positioned under a sheet of clear perspex at a height h cm above a similarly textured background (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 percentages of landings occurring within the disc, for various heights (h) of the disc above the background. The detectability of the disc reduces as h decreases, reaching the random-hit level (dashed line) when $h = 0$, i.e., 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. [Adapted from Srinivasan et al. (241), with permission from The Royal Society.]

A. Color Blindness of the Optomotor Response

In the honeybee, the pathway that drives the optomotor response is driven almost exclusively by the green-sensitive photoreceptors. Measurements of the spectral sensitivity of the honeybee's optomotor response, determined by recording the yaw torque elicited by a stimulus consisting of a moving striped grating, reveal a sensitivity that matches that of the bee's green photoreceptors (116, 119). Further evidence for color-blindness of the optomotor response comes from elegant experiments in which the in-flight optomotor behavior of bees was measured in response to moving patterns composed of two alternating colors of stripes (116, 119). When the stripes of one color (A) were held invariant and the intensity of the stripes of the other color (B) was varied systematically, it turned out that there was one particular intensity at which the optomotor response disappeared, even though the two colors comprising the pattern continued to be clearly discriminable. It turned out that, at this "balance point" the two colors excited the green photoreceptor equally strongly, the excitations could be calculated from the

known spectral sensitivity functions of the green photoreceptors. This finding, which suggested that the optomotor response is driven by the green receptor channel, was corroborated by repeating the above experiment for a range of different colors of A, and determining for each case the intensity of color B at which the optomotor response disappeared. All of the balance points so obtained were consistent with the hypothesis that the optomotor response is driven exclusively by the green receptor (119). This is true regardless of whether the optomotor behavior is measured in terms of the yaw torque that is exerted by tethered, flying bees (119) or in terms of the relative frequencies of left versus right turns made by tethered walking on a so-called Y-maze globe (117).

Further confirmation of this idea comes from measurements of the spectral sensitivity of a large-field movement-sensitive neuron in the lobula of the bee, thought to be involved in the optomotor pathway. Analysis of the responses of this neuron to moving striped patterns of various monochromatic colors revealed a spectral sensitivity identical to that of the bee's green photoreceptors (159). It should be pointed out, however, that not all of the movement-sensitive neurons in the honeybee optic lobe are exclusively green-sensitive. Some neurons display other spectral sensitivities, and their precise visual functions remain to be ascertained (180).

The movement avoidance response, described above, also appears to be driven primarily by the green receptors. When alternate sectors in the discs were composed of colors selected to provide a strong contrast to the green receptors (but not the blue receptors), the movement avoidance response was strong and persisted up to rotational speeds that generated flicker frequencies of up

to 200 Hz (240). However, when the sectors in the discs were composed of colors selected to provide a strong contrast to the blue receptors (but not the green receptors), the movement avoidance response was substantially weaker, and disappeared at ~ 100 Hz (240). These findings demonstrate that the movement avoidance response is also likely to be mediated exclusively by the green photoreceptor channel.

B. Color Blindness in Edge Detection

The ability of bees to detect visually contrasting edges, and to target them while landing, also appears to be mediated by a color-blind system that is driven primarily by the green receptor channel (146). When bees are trained to feed at, say, a black disc placed on a white background by offering them a drop of sugar water as a food reward at the center of the disc, they do not land at the center of the disc, but, rather, at its boundary, and then walk to the center to collect the food (see Fig. 10). Evidently, their landings are directed toward the high visual contrast at the boundary, presumably because 1) the contrasting boundary provides motion cues that can be used to gauge the distance to this feature, and thus to orchestrate a smooth landing; and 2) the boundary may be an indication that the disc has a physical edge, which will offer a secure grip upon landing. When the colors of the disc and the background are chosen such that the disc boundary offers a strong contrast to the green receptors (but not to the blue receptors), the bees show a strong tendency to land at the boundary (Fig. 11, bottom panel), as in the case of the black discs on the white background.

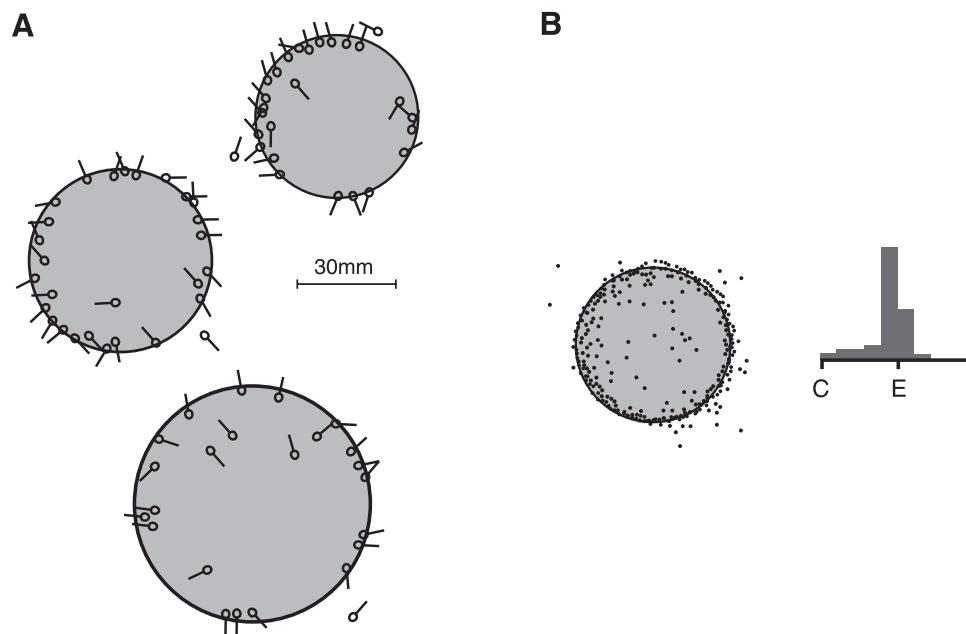


FIG. 10. Visual edge detection in landing honeybees. *A*: distribution of positions and body orientations at landing of bees trained to feed at a drop of sugar water placed at the center of each of three black discs placed on a white background. *B*: distribution of landing positions over a disc, where each dot marks the position of the head in a landing (*left*). Radial distribution of landing density over the disc, where C represents the center and E the edge. [Adapted from Lehrer et al. (146), with permission from The Royal Society.]

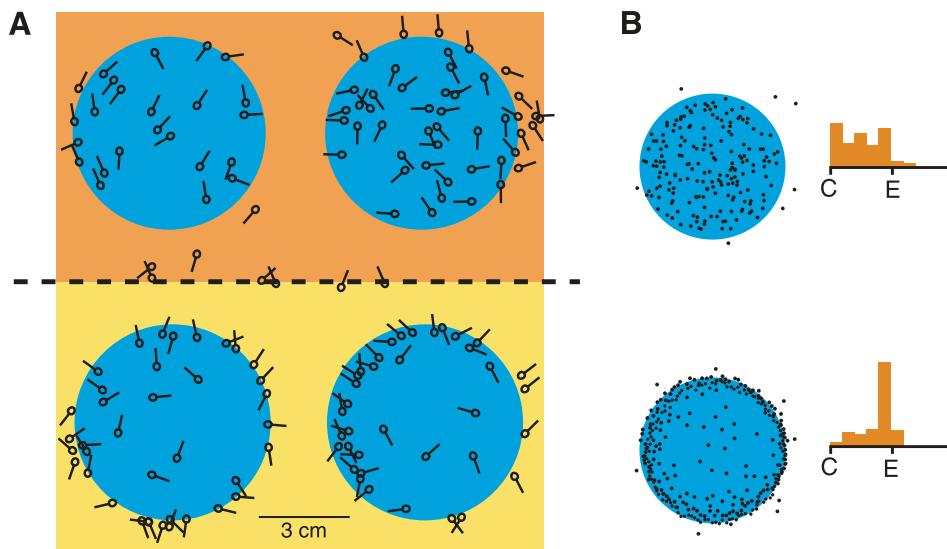


FIG. 11. Chromatic properties of edge detection in landing honeybees. *A:* bees trained as in Figure 9 to collect food rewards on blue discs tend to land preferentially at the boundaries of the discs when the color of the background is chosen such that the boundary between the disc and the background presents a substantial contrast to the green receptor channel, but negligible contrast to the blue receptor channel (*bottom panel*). However, when the color of the background is chosen such that the disc boundary presents a substantial contrast to the blue receptor channel but negligible contrast to the green receptor channel (*top panel*), the same bees show no preference for the boundary and land uniformly all over the area of the discs. *B:* radial distribution of landing densities in the two conditions. This experiment demonstrates that edge detection during landing is color-blind and mediated primarily by the green receptor channel. [Adapted from Lehrer et al. (146), with permission from The Royal Society.]

However, when the colors are such that the boundary offers a strong contrast to the blue receptors (but not to the green receptors), the bees show no particular preference for the boundary; they land uniformly all over the surface of the disc (Fig. 10, *top panel*). Thus edge detection for landing appears to be mediated by a color-blind visual pathway that receives its input primarily from the green photoreceptors (146). Interestingly, visually guided landings in budgerigars also appear to be driven by a color-blind visual pathway, although the bird as a whole possesses tetrachromatic color vision (13).

C. Color Blindness in the Perception of Depth From Motion

The “artificial meadow” experiment, described above, showed that bees can learn to distinguish between discs at various distances (depths) when they fly above them (147, 243). Lehrer et al. (147) went on to examine whether this capacity depended on the color of the disc, and on the color of the background against which it was presented. When the colors of the disc and the background were chosen such that the boundary between the disc and the background provided a strong contrast to the green receptors, but not to the blue receptors, the bees were able to discriminate the depths of the various discs very well. However, when the colors were such that the boundary between the disc and the background provided a strong contrast to the blue receptors, but not to the green receptors, the bees’ ability to discriminate depth disappeared (147). This finding reveals that, in the honeybee, the ability to extract depth from motion cues is, again, color-blind, and driven primarily by the green receptor.

D. Color Blindness in Estimating Distance Flown

Finally, there is evidence that the honeybee’s “odometer” is also driven exclusively by the green receptor channel. This odometer, as we shall describe later below, is a visually driven mechanism that evaluates how far the bee has flown to get to a food source, by gauging the total extent of image motion that the eye has experienced en route. The visual pathway that measures the rate of image motion experienced by the eye, and integrates it over time to obtain the total amount of image motion, is driven by the green channel (34).

It is evident from the above discussion that virtually all of the motion-sensitive behaviors that have been studied so far in the honeybee are color-blind (143, 144). Curiously, the same is true for the perception of motion in humans. Although we possess trichromatic color vision, our motion sensitivity again appears to be largely color-blind and is driven primarily by the so-called “luminance” pathway, which sums signals from the red and green cones (152, 187, 297; see, however, Refs. 27, 164). Color-blindness in motion perception has also been reported in a variety of other animals such as goldfish (202), lizards (203), and frogs (14).

E. Why Color-Blindness?

Why are many of the movement-dependent behaviors so pervasively blind to color? One can think of two possible reasons. First, it can be shown mathematically that correlation-based motion sensors of the type described by the Hassenstein-Reichardt model (see above) will produce the strongest response if the two input pathways A and B that feed into the correlation mechanism (see Fig.

5) possess the same spectral sensitivity (234). In other words, the response of a movement detector will be stronger if both of its inputs are derived from blue-sensitive photoreceptors, or from green-sensitive photoreceptors, than if one input comes from a blue receptor and the other from a green receptor. This is because, for most natural moving scenes, the signals induced in neighboring ommatidia are most strongly correlated if they are sensed by photoreceptors of the same spectral class, the time-varying signal from the photoreceptor in one ommatidium will then be identical to that from the photoreceptor in the neighboring ommatidium, except delayed (or advanced) in time (234). Second, it turns out that in most natural scenes, which are dominated by green or brown landscapes, the visual contrast is highest in the green part of the spectrum. This implies that the response of a motion sensor will be strongest when its inputs are tuned to the green part of the spectrum. Interestingly, the spectral sensitivity of the honeybee's green photoreceptor (see Fig. 2.12 in Ref. 88) coincides very well with the envelope of the spectral sensitivities of the human red and green photoreceptors which comprise the luminance pathway (see, for example, Fig. 1.2b in Ref. 297 or Fig. 2.12 in Ref. 88). Thus the visual systems of humans, bees, and perhaps many other terrestrial organisms may have evolved to sense motion in similar environments.

IX. NAVIGATION

A. The Honeybee's "Waggle Dance"

Navigation in flying insects has been studied most intensely in the honeybee. The reason for this probably arises from the famous "waggle dance" that a bee performs after returning home from a newly discovered, attractive food source, to advertise to its nestmates the distance and direction of the goal (268). The dance is performed on the vertical surface of the honeycomb. The bee moves in a series of alternating left- and right-hand loops, each pair of loops shaped roughly like a figure eight (Fig. 12A). At the end of each loop, the bee enters a so-called "waggle" phase in which she waves her abdomen rapidly from side to side. The angle between the axis of the waggle and the vertical direction represents the angle between the sun and the direction in which a bee should fly to find the goal (Fig. 12A). The duration of the waggle phase is proportional to the distance of the food source from the hive. Thus, if marked bees are trained to forage at a sugar water feeder and their dances upon returning to the nest are recorded and analyzed, the waggle duration will be found to increase as the feeder is moved progressively further away from the nest, roughly proportional to the distance (Fig. 12B). Thus the dancing bee conveys information about the location of the food

source to her nestmates in this highly symbolic way, with the vertically upward direction representing the direction of the sun. If the food source is very close to the hive (within a radius of ~50 m), the waggle phase disappears and the dance consists of a series of irregular loops (Fig. 12B). This so-called "round dance" provides no directional information, but implies that the food source is close to the hive, within a radius of ~50 m, which is adequate for the nestmates to locate it. The distance at which the transition from the round dance to the waggle dance occurs is ~50 m for the Carniolan honeybee (*Apis mellifera carnica*), but can vary somewhat with the species and race of honeybee; it can be as low as 20 m in the Italian honeybee (*Apis mellifera ligustica*) or 2 m in the case of the Indian honeybee (*Apis Indica F.*) (268). In many species, bees perform a differently shaped dance, termed the "sickle dance," in this transition phase (268).

The waggle dance, in addition to encoding the distance and direction of the food source, is also used by the dancer to convey information about the "attractiveness" of the food source. The attractiveness, as assessed by a bee, can depend on the quality (sweetness) of the nectar that the flower bears, the time (or energy) that is required to fly to the flower, and the time (or energy) that is required to get to the nectar after having landed on the flower (this is known as the "handling time") (91, 200, 204). The attractiveness of a flower increases with the quality of its nectar and its proximity to the hive, but decreases with increase of handling time. The attractiveness is signaled by two dance parameters, namely, 1) the number of loops performed and 2) the duration of time that elapses between successive waggles (the inter-waggle duration). Food sources that are more attractive generate a greater number of loops, and a shorter inter-waggle duration (212, 213). These two parameters together characterize the so-called "liveliness" or "intensity" of the dance (268), which is a measure of the flower's attractiveness.

There is good evidence that potential recruits choose between different food sites, as advertised by different dancing bees, by favoring dances of higher liveliness. This behavior ensures that the foraging resources of the colony are used in an optimal way, by maximizing the ratio of the energy that is obtained from a food source, to the energy that is expended to fly there and extract the nectar (91, 204). There is also evidence that bees that bring in high-quality food are attended to more readily and quickly not only by potential recruits, but also by nectar-unloading bees. Thus the colony gives the dancing bee quick feedback about the quality of the food that she is bringing in, relative to the food that others might be fetching from other sources, and will help her decide whether to continue to forage at her present site or to seek out a better one, either by searching on her own, or by attending to other dances (91).

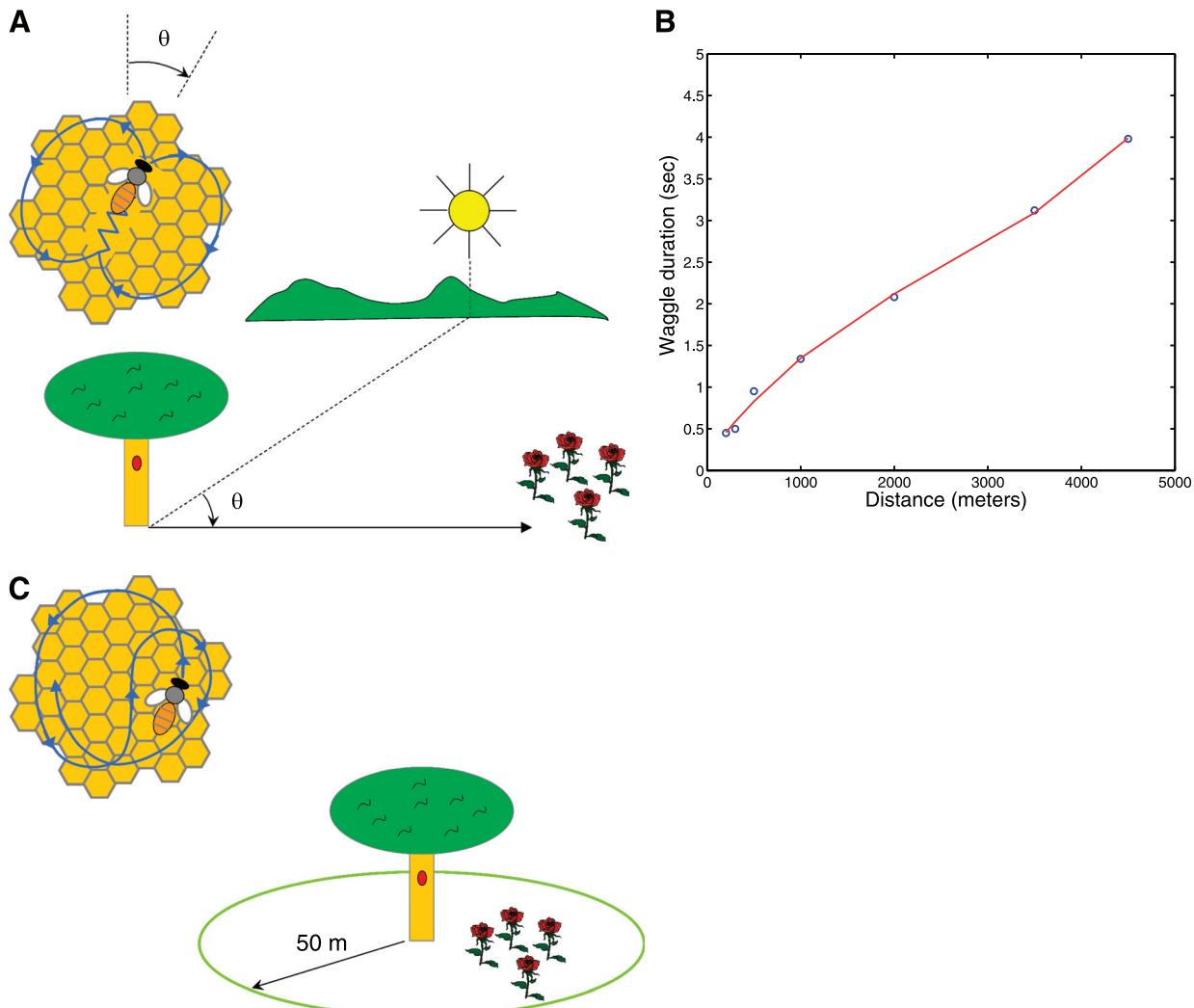


FIG. 12. Illustration of the symbolic navigational information that a dancing honeybee provides to its nestmates. *A*: the “waggle dance,” which conveys information on the distance and the direction to a food source. *B*: the waggle duration increases approximately proportionally to the distance of the food source from the nest. *C*: the “round dance,” which implies that the food source is close to the hive, within a radius of ~50 m. See the description in text. [*A* and *C* modified from Veeraraghavan et al. (263), copyright 2008 IEEE; *B* plotted from data in Table 13 of von Frisch (268).]

Let us return to the specific symbolic instructions that are conveyed by a dancing bee to the potential recruits, to inform them about the location of a food source. To use the vertically upward direction as a reference to the direction of the sun, the dancer, as well as the potential recruits observing the dance, must be able to sense the direction of gravity. There is evidence for three ways in which this might be done. First, there are mechanosensory hairs in the front of the thorax, which are in contact with the back of the head. These “neck” hairs could convey information on the orientation of the bee relative to the vertical by sensing the pitch and yaw of the head relative to the thorax. Because the dance is performed on the vertical surface of the honeycomb, the weight of the head would cause the head to pitch maximally down relative to the thorax when the bee’s body is directed upwards, and maximally up relative

to the thorax when the body is directed downwards. Intermediate orientations would generate intermediate amounts of pitch of the head, in addition to yaw. Thus the orientation of the head relative to the thorax should provide sufficient information for the bee to assess the orientation of her body relative to gravity. Indeed, ablation of the mechanosensory hairs (or gluing the head rigidly to the thorax) disorients the bees’ dances (151, 268). Second, body orientation may also be gauged by monitoring the orientation of the abdomen relative to the thorax. When the bee is oriented facing upwards, the abdomen would hang vertically down, parallel to the long axis of the thorax. On the other hand, when the bee is oriented to the right of the vertically upward direction (for example), then the tendency of the abdomen to continue to hang vertically downwards would cause the abdomen to de-

flect to the right, relative to the thorax; and the opposite would be true if the bee was oriented to the left of the vertical. There is evidence that the angle between the thorax and the abdomen; that is, the angle of the "waist" joint, is also sensed and used to infer the orientation of the body relative to the vertical (88, 151, 156, 157, 199). Sensory interneurons have been observed to innervate mechanosensory hair cells in the neck and waist areas (22, 199). Finally, proprioceptive information from the joints in the legs may provide additional information on body posture relative to gravity (88, 151).

Given the paucity of visual information in the darkness of the hive, it is likely that recruits sense the waggle of the dancing bee's abdomen mechanically and/or acoustically, rather than visually. Potential recruits follow the dancer and often touch the dancer's abdomen with their antennae (190, 259), suggesting that this mechanical contact might provide orientational cues. There is also evidence that the Johnston's organs at the base of the antennae play a role in sensing the airborne vibrations generated by the waggling abdomen (88, 165).

How did the vertically upward direction come to symbolize the direction of the sun? The prevalent theory is that this representation evolved originally as a modification of an "*Urtanz*" that the ancestral, tropical species of honeybees performed on their honeycombs, which were built horizontally and exposed to the sky. In the original form of the dance, a bee, dancing on the horizontal honeycomb, would point its waggle axis directly at the food source, mimicking a scaled-down journey to the destination. This is the form of dance that the tropical bee species *Apis florea* exhibits when it advertises food sources on the horizontal honeycombs of its nest (268). As the tropical species evolved and moved northward to cooler climates, their nests could no longer be built outdoors; they had to be built in tree cavities, for protection from the cold. As the theory goes, it was at this time that the bees made a transition to the construction of vertical honeycombs (62, 91, 150, 178). In the darkness of their new abodes, the sun was no longer visible and could no longer provide a direct directional reference. Consequently, the bees evolved to use the upward vertical direction (the direction of negative gravity) to symbolize the direction of the sun. This is the dance of the modern honeybee species, *Apis mellifera*. Indeed, even *Apis mellifera* reverts to the ancestral dance when it is forced to dance on a horizontal honeycomb (268). This theory of the evolution of the dance is, however, not uncontroversial (see, for example, Refs. 63, 186).

The information in the honeybee's waggle dance is decoded and used by the nestmates to locate the food source, and to harvest it efficiently. But the waggle dance is also useful for the researcher who wishes to unravel the mysteries of the honeybee's navigation systems, because it provides a window into the bee's perception of how far,

and in which direction, she "thinks" she has travelled. We now examine how bees gauge the direction distance of their flight to the food source.

B. Determining the Direction of the Food Source: the "Celestial Compass"

The direction of the food source is established in relation to the position of the sun, and of the pattern of polarized light that it creates in the sky (268). We describe below how bees obtain compass information from each of these cues that the sky provides.

1. The sun compass

When the sun is clearly visible in the sky, it is used as a directional reference, by a forager to return to a food site that it has visited previously, by a dancing bee to signal the direction of a food source to its nestmates (as described above), and by a new recruit that has just witnessed a dancing bee, to set the course of its outbound foraging flight. A forager returning to a previously visited feeding site sets its flight direction by orienting itself such that the sun is in the same position in its visual field as it was in the previous flight. When *Apis mellifera* dances on a vertical honeycomb in the nest to advertise a food source, she needs to transpose the azimuthal bearing of the sun (relative to the direction of her flight to the food source) to the angle between the waggle axis of her dance and the vertically upward direction on the honeycomb. A naive bee, freshly recruited by a dance, must make the opposite transposition: she must fly in a direction such that the azimuthal bearing of the sun (relative to her flight direction) corresponds to the orientation of the waggle axis of the dance that she has just observed in the hive (see Fig. 12A). Interestingly, the waggle dance is also used by scout bees in a swarm to indicate the direction and distance of potential new homes for the swarming colony (211). At the neural level, we know relatively little about how the azimuthal bearing of the sun is registered and represented, how the dance direction is sensed and represented by a fresh recruit, or how bees make the transitions between these two frames of reference.

In setting their compass direction, bees possess an internal clock that enables them to allow for the movement of the sun in the sky during the day. Thus, in a situation where a bee dances for prolonged periods to advertise the location of a food source that it has discovered (without returning to revisit it), the bee has been observed to shift the orientation of its waggle axis systematically and appropriately with the progress of time, thus revealing the use of an internal clock to adjust the reference orientation of the sky compass according to the time of the day (148, 149, 280). Furthermore, when a colony of bees that has been foraging at an attractive food

source is abruptly transported to a new, unfamiliar location in which there are no familiar landmarks and released to forage there, they fly out in the same compass direction irrespective of when in the day they are released, indicating 1) that they are relying on the sun compass to set a course in the novel environment and 2) that they have compensated for the predictable motion of the sun in the sky (91, 149, 150). Another piece of evidence that strongly supports time compensation of the celestial compass comes from experiments in which bees that have learned a food site are prevented from foraging for a few hours, and then given a taste of the nectar that they had collected when they last visited it (149, 150). Some of these bees then break into a waggle dance, recalling the position of the food source, even without revisiting it. In these “recapitulatory” dances, the bees indicate the direction of the food source by allowing for the motion of the sun during their period of imprisonment. Indeed, bees can also be induced to dance in this way at night, long after the sun has set. In these dances, they seem to use an appropriately extrapolated azimuthal position of the sun, which is now below the horizon, as a reference to set the direction of their dances. Clearly, then, these bees are relying on an internal clock to achieve this time compensation. The internal clock is believed to reside in the central complex (see below).

2. The polarized-light compass

When the sun is hidden by a cloud, bees can still derive compass information from a patch of blue sky, by making use of the pattern of polarized light that the sun produces in the sky (Fig. 13). Light from the sun is unpolarized, but the atmosphere scatters and polarizes this light, a phenomenon initially studied and quantified by Lord Rayleigh, and known as Rayleigh scattering (Fig. 13A). Light propagates as an electromagnetic wave in which the electric and magnetic fields, denoted by vectors, are oriented orthogonally to the direction of propagation (see, for example, Ref. 288). When light is unpolarized, the electric field vector (denoted by “e-vector”) is oriented randomly within a plane that is perpendicular to the direction of propagation. (The same is true for the magnetic field vector, but we shall consider only the e-vector from here on.) When light is polarized, the e-vector has a preferred orientation within this plane, exhibiting a maximum amplitude along one axis and a minimum amplitude in the perpendicular axis. In the case of fully polarized light, the e-vector is oriented along a single axis.

As mentioned above, light from the sun is unpolarized, as shown in Figure 13A. The light that is scattered by the atmosphere in a direction perpendicular to the incident sunlight is maximally polarized in a direction perpendicular to the plane containing the sun, the observer and the point of scatter (Fig. 13A). Light passing undeflected through the

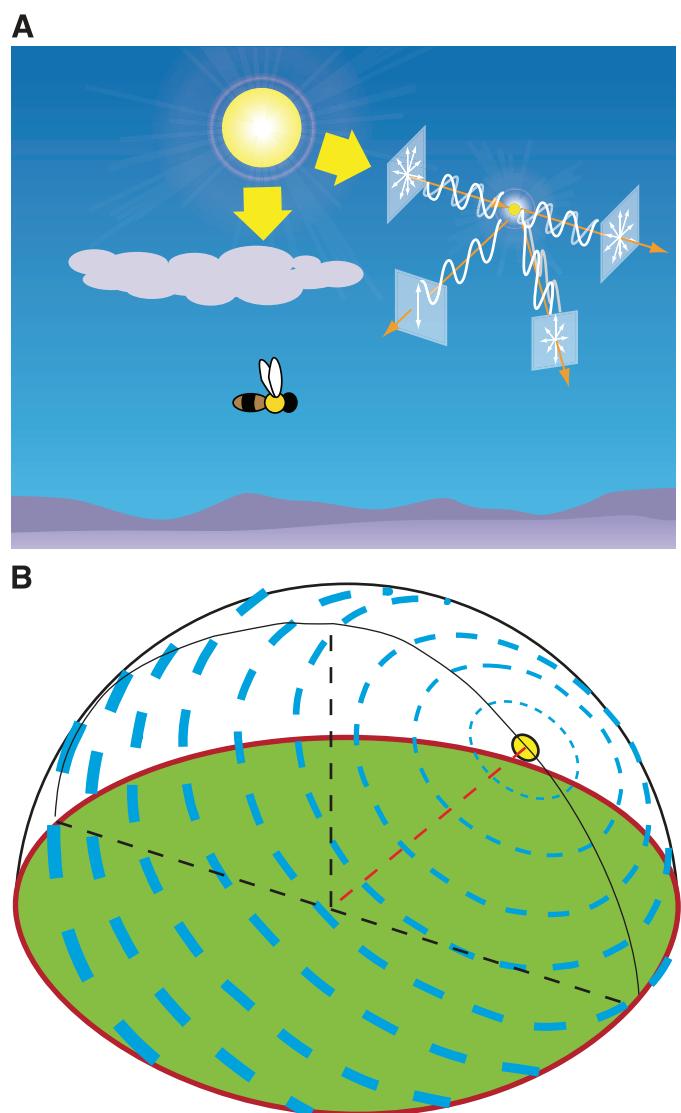


FIG. 13. A: unpolarized light from the sun is polarized by atmospheric scattering, with the degree of polarization depending on the observer's direction of view relative to the sun. B: as a result, the light from the sky possesses a characteristic pattern of polarization in which the light is unpolarized in the direction of the sun (yellow dot) and is most strongly polarized in an equatorial ring corresponding to viewing directions that are perpendicular to the direction of the sun. The thickness of the dashed blue lines denotes the degree of polarization. See details in text. [Modified from Wehner and Labhart (288), with permission from Cambridge University Press.]

atmosphere remains unpolarized (Fig. 13A). As a result, skylight, as viewed by an earthbound observer, is unpolarized in the direction of the sun and is maximally polarized in the equatorial ring corresponding to viewing the sky in directions that are 90 degrees away from the sun, as shown in Figure 13B. In this figure, the yellow dot represents the position of the sun, and the dashed lines depict the directions of polarization (the e-vector directions) of light incident from various points in the sky, from the point of view of an observer at the center of the celestial sphere. As the sun moves across the sky, the pattern of polarization that the

sun induces in the sky moves with it, the pole of the pattern always being located at the sun and the equatorial ring lying in a plane perpendicular to the line joining the observer and the sun (288). When the sun is obscured by a cloud, honeybees are able to analyze the pattern of polarization in the clear part of the sky and use this as a directional reference, in lieu of the sun (268).

To understand how the pattern of polarized light in the sky is sensed by the honeybee's visual system, we need to consider in greater detail the structure of the compound eye and its photoreceptors. In the DRA of the honeybee's compound eye, the rhabdom of each ommatidium is dominated by microvilli from the ultraviolet (UV) photoreceptors. The UV photoreceptors are ideally suited for polarization vision, because scattered light from the sky is polarized most strongly in the UV. Indeed, there is evidence to suggest that most insects, including honeybees, show behavioral responses to polarized light mainly in the short-wavelength region of the spectrum: UV for bees (134, 163, 271) and blue for crickets and locusts (70, 104, 105, 135, 139).

We mentioned at the beginning of this article that the light-absorbing photopigment is situated in the microvillar membranes of the photoreceptors (Fig. 1C). In the dorsal rim area, the microvilli within each photoreceptor are all aligned in the same direction and are oriented transversely with respect to the long axis of the rhabdom. When an ommatidium is illuminated by polarized light, a photoreceptor in the ommatidium absorbs light maximally if the e-vector of the incident light is parallel to its microvilli, and minimally if the e-vector is orthogonal to them. The polarization sensitivity of the photoreceptor is explained by the following model. We assume that the efficiency with which light is absorbed by a photopigment molecule depends on the orientation of the e-vector with respect to the molecule, and that the molecule absorbs light maximally when the e-vector of the incident light is oriented in the molecule's "preferred" direction, and not absorbed at all when the e-vector is oriented in a perpendicular direction (168). The microvillus can be modeled as a cylindrical tube with the photopigment molecules aligned randomly over its membranous surface (168, 220). Such a model predicts that the photopigment molecules in the microvillus would collectively absorb twice as much light when the e-vector of the incident light is parallel to the microvillus, compared with when it is orthogonally oriented, producing a polarization sensitivity (ratio of maximal to minimal light absorption) of between 1.6 and 2.0 (168, 220). However, intracellular recordings of short-wavelength-sensitive photoreceptors in the honeybee's dorsal rim area reveal polarization sensitivities exceeding 10 (134), and in the cricket they are as high as 29 (16). This suggests that the photopigment molecules are not oriented randomly within the microvillar membrane, but are preferentially aligned parallel to the long axis of the

microvillus (220). This alignment substantially boosts the polarization sensitivity of the photoreceptor from 2 to a median value of nearly 10 (16).

The arrangement described above endows each UV photoreceptor in the dorsal rim area of the compound eye with strong polarization sensitivity. Within each ommatidium in the DRA, there are two groups of UV photoreceptors. One group has its microvilli oriented in a specific direction, and the other in the orthogonal direction, as is illustrated schematically in Figure 13 (136, 288). It has been postulated that these two groups of photoreceptors interact antagonistically at the early stages of the visual pathway (133). We could regard the neuron, or neural circuit that implements this antagonistic interaction, as an "Elementary Polarization Detector" (EPD). If one group of photoreceptors excites the EPD while the other group inhibits it, then the EPD will be strongly excited when the e-vector of the incident light is parallel to the microvilli of the excitatory group, and strongly inhibited when the e-vector is parallel to the microvilli of the inhibitory group, as shown in Figure 14. This antagonistic interaction has two advantages. First, the push-pull effect amplifies the output of the EPD when the direction of the illuminating e-vector is varied, thus enhancing the polarization signal. Second, it eliminates or strongly reduces any potential sensitivity of the EPD to changes in the intensity of the incident light. Consequently, the EPD will signal the true direction of the e-vector irrespective of light intensity, and will not confound changes in the e-vector orientation with changes in intensity.

Each ommatidium in the dorsal rim of the honeybee's compound eye can thus be regarded as a polarization analyzer, with a preferred e-vector orientation that generates a strong excitatory response in the underlying EPD, and an orthogonal, nonpreferred e-vector orientation that generates a strong inhibitory response in the EPD. An analysis of the ommatidia in the dorsal rim area of many insects, including the honeybee, reveals that there is a systematic shift of the preferred e-vector direction of the rhabdom as one moves from one ommatidium to the next, resulting in a fan-shaped pattern of preferred orientations across the array (137, 139, 288). This pattern is illustrated in Figure 15A for a field cricket.

How are the polarized-light signals from the dorsal rim area analyzed at higher levels of the visual pathway? To date, there is not much information on this question with regard to the bee. However, in the cricket, electrophysiological recordings of neurons in the next stage of processing, the medulla, have revealed three populations of polarization-sensitive neurons (POL neurons), with three distinct preferred e-vector orientations separated by ~120 degrees (Figs. 15B and 16). All of these neurons have large visual fields, covering a substantial area of the upper sky (16, 106, 138, 139, 181). It is believed that each of these medullary neurons pools (i.e., spatially sums) the

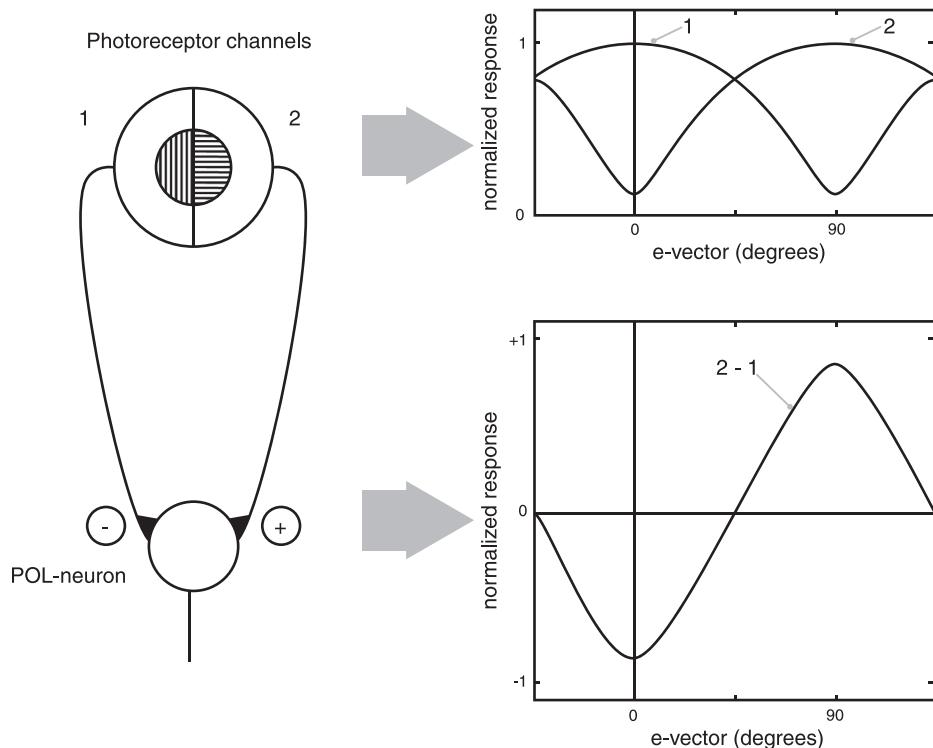


FIG. 14. Analysis of polarized light at the first stage of the insect visual pathway involves a mutually antagonistic interaction between signals from two sets of photoreceptors with orthogonal preferred e-vector orientations. This enhances sensitivity to changes in e-vector orientation and suppresses sensitivity to changes in light intensity. The neuron or neural circuit that implements this antagonistic interaction may be regarded as an “elementary polarization detector” (EPD). See description in text. [Modified from Labhart (133), with permission from Macmillan Publisher Ltd.]

outputs from a large number of EPDs that have similar preferred e-vector orientations within the dorsal rim array. Most of the POL neurons are strongly excited when the e-vector is oriented in their preferred direction, and strongly inhibited when the e-vector is orthogonal to the preferred direction (Fig. 16A) (105, 133, 137, 139, 183). The relatively large visual field of each POL neuron (often exceeding 60 degrees in width) allows it to ex-

tract a reliable e-vector signal from a moderately large patch of the sky, uncontaminated by local errors arising from small cloud patches or atmospheric abnormalities. The three classes of POL neurons, with preferred orientations 120 degrees apart (Fig. 16B), are ideally suited for analysis of the e-vector orientation in the upper region of the sky. It should be mentioned that, so far, recordings from POL neurons have been performed

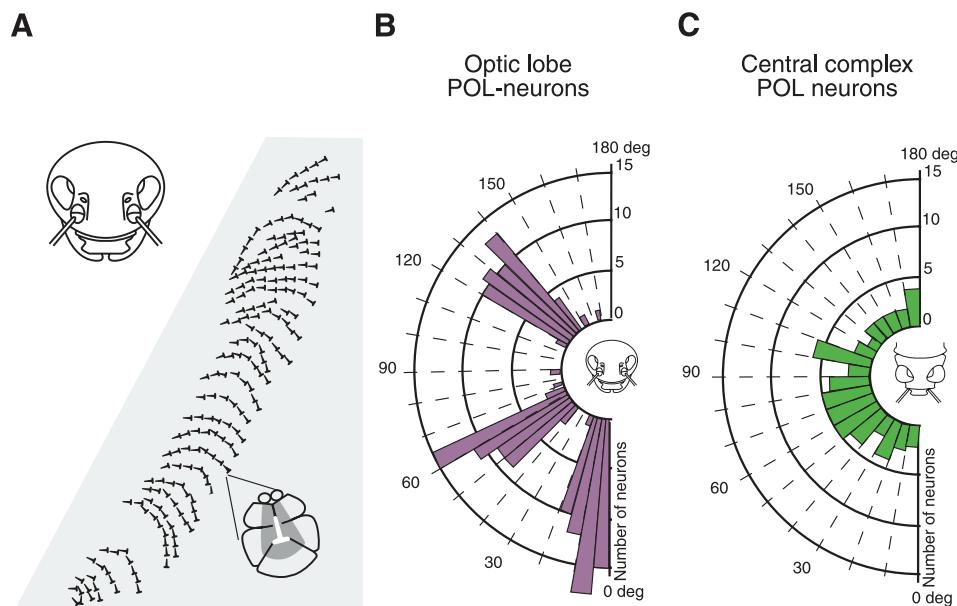


FIG. 15. A: illustration of microvillar orientations in the array of ommatidia in the dorsal rim of the compound eye of a field cricket. B: histogram of the preferred e-vector orientations of polarization-sensitive interneurons in the medulla reveals three distinct classes, with preferred directions separated by ~120 degrees in angular space. C: interneurons at a higher level of processing, the central complex, show a continuum of preferred orientations, distributed more or less uniformly over the entire orientation domain. [Redrawn from Labhart and Meyer (137), with permission from Elsevier.]

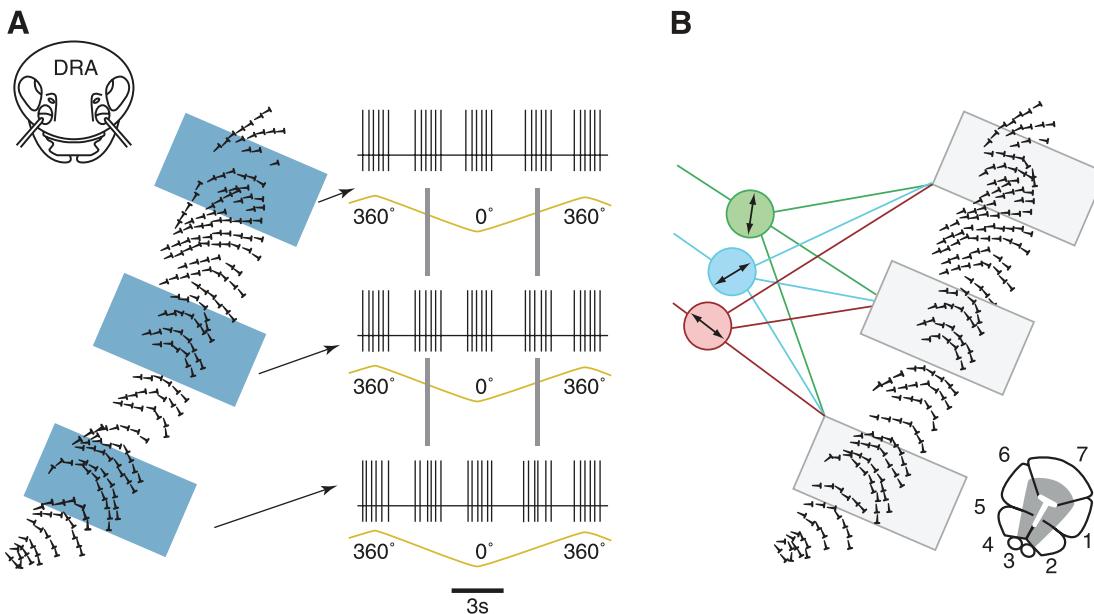


FIG. 16. *A*: responses of a polarization-sensitive interneuron (POL neuron) to polarized light with its e-vector rotating continuously. The traces show responses when the neuron is stimulated in this way at three different regions (rostral, medial, and caudal) within the dorsal rim area. *B*: POL neurons with three distinct preferred e-vector orientations separated by 120 degrees are postulated to pool differently weighted collections of responses from the three regions. [Redrawn from Labhart et al. (139), with permission from The Company of Biologists.]

only in orthopterans (crickets and locusts), and not in the honeybee.

A little reflection will reveal that a minimum of three POL neurons, each with a distinct preferred direction, is required to establish the orientation of the e-vector unambiguously and instantaneously (125) and that three preferred directions that are equally spaced in the angular domain would be optimum. However, a single POL neuron would suffice if the bee adopts a strategy of "scanning" the e-vector of the sky by continuously changing its head orientation (e.g., by turning in a circle) whilst monitoring the variation of the POL neuron's response. The insect should then be able to determine the direction of the e-vector by noting the head orientation at which the response of the POL neuron reaches a maximum or a minimum. These so-called "simultaneous" and "scanning" models are discussed, for example, in References 65, 195, and 288. It is presently unclear whether bees use the instantaneous method or the scanning method, or both, although there is some evidence to favor each. The use of the instantaneous method is an attractive hypothesis, at least in the insects that are known to possess the three classes of POL neurons in the optic lobe.

In locusts, the responses of neurons to polarized light have also been examined at a much higher level, namely, that of the central complex. At this level, the neurons no longer show just three distinct, preferred e-vector orientations. Rather, each neuron is more sharply tuned to a preferred orientation, and collectively, these neurons exhibit a continuum of preferred orientations, distributed more or less uniformly over the entire orientation domain,

ranging from 0 to 360 degrees (Fig. 15C) (98, 99, 105, 264). This set of so-called "compass" neurons presumably receives appropriately weighted synaptic inputs from the three sets of POL neurons described above. The compass neurons appear to be involved in a "winner take all" type of neural network that provides a compass-like representation of the e-vector, where the unit with the strongest response signals the e-vector direction. Models of such neural networks have been proposed (288) and partially validated (99, 198).

There is evidence that, apart from the position of the sun and the orientation of the polarized-light pattern in the sky, bees use additional cues based on the variations of intensity and color across the sky that depend on, and vary with, the sun's position (21, 66, 194, 283). The intensity of the sky is obviously highest at the sun and decreases systematically and predictably in regions further away from it. When the sun is high in the sky, the color of the sky is a whitish, unsaturated blue in the vicinity of the sun and becomes a deeper, more saturated blue in regions further away. When the sun is near the horizon, the sun and the immediately surrounding sky are reddish orange in color, whereas regions in the opposite hemisphere tend to be deep blue. Therefore, even when a cloud obscures the sun, the gradients of intensity and color that exist in the visible parts of the sky are used to infer the sun's position to obtain a reference direction for the sky compass (21, 66, 194, 283). Cues derived from these gradients would also help eliminate the 180-degree ambiguity that arises when using the measured direction of the e-vector in a patch of sky to determine the direction of the sun

(182, 284). The central complex of the locust also features neurons that respond not only to the e-vector direction, but also to the azimuthal position of a light source, as well as to spectral gradients in extended visual stimuli (182, 184). Some of these neurons exhibit preferred e-vector orientations that vary with the time of the day, suggesting that they receive input from an internal clock (182). The central complex is likely to be the region of the brain in which celestial information is combined with clock information to set a course of flight that is always directed toward the desired target, regardless of the time of the day. Exactly where the clock resides is an open question, yet to be answered; it may well be distributed across several brain ganglia.

In the context of polarized-light vision, we should highlight an important structural difference between the ommatidia in the DRA, and those in the rest of the compound eye. In the rhabdoms of the DRA, the microvilli of an individual photoreceptor maintain a constant orientation throughout the depth of the rhabdom (136). This alignment ensures that the photoreceptors in the DRA possess high polarization sensitivity. On the other hand, in the ommatidia in the rest of the compound eye, the rhabdoms tend to twist about their long axis (136, 286). Therefore, the orientation of the microvilli of a photoreceptor can vary by as much as 180 degrees in going from the top of the rhabdom to the bottom. This twist tends to make the photoreceptor equally sensitive to all e-vector directions, thus destroying its polarization sensitivity. The obliteration of polarization sensitivity in regions outside the DRA may actually be an advantage, given that the rest of the eye is not involved in the analysis of the polarization of the incident light but, rather, in evaluating other attributes of the image, such as its color, texture, and motion (285). Bearing in mind that polarized light can arise not just from the sky, but also from shiny surfaces on the ground, such as water surfaces and certain types of leaves and flowers, it becomes clear that the photoreceptors that are used for the analysis of the color of a flower must not be additionally sensitive to any polarization of the light coming from it. This is because any sensitivity to polarization would contaminate the perception of the true color of the flower. The same would be true for the perception of shape, or motion. It has been argued, therefore, that the twist that is consistently observed in the non-DRA regions of the compound eye is an adaptation to prevent this cross-contamination (285, 286). This being said, there are certain insects such as the water inhabiting beetle *Notonecta*, which detects and lands on water surfaces by making use of special adaptations in the ventral region of the eye for the detection and analysis of the polarized light that is reflected by such surfaces (208–210).

C. Estimating Distance Flown: The Honeybee's "Odometer"

As we have described above, the waggle dance that is performed by a bee carries information on the distance and direction of an attractive food source from which it has just returned. The preceding section has described how bees establish the direction of the food source, and the nature of the underlying compass. How does a bee gauge how far it has flown to reach the food source? That is, how does its "odometer" function? Early studies of the waggle dance suggested that distance travelled is measured in terms of the total energy expended during flight (102, 103, 268). The evidence for this was twofold. First, if a foraging bee was made to carry an extra load, by attaching a small steel ball to her thorax, she signaled a greater flight distance in her dances. Second, bees signaled larger distances when they flew to food sites located uphill from the hive, than when they flew to food sites positioned downhill at the same distance. However, recent findings question this hypothesis (73, 87, 174) and suggest that an important odometric cue is the extent to which the image of the environment moves in the eye as the bee wings her way to the target (72, 74, 75, 206, 228, 248, 249, 254). In other words, the odometer is driven by a visual rather than an energy-based signal. Here we shall describe some of the recent work that led to this insight.

About 15 years ago, Srinivasan et al. (254) trained bees to find a food reward placed in a tunnel, and then explored the cues by which they inferred how far they had flown to get to the food. The walls and floor of the tunnel were lined with black-and-white stripes, usually perpendicular to the tunnel's axis (Fig. 17A). The reward consisted of sugar solution offered by a feeder placed in the tunnel at a fixed distance from the entrance. 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 a fresh tunnel that carried no reward and was devoid of any scent cues. The training and test tunnels were covered by a transparent sheet of perspex, and subdivided into numbered sections for the purposes of analysis. In the tests, the bees' behavior whilst searching for the reward was recorded by noting the locations of the first four U-turns that they made in the tunnel, as they zig-zagged back and forth across the position of the (now absent) feeder (249, 254). From this data it was possible to estimate the mean searching location, and the extent to which the search was distributed about this mean. Each bee was tested separately, to avoid interference effects.

Bees trained in this way showed a clear ability to search for the reward at the correct distance, as shown by the searching distribution (Fig. 17B, thick curve). How

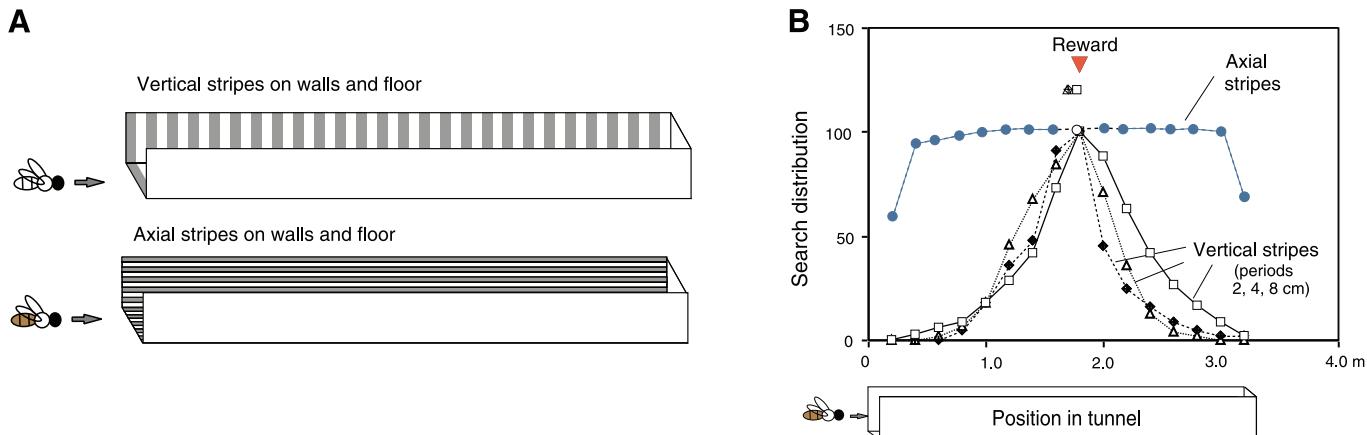


FIG. 17. *A*: experiment investigating how honeybees gauge distance flown to a food source. Bees are trained to find a food reward placed at a distance of 1.7 m from the entrance of a 3.2-m-long tunnel of width 22 cm and height 20 cm. The tunnel is lined with vertical black-and-white gratings of period 4 cm. *B*: when the trained bees are tested in a fresh tunnel with the reward absent, they search at the former location of the feeder, as shown by the bell-shaped search distributions. This is true irrespective of whether the period of the grating is 4 cm (as in the training, square symbols), 8 cm (triangles), or 2 cm (diamonds). The inverted triangle shows the former position of the reward, and the symbols below it depict the mean values of the search distributions in each case. Bees lose their ability to estimate the distance of the feeder when image-motion cues are removed by lining the tunnel with axial (rather than vertical) stripes (circles). These experiments and others (218, 249) demonstrate that *1*) distance flown is estimated visually, by integrating over time the image velocity that is experienced during the flight, and *2*) the honeybee's odometer measures image velocity independently of image structure. [Adapted from Srinivasan et al. (249), with permission from The Company of Biologists.]

were the bees gauging the distance flown? A number of hypotheses were examined, as described below.

Were the bees learning the position of the feeder by counting the stripes en route to the goal? To examine this possibility, bees were trained in a tunnel lined with stripes of a particular spatial period and tested in a tunnel lined with stripes of a different period. The test bees searched at the correct distance from the tunnel entrance, regardless of stripe period (Fig. 17*B*, thin and dashed curves). Therefore, distance is not gauged by counting the number of stripes or other features passed whilst flying through the tunnel (249, 254).

Were the bees measuring distance flown in terms of the time required to reach the goal? To examine this possibility, bees were trained as above and tested in a tunnel that presented a headwind or a tailwind, generated by a fan at the far end of the tunnel. In a headwind, bees flew slower and took longer to reach the estimated location of the reward. The opposite was true in a tailwind (249). Therefore, distance is not estimated in terms of time of flight, or other correlated parameters such as number of wing beats. Interestingly, in a headwind, bees overshot the location of the reward; in a tailwind, they undershot it. Thus, in each case, the bees overcompensate for the effects of the wind, and exactly why they do this is not yet clear. Nevertheless, the existence of the overshoot and undershoot demonstrate convincingly that distance flown is not measured in terms of energy consumption. This is because, in the case of the headwind, the bees are experiencing a greater resistance to forward motion, as well as flying a greater distance, compared with the tailwind, which implies that they must be expending more energy in the former case than in the latter (249).

Were the bees measuring distance flown by gauging the extent of motion of the image of the surrounding panorama as they flew to the goal? To investigate this possibility, bees were trained in a tunnel of a given width and then tested in a tunnel that was narrower or wider. In the narrower tunnel, the bees searched at a shorter distance from the entrance; in the wider tunnel, they searched farther into the tunnel (249, 254). These results suggest that distance flown is gauged by integrating the speed of the images of the walls and floor on the eyes whilst flying through the tunnel.

To test the image motion hypothesis critically, bees were trained and tested in conditions where image motion was eliminated or reduced. This was done by using tunnels that carried axially oriented stripes on the walls and floor. Such tunnels provided no information on image motion, because the bee's flights in them were parallel to the direction of the stripes. In the experiments using axial-striped tunnels, the bees' behavior was strikingly different: they showed no ability to gauge distance travelled. The bees searched uniformly over the entire length of the tunnel, showing no tendency to stop or turn at the former location of the reward (Fig. 17*B*, dashed curve). Evidently, when bees are deprived of image-motion cues, they are unable to gauge how far they have flown. This finding provides direct and rather compelling evidence that the honeybee's odometer is driven by image motion, and that the distance traveled is estimated by integrating the amount of image motion that is experienced over time (249, 254). Experiments similar to those described above have been conducted on stingless bees (*Melipona seminigra*) and have yielded similar results (109).

What are the consequences of measuring distance travelled by integrating optic flow? One consequence would be that errors in the measurement and integration of image speed accumulate with distance so that larger distances are estimated with greater error. To test this prediction, Srinivasan et al. (249) examined the accuracy with which bees were able to localize a feeder when it was placed at various distances along a tunnel. The results (Fig. 18) show that the width of the search distribution indeed increases progressively with the distance of the feeder from the tunnel entrance. Thus the error in estimating distance increases with distance flown, as would be expected of any mechanism that measures a velocity, or a rate, and integrates it over time to obtain a measure of the total distance traversed.

An integrative mechanism for measuring distance travelled would be feasible only if the cumulative errors are somehow prevented from exceeding tolerable levels. One strategy, which could be employed when traversing familiar routes, would be to recommence the integration of image motion whenever a prominent, known landmark is passed. Do bees adopt such a tactic? To investigate this, Srinivasan et al. (249) examined the bees' performance when they were again trained to fly to a feeder placed at a large distance into a tunnel (Fig. 18), but now had to pass a prominent landmark (a baffle consisting of a pair of overlapping partitions) occurring en route to the feeder. If these bees reset their odometer at the landmark, they should display a smaller error because they would then only need to measure the distance between the landmark and the feeder. This is precisely what occurred: the search

distribution was then significantly narrower (green circles, Fig. 18). Furthermore, when the trained bees were confronted with a test in which the landmark was positioned closer to the tunnel entrance, the bees' mean search position shifted toward the entrance by almost exactly the same distance (249). These results confirm that bees recommence computation of distance when they pass a prominent landmark and that such landmarks are used to enhance the accuracy of the odometer.

Further experiments are required to determine whether bees use a single odometer, resetting it to zero each time a landmark is passed, or start a new odometer at each landmark, leaving some or all of the earlier ones running. In conditions where landmarks are poorly visible or not stable, it may be advantageous to combine odometric readings referenced to a number of different landmarks encountered en route, as well as to the total distance from the start to the goal, to obtain a reliable estimate of the distance flown. Indeed, there is evidence that desert ants combine various odometric readings in this way (38, 39). Furthermore, as we shall see later below, honeybees also behave as though they run two odometers concurrently: one for their own personal use and the other for indicating the distance of the route their nestmates.

A number of studies (32, 33, 40, 42, 45, 51) indicate that foraging bees "expect" to see a specific sequence of landmarks situated at specific distances on the way to the food source and that they monitor their progress toward the destination by checking whether the expected landmarks show up at the appropriate distances. Thus bees

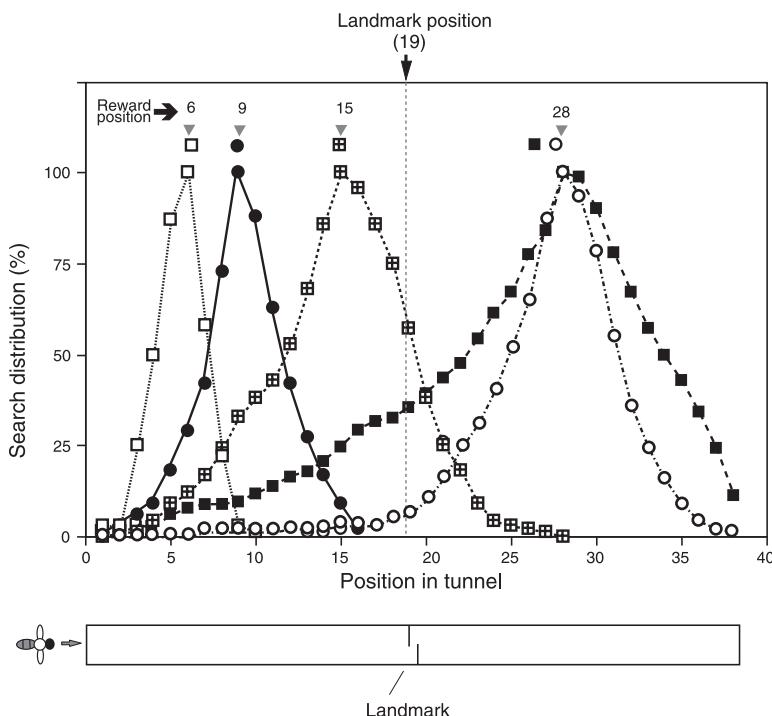


FIG. 18. Experiment investigating variation of the accuracy of the honeybee's odometer with the distance travelled. Bees were trained, in separate experiments, to find a food reward in a long tunnel at a feeder positioned at various distances from the entrance: 6, 9, 15, and 28 units, where 1 unit = 10 cm. The searching distributions of the trained bees became progressively broader with increasing feeder distance, indicating that the accuracy of the odometer in pinpointing the goal deteriorates with longer flights, due to increased accumulation of odometric errors. However, when bees are trained with the feeder at the largest distance (28 units) but with a prominent landmark placed en route to the feeder, the searching distribution of the trained bees is substantially sharper (green circles, dot-dashed curve), indicating that in this situation the bees are able to reset their odometer at the landmark (or start a new odometer there), and start measuring distance afresh from that point to the goal. [Adapted from Srinivasan et al. (249), with permission from The Company of Biologists.]

may improve the robustness of goal-finding by combining and cross-checking information on landmark sequences and distances. If a landmark appears roughly at the expected distance, it is used to recommence integration of image motion and to thereby improve the accuracy of distance estimation. On the other hand, if a landmark appears much earlier than expected, or does not appear at all, the bee might resort to using the prevailing odometric signal to determine where to look for the target (265). Further investigation is needed, however, to fully understand the interplay between odometry and landmarks in navigation.

Esch and Burns (72, 74) investigated odometry in honeybees through a different experimental approach, namely, that of filming the bees' dances in the hive when they returned from an artificial feeder placed outdoors in an open meadow. They examined how these dances changed when the height of the feeder above the ground was varied systematically, by attaching the feeder to a weather balloon (Fig. 19). When the feeder was on the ground, 70 m away from the hive, the bees correctly indicated a distance of 70 m. However, when the altitude of the feeder was increased, the bees did something quite unexpected. Instead of signaling a larger distance, as one

might expect, since they were now flying a longer route to the feeder, and expending more energy to get to it, they signaled a shorter distance. When the feeder was 90 m above the ground, and at a horizontal distance of 70 m from the hive, the bees indicated a flight distance of only 25 m, when the shortest distance to the feeder in this situation was in fact 114 m (dashed line, Fig. 19). From this surprising finding, Esch and Burns (74) inferred that distance flown is gauged in terms of the motion of the image of the ground. The higher the bee flies, the slower the ground beneath her appears to move. This conclusion is consistent with the results of the tunnel experiments. Evidently, then, visual odometry is used not only in short-range navigation, as in the tunnel experiments, but also in situations that typify natural, outdoor foraging.

The above findings may partly explain why the early studies erroneously concluded that the honeybee's odometer uses energy consumption as the primary cue. Burdening a bee with a steel ball would tend to make her fly closer to the ground, thereby increasing the image motion that she experiences from the ground and causing her to report a larger distance in her dance (72). Similarly, when a bee flies in a headwind she may fly closer to the ground, either to maintain the same image velocity as she would in still air, or simply to "duck the breeze." This would, again, increase the image motion and, therefore, the odometric reading. While these explanations are presently only speculations that need to be checked, they illustrate, rather disturbingly, how easily one can be led to false conclusions about mechanisms.

We have seen above that the balloon experiment caused bees to underestimate the distance they had flown, because they experienced an optic flow that was weaker than what they would normally experience during normal, level flight. What happens when bees encounter the opposite situation, namely, one in which image motion cues are artificially exaggerated? Srinivasan et al. (248) explored this question by training bees to fly directly from their hive into a short, narrow tunnel that was placed very close to the hive entrance (Fig. 20). The tunnel was 6 m long, 11 cm wide, and 20 cm tall, and its entrance was 3 m from the hive. The walls and floor of the tunnel were lined with transversely oriented black-and-white stripes (or, in some instances, a random texture). When the bees were trained to a feeder placed at the tunnel entrance, they performed a round dance when they returned home (Fig. 20, top panel). This is what one would expect, given that the feeder was only 3 m away from the tunnel entrance. The feeder was then moved step by step along the tunnel to its far end, which was 6 m from the tunnel entrance (Fig. 20, middle panel). Surprisingly, when the bees returned to the hive after foraging at this location, they performed a waggle dance signaling that they had flown a distance of 200 m! Evidently, the bees were massively overestimating the distance they had

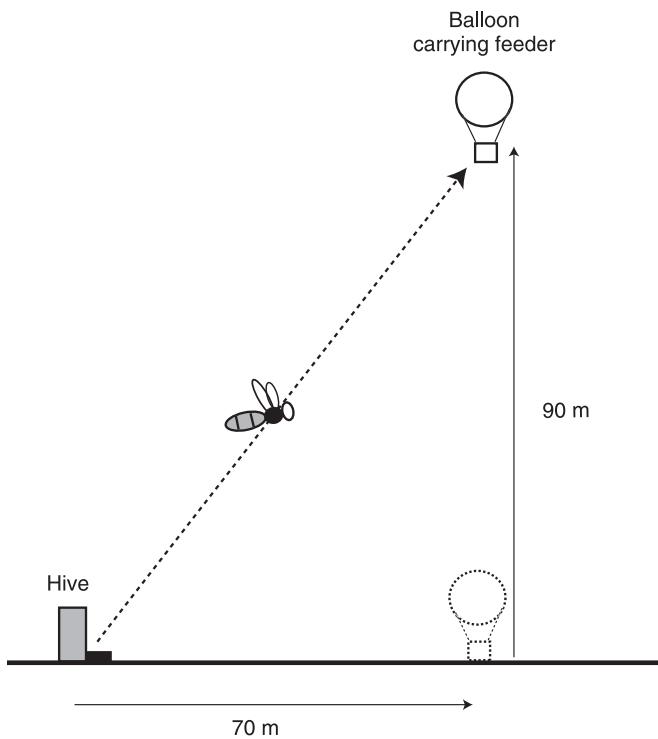


FIG. 19. Experiment in which bees were trained to find a food reward in a balloon positioned 90 m above the ground, at a horizontal distance of 70 m from their hive. The returning bees signaled a distance of 25 m in their waggle dances, a distance far lower than the shortest distance to the balloon (114 m, dashed line). This experiment indicates that the bees were not measuring the physical distance that they had flown. More likely, they were gauging distance flown in terms of the movement of the image of the ground in their eyes.

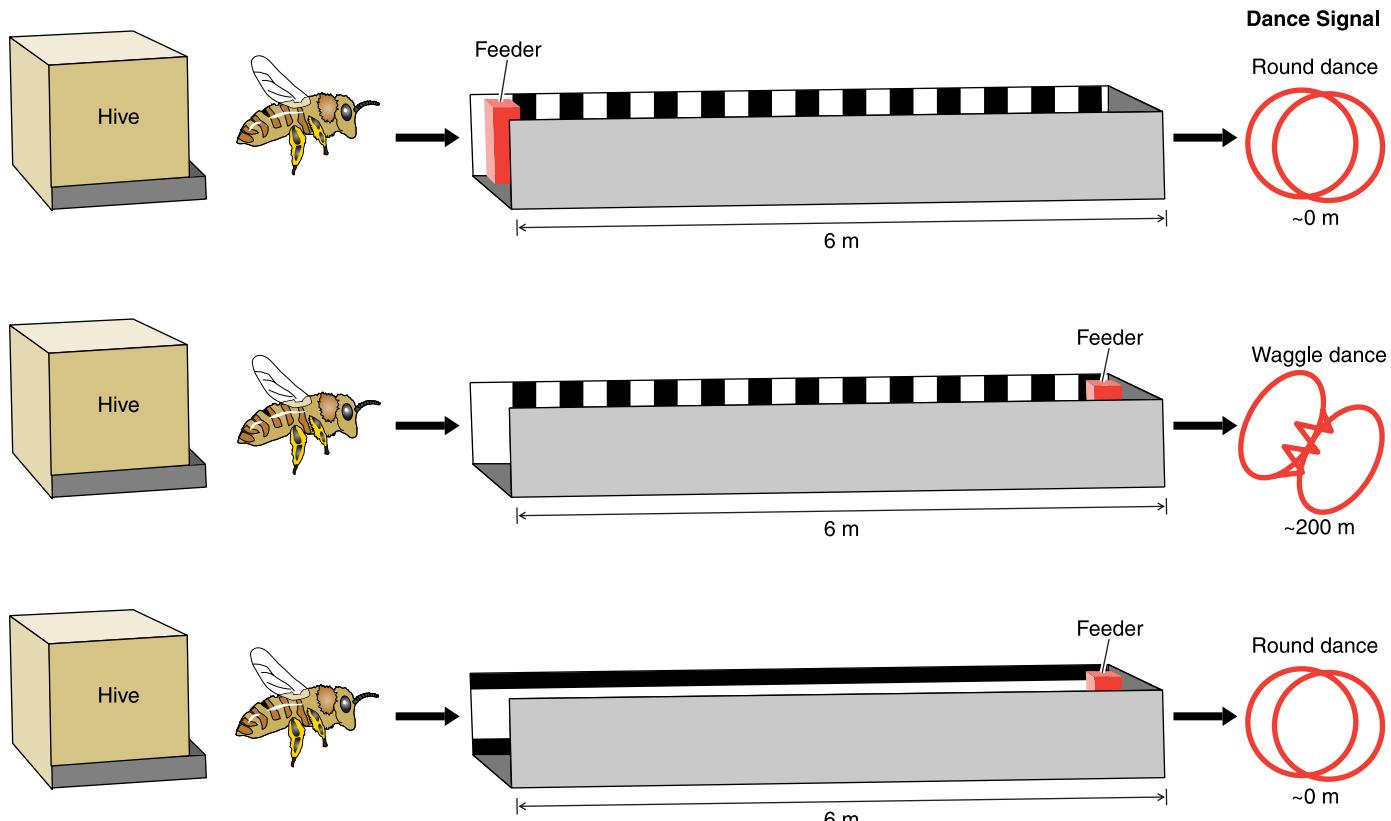


FIG. 20. A test of the hypothesis that bees measure distance flown to a food source in terms of the optic flow experienced en route. Bees were trained to forage in a narrow tunnel, 6 m long, placed very close to the hive. When trained to a feeder placed at the tunnel entrance, they performed a round dance (*top panel*). However, when the feeder was moved to the end of the tunnel, the bees performed a waggle dance, indicating a distance of 200 m, hugely overestimating the distance that they had actually flown (*middle panel*). When the feeder was kept at the same position but the transverse stripes lining the tunnel were replaced by axially oriented stripes (which induced little or no optic flow), the bees performed a round dance, signaling that they had now flown a negligible distance (*bottom panel*). This experiment (248) confirms the hypothesis that the honeybee's odometer is driven by optic flow.

flown in the tunnel because the proximity of the walls and floor of the tunnel greatly magnified the optic flow that they experienced, compared with what would normally occur when foraging outdoors. On the other hand, when the walls and floor were decorated with axially oriented stripes, bees trained to a feeder at the same position, 6 m into the tunnel, performed a round dance (Fig. 20, bottom panel), indicating that they had flown a very small distance, despite the fact that they had flown the same physical distance as when the tunnel carried vertical stripes. Evidently, in the experiment with the axial stripes, the bees experienced little or no optic flow, and therefore indicated in their dances that they had flown a very small distance. These experiments again drive home the point that image motion is the dominant cue that bees use to gauge how far they have travelled.

Experiments in which the tunnel was lined with periodic black-and-white stripes, and the spatial frequency or the contrast of the patterns was varied, revealed that the distance flown, as indicated by the duration of the dance, was largely invariant to these parameters (218). The indicated distance was also largely invariant to

changes in the texture of the patterns, for example, checkeredboards, vertical black-and-white stripes, or vertical sinusoidal gratings. On the other hand, the indicated distance depended strongly on the width of the tunnel, doubling the tunnel width halved the bees' estimate of how far they had flown (218).

The above findings indicate that bees measure their travel distance by obtaining a robust estimate of the total extent of image motion that their eyes have experienced on the way to the food source. Consequently, the "true" calibration of the honeybee's odometer cannot be in terms of absolute distance to a food source. Rather, it must be in terms of the image motion that the bee experiences en route. The tunnel-dance experiment provides us with a convenient means of obtaining the desired calibration, because the tunnel environment, as well as the trajectory of the bee in it, are very well defined. Taking into account the geometry of the tunnel and the bee's flight path within it, one can calculate a calibration factor for the honeybee's dance as ~ 18 degrees of image motion per millisecond of waggle duration (248). In other words, one millisecond of wag-

gle represents an 18-degree movement of the image of the environment in the eye.

Do hivemates pay attention to the “erroneous” dances made by bees returning from the tunnel, and if so, how do they respond? It turns out that the dances indeed recruit other foragers (75). Furthermore, the foragers do not fly into the tunnel in search of the advertised food: they search at the distance indicated by the dance, i.e., almost 200 m away! This finding reveals that the dance does not signal an “absolute” distance to potential recruits; rather, it specifies the amount of image motion that they should experience en route to the food. The recruits simply fly outdoors, in the appropriate direction, until they have “played out” the prescribed amount of image motion.

The above experiment also addresses another controversy that has lingered in the literature for many years in relation to the significance of the honeybee’s waggle dance. An alternative hypothesis (292) proposes that, although the dance undoubtedly bears information about the distance and direction of the food source, this information is not used by the recruits to find the food. Rather, they home in on the food source by following scent cues acquired from the nectar or pollen that she has brought back, or by following the dancer herself to the food, using visual or olfactory cues (293). According to this view, the waggle dance that is orchestrated by a bee is simply a device to gather the attention of potential recruits, to convey food samples to them, and to induce them to follow her, or the scent of the food, to the destination. While it is possible (and even likely) that the recruits use these alternative strategies to help find the destination, they cannot account for the entire phenomenon of recruitment. In the tunnel experiment described above, if the recruits were relying purely on olfactory or visual cues to lead them to the food, they should have all arrived at the feeder in the tunnel. In fact, none of the recruits arrived at this feeder; all of them searched for the food at the dummy feeders that were located outdoors, far away from the tunnel feeder. Therefore, these recruits must have indeed been interpreting the dance in the symbolic, geometric fashion that von Frisch had initially postulated. In summary, the recruits derive abstract information about the location of the food source from the dance and, where feasible, they take advantage of additional olfactory and visual cues to find the destination.

What are the advantages and disadvantages of a visually based odometer? Unlike an energy-based odometer, for example, a visually driven odometer would not be affected by wind (unless the wind causes the flight altitude to change). It would also provide a reading that is independent of the speed at which the bees flies to the destination, because the reading depends only on the total amount of image motion that is registered by the eye, and not on the speed at which the image moves. However, as

we have seen above, a visual odometer would work accurately only if the bee followed a fixed route each time it flew to its destination (or if a follower bee adhered to the same route as a dancing scout bee). This is because the total amount of image motion that is experienced during the trip would depend on the distances to the various objects that are passed en route. Indeed, the dances of bees from a given colony exhibit substantially different distance-calibration curves, when they are made to forage in different environments (75). The strong waggle dances of bees returning from a short, narrow tunnel illustrate this point even more dramatically. However, the unavoidable dependence of the dance on the environment may not be a problem in many natural situations, because bees flying repeatedly to an attractive food source tend to remain faithful to the route that they have discovered (e.g., Ref. 41). Since the dance indicates the direction of the food source as well as its distance, there is a reasonably good chance that the new recruits, which fly in the same direction as the scout that initially discovered the source, will experience the same environment, and therefore fly approximately the same distance.

There is another complication, however. Even if all bees take the same route to a food source, they may not necessarily fly at the same height. And if they derive their odometric signal from the motion of the image of the ground, the signal will vary substantially, depending on the height of flight. Indeed, when Esch and Burns (72) placed a beehive on the roof of one tall building and trained them to forage at a feeder atop another tall building, the bees indicated a shorter travel distance in their dances, than when they flew the same distance close to the ground. At present, we do not know whether, and, if so, how bees deal with this problem in a real-life situation, which is unlikely to involve a sudden transposition of the nest or the food source to a different height, but could nevertheless lead to different estimates of travel distance, depending on the height at which the bee chooses to fly to its destination. One possibility is that all bees tend to fly at a more or less constant height above the ground, thus “standardizing” the odometric measurement. Another possibility is that flight altitude is not fixed, but is measured continuously and taken into account in calculating the distance travelled. Whether either of these strategies is adopted, and if so, how the altitude is regulated or measured, remains to be explored.

Do foraging bees gauge the distance to the food source on the way to it, or on the way back to the hive? This question, which has a long history (see Ref. 268), was examined more recently in an experiment in which the outbound and inbound distances were manipulated independently (249). Bees were trained to fly into a tunnel to a feeder that was placed at a certain distance (X) from the entrance. After a bee had entered the tunnel and alighted at the feeder, the tunnel was quickly extended by placing

an additional section (of length Y) at the entrance. Thus, when leaving, the bee had to fly a distance ($X + Y$) to leave the tunnel. This procedure was carried out for each bee that was trained. When a bee trained in this way was tested in a fresh tunnel that carried no reward, it searched for the reward at a distance X from the entrance, after entering the tunnel. When the same bee was tested by allowing it to feed at a reward placed at a distance X from the entrance, and then quickly adding a long tunnel section to the front of the tunnel before it departed, the departing bee searched for the exit of the tunnel at a distance X from the feeder, in the homeward direction (249). These findings indicate that, at least in this kind of experiment, honeybees register only the outbound distance to the food source, and not the return distance. However, similar experiments conducted with stingless bees (*Melipona seminigra*) reveal the opposite, namely, that the learned distance is that corresponding to the return flight (109). It is unclear whether this discrepancy is due to species differences, or other, as yet unknown factors. The results with the honeybees are in agreement with most of the earlier field studies in which honeybees were trained to forage at distant feeders under various environmental conditions, and their dances were recorded. For example, bees exhibited longer waggles in their dances when they flew uphill (or upwind) to a feeder, rather than downhill (or downwind) to it (102, 103, 268). These findings suggest that distance is inferred on the way to the food source rather than on the way back, regardless of the mechanisms that might be involved in estimating the distance (see Ref. 249 for a detailed discussion). The results of these experiments are consistent with the hypothesis that bees gauge distance primarily on the outbound flight. Otto (179) trained bees outdoors to fly one distance to a feeder on their outbound flight, and a different distance in the return flight by quickly moving the feeder, with the feeding bees, to a different location before allowing them to return home. He found that the bees signaled in their waggle dances a distance that was intermediate in value between the outbound and the return distances, suggesting that they were using an average of the two distances. Further investigation is required to understand why Otto's findings are at variance with most of the others.

When a scout bee first discovers a new food source, its initial outbound trajectory is likely to be tortuous, because it would not have known the location of the food. However, the return flight is likely to be closer to the proverbial "bee line," if the bee's path integration system has functioned properly (see below). From this standpoint, it would be more sensible for the scout bee to signal the direct, return distance to the recruits in her dance, rather than the tortuous distance measured during the outbound flight. Furthermore, since the recruited bees are meant to follow the direct route to the feeder, it would

make sense to convey the distance as inferred by the optic flow signals that are experienced along the direct route. On the other hand, it should be noted that bees rarely dance upon their first return from a newly discovered food source. Typically, they begin to advertise the source only after they have visited it at least four or five times (258, 268). Presumably, this delay ensures that 1) the food supply is steady and reliable and 2) the direct route to the food source has been learned accurately, and flown repeatedly. Once this has occurred, it should not matter whether the distance is reckoned from the outbound or the inbound route, because the two routes coincide. Nevertheless, two further considerations favor the use of the outbound route. First, the series of images captured by the eyes during the outbound flight should be exactly the same as that captured on the return flight, only reversed in sequence. However, this will be strictly true only if the eyes capture a fully panoramic snapshot of the scene at each step along the route. If, on the other hand, flight distance is reckoned primarily from the flow experienced by the frontal and lateral fields of view (and not the rear field), then the outbound view from any point along the journey will, in general, be different from the homeward view at the same point. This is likely to be the case, because of the blind zone in the rear of the bee's visual field (see above). Hence, the sequence of images experienced during the return flight will not be simply the reverse of the sequence experienced in the forward flight. Consequently, there is no guarantee that the integrated readings of optic flow will be the same in the two directions, unless the landscape and the illumination satisfy rather stringent symmetry requirements. Given this, it would be preferable to use visual information derived from the outbound flight to compute and signal the flight distance to a potential recruit, whose first journey will obviously be along the outbound route. Second, a bee will most likely fly with an empty crop to the food source, and return fully laden with her weight nearly doubled. If she uses energy consumption even only as a partial cue to obtain an estimate of the distance flown, this estimate will be considerably lower on the way to the food source, than on the way back (268). Even if the distance estimate is based solely on optic flow information and not on energy consumption at all, it is likely that a fully laden bee returning home will fly closer to the ground and therefore experience a greater optic flow from it, than a lighter individual that flies from the hive to a food source (72). Since recruits leave the hive with a nearly empty crop, it would make sense for a dancing bee to signal the distance as estimated from its outbound journey, so as to match the conditions that would be experienced by the new recruit.

D. Path Integration

So far, we have surveyed the means by which bees determine 1) the direction of their flight to a food source and 2) the distance they have flown to get to the food source. What remains to be done is to establish how the information on direction and distance are combined to determine the position of the food source in relation to the hive. If the bee flies a straight line to the food source (as shown in Fig. 21A), the distance flown is simply the odometric signal that is obtained by integrating the optic flow measured over the entire flight, and the direction to the food source is that signaled by the bee's compass neurons (see above). On the other hand, if the bee flies a tortuous route to the food source (as in Fig. 21B), determining the position of the food source in relation to the hive becomes a more complex task. Nevertheless, there is evidence that bees are able to perform this computation. When a bee returns home after visiting a food source located behind a large hill or other intervening obstacle which forces a detour, she signals the short-cut (or "bee-line") direction in her dance (268). The desert ant *Cataglyphis bicolor* also possesses this capacity. At the end of a tortuous, winding forage in the Sahara desert, it runs in a straight line directly back to its nest when it has found food (see Ref. 280, Fig. 3.19).

In each case, the animal appears to have performed what is known as "path integration"; it has kept a running record of its translatory and rotatory movements and turns over the entire outbound journey so as to know exactly how far away its nest is, and in which direction, so that it can return home in a straight line immediately after food is found.

How is path integration accomplished? In the case of the bee, the sky compass provides information on the bee's instantaneous heading direction, and the optic flow signal that feeds into the odometer provides a measure of the instantaneous flight speed (e.g., Refs. 37, 45, 289). If a bee makes a straight flight from the hive to a familiar food source, the distance to the food source is indicated by the odometer, and the direction of the food source is indicated by the celestial compass. These two items of information define a vector that specifies the position of the food source relative to the hive (Fig. 21A). On the other hand, if a scout bee sets out on an exploratory journey to seek a novel food source, the outbound path will most likely be a tortuous one, complicating the process of path integration. In this case the curved trajectory of the bee can be approximated by a sequence of short, straight, translatory motions, as illustrated by the vectors in Figure 21B. The current position of the bee with respect to the

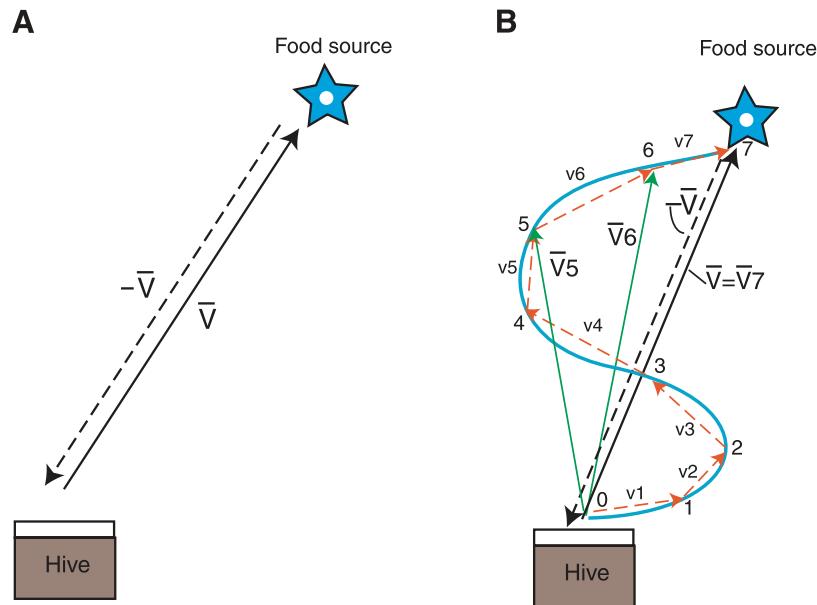


FIG. 21. Illustration of path integration in navigation. *A*: if a bee makes a straight flight from the hive to a familiar food source, the distance to the food source (as indicated by the odometer) and the direction of the food source (as indicated by the celestial compass) determine the goal vector \bar{V} , which defines the position of the food source relative to the hive. The homing vector ($-\bar{V}$) is simply the negative of the goal vector \bar{V} . *B*: if a bee makes a tortuous, searching flight to ultimately find a novel food source (blue trajectory), the goal vector \bar{V} is obtained by performing a vector integration of the curved path to the goal. If we consider this path to be composed of a series of short linear segments, the goal vector is given by $\bar{V} = \bar{v}_1 + \bar{v}_2 + \dots + \bar{v}_7$, where \bar{v}_1, \bar{v}_2 , etc. are the elementary vectors representing the individual linear segments. These elementary vectors are measured by recording the direction of each segment (as registered by the celestial compass) and the incremental distance traveled along it (as reported by the odometer). At any point *i* along the trajectory, the vector v_i defining the bee's current position relative to the hive is updated by adding the vector v_{i-1} , defining the bee's previous location, to the vector v_i describing the incremental change in the bee's position in moving from location *i*-1 to location *i*. For example, $\bar{V}_6 = \bar{V}_5 + \bar{v}_6$ (see Ref. 171).

hive is then given by the vector that represents the sum of the individual vectors.

To perform path integration, one does not need to obtain an absolute directional heading from an external frame of reference, such as the celestial compass. In principle, one can monitor the turn rate continuously as an angular velocity, through visual or proprioceptive signals, and integrate the angular velocity signal to obtain an estimate of the heading direction at all points along the journey. However, such a strategy is very susceptible to the errors in the measurement of turn rate and translation rate, which would inevitably accumulate as the length of the journey increases. Recent theoretical analysis has shown that this style of path integration will lead to unacceptably large errors, except when the travel distances are very small (30, 31). In fact, it is surprisingly difficult to move in a straight line without the aid of an externally based directional reference (223). It is very likely, then, that most navigating animals use an externally based directional reference, whenever possible, to carry out path integration. Indeed, mole rats performing path integration while traversing underground tunnels rely purely on vestibular information when travelling short distances, but include information on absolute heading (based on a magnetic compass) when travelling longer routes (122). There is clear evidence that desert ants perform path integration (280). If a desert ant is displaced to a new, unfamiliar location immediately after it has found food, it will run a homing course parallel to the original direction, and when it has travelled a distance that approaches the length of the expected homing vector it will begin to look for the (missing) nest in a stereotyped searching pattern (290). This demonstrates that the ant's path integration system has evaluated the distance as well as the direction of home, in rough accordance with the scheme illustrated in Figure 21B, or a computationally simpler approximation thereof (171).

Bees, too, appear to perform path integration, although the analogous experiments are more difficult to perform because they fly long distances in three dimensions, making it difficult to track them manually. In a pioneering early study, Bisetzky (15) observed the dances of bees after they returned from walking short distances along various straight and curved tunnels to reach a food reward. The distances and directions indicated by these waggle dances showed some indication of an ability to integrate paths, although not all of the results were consistent with this hypothesis. Recent advances in harmonic radar tracking technology (e.g., Refs. 24, 189) are making it feasible to begin to investigate path integration in flying insects. A harmonic-radar study in which bees were displaced from a feeding site and released at another location indicated that they, too, showed a homing behavior similar to the displaced desert ants (189), thus demonstrating an ability to integrate paths.

In the meantime, the bulk of our knowledge about path integration in flying honey bees has come from observing the waggle dance, which provides an excellent readout of the bee's path integration system; it opens a window into the bee's mind to reveal how far the bee thinks she has travelled, and in which direction. We have seen that dancing bees always signal the bee-line direction to a food source even if they have to circumvent a large obstacle to reach it, as explained above. Interestingly, however, the distance that these bees signal in their dances is not the length of the resultant (short cut) vector, but the total length of the circuitous path that they are forced to take as a result of the detour, a much larger distance. Thus, when bees are trained to fly around a hill to find a feeder on the other side, by moving the feeder step by step around the perimeter of the hill, thus making a large detour on the way to the food, they signal in their waggle dances the vector direction of the food source from the nest, but the perimeter length of the circuitous journey, rather than the vector distance (268). However, the bees that are recruited by the dance never take the detour; they heed the dancer's instructions and take the short cut over the hill, rather than fly around it (91, 268).

When bees are forced to make detours, why do they signal the total path length to the target rather than the direct vector distance, given that the recruits take the short cut? One reason may be that even the short-cut route over the hill is likely to be longer than the direct distance between the hive and the nest in the horizontal plane, because the short-cut actually involves flying up and down the hill. In one such detour experiment conducted by von Frisch and Lindauer in 1950, the route around the hill was 133 m, the length of the short-cut vector in the horizontal plane was 80 m, and the length of the actual flight along the short-cut route that the recruits took (up and down the hill) was 150 m (268).

Signaling of the perimeter distance in dances is also observed when bees fly journeys in the vertical plane. In one investigation, bees were trained to fly through an L-shaped tunnel that required them to fly initially through a vertical section (during which their eyes experienced vertically directed optic flow) and then through a horizontal section (during which the eyes experienced horizontally directed optic flow). The distance that the bees then signaled in their waggle dances corresponded to the optic flow that was experienced over the total distance flown in the tunnel, rather than the distance corresponding to the hypotenuse (52).

E. More Than One Path Integrator?

It therefore appears that the direction of the food source is computed and signaled by a vector-based system of path integration, while the distance to the food

source is computed and signaled by a scalar-based system of path integration. This suggests that bees may carry more than one form of path integrator. Further evidence in support of this notion comes from recent experiments by Dacke and Srinivasan (53), who manipulated the amount of celestial compass information available to bees during a foraging flight and analyzed the encoding of spatial information in the waggle dance as well as in the navigation of the trained bees. They found that the waggle dance encodes information about the total distance flown to the food source, even when celestial compass cues are available only for a part of the journey. This was in contrast to how a bee gauged distance flown when it navigated back to a food source that it already knew. When bees were trained to find a feeder placed at a fixed distance in a tunnel in which celestial cues were partially occluded and then tested in a tunnel that was fully open to the sky, they searched for the feeder at a distance that corresponded closely to the distance that was flown under the open sky during the training. Thus, when navigating back to a known food source, information about distance travelled was disregarded when there was no concurrent input from the celestial compass. In other words, when an individual bee flew back to a known food source, its path integrator was "gated" by signals from the sky compass. This is very similar to the path integration mechanism that controls homing behavior in desert ants (191, 222).

Additional data in support of the existence of two (or more) path integrators comes from the reward-searching experiments in the tunnel, as described above. When a bee is trained to fly past a landmark to visit a food source, it pinpoints the location of the food by measuring and using the distance from the landmark to the food, as described above. But when the bee returns to the hive, she signals the total distance to the food source in her dance, not just the final leg.

All of the above evidence suggests that the honeybee may possess two different path integrators: 1) a "community" path integrator that the bee uses to signal the correct direction and the total (possibly circuitous) distance of a food source to its nestmates through the dance, and 2) a "personal" path integrator that the bee uses for its own navigation, which delivers the correct direction and the vector distance to the food source, thus enabling it to return repeatedly and accurately to a known source (53). It is possible that the personal path integrator is of a flexible and adaptive nature, tailored to the route that an individual bee learns.

To summarize the results of this section, one can think of the odometer as the "lowest level" component of the honeybee's navigational apparatus. It is a scalar distance-measuring device that simply registers the incremental distances that are travelled along the route, regardless of the heading direction. The output of this basic

system could be used concurrently by several path integrators, to represent the position of the food source relative to the nest in different ways. One path integrator, for example, might combine instantaneous distances travelled (as indicated by the odometer) with instantaneous heading direction (as indicated by the celestial compass) and accumulate the resulting elementary vectors to give a vector that represents the true distance and the true direction of the food source relative to the hive. This path integrator would deliver the correct direction of the food source relative to the hive, and the distance "as the crow flies." Another path integrator might combine the instantaneous travel distances and heading directions (as described above) to obtain a vector that gives the true direction of the food source, but it may report the total distance travelled by summing the incremental distances as scalar quantities, without regard to the direction of travel. This path integrator would deliver the correct direction of the food source relative to the nest, but indicate the perimeter length of the route that is actually taken to get to the food source, as when a bee circumnavigates a mountain.

More work is required to test the hypothesis of two (or more) distinct path integration systems, and, if they indeed exist, to better understand their individual characteristics and roles.

X. ROBOTICS

Over the past decade there has been considerable interest in implementing some of the insights gained from the study of vision and navigation in honeybees and other insects to the guidance of terrestrial and aerial vehicles. The reasons for doing this are twofold. First, robotic platforms offer a means of testing rigorously our concepts of visual guidance and navigation in insects, under real-world conditions. Second, there is the possibility that some of these biologically inspired principles will provide novel solutions to difficult and persistent problems in the design of navigation systems for autonomous vehicles.

A. Guidance of Robots Along Corridors

The "centering" response in bees offers a simple strategy for visually guiding a robot along a corridor. By balancing the speeds of the images of the two side walls, one can ensure that the robot progresses along the middle of the corridor without colliding with the walls. Furthermore, the speed of the robot can be adjusted to a safe value by holding constant the average velocity of the images of the two walls.

Following the publication of the studies on the centering response of the bee, several laboratories have built land-based robots that navigate through corridors by us-

ing the principles of balancing lateral image motion to steer through the middle of the corridor, and maintaining a constant image velocity to regulate the speed of locomotion (1, 25, 50, 61, 112, 217, 279). Computationally, this approach is more amenable to real-time implementation than methods that use stereovision to calculate the distances to the walls. The design and performance of one of these robots (279) is shown in Figure 22. The robot is approximately the size of a small skateboard, with a single video camera mounted facing upwards (Fig. 22A). This camera captures views of the side walls (one of each wall) through a mirror assembly positioned above the lens. Video information from the camera is transmitted to a computer, where the image velocities of the two walls, induced by the motion of the robot, are measured. The algorithms for measuring image motion are described in References 230, 231, 237. The computer then issues appropriate steering commands to the robot to ensure that it stays close to the midline of the tunnel. The tunnel-following performance of the robot is illustrated by the examples shown in Figure 22, B–E. In all cases, the robot follows the axis of the corridor reliably. The presence of an obstacle next to one of the walls causes the robot to go through the middle of the gap remaining between the

obstacle and the other wall. Additional control algorithms have been developed for controlling the speed of the robot. Speed control is achieved by holding constant the sum of the image speeds from the two walls (279), thereby ensuring that the robot automatically slows down to a safe speed when the corridor narrows. Visual odometry, using the honeybee-inspired principle of integrating optic flow, has also been implemented successfully in this robot (279) as well as in automotive vehicles (e.g., Ref. 176).

Thus the strategies used by flying bees to negotiate narrow gaps, to regulate flight speed, and to estimate travel distance appear to be feasible for guiding robots through corridors. The principle of balancing lateral optic flow to steer through corridors is, of course, equally applicable to the guidance of airborne vehicles through gorges, or streets lined with buildings (e.g., Refs. 92, 108) and for obstacle avoidance (e.g., Ref. 299).

B. Terrain Following Guidance for Aircraft

Flying at a constant, low height above the ground is important when there is a need to prevent detection by

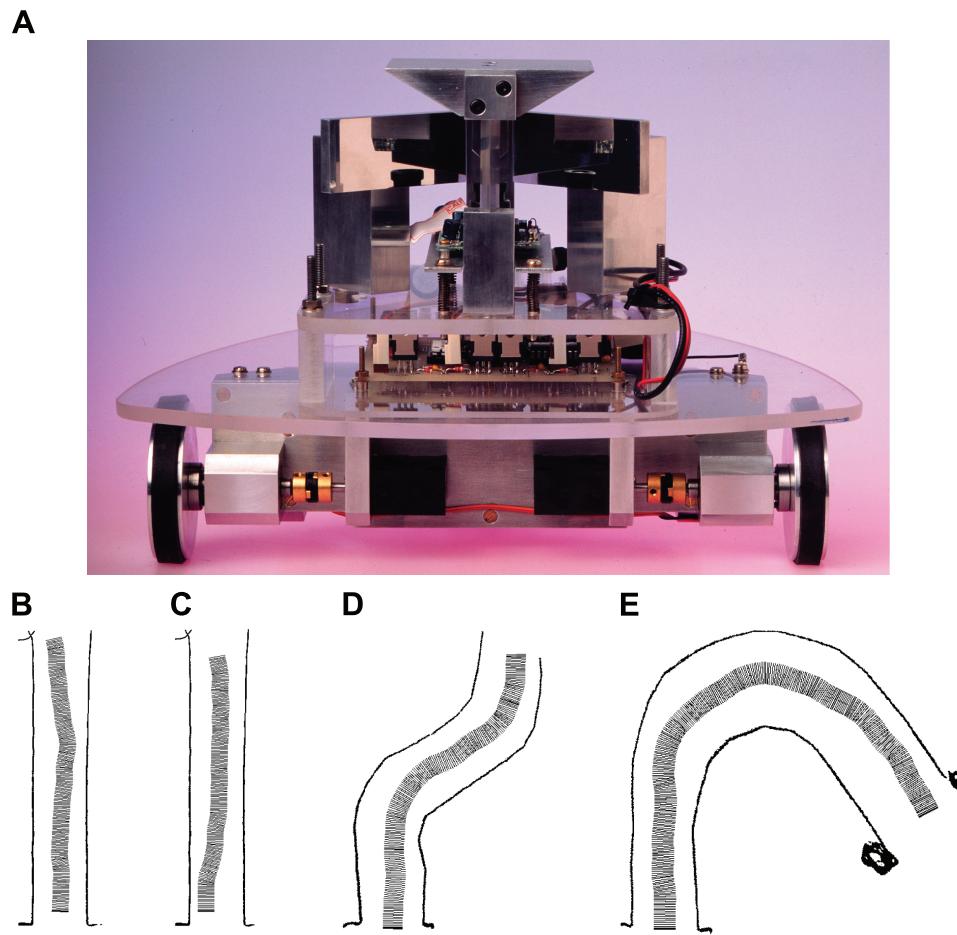


FIG. 22. A: frontal view of a corridor-following robot. B–E: performance in variously shaped corridors, of width ~80–100 cm. [Adapted from Weber et al. (279), with permission from Oxford University Press.]

enemy radar, or to carry out close-up photographic exploration of terrain. If the ground speed of the aircraft is known (for example, from measurements of airspeed, or from GPS information), then the height above the ground can be computed from the optic flow generated by the image of the ground. This strategy can be used to control the aircraft's height above the ground and to achieve terrain following. This approach is attractive because it only requires the presence of a small, inexpensive, low-resolution video camera on board. It is thus cheaper and requires a smaller payload compared with other strategies for height measurement such as radar or ultrasound. Terrain following has been, and continues to be, implemented and tested in fixed-wing as well as rotary-wing aircraft models (e.g., Refs. 10, 252). Figure 23 shows an example of a helicopter (Hirobo Eagle X, 1.5 m fuselage length, 1.5 m rotor blade diameter) equipped with a downward-looking camera that is used to compute the optic flow generated by the ground. The craft carries a suite of other sensors (gyros, accelerometers) to augment stability. Video and mechanical signals are transmitted to a ground-based control station. There this information is processed in real time (at video frame rates) to generate command signals that are transmitted back to the helicopter via the radio link that would normally be used to pilot the craft if it were being flown manually. Thus the ground

station forms a part of the autonomous control loop. A view of a flight test at 50 km/h is shown in Figure 24A. Here the aircraft is followed by a truck that carries the ground-based control station and moves at the same speed, so as to maintain radio contact. The aircraft is taken off manually (piloted under radio control), after which control of height is passed on to the terrain-following controller. Ground speed is measured from an on-board GPS receiver. Figure 24B shows a view of the ground, as captured by the downward-looking camera. Figure 24C shows height computed from ground speed and optic flow data. Optic flow is computed by using an "Image Interpolation" algorithm, details of which are given in Reference 230. In this particular example, the loop was not closed. Closed-loop terrain following has been achieved in fixed-wing as well as rotary-wing machines. However, performance in terrain following has not yet been evaluated accurately, owing to the difficulty of obtaining the "ground truth" (the actual height of the aircraft above the ground). Other studies investigating the use of optic flow to regulate height above ground are described in References 10, 79, 169, 170, 175, 196, 221, 226, 245.

C. Control of Aircraft Landing

The feasibility of the honeybee's landing strategy has been tested by implementation in a computer-controlled

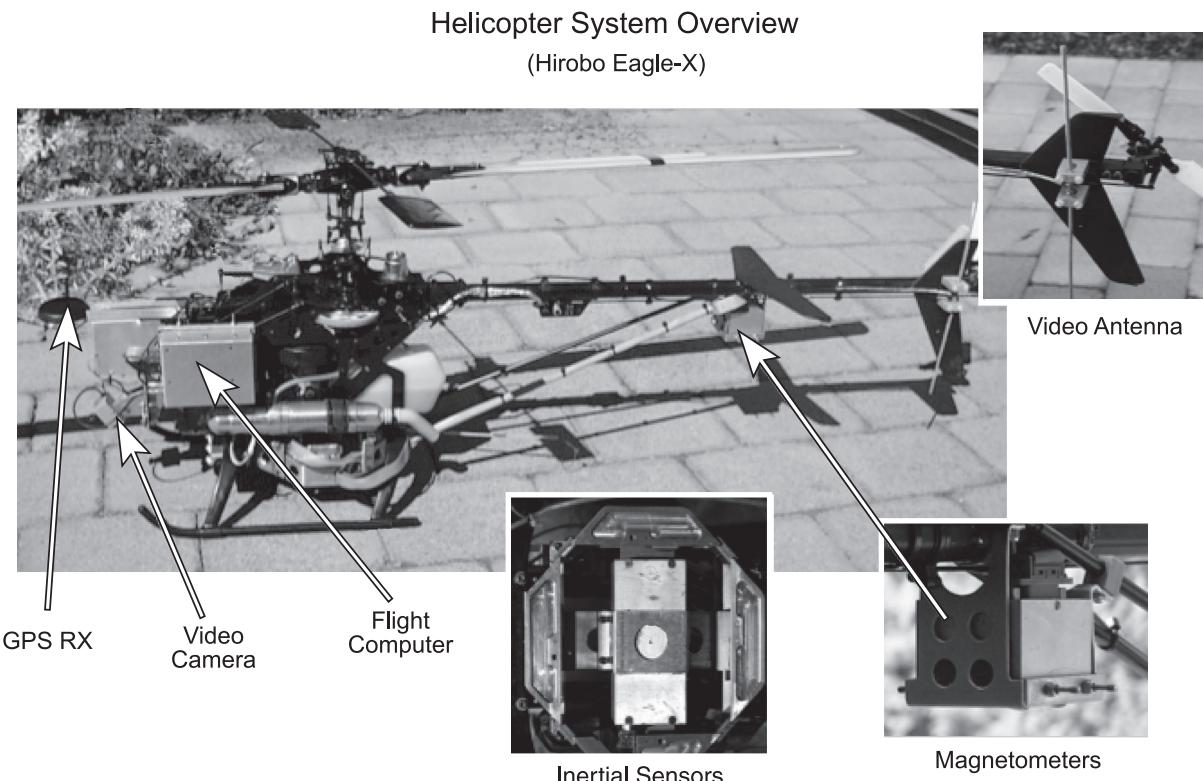


FIG. 23. View of one of the model helicopters used to test terrain following and landing algorithms. The helicopter, a radio-controlled Hirobo Eagle X, was augmented for semi-autonomous flight by addition of the indicated items. [Adapted from Srinivasan et al. (252), with permission from Professional Engineering Publishing.]

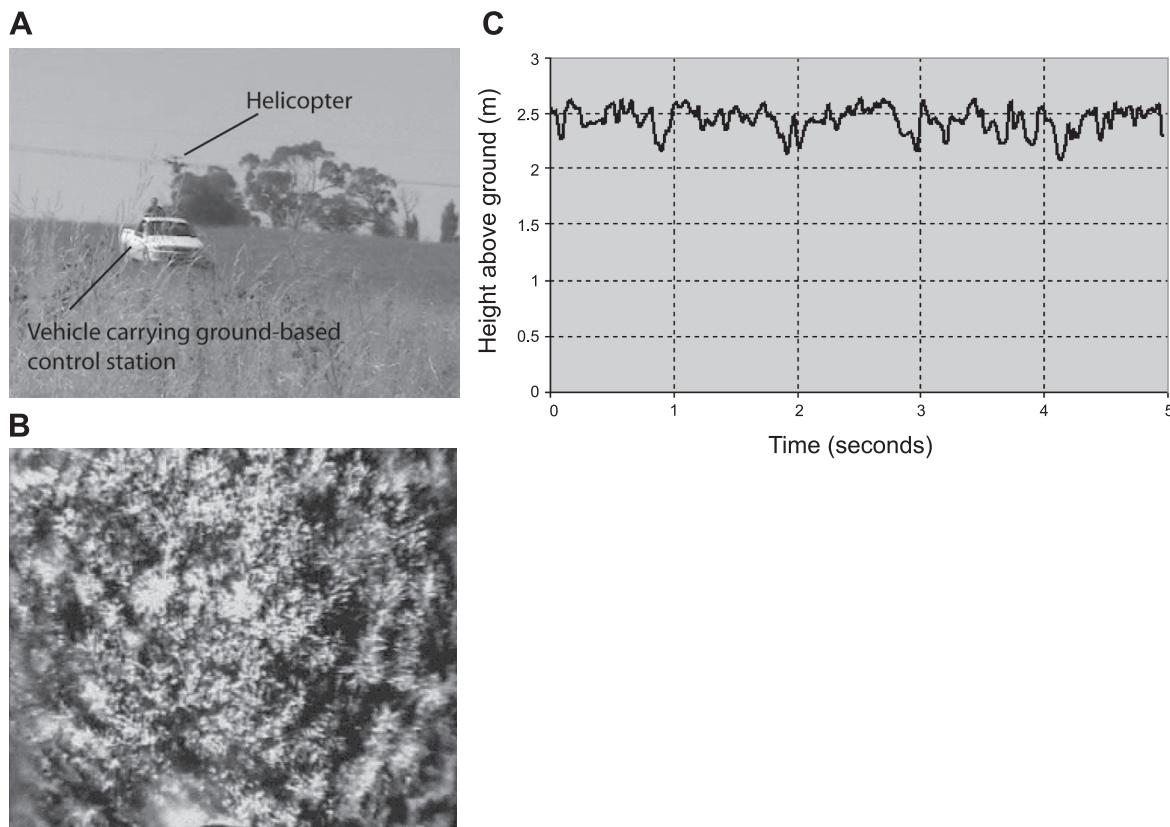


FIG. 24. A: terrain-following test of model helicopter at 50 km/h. B: image of ground as seen by a downward-looking camera. C: helicopter height, computed from ground speed and optic flow data. [Adapted from Srinivasan et al. (252), with permission from Professional Engineering Publishing.]

gantry robot carrying a visual system (251). Vision was provided by a downward-looking video camera mounted on the gantry head, which could be translated in three dimensions (x , y , and z). For the purpose of implementing the landing strategy, translatory motion of the camera was restricted to the forward (x) and downward ($-z$) directions. There was no lateral (y) motion and no rotation about the z -axis. The system was 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. The floor, defined to be the landing surface, was covered with a random visual texture. The velocity of image motion was measured by using an Image Interpolation algorithm (230).

Landing was controlled by maintaining a constant descent angle, and adjusting the forward (x) component of camera velocity at each time step to keep the velocity of the image of the ground in the camera constant at the “set-point” value of 300 degrees/s (see above). It turned out that the resulting motion of the camera replicated the motion of a landing bee very well: the altitude decayed exponentially as a function of time, as did the forward and descent speeds (250). Comparable results were obtained when the floor was covered with other visual textures such as a newspaper, or with twigs, bark, and leaves to

simulate a natural outdoor environment. These results demonstrate the validity and feasibility of the honeybee’s landing strategy.

Autonomous landing approaches have been achieved on a fixed wing aircraft (29). As in terrain following, a downward-looking camera is used to acquire ground images and compute optic flow. It is difficult to implement the honeybee landing strategy literally on a fixed-wing aircraft, because the strategy requires the ground speed to approach arbitrarily small values (below stall speed) as the aircraft nears the ground. Consequently, a modified landing strategy has been tested, in which the throttle is cut and the elevator setting is adjusted in closed loop to hold the magnitude of the optic flow from the ground constant as the altitude drops. The result is that altitude and forward speed decrease approximately linearly with time as the ground is approached. A similar approach has been used in Reference 12.

D. Robot Navigation Using a Polarization Compass

The efficacy of using the polarized light pattern in the sky for navigation has been tested by incorporating an insect-inspired polarization compass into autonomous ro-

bots (140, 141). Figure 25 shows views of "Sahabot," a robot steered by a polarization compass. Like the insects (Figs. 15 and 16), this robot used three sets of polarization-opponent channels, with preferred directions separated by 120 degrees. Each polarized-light sensor consisted of a polarizing filter placed over a photodetector, and each polarization-opponent channel was created by combining antagonistically the signals from two sensors with orthogonally oriented polarizers. The robot also incorporated a ring of eight light-intensity sensors looking all round the robot at the sky just above the horizon. The pattern of intensity recorded by these light sensors was used to discriminate the solar direction from the anti-solar direction, and thus eliminate the 180-degree ambiguity that is inherent in the polarization compass (see above). Wheel encoders were used to measure and control the translation and rotation of the robot. Lambrinos et al. (140) used this robot to test the efficacy of the "scanning" method as well as the "simultaneous" method of establishing a desired compass heading, as described above, to navigate a course to a prescribed destination and back. In the scanning method, the robot only used the signal from one polarization-opponent channel. The robot began by turning in a tight circle near the starting point, recording the time-varying signals from this polarization-opponent channel and from the intensity-sensing ring as it scanned the whole spectrum of orientations ranging from 0 to 360 degrees. This scan was used to establish the direction of the solar meridian, and to calibrate the absolute heading direction in relation to the robot's orientation, as determined by its wheel encoders. Information from the wheel encoders was then used to set and maintain the prescribed heading direction towards the goal. Navigation toward the goal was "blind," in the sense that no visual signals were used; steering was accomplished purely through proprioceptive information provided by

the wheel encoders. In the middle of the journey (as inferred from the wheel-based odometry), the robot performed another scan to recalibrate the direction of the solar meridian and to reset its course direction, correcting for any drifts in heading direction that might have occurred on the way. When the goal was reached (again, as inferred from the wheel-based odometry), the robot performed a second calibration scan before heading back in the homeward direction. When it was halfway home, the robot did a final scan to readjust its homeward course and complete the journey. Two examples of the trajectories followed by the robot in these tests are shown in Figure 26.

In the "simultaneous" method, the robot again began by performing a scan, but this time the signals from all three of the polarization channels were recorded, along with the signals from the light-intensity ring and the wheel encoders. This calibration allowed any desired heading direction to be set (and maintained) by achieving (and maintaining) the appropriate ratios of signals in the three polarization-opponent channels. In this case, the robot was not blind during the journey; the heading direction was maintained and constantly corrected by monitoring the signals from the three polarization-opponent channels. A single scan was performed at the start of the journey, and there were no further scans. When the robot reached its goal (as signaled by the wheel-based odometry), it made a U-turn and headed back home by setting a course in the opposite direction, and maintaining the appropriate (new) ratios of signals in its three polarization-opponent channels. Two examples of the trajectories followed by the robot in these tests are shown in Figure 27.

The navigational performance of each method was assessed quantitatively by measuring the positional error between the starting and the finishing points of the journey. The overall error in heading direction was estimated by dividing the positional error by the total distance trav-

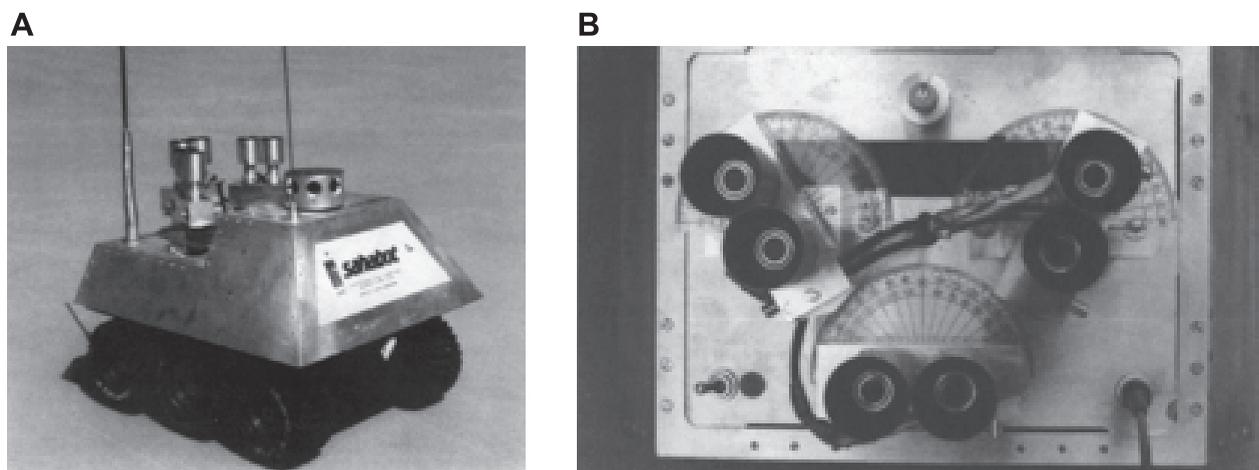


FIG. 25. *A*: view of "Sahabot," a robot steered by a polarization compass, tested in the Sahara desert. *B*: top view of sensor panel, showing three sets of polarization-opponent input channels separated by 120 degrees in preferred orientation. [From Lambrinos et al. (140), with permission from Sage Publications.]

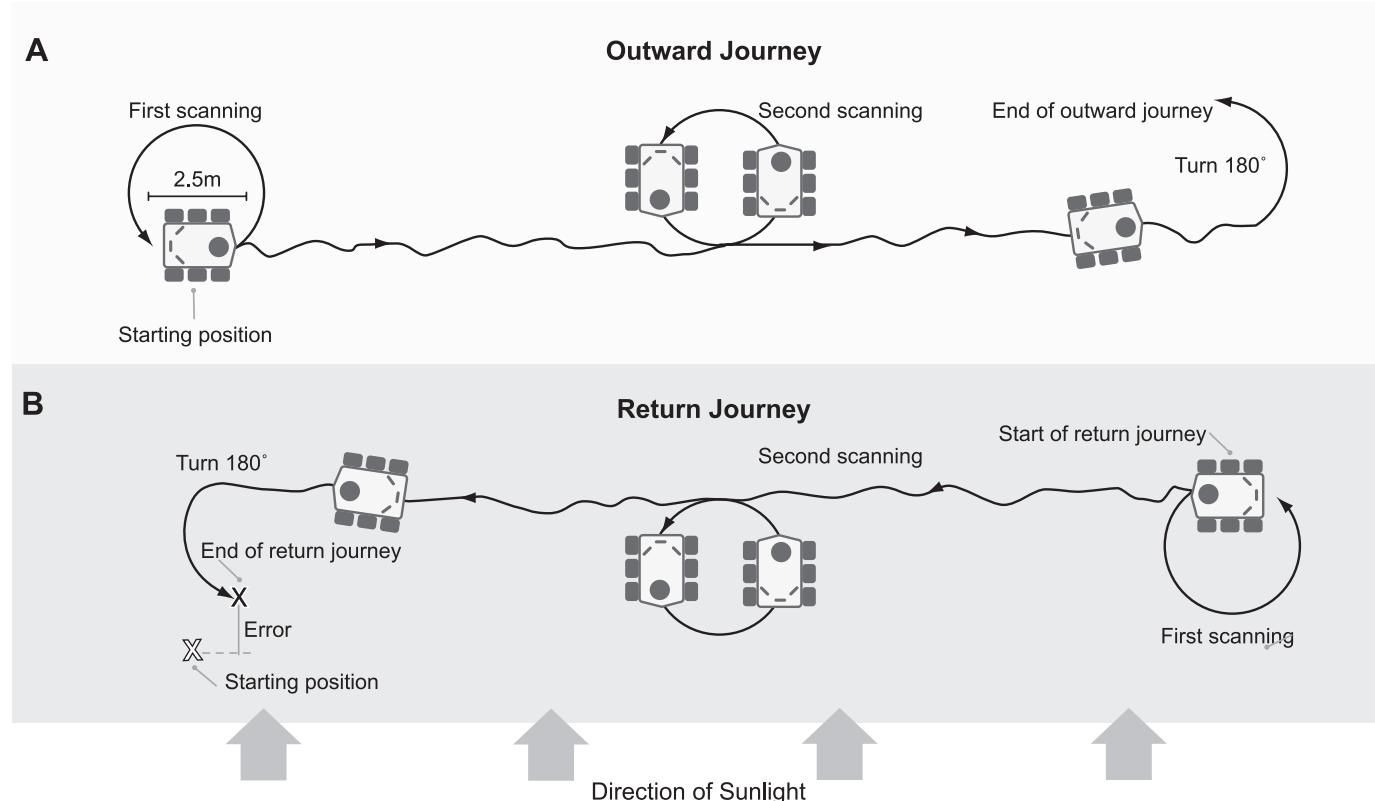


FIG. 26. Example of robot navigation using a polarization compass in the scanning mode. See the description in text. [From Lambrinos et al. (140), with permission from Sage Publications.]

elled. Both methods revealed good performance, thus validating the efficacy of a polarization-based compass for navigation (140). The simultaneous method was found to be more accurate than the scanning method. This is not surprising, given that in the scanning method the robot

was travelling blind between scans, whereas in the simultaneous method it was monitoring and correcting its heading throughout the journey (140). However, it might have been possible to improve the accuracy of the scanning method by steering the robot between scans so as to hold constant the amplitude of the signal from the single, polarization-opponent channel. An improved version of an optoelectronic polarization compass is described in Reference 141. Other investigations of the use of the polarization compass for robot navigation are described in References 205 and 262.

To summarize the results of this section, we may say that the study of visual guidance in the honeybee has so far led to new algorithms for the guidance of robots along corridors, for equipping robots with a biologically inspired celestial compass, for the control of altitude in aerial vehicles, and for guiding a safe landing.

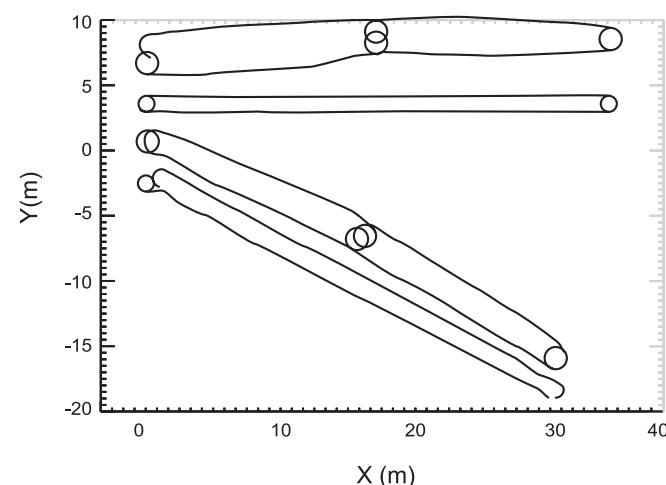


FIG. 27. Comparison of performance of robot navigation with a polarization compass using the scanning method (trajectories with central loop) and using the simultaneous method (trajectories without central loop). See the description in text. [From Lambrinos et al. (140), with permission from Sage Publications.]

XI. CONCLUSIONS, UNANSWERED QUESTIONS, AND OUTLOOK

Over the past hundred years or so, the study of honeybee behavior has revealed more and more about a creature with remarkable and unexpected capacities with regard to its ability to 1) guide and control its flight;

2) navigate to distant food sources; 3) learn and memorize colors, shapes, and scents of food sources; and 4) perform tasks that are arguably “cognitive” in many respects. This review has focused primarily on *areas 1* and *2*; another recent review (232) describes recent progress in *areas 3* and *4*.

It is now clear that the compound eyes of the honeybee are regionally specialized to perform various tasks. While the frontal and ventral fields of view appear to be specialized for the perception of color and shape, the frontal and lateral fields of view seem to be involved in the perception of image motion that is used to control flight speed, to avoid obstacles, and to estimate distance flown. The ventral field is also important in measuring the image motion that is used to guide the bee to a smooth landing on a horizontal surface. Indeed, research over the past 20 years has revealed that honeybees, and possibly all flying insects, use cues based on image motion in far more subtle ways than previously believed. While the early studies of optomotor behavior demonstrated the importance of image motion in stabilizing flight with respect to roll, pitch, and yaw, we now know that other cues derived from the pattern of image motion that is experienced during flight are used to control the speed of flight, to negotiate narrow gaps safely, to gauge journey distance, to avoid obstacles, and, indeed, to perceive the world in three dimensions.

A. The Neural Basis of the Optomotor Response

While the neurons in the visual pathways underlying the optomotor behavior are now beginning to be well characterized and moderately well understood, at least in flies, as we have described in this review, there are still major gaps. For example, we still do not know where along the movement-detecting pathway the EMD resides, or how this detector performs, at the physiological level, the multiplication-like operation that is crucial to the neuron’s ability to distinguish between movement of the image in the preferred direction and in the null direction, although models have been proposed (e.g., Refs. 235, 261).

The responses of the movement-detecting neurons that mediate the optomotor response (and the responses of the Hassenstein-Reichardt model) confound various properties of the moving stimulus, such as the speed of the image, its contrast, and its spatial frequency content. Therefore, they are not capable of encoding the velocity of the image unambiguously (188, 233, 244). However, neurons such as these, that are thought to be involved in the stabilization of flight orientation, may not need to measure the speed of motion of the image on the retina veridically. It may

suffice to determine just the direction of image motion reliably, and from this to generate a signal that is appropriate for correcting deviations from the intended flight direction or the desired flight attitude.

B. The Neural Basis of Other Movement-Sensitive Behaviors

A major unresolved puzzle concerns the neural basis of the other movement-sensitive behaviors such as obstacle avoidance, control of flight speed, and visual odometry. It appears that all of these behaviors are mediated by movement-detecting systems that measure the speed of the image rather reliably, largely independently of the spatial texture of the image, or of its contrast. As we have seen in this article, this ability to measure image speed robustly is critically important in controlling behaviors such as collision avoidance, flight speed regulation, and visual odometry. This property is very different from those of the movement-detecting neurons that are presumed to mediate the optomotor response. The responses of these neurons, which are the best-characterized interneurons in the insect visual pathway, do not appear to encode the speed of the image faithfully. Their responses depend strongly on the visual texture of the image (e.g., its spatial frequency content), as well as its contrast.

How does the visual system extract veridical information on image speed from the responses of these interneurons to control the bee’s velocity-sensitive behaviors? One possibility is that the information on image speed is represented not just in the response of a single neuron, but across an array of interneurons with different spatiotemporal frequency sensitivities, as described, for example, in Reference 244. The speed of the image can then be represented by the relative strengths of the responses across the array of interneurons, just as the wavelength of a light source is represented by the relative strengths of the responses that it elicits in an array of photoreceptors with different spectral sensitivities. Another possibility is that these interneurons, which have so far been probed mainly by using stimuli consisting of sinusoidal gratings moving at a constant velocity, exhibit velocity-sensitive properties when they are exposed to more realistic visual stimuli, such as natural scenes that move at changing velocities (113, 256). A third possibility is that image speed is computed by an entirely different set of neurons, in a parallel movement-detecting pathway that mediates the behaviors that require robust measurement of image speed. This possibility is supported by the observation that many of these latter behaviors exhibit characteristics that are rather different from those of the optomotor response. As described earlier in this article, many of the speed-sensitive behaviors are characterized by nondirectional sensitivity to motion, small-field sensi-

tivity, and sensitivity to higher temporal frequencies. Further investigation is required to determine whether the so-called "movement-detecting pathway" in insects actually consists of a number of distinct movement-sensitive pathways, tailored to different behaviors.

It is now becoming apparent that visual stimuli can evoke rather different electrophysiological responses from neurons in the insect visual pathway, depending on the behavioral state of the animal (192). These responses are also modulated by octopamine, a biogenic amine likely to be associated with arousal and flight (128, 153). Therefore, caution must be exercised when attempting to relate behavioral data to electrophysiological responses obtained from restrained, immobile animals.

C. The Neural Basis of the Honeybee's Odometer

There is a major mystery surrounding the neural basis of the honeybee's odometer. What are the neural mechanisms by which the distance signal is computed? Where, in the insect's brain, is the odometer located? At present, we are completely in the dark about these questions. As we have discussed above, the visual systems of flying insects, in particular, flies (67, 69) and bees (59), contain interneurons that respond strongly to image motion. Ibbotson (113, 114) has reported the existence of spiking visual interneurons in the bee that respond to the movement of patterns in the front-to-back direction in each eye. The firing frequencies of these neurons increase approximately linearly with pattern velocity. If the output of such a neuron is integrated over the time of flight, the result would provide an indication of how far the bee has flown, independently of the speed at which the bee flies to the destination. In other words, the total number of spikes fired by the neuron would be a representation of the distance covered. Such a mechanism, however, would require a means of counting spikes over the rather long time that is characteristic of a bee's outdoor flights, typically at least a minute. Furthermore, this information on travel distance would have to be retained at least until the bee has returned home and completed her dance, and possibly for the additional duration required to return to the food source. How the bee's nervous system accomplishes this task, if this is indeed what it does, remains a mystery.

D. The Neural Basis of Path Integration

There are gaps in our understanding of how the directional information derived from the celestial compass is represented in the nervous system, and how this information is combined with the odometric (distance) signal to compute and represent the bee's current location with respect to the hive at any point along her journey. As

discussed earlier in this article, we have some information on how the POL neurons are used to extract heading information from the polarized-light pattern in the sky, and how this heading direction is represented by the "compass" neurons. But exactly how the insect combines the moment-to-moment information on distance and direction of travel, to estimate its current position in relation to home, remains a major mystery. Quite apart from the intriguing question of how the nervous system executes the computational exercise of path integration, we also do not know how or where in the brain the location of home (or of a known food source) is represented. One possibility is that the distance and direction of known locations are represented as signals that encode the distances and directions to these locations, i.e., as vectors. Another possibility is that the honeybee's brain encodes location information in terms of the activity of an array of "place" neurons, rather like in the hippocampus of a rodent or a primate (e.g., Refs. 71, 177). As the bee progresses along her journey, activity would shift from one place cell to the next, thus providing a direct spatial representation in real time of where the bee is in relation to its home and to a food source. There is evidence for the existence of placelike neurons in the mushroom bodies of the cockroach (166, 167). Whether honeybees also possess such place neurons, and whether those neurons are used in this way, is an exciting area of future investigation.

E. The Role of Landmarks in Honeybee Navigation

It is known that bees use landmarks for navigation in a variety of different ways. For example, bees that repeatedly visit a familiar feeding site can set their course to it by using a distant landmark as a beacon, if this landmark happens to lie close to the desired bearing (e.g., 32, 33, 43, 83, 268). When a bee nears the feeding site, it pinpoints the goal with reference to prominent surrounding landmarks that it has learned during the first few visits. Indeed, during these initial visits, it appears that bees acquire panoramic "snapshots" of the environment surrounding the goal as they depart after feeding from it, by using patterns of flight that seem to be specially tailored to acquire the appropriate snapshots (145, 296). When in the vicinity of a feeding site, bees use distant landmarks to set their bearing, and nearby landmarks to help guide them to the correct location. They home in on the goal by adjusting their spatial position such that the currently viewed panoramic scene matches the previously memorized snapshot of the image acquired at the goal (26). Indeed, bees can remember several feeding sites simultaneously, and recall the landmark constellations that are appropriate to each site in a context-dependent manner (e.g., Refs. 48, 298). How landmarks

are represented at the neural level, and recalled at the appropriate places and times, remains a major unsolved mystery.

There is a rich and fascinating body of work on landmark-based navigation in bees (and ants) that is far too extensive to discuss comprehensively in this article, and which should be the topic of a separate review. We refer the reader to some of the excellent reviews that exist in the literature, for example, References 36, 44, 46, 49, 115, 280, 282, 287.

F. The Ocelli

Another enigmatic question concerns the role of the ocelli, the three light-sensitive organs that are positioned above the compound eyes. Each of these structures resembles a “simple” eye, comprising a single lens and an underlying retina (reviewed in Ref. 88). The frontally located ocellus looks in the forward direction, while the two laterally positioned ocelli capture lateral views of the environment, one looking towards the left and the other towards the right. While the function of the ocelli in the honeybee remains largely a mystery, evidence from other flying insects, such as locusts and dragonflies, suggests that the ocelli may be used to monitor the position of the horizon relative to the head, and to use this information to achieve and maintain horizontal flight by stabilizing roll and pitch (11, 295). Optoelectronic ocelli with characteristics mimicking insect ocelli have already been tested successfully in model aircraft (e.g., Refs. 28, 260).

G. Gyroscopic Organs for Flight Stabilization?

In the dipteran flies, it is well known that there are additional, mechanosensory organs that aid in the stabilization of flight attitude. While many insects possess two pairs of wings, the hind pair in dipteran insects have been modified into tiny, club-shaped structures, barely visible to the unaided eye, that oscillate up and down in synchrony with the front wings, but in antiphase. These structures, known as the halteres, are believed to function as gyroscopes which sense the coriolis forces that accompany the insect’s rotations about the yaw, pitch, and roll axes (60, 101, 172, 173). Behavioral experiments with houseflies indicate that the haltere system senses rapid rotations, thus augmenting the contribution of the visual system, which responds only to slower rotations, in stabilizing attitude. Since the haltere system does not rely on vision, it can, in principle, help stabilize attitude even during flight in the dark or in a featureless environment. Honeybees and other hymenopteran flying insects, on the other hand, possess two pairs of wings. This raises a number of questions: Do honeybees lack a gyroscopic sense, given that they do not possess halteres? Do the

hind wings provide a haltere-like function in these insects? Or are there other organs or structures that serve this purpose? In the hawkmoth, for example, it has recently been suggested that the antennae may function as gyroscopic sensors (201), in addition to playing an important role in olfactory, anemometric, and tactile perception.

H. A Magnetic Compass?

Equally intriguing is the emerging possibility that honeybees may use a magnetic sense to aid their orientation and navigation. Early experiments showed that honeybees can be trained, by reward in a dual-choice paradigm, to distinguish between different patterns of magnetic fields (127, 276–278) and that this discrimination ability can be impaired by attaching a magnet to the bee (275). Furthermore, there is evidence that bees sense the earth’s magnetic field and use it as an earth-based orientational reference, while learning the visual environment around a recently discovered food source (43). Thus, when bees discover a new food source, they always approach it from the southerly direction during the first few visits. This consistency in the direction of approach may facilitate learning of the relative locations of salient landmarks around the target as a visual “snapshot” that would allow the target to be located and homed in more easily on subsequent visits, because the direction of approach is always from the south. Collett and Baron (43) found that the bees’ approach direction could be altered by placing permanent magnets on the floor near the food source. The bees then faced southward as defined by the artificially imposed magnetic field, rather than by the geomagnetic field. This finding demonstrates that, in the absence of the magnets, the bees were orienting themselves by sensing the direction of the earth’s magnetic field. It has been found that trophocyte cells in honeybees contain granules super-paramagnetic magnetite, and that these cells receive sensory innervation (111). Furthermore, these granules change in size upon application of a magnetic field and lead to an increase in the intracellular calcium levels in the trophocyte cells (110). Thus there is evidence for the existence of a magnetic sense in the honeybee, and for a plausible neural substrate that might be involved in the transduction of the magnetic signal. The next steps will be to 1) design behavioral experiments to better understand the contexts in which bees sense and use the earth’s magnetic field, 2) investigate the physiological substrates that underlie transduction of the magnetic field, and 3) examine how the direction of the geomagnetic field is represented in the nervous system and to determine whether, and if so how, this information is combined with information from the polarization compass to mediate navigation. It should also be noted that some of the navigational feats of worker honey-

bees, which suggest the use of a time-compensated celestial compass, could, at least in principle, also be explained by the use of a magnetic compass. However, the observation that imprisoned bees time-compensate for the motion of the sun in the sky in their delayed dances (as described above) must mean that they are using the celestial compass, and not a magnetic compass, as the reference with which to signal the direction of the food source to their colleagues.

Recent research on certain insects, notably *Drosophila*, is revealing the presence of an additional magnetoreceptive mechanism, which is light dependent and based on cryptochrome photopigments (84, 85, 185, 274), but its presence in the honeybee is yet to be investigated.

I. Navigation of Drones and Queens

In this review we have only discussed the visual and navigational abilities of the female (worker) honeybee. Relatively little is known about the vision and navigation of drones, or of the queen. Part of the reason for this is that neither the drone nor the queen has a foraging lifestyle. Consequently, it is difficult to train them by providing a food reward, as can be done with a worker honeybee. The structure of the compound eyes of drones differs from that of female workers in that the eyes are much larger and meet almost seamlessly at the top of the head (88), producing a binocular zone of high visual acuity in the dorsofrontal field of view (158, 214, 215). This eye region appears to be specialized to detect small objects against a uniform background. It is believed to facilitate the detection of high-flying queens against the blue background of the sky, and the chasing and the interception of a queen in her mating flight (88). Drones tend to collect in specific spots known as "congregation sites," where they await queens (154). So far, we know relatively little about how the congregation sites are chosen, or how queens from various colonies find them (197). These questions are especially intriguing because drones and queens, unlike the worker honeybees, do not forage and therefore have less opportunity to learn their environment. The queens probably have even less navigational knowledge than the drones because they rarely leave the hive, except during a nuptial flight (or when the colony swarms). It is believed that many queens perform just a single nuptial flight in their entire life. How, then, do such navigationally inexperienced queens find the congregation sites and return home? The ability of a mated queen to return home reliably and unerringly is critical to the survival of the colony. These are fascinating puzzles that beg investigation.

J. Robotics

Finally, we have seen that the study of vision and navigation in simple natural systems, such as those found

in honeybees and other flying insects, is suggesting novel ways of tackling tenacious problems in autonomous navigation. This is because insects, with their "stripped down" nervous systems, have been forced to evolve ingenious and computationally efficient solutions to these problems. This rapidly growing field of interdisciplinary research has two major thrusts. One thrust is to build "biomimetic" machines, devices that mimic biological design in toto, or as closely as possible, to examine how the machines perform compared with the real animal, and thereby to test whether we indeed understand how the animal works. Another thrust is to use inspiration from biology, rather than mimicking biology totally, to come up with novel approaches and algorithms that will aid in the design and development of autonomous robots with a variety of applications such as surveillance, rescue, exploration, and monitoring of infrastructure. Many of these studies are revealing that the insect-inspired approach to aerial robotics leads to solutions that are lighter, less bulky, less computationally demanding and less expensive than the traditional, engineering-based approaches (78, 246, 247).

The honeybee is thus proving to be a valuable model organism in which one can study fundamental and general principles of vision, visual guidance, and navigation, as well as apply the insights gained to the development of the next generation of autonomous vehicles (78, 247).

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