

# 07

## PILOTING: THE VISUAL CONTROL OF FLIGHT<sup>1</sup>

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What a delight it is to watch insects go about their daily life on a summer day. Most obviously, a large male butterfly flutters by on regular patrol around its territory and suddenly it recognises a female of its own species. A group of hoverflies hovers in separate stations in a shady place between trees; bees move from one flower to another of the same kind; a large fly weaves from side to side as it dashes past; and along the footpath a dragonfly hunts for mosquitoes. They all appear to see quite well and, after centuries of discussion about insects' perception of their visual world, it is now possible to outline some of the mechanisms that coordinate their manoeuvres in flight. We can distinguish more than a dozen kinds of generalised visual tasks in relation to their three-dimensional world and can offer details of some of them. Bees control their flight manoeuvres visually and by a variety of receptors of the joints, hairs and muscles. All of these mechanisms are strongly modified by learning. Here, we will stick to the visual control of flight.

When we examine the nineteenth-century works of Fabre, Lubbock, Forel and others, we find descriptions of performance but no clear ideas about mechanisms of control. The twentieth century brought some experiment but much of it beside the point. The works of Loeb, Crozier, Mast and others, summarised in the textbooks by von Buddenbrock and Wigglesworth, contain numerous accounts of varied responses to light but few that can be related to mechanisms of normal behaviour. There were discussions of reflexes versus central nervous pattern generators (from Sherrington to von Holst) and classifications of responses (from Kühn to Fraenkel and Gunn)—now mostly forgotten. In mid-century, the new techniques of electrophysiology (Autrum, Burkhardt, Burt and Catton, Pumphrey, Pringle and Roeder) were diverting but revealed little more about visual control of motion than did the behaviour itself (Autrum 1979–81).

From the 1950s, motion perception became the basis of insect vision. A part of that story was the huge diversion of resources to the optomotor response—that is, when an insect responds to the rotation of a drum around it by turning in the

same direction. More recently, we have clear-cut examples of analysis of visual behaviour in free flight. The main reason why there has been so much discussion, even acrimony, about how insects in nature perceive the three-dimensional world is that several mechanisms always operate in parallel and it is hard to demonstrate the relevance of a response to a laboratory stimulus. One reason for the slow progress is that for obvious reasons insect vision is narrowly dedicated to the real tasks required in the ecological context and we are usually ignorant of these.

## Responses to light

In the classification of movements that bring insects to their preferred places (Kühn, Fraenkel and Gunn), the responses affected by the direction of the light are called taxes and those that are undirected are called kineses. Orthokinesis is a dependency of locomotion speed on stimulus intensity, so the insect finally stops in the dark or light, and stays there. Klinokinesis is when the frequency of turning depends on the intensity. Klinotaxis is when the insect compares the stimulus on two sides by making successive movements to left and right. Tropotaxis is when the comparison is simultaneous. Telotaxis is fixation on one goal at a time. The old term 'tropism' vaguely covers all these and is sometimes more convenient because the human categorisation is not sharp.

As a student, I had to learn this classification, but it did not help in understanding insect vision. The experiments scarcely approximated the natural situations and the results were described in behavioural terms that failed to connect to the anatomy, physiology or life history of the same animal. In brief, there was too little thoughtful experimental analysis and too much naming and categorising of the performance.

Freely flying vehicles need a cue for staying the right way up. Having little gravity sense in flight, many insects use the dorsal light response and the general brightness of the sky as a sign of 'up'. Some make use of the direction of the light beams rather than the intensity of the sky above. Insects that swim upside down have the reflex reversed. Some insects can fly in complete darkness, but most, like locusts and dragonflies, cannot.

The UV light of the sky is poorly reflected from natural objects, so it comes almost entirely from above. Most insects studied have more blue and UV receptors on the dorsal part of the compound eye than elsewhere. A disturbed bee flies towards the brightest UV part of the sky to escape and uses the ultraviolet of the sky to help it stay the right way up in flight. Bees turn a forward somersault in flight if they fly over a mirror that reflects ultraviolet upwards.

Many insects have three small eyes called ocelli at the top of the front of the head. In the dragonfly, they are detectors of the average position of the sky and they stabilise flight in dim light. In some species, they are partially focused

laterally, in the expected direction of the horizon. The large apertures of the ocelli and the summation of the receptors on the neurons below account for the extraordinary sensitivity to the position of the sky, earth and horizon. In the locust, the ocelli detect deviations from the direction of the horizon even in starlight, but in the bee, their functions and interactions with the compound eyes are not yet clear.

## Binocular vision

Because insects have two eyes does not mean that they have the vertebrate binocular mechanisms to measure range. Insects have no accommodation of the lens, convergence of eye movements or receptors at different focal planes. Cats and primates have an array of binocular neurons in the visual cortex with a variety of angular offsets in the visual axes of the two eyes—so-called disparity units. Combinations of these disparity neurons can measure range even off the midline. Insects do not have this mechanism.

The most skilful fast-flying insects that catch prey in the air commonly have some binocular overlap of axes at the front and top of the eyes but little separation between them, and they measure range by moving in flight. At the opposite extreme are the mantids, dragonfly larvae and a number of predatory insects that have two widely separated eyes. They slowly assess the situation for grabbing prey by turning the head and use triangulation for range estimation (Figures 5.12, 5.12d, 5.12e). As far as we know, the triangulation is done by coincidences of corresponding visual outputs on motor centres, not by a congruent mapping of the spatial array of one eye into the opposite optic lobe. The direction of the mantid's leg extension is controlled partly by hairs at the neck. Finally, there remain a vast number of insects with a little binocular overlap, but they can triangulate over short distances for the operation of their own mouthparts (Figure 1.3).

## Saccades

Saccades are spontaneous jerks of the eye at intervals of up to a few seconds—so small as to be scarcely noticeable, so they were ignored until recently. The word 'saccade', from old French, meaning 'twitch', is not in my edition of the *Oxford English Dictionary*. In 1963, David Sandeman noticed that in crabs a saccade was initiated by bringing a contrasting object into view. Land described them in the fly in 1975 (Figure 3.5), and their role in the vision of *Drosophila* was analysed in detail by Heisenberg and Wolf in the 1980s. They serve three essential purposes in active vision.

First, saccades give the fly a way to calibrate the motion detectors by making a voluntary motion of a standard size. Second, a saccade activates a synchronous

input along all visual axes that look at contrasts in the visual world, so that the retinotopic location of every contrast is renewed. The saccade is the engine that arouses the feature detectors when insects take a snapshot of the angular distribution of landmarks.

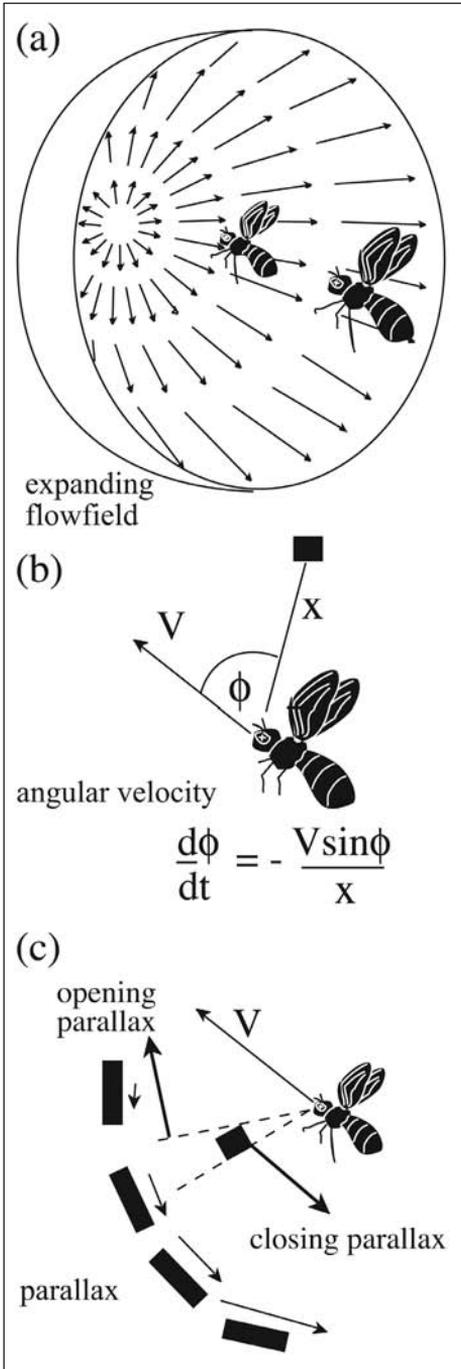
Third, in the flies *Drosophila* and *Musca*, a voluntary turn is initiated by making a fast saccade towards the direction of the intended turn, overriding the optomotor system's visual control of the head position, and the body then follows. In this action, the saccade is the unit of self-directed turning (see Figure 7.7). In the flying locust, active turning of the body begins at the same time as the saccade of the head. No doubt, voluntary turns will be found that are not accompanied by a saccade, as in the smooth tracking by the head of a mantis that follows a moving fly on a featureless background. On the other hand, when tracking a prey against a patterned background the mantis is obliged to make a series of saccades (Rossel 1979). Spiders move the retina inside the head to make saccades and to fixate on prey. In most insects, the saccades have not been studied.

## The optomotor response

The optomotor response is limited to the visual stabilisation of the head position when there is an unexpected displacement. Traditionally, it keeps a moving insect on a straight course and a hovering or floating insect on station in spite of wind or water currents. The classical systems analysis (Figures 3.1c and 3.2.a) was in terms of the perceived angular velocity at the eye although at the time it was also inferred that the motion detectors responded to contrast frequency, not velocity. How this was resolved was not explained. The optomotor response is rather delayed, with a latency of 40–50ms in the fly, and is also tuned to low temporal frequencies, rising rapidly to a peak near 1Hz, then falling off to zero near 10Hz, so any particular response can arise from two different stimulus situations. A fly hovering in a drum will not oscillate faster than 0.1Hz, which is useless for the control of flight. The response is to the passing of edges, so, within limits, it is similar if the number of edges is halved but their velocity is doubled. It adapts to a steady motion and then responds afresh at each unexpected change in frequency of the passing of edges. The optomotor response signals direction but not angular velocity and is dependent on a residual slip motion, so that it alone never completely compensates for a deflection from a straight track and never recovers the original direction of heading.

For all these reasons, the optomotor response cannot account for the way insects fly in a constant direction at a preferred speed over the ground or how they total their successive turns. Finally, as described below, the optomotor response is learned, like all short-term postural control of the legs, head or antennae. It is a stabilising mechanism with directionally sensitive motion detectors and a learned control of the steering muscles (see Chapter 3).

Figure 7.1 Situations encountered during flight. a) The optic flow in forward flight. b) The relation between the forward air speed,  $V$ , the angular velocity,  $d\phi/dt$ , and range,  $X$ , of a nearby object. c) Opening and closing parallax when seeing an object against a background.



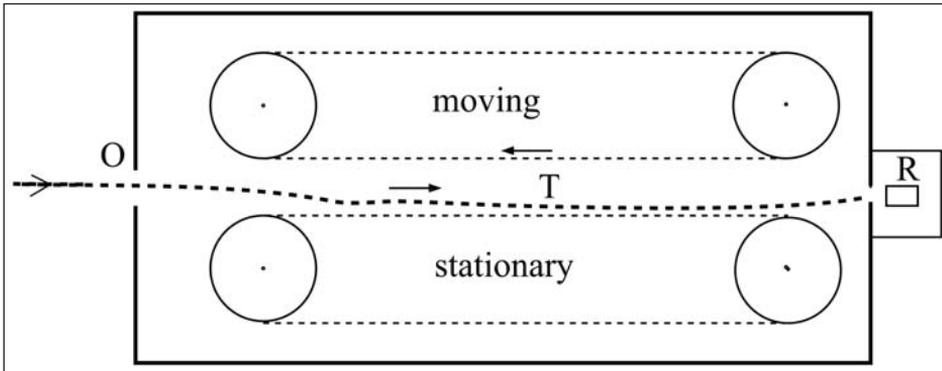
## Optic flow and the avoidance and centring responses

In the past decade, the central factor in flight control has turned out to be the optic flow (Figure 7.1). The first indication was an accidental discovery of the fact that bees refused to approach rotating sector wheels, but were not concerned about the flicker of a light at the same temporal frequency without motion. The avoidance response was not at first linked to the perception of the three-dimensional world, but the general idea now is that insects interpret relative motion as the nearness of something and their three-dimensional world is composed of the ranges of different contrasts in different retinotopic directions around the head, irrespective of the real patterns.

In 1950, J. J. Gibson published a groundbreaking book suggesting that we recognised the three-dimensional arrangement of our surroundings directly from the gradient of velocities in our visual field as we moved about. The null point in the flow field is the place we aim for and the induced angular velocity at any point in the visual field is a measure of the nearness or inverse of the range (Figures 7.1 and 7.3). Gibson, who at the time was working for the US Air Force, took these ideas from classified work at Farnborough by G. C. Grindley, who died in 1976 leaving no published record of his work (Mollon 1997).

To fly in a cluttered, unpredictable three-dimensional world, insects must have mechanisms in different parts of the eyes to measure perceived angular velocity irrespective of pattern, so that they can control speed, range and steering. To control the visual input and also record the flight position and speed, the first analysis was made with bees trained to fly along a tunnel in which the walls on either side could be moved in either direction separately (Figure 7.2). Later, large television screens replaced the walls so that the patterns could also be moved up or down. The bees flew as though they equalised the angular velocities on their two sides, irrespective of the pattern or the direction of motion that they saw. Somehow, with contrast frequencies up to 150Hz, they measured angular velocity but ignored its direction. The mechanism is therefore faster than the optomotor response, but both responses are colourblind and based on green receptors. The avoidance response enables insects to fly rapidly between objects without risk of collision. In addition, anything coming into view causes a sudden turn. Self-guided mobile robots that negotiate between obstacles and walls were made with this design in the early 1990's.

Figure 7.2 The apparatus for experiments with the angular velocities on the two sides of the flying bee. The bees learn to enter on the left and fly along the tunnel to obtain the reward in the box, R, on the right. They then return by the same route. The side walls can be moved either way at a controlled speed and the patterns on them can be changed. A video camera tracks the bees from above. The average track, T, of the bees is such that the angular velocities are equal on the two sides, irrespective of the pattern.



Source: After Srinivasan et al. (1991).

## The analysis of the visual feedback

A mechanism based on saccades has been worked out for the fly *Drosophila* (see Chapter 3), but saccades give information about location and angular spatial frequency of surrounding contrasts, not about range or flight speed.

Forwards or sideways motion of an insect in flight, if stabilised against rotation, causes an induced relative angular velocity of surrounding objects that is inversely proportional to range (Figure 7.3a); so, distant objects appear to move little and slowly. Like a one-eyed man who estimates the range of objects of unknown size dead ahead, the insect makes a lateral movement by a known or predetermined amount (Figure 7.3b). When the flying insect sees a regular striped pattern of constant stripe period at the side, the perceived angular velocity is inversely proportional to the range, but the contrast frequency—that is, the rate of passing of stripes—is independent of range (Figure 7.3c).

The analysis of the ways that bees use the perceived angular velocity began with the observation that they fly through a gap between obstacles, along the side of a wall without collision or without turning into the wall, irrespective of the pattern on either side, and they can be trained to come to a target at a particular range. To measure the range of an arbitrary pattern, it is essential to move the eye without rotating it and measure the resulting apparent angular velocity of the target. For an object in front, at the side or below, one way to do

this is to use the fact that the range is inversely proportional to the perceived angular velocity (Figure 7.3). This calculation requires a measure of the forward speed in relation to the ground.

To measure the range at an angle to the direction of motion there is a sine or cos function to consider (Figure 7.3). The range to an object dead ahead can also be measured from the perceived rate of expansion on the eye, which is another simple relation (Equation 7.1).

#### Equation 7.1

$$\text{Range } R = (\text{forward velocity})/(\text{angular velocity of the edge})$$

$$\text{Or: (time to contact)} = 1/(\text{angular rate of expansion})$$

In these relations, flight speed over the ground is measured in metres per second, angular velocity in radians per second and range in metres.

Air speed is measured by sensitive mechano-receptors that detect the bending of the first joint at the base of the antenna, due to the air pressure in flight. Similarly, hairs on the head detect air movement, but these cannot report speed over the ground.

A problem arises from the fact that the most easily observed motion detectors, in the optomotor system, are sensitive to the rate of the passing of contrasts (called the contrast frequency) and also the direction of passing, but not to angular velocity. For an eye looking at a textured background at the side or directly downwards, Equation 7.2 applies.

#### Equation 7.2

$$\text{Angular velocity} = (\text{contrast frequency})/(\text{angular spatial frequency})$$

For regularly repeated edges, as in a grating, the spatial frequency is the reciprocal of the period. This relation implies that the absolute value of the average period in the pattern passing by is part of the calculation, but the bee in the air does not have a measure of it. The bee does, however, measure its perceived velocity over the ground, as shown by many experiments. It must learn to use a preferred angular velocity that suits its preferred or real flight speed.

How is the angular velocity measured? The bees clearly measure their speed over the ground by non-directional detectors and they learn the speed at which they negotiate a familiar route. Several authors have recorded from deep optic neurons that show an increasing response to increasing angular velocity, irrespective of the spatial frequency, but so far all the neurons sensitive to high velocities are directional. A possible mechanism can be designed in several ways—for example, by measuring the delay as a contrast passes from one visual receptor to the next, or the next but one (called the stopwatch method), but there is no evidence that this happens or that arbitrary times are measured.

Figure 7.3 Relations between flight speed,  $V$ , range,  $R$ , and the induced angular velocity for different directions relative to the direction of flight. If rotation is eliminated, (a) forward flight or (b) sideways scanning causes an induced relative angular motion of surrounding objects. This visual feedback is inversely proportional to range. c) The frequency of passing stripes (the induced contrast frequency) is proportional to forward velocity,  $V$ , and inversely proportional to the pattern period,  $P$ , but independent of range,  $R$ . Angles are measured in radians.

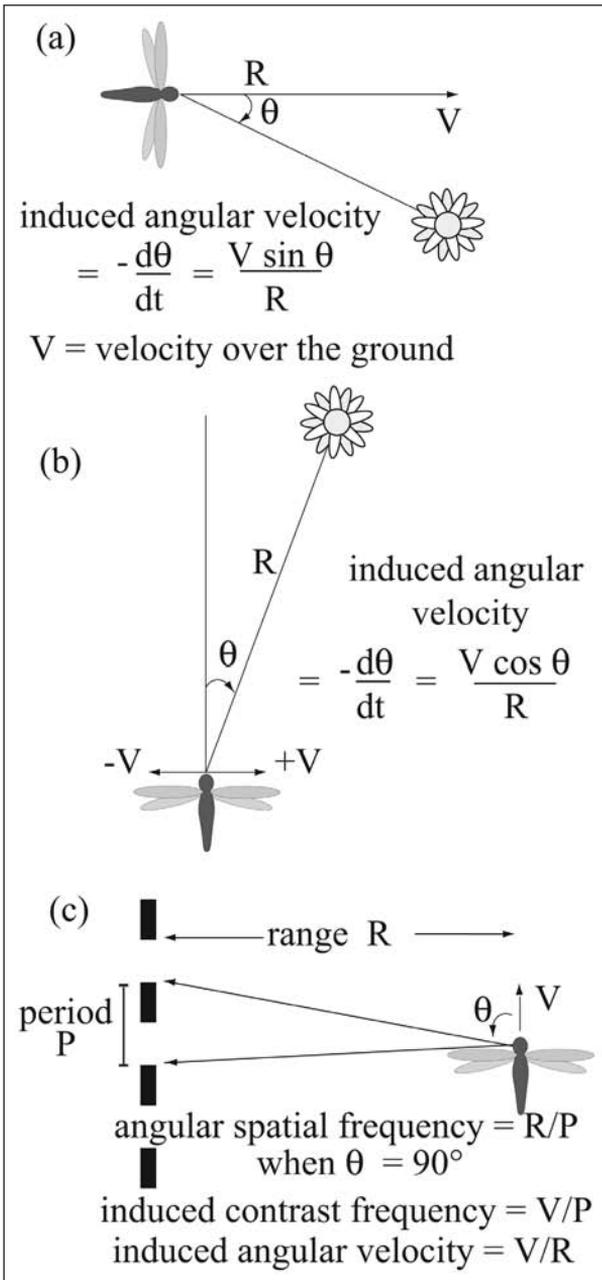
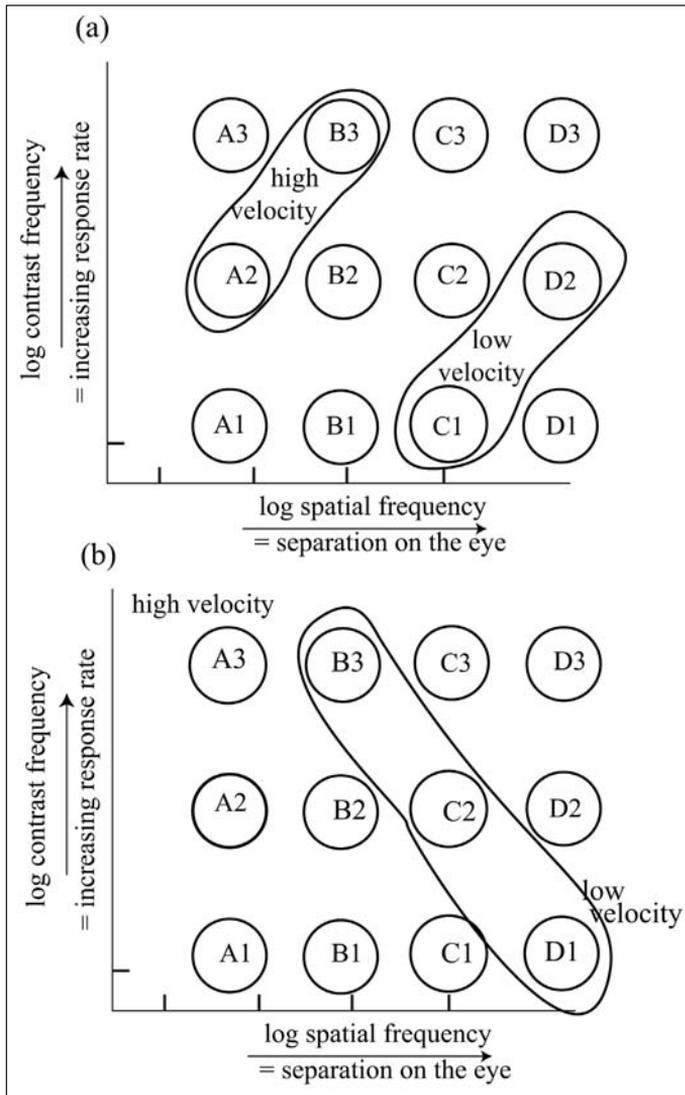


Figure 7.4 Measurement of angular velocity. Four motion-detector neurons, A, B, C and D, have different retinal spacing of their inputs, so they are tuned to different spatial frequencies. They have an increased response (A1, A2, A3) to increasing temporal frequency. a) The high-level neurons that detect appropriate coincidences (A1, B2, C3) are detectors tuned to different angular velocities. b) The higher-level neurons that detect appropriate coincidences (C1, B2, A3) have an increased response to increasing velocity irrespective of spatial frequency.



More likely there are several motion-detector channels in parallel, with different spacing on the retina (Figure 3.4). Consequently, they have response curves tuned to different spatial frequency peaks (cells A, B, C and D in Figure 7.4). Each of these types occurs with different contrast frequency peaks (cells A1, A2 and A3 in Figure 7.4). We can imagine various combinations of spatial frequency and temporal frequency tuning to the optic flow. If there is a higher-level neuron that detects the coincidence between a strong response of detector B3 with a weak response of detector A2, the insect responds to the high angular velocity (Figure 7.4a). If there is another higher-level neuron that detects the coincidence between a strong response of detector D2 with a weak response of detector C1, the insect responds to the low angular velocity. Even two different channels with different spatio-temporal constants would allow some estimation of the perceived angular velocity.

We need a mechanism, however, that yields *an increasing response to increasing velocity irrespective of the spatial frequency* of the pattern. This could be achieved by a higher-level neuron that detects the coincidences between responses of detectors D1, C2 and B3 (Figure 7.4b).

Significantly, when the flying bee measures the perceived angular velocity to get the range or the distance flown, she appears to be unaware of the direction of the perceived motion, but at the same time, her body position is stabilised around three axes by the quite separate optomotor response that is sensitive to the direction but not the perceived angular velocity. The automatic stabilisation of yaw, pitch and roll in the flight posture is separate from the choice of direction. At present, some models of the control of flight in the fly appear to put the whole signal through a single channel. Further channels—for example, from the halteres and antennae—also play a part.

The channels that detect looming, avoidance of collision and active control of direction are all faster than the optomotor response. As in all insect motor systems, in the bee, there are slower tonic and faster phasic (twitch) motor neurons in the bee's control of neck movements, but much remains to be analysed in these responses.

These ideas omit the fact that the compound eye is an ideal device to measure the angular spatial frequency in a local region of a scene. For example, at every saccade of the head, each contrast in the image stimulates a modulation detector. We know that these responses are summed in local eye regions in the bees, which can learn local modulation quantitatively and remember the different modulation in separate regions of the eye when landmarks are distinguished. The sum of the modulation is a measure of the average spatial frequency in each local region. We do not know whether insects make use of saccades in this way.

In the fly, the fields and directional sensitivities of the different neurons that measure direction of motion and its temporal frequency are well known from recordings in the lobula plate, but the eye regions and neurons that measure range and apparent angular velocity have not been distinguished.

## Direction and speed over the ground

The tendency of insects to fly upwind has been known for more than a century and it was not a mystery until work by the Reichardt group, from 1956 onwards, turned the emphasis to the optomotor response. Kennedy (1940) made the basic discovery that the control was entirely visual, showing that the speed and direction of freely flying mosquitoes in a wind tunnel could be controlled by letting them see a moving pattern. In slowly moving air, the insects overtook the apparent movement of the ground, which ensured that they flew upwind at a preferred ground speed. If the wind was strong, the insects turned around and flew with it or settled. The results were later repeated on aphids, moths and several flies including *Drosophila*. In the early work, the flight height was not controlled, unless there was an odour plume. A wide range of behaviour—from the migration of butterflies or locusts to the dispersal of aphids or the behaviour of flies in tunnels—was governed by the visual response to the perceived motion of the ground. Some insects that migrate, and swarming locusts, turn to fly downwind and are assisted by it. In a locust swarm, the individuals at the top fly faster, overtake their fellows and then descend at the front of the swarm. In light wind, the swarm tends to drift downwind and compensates for any change in speed over the ground.

Within the range of wind speeds that they can exceed, flies or bees flying upwind in a horizontal wind tunnel have a preferred upwind speed relative to surrounding objects, irrespective of the pattern that they see. When there is a sudden step in the period of the pattern on the tunnel wall or floor, they maintain the same perceived angular ground speed as before.

Bees fly faster when higher and slow down as they approach a landing. They fly slower in narrower tunnels, faster in wide ones or in the absence of strong visual feedback. They are slowed down by the angular velocity component of the visual feedback irrespective of the spatial frequency of the pattern. The preferred angular velocity is in the range 250–750 degrees per second and is controlled from moment to moment by the range of nearby contrasts. Two important points follow from all this: first, the optomotor system does not control the flight velocity or direction; and second, because the dance cannot code the height at which they fly or the effect of the wind, the bees' dances convey the perceived distance to the goal over the ground, which makes the instruction in the dance independent of the wind, but the recruits must fly the same route at the same height as the dancers.

In each situation along their route, flying bees have a preferred forward flight speed and a preferred flight height, and these are both related to the perceived angular velocity. There are other factors—for example, they learn how to negotiate a convenient route and when to slow to anticipate a turn; and all flying insects have airspeed detectors in the antennae and head hairs. They might also follow an odour plume at a certain height.

## Following an odour plume

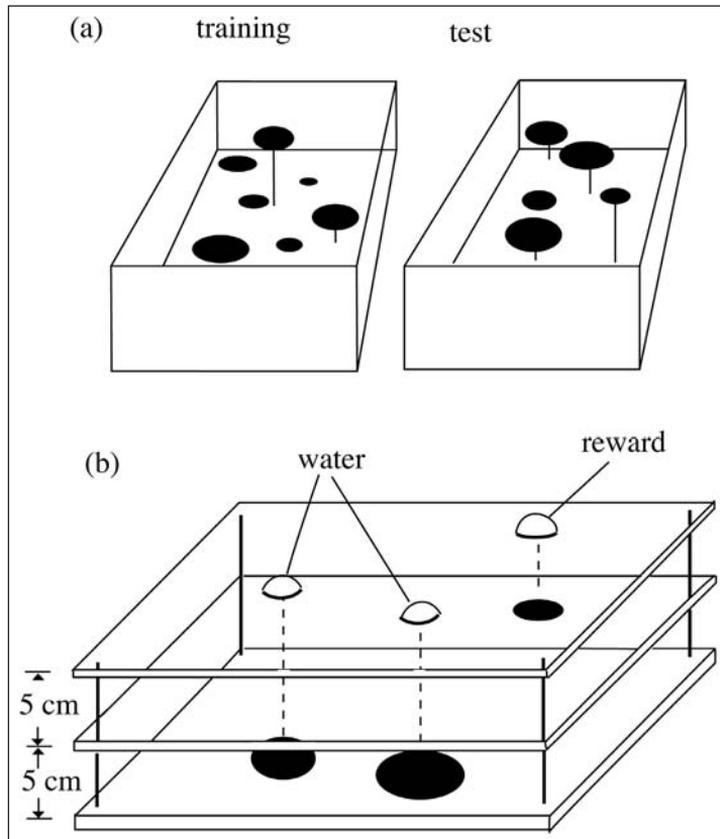
Although the primary stimulus is the odour of water, a flower, scent mark, dung pile, carcass, male's pheromone or animal sweat, many insects including bees fly upwind towards an odour source by visual control from the feedback from the motion of the ground. In general, the odour receptors initiate the search but they are not directional. When the insect comes to the edge of the odour plume and loses the scent, it casts about or scans from side to side or up and down under visual control until it finds the odour again and turns upwind. There is no question of holding a station by the optomotor response or of using an odour gradient. Aquatic animals behave similarly.

## Other ways to measure range

It has been known since Wallace (1959) that grasshoppers sway from side to side to measure the range before they jump. In 1977, I proposed that to measure the range of nearby objects, flying insects also made use of the apparent motion caused by similar relative movement in flight because they lacked other means. There are two mechanisms involved—one based on induced lateral motion, which is hard for humans to do because they fixate with a moveable eye, and the other on observing the parallax as an object appears to move against a background, which is the way that a one-eyed person usually estimates range. Without parallax, many kinds of insects can catch a mate or prey as seen against the sky and mantids and locusts can also estimate range by peering from side to side at an object against a featureless background.

In 1986, we began a series of experiments that demonstrated range discrimination in a number of ways. The first experiment was to train flying bees to discriminate paper 'flowers' raised on stalks (Figure 7.5a). The bees were able to distinguish the correct length of stalk and land over the one with a reward of sugar solution; other flowers had only a drop of water. The flowers were randomised in size and position but the rewarded flower always had the same length of stalk. Later, we put paper discs on flat shelves of perspex (Figure 7.5b) and also showed that bees could discriminate different horizontal ranges of black discs of randomised size when they were on a vertical surface.

Figure 7.5 The discrimination of range irrespective of the position, absolute size or angular size of the disc. a) The first experiments were done with discs of different sizes on stalks of different heights in a box over which the bees could fly. b) Later, the discs were arranged on thin, clean sheets of perspex. The bees were trained to land over a disc of random size at the specified vertical range, while the heights, positions and sizes of the other discs were repeatedly randomised during the training. The reward of a drop of sugar solution is always over the target disc and drops of plain water are offered in random places to ensure that the bees do not search for the reward.



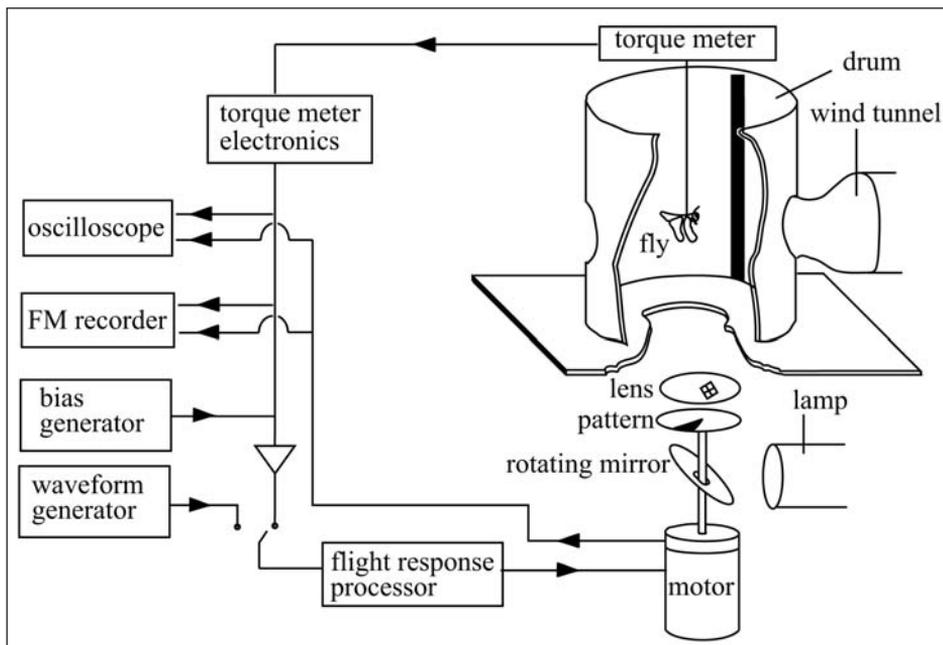
Source: Horridge et al. (1992).

With a similar arrangement, bees discriminate the absolute size of a black disc, presumably by combining the range with the angle subtended at the eye. When the angle subtended at the eye and the range of the target are randomised, bees learn to discriminate the correct absolute size and, when size and range are both randomised, they can learn to select the correct angular size. Bees can also do these tasks looking horizontally at vertical targets. It appears that absolute size is important in the three-dimensional world of bees and wasps, especially for control of flight height, locating self relative to landmarks and recognition of familiar places.

## Control of straight flight

A human learning to steer a car or a boat with a wheel or a tiller must learn which direction of steering causes which direction of turning, and further, what happens when going backwards, which many insects, including bees, can do. Learning by trial and error is involved (or not, as the case may be). Insect flight in a straight line is dependent primarily on visual feedback from the surroundings and fixation on a target, although factors such as odour plumes can initiate it. In free flight, the fly *Drosophila* makes saccades with angular velocities between 1500 and 4000°/s randomly in either direction. The fly, like the bee, can integrate successive turns in free flight, steer towards local contrasts and return later to its original track.

Figure 7.6 The essentials of the flight simulator with the fly mounted on a torque meter in a white drum, and a motor that moves the black bar as instructed by the computer. The only measurements are of yaw torque, drum velocity and drum position; therefore, any theory must be expressed in these terms. The fly can learn to fly on a straight course in this apparatus and also to select one of several different patterns.

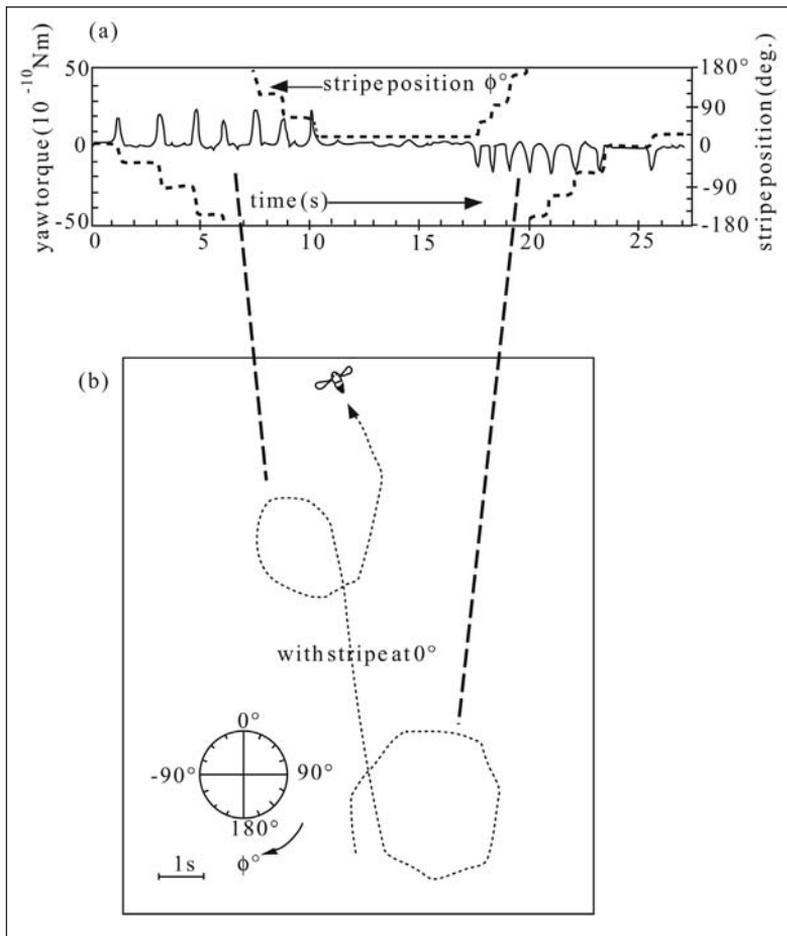


Source: After Wolf and Heisenberg (1991).

To analyse the mechanism of steering, Wolf and Heisenberg (1990) fixed the *Drosophila* within a drum on a device that measured the turning torque generated by the wings in the horizontal plane and converted this torque into the expected rotation of the visual field that the torque would cause (Figure 7.6). Neither the head nor the body moved, but the fly's efforts to turn now appeared to it to have

been effective. The coupling ratio was not critical. There was continual jitter and fluctuation of the output. The fly's effort to make a saccade appeared on the recording as a brief pulse of torque, which was converted to a drum rotation up to  $60^\circ$  in the opposite direction (Figure 7.7), but there was no optomotor response to the movement of the drum that was initiated by the saccade.

Figure 7.7 The behaviour of *Drosophila* in the flight simulator, with a single black strip visible to it (Figure 5.9). a) Traces of yaw torque (left scale) and pattern position (right scale) showing torque spikes and small adjustments of torque between them. b) A reconstruction of the trajectory that the fly would have made if free, assuming constant forward flight velocity and adding the turns.



Source: After Heisenberg and Wolf (1992).

On the other hand, an unexpected imposed rotation of the whole visual field by as little as  $0.1^\circ$  causes a torque response with 40–50ms latency and high gain. If one wing is damaged, causing continual turning in flight, the fly readjusts again to the new relation between the eyes and the torque. The visual input generated by a saccade informs the fly within 50ms whether there has been a change in position of contrasts in the visual field apart from that which was expected, and it adjusts the output. Any low contrast in the visual field is sufficient for visual stabilisation on a straight course. There is no fixed cancellation of the optomotor response to allow for voluntary turning, for that would fail to compensate for damaged wings.

The fixed fly can also learn to control the position of a vertical bar, which it prefers to bring to the front and then fly towards it. If the bar is displaced sideways, the fly exerts torque to bring it back to the front (Figure 7.7). The angular motion input resulting from the saccades is ignored, probably because it is too fast. Careful analysis of the wild type, supported by work on the double mutant *rol sol*, suggested that the single bar was controlled by its position, but the background was controlled to reduce its perceived motion, with a slip speed, so displacements were not fully corrected. If the coupling between the fly's effort to turn (the torque) is reversed, with a bar moving in front of the background of the drum (the figure/ground stimulus), a normal *Drosophila* can learn to control the position of the bar but not the position of the background. The double mutant *rol sol*, however, lacks the optomotor system but still retains the faster non-directional system that normally detects the position of a bar and, with this, it can learn to stabilise either the bar or a textured background despite the reversed coupling.

If the apparatus is rearranged so that the movement of the bar is controlled by the forward thrust in flight instead of by the turning torque, the fly learns the new controls in a few seconds of trials. The fly can also learn to control its visual field by pushing with its legs on a table below or in response to warmth as reward or cold air as a punishment. Long ago, I showed that the leg posture of locusts and cockroaches was learned by operant conditioning in a similar way. We can conclude that when there are several motor outputs to legs and wings, it is necessary to have a learning mechanism so that they function effectively in an unpredictable world. Even humans relearn quickly if placed on a bicycle or stilts or if their vision is inverted by prisms.

## Visual measurement of distance flown

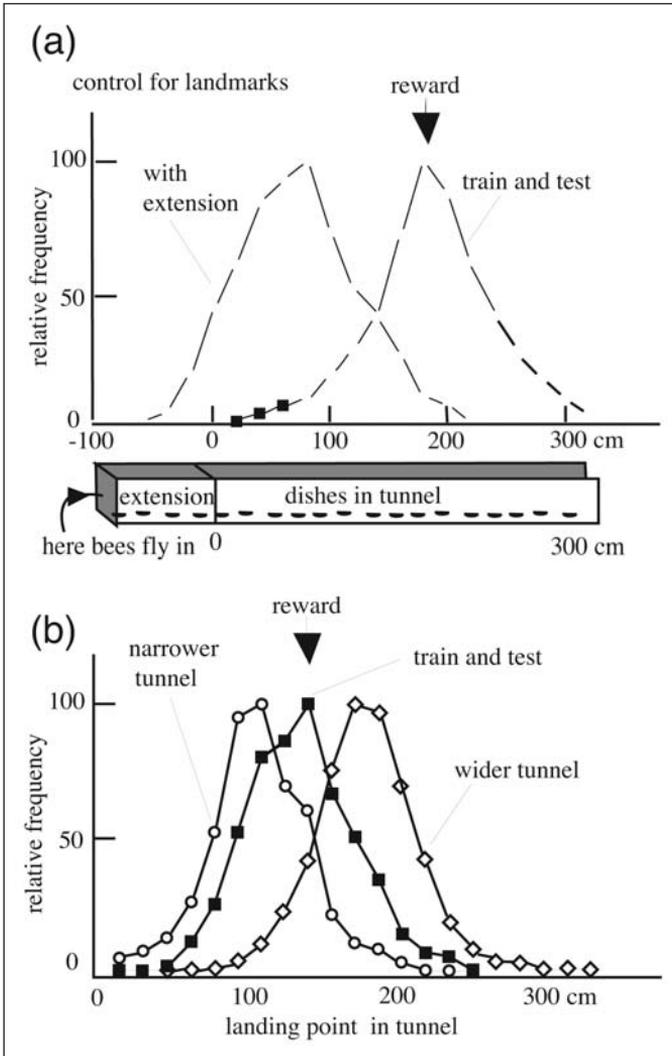
In their dance, bees signal the direction and distance to a worthwhile food source from which they have just come. Despite the observations of his students, von Frisch believed that the bees measured the energy used to reach the food source, irrespective of the distance over the ground, although the latter was the most

reliable cue in a windy world. Recent work has shown that bees use their eyes to measure the distance they have travelled over the ground, not the energy used. Esch and his colleagues made use of the fact that bees coded the outward distance from the hive to a reward by the number of abdomen wobbles in the dances on their return. They flew bees to a reward in a balloon. As the balloon was raised, the bees were obliged to fly higher and this reduced the optic flow, so their dances indicated a shorter distance. Also, flights between the tops of tall buildings were coded as too short by the dances of the returning bees. The oxygen usage was strongly influenced by temperature but was related only indirectly to the distance coded by the dances.

When trained bees flew down a long tunnel with patterned walls, along which small dishes were distributed, they learned to fly for the correct distance to the particular dish where they expected the reward of sugar to be (Figure 7.8). They flew the same total distance if an extra length was added at the entrance of the tunnel (Figure 7.8a). They learned the distance on the way in, not on the way out (Srinivasan et al. 1996). There was no effect on the distance flown by the bees when the period of the pattern was changed on the inside walls of the tunnel or when a wind was blown along it, although a wind changed the duration of the flight. The bees do not count landmarks along the tunnel nor do they fly at a constant speed irrespective of the wind, but if bees trained in one tunnel are tested on a wider tunnel, they fly too far. Conversely, if given a narrower tunnel, they do not go far enough (Figure 7.8b). These effects show that the bees measure distance by integrating the apparent velocity of the optic flow at the side of the eye over time. If the optic flow is made useless by putting stripes horizontally along the sides of the tunnel, the bees do not know how far to go and also they fly at great speed.

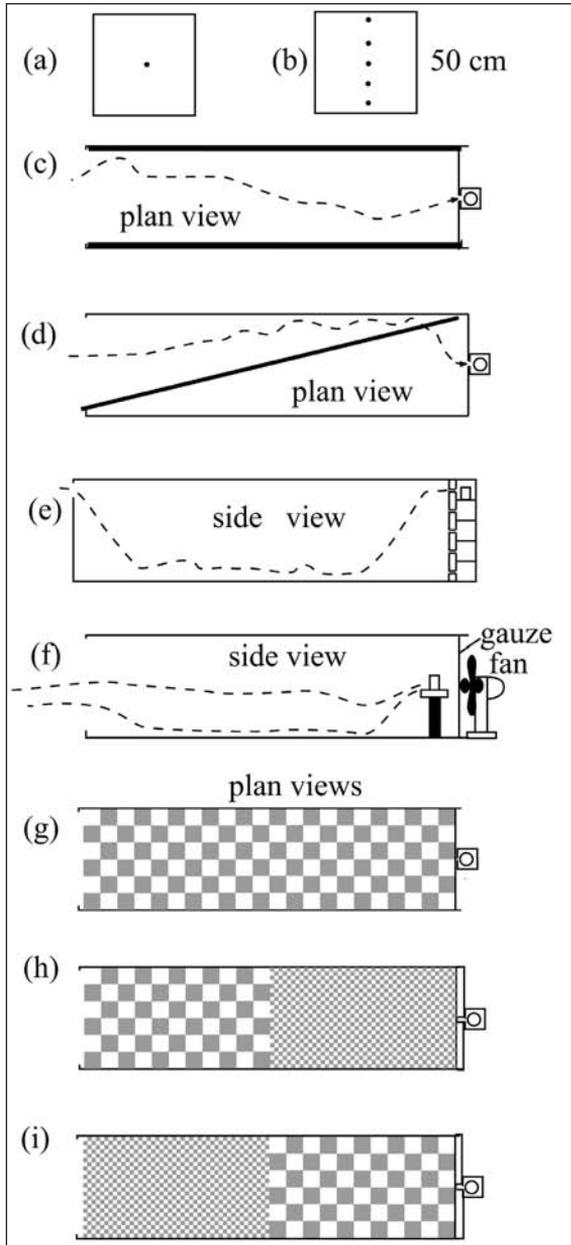
Recent measurements by Srinivasan, Zhang and others have shown that outdoors the bees give about 1.6ms of waggle dance per metre travelled, and 1 metre of flight in a tunnel 30cm wide is equivalent to 25m outside. In terms of angle, one millisecond of waggle encodes about  $18^\circ$  of image motion on the eye in any situation.

Figure 7.8 Bees learn to fly the correct distance in a 3m tunnel to the dish that contains the reward. a) Results of training followed by testing with a 1m extension of the tunnel. They fly the same distance as before but to the wrong place, showing that they do not use landmarks. b) There is no effect of changing the period of the stripes in the tunnel, so they do not count stripes.



Source: After Srinivasan et al. (1996).

Figure 7.9 Bee flight paths in a large, featureless tunnel. a) and b) Positions of the reward holes on the end wall. c) Flight between two black lines. d) Flight deflected by the black line. e) In side view, they drop to the floor if it is featureless. f) They fly low to avoid a wind. g) The textured floor. h) and i) Sudden change of the spatial frequency makes them aim (h) too low or (i) too high, without change of flight speed.



Original unpublished observations

## Control of flight altitude

In their normal terrain, bees have a preferred flight height, which depends partly on what they have experienced in previous flights at the same place—for example they will fly low or in the shelter of a wall to avoid a strong wind (Figure 7.9f). When bees fly along a familiar route, they have learned the familiar average period of the pattern below them and use it to bring them back to a preferred flight height. When bees were trained to fly into a large featureless tunnel, 1m high and 1m wide, they flew along the centre near the floor if it was white, but at a height of about 50cm if there was a pattern on the floor, irrespective of the pattern. They learned to fly higher or lower if they anticipated meeting obstacles in the way and they learned to follow a black line sloping up or down (Figures 7.9c and 7.9d). When given a choice of several holes at different heights, but only the top one with a reward, they learned to fly at the height of the anticipated reward hole (Figure 7.9). When they had thoroughly learned the correct height to fly over a coarse pattern (Figure 7.9g), the floor below the reward hole was unexpectedly changed to a pattern with a smaller period (Figure 7.9h). The bees then aimed too low until they relearned the correct height of the reward. They therefore learned the perceived temporal frequency of the ground at their preferred flight speed. Bees learn to go to a reward at a certain height but they cannot recruit to a food source that is high above the ground, so the dance apparently contains no information about altitude.

## Control of flight speed

In each situation, bees have a preferred speed of passing the panorama that they see. They fly faster in a head wind, fast when familiar with the terrain and slowly in an unfamiliar place. Outdoors, they fly fast when high up and slower when closer to neighbouring contrasts. They fly slower when exploring or uncertain and faster when certain of their route. As the bee flies along, it adjusts its speed and direction by the perceived optic flow, forming a feedback loop that again changes the optic flow. In the tunnel experiments, they fly slowly because the walls are close and appear to pass faster, but by the time the measurements are made, they have also learned the dimensions of the tunnel. When there is a constriction in the tunnel, the bees slow as they pass it then return to the same speed as before, but the perceived angular velocity remains approximately constant. Because continuous learning is involved and the internal state of the bee is unknown, it is difficult to discover how the preferred speed is decided.

The front and the sides of the eyes are clearly instrumental in measuring the optic flow as the bee flies along, but the optic flow has a distribution around the eye—slow at the front but faster at the sides and below. The directional effects also differ with the region of the eye, as lateral motion at the front causes

turning, at the side it affects only the speed, and ventral motion makes the bee turn and fly upwind. In experimental unmanned planes and helicopters, it is sufficient to control landing by the optic flow in a solid angle looking forward and downward, and to prevent collisions via an eye with 360° vision looking towards the horizon.

As well as visual control via the optic flow, bees and flies have head hairs and a special mechano-receptor system at the base of the antennae, both of which are sensitive to air speed. How the three systems interact has not been studied.

## Hovering

In several groups of insects, some adept fliers can hover in flight while they examine an object visually, feed from a flower, lie in wait or guard a nest entrance. It is no more of an achievement than flying; exactly the same parallel mechanisms are in action, including learning each familiar situation. In various hovering insects, a suitably tuned optomotor response for stability against unexpected perturbations, fixation on a target to stabilise the direction of looking and a shift sideways or a measure of target size for range estimation have all been described as contributory mechanisms. Expansion of the image on the retina is a sign of an approach towards something. Locomotion in any direction is reduced to zero by detecting and moving away from each centre of expansion, combined with keeping landmarks at fixed positions on the eye.

The interesting questions about hovering to fixate on a contrast are how much it improves vision and to what extent stationary images at the front of the eye can be better processed and remembered. Some dragonflies have more than one fovea. In some situations when insects hover, the image is fixated with deliberation by the fovea and this behaviour is somehow related to the improved discrimination of a mate, a flower or prey. Almost always these insects 'turn and look' at a specific object; however, it has not been shown that they partition their visual world into separate objects.

Male hoverflies and dragonflies, hovering in wait for a passing female, fly in exactly the appropriate direction to intercept her. The response is simpler than it appears at first sight, because the line of interception is selected on the assumption (perhaps learned) that the target is a female of standard size flying at a predictable speed. Bees commonly use landmarks at the side or the lateral parts of a target to localise a reward that is in front of their eyes, but they turn to centre their vision on a spot of blue colour, a radial hub, a source of parallax or an expected cue. All of these reactions are strongly influenced by learning during the course of the experiment.

## Landing

As a flying or swimming insect approaches an object, it slows long before the legs are extended for landing. When a fly sees something in its path, it unfolds its forelegs, brings the other legs down and then extends the forelegs to break the shock on contact. Any strong addition into the flow field at the front of the eyes is an adequate input. Although the necessary trigger for the landing response has been studied in detail in the fly, we are still not clear how it controls its own dedicated motor pattern. There appear to be fixed or learned motor sequences for the initial stages of landing, triggered by looming and net darkening, which are preset for the task. Flying flies held by the thorax go through these motions repeatedly but tethered bees soon learn that they are fixed.

The motion perception for the landing response is tuned to a higher contrast frequency than that for the optomotor response. There are several vision mutants of *Drosophila* in which either the landing or the optomotor response is ineffective—again suggesting they are separate systems. Selective habituation of neurons suggests that the optomotor and landing pathways have separate motion-detector pathways. The landing is best stimulated by fast motion of a single edge or by a spatial period greater than  $20^\circ$ , whereas the optomotor response is most sensitive to slower motion of intermediate periods. Although it is an attractive idea, it has not been demonstrated that any insect computes the time to contact when landing and slows accordingly.

A honeybee coming in to land on a flat, patterned surface detects the increased speed of the ground beneath it and turns to land at right angles to an edge. As it loses height, it slows to its preferred angular velocity over the ground. Analysis of numerous landings by high-speed photography shows that the average bee keeps the average angular velocity of the surface constant as it approaches, until the flight speed is zero at touchdown. There is one input variable, the perceived angular velocity, and one controlled variable, the flight speed over the ground—both ending at zero. For most of the way, the angular velocity is maintained at 400–600°/s, but there is great variability in the response and a lot of unknown factors. Obviously, the relations between the instantaneous perceived angular velocity, flight height and instantaneous airspeed are not as consistent as the averages. How this translates into other situations, like landing on a thin twig, has still to be worked out.

## Scanning and peering

When dropped on the ground, many insects make exploratory head movements. Before they reach out to step across a gap, young praying mantis make a few

lateral scans of the head—sometimes called peering—direct their gaze at the other side and prevent head rotation while they move the head sideways to measure the range.

When the mantis sees a potential prey, it behaves quite differently: it freezes and uses triangulation by the two eyes to manoeuvre very cautiously into the predetermined range for a strike with a foreleg. A mantis can track the movements of a small prey on a featureless background by smoothly tracking it with movements of its neck and legs, but if the prey is on a textured background, the mantis tracks it with short jerks of the head, like saccades, that overcome the visual stabilisation by the background.

Before they jump, grasshoppers, locusts and young mantids make a similar lateral movement of the head as they measure the range ahead (Figure 7.10a). The velocity at take-off and the distance jumped depend on the range measured visually. Peering or scanning by standing insects appears to be the same mechanism as range measurement and segmentation of the three-dimensional cluttered world by flying bees: it involves non-directional relative motion irrespective of pattern and it is also sensitive to the parallax when an object moves across the contrasts of the background.

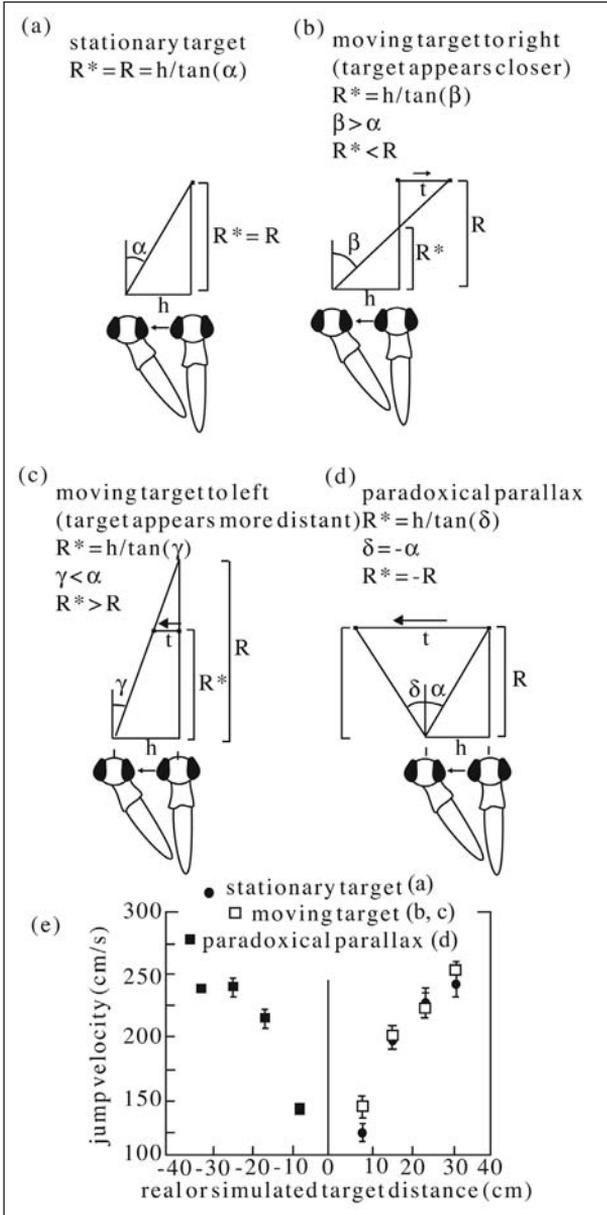
A fovea at the front of the eye is an advantage for peering because it increases the number of receptors involved. Locusts have a small, forward-looking fovea.

Two types of experiments show that the measurement of range from the relative motion on the eye is done by non-directional (that is, scalar) motion detectors. When a locust peers from side to side to estimate the range for a jump, the target can be moved as the locust moves its head (Figures 7.10b–d). The added motion reduces the apparent motion on the eye and the locust jumps short, according to the motion it sees. When the added motion is so arranged that the apparent motion is reversed (Figure 7.10d), the locust will still jump according to the amplitude of the net motion. The visual system measures the range irrespective of the direction of the induced motion on the eyes.

Flying insects also scan in flight and, like peering in mantids and locusts, the scanning detects the range, but we have no evidence that they see shapes. They identify biologically important objects by detecting cues. A good example of peering in flight is the flight of a fast fly, weaving from side to side as it goes, or the lateral movement of a hoverfly or hovering dragonfly when an intruder comes into view.

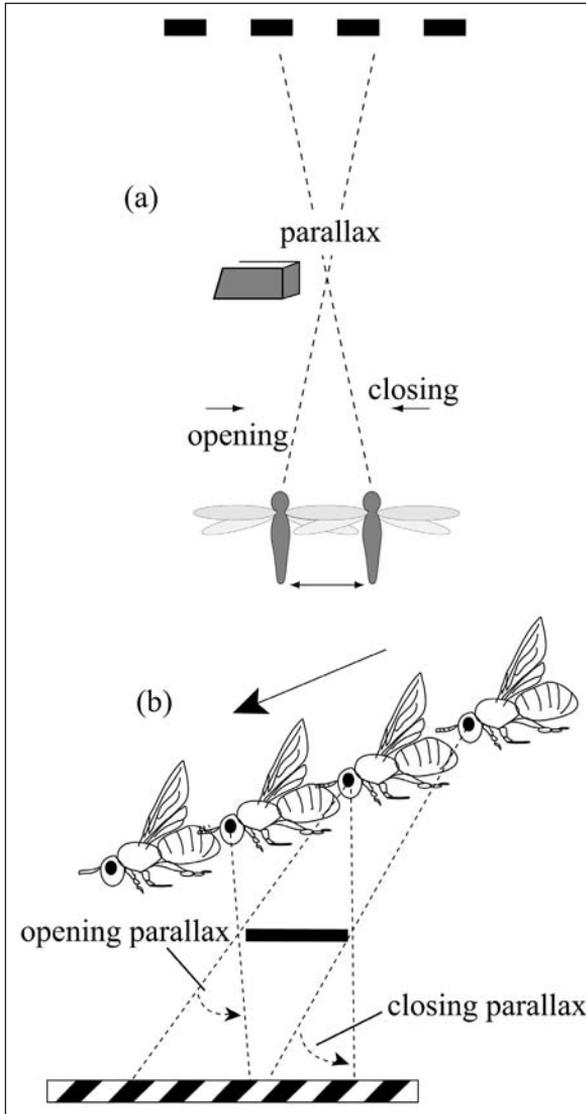
Another kind of scanning is seen when bees fly over striped patterns in search of a reward. They tend to follow the edges, as a way of reducing the relative motion and flicker on the eye, whether trained to the pattern or seeing it for the first time. We know nothing about neural mechanisms of saccades, peering or scanning, or their use out of the horizontal plane, and few species have been studied.

Figure 7.10 Range measurement by the locust before it jumps. The locust peers by moving its head sideways by a distance ( $h$ ), keeping the midline of the head pointing directly forward. In (a) the target is stationary and the angle,  $\alpha$ , indicates the range. In (b) and (c) the target is moved when the locust peers so that the angle,  $\beta$ , is too large and  $\gamma$  is too small. In (d) the target is moved to the other side so that the angle,  $\delta$ , is in the opposite direction to  $\alpha$ . The locust still estimates the range as  $R$ , so it uses the other eye. e) The jump velocity is related consistently to the apparent target distance.



Source: Partly after Sobel (1990).

Figure 7.11 a) Sideways motion of a hovering insect induces opening or closing parallax as well as relative motion. b) When an insect is approaching an object or coming in to land, the nearer edge presents an increased velocity coming into view and also the closing parallax as contrasts in the background are obscured. Either stimulus is accepted as a measure of range, but the insect never lands on the far edge, which presents opening parallax.



## Self-motion generates parallax

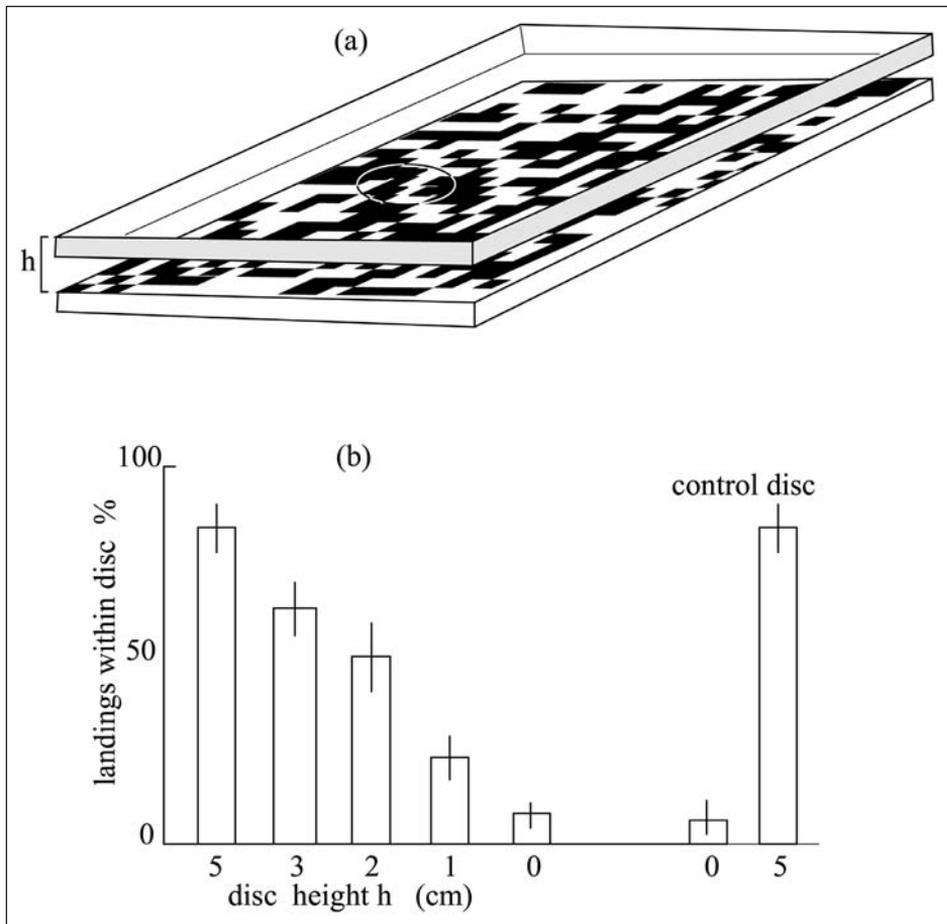
When an eye moves, nearer objects appear to move faster against the slower motion of the more distant background. Relative motion between two objects caused by sideways motion of the observer is called parallax. For centuries, this was the term employed by astronomers to describe the apparent motion of near stars against the positions of more distant stars caused by the motion of the Earth around the Sun. Two components of parallax are important in ordinary vision: a) the covering or revealing of the more distant contrasts by the nearer object (Figure 7.11c), so that there are local changes in intensity, contrast or colour; and b) the step in relative velocity at the step in the range (Figure 7.11b). Insects tend to fixate on a contrasting edge and head towards it, but it is less certain whether they perceive the edge as part of an object.

When locusts prepare to jump, they peer equally well at textured or black targets, seen against a textured background, and at the edge of a wide target (Figure 7.11a). When the difference in perceived velocity is made smaller by bringing up the background closer to the target, but keeping the target range constant, the locust jumps harder as though it interprets the smaller parallax as a measure of a greater range. It therefore assumes that the background is stationary and far away (Collett and Patterson 1991).

Bees can be trained to come for sugar to a platform bearing a pattern of stripes or random contrasts, seen against a similar more distant patterned background. They discriminate the platform by parallax (Figure 7.12). Their behaviour towards a moving contrast on a moving textured background also reveals that they detect the edge by the difference in motion, not merely by increased flicker. They land on a boundary that provides closing parallax (Figure 7.11b) and will not land on the far edge of a patterned surface beyond which they can see a more distant patterned background (opening parallax).

Bees can also be trained to come to an edge between two moving patterns or between a moving and stationary background. They land at right angles to the line of increasing velocity, whatever its direction. Once again, we see that bees recognise velocity and edges separately irrespective of direction or pattern and measure range by using a non-directional measure of angular velocity. They have several separate and parallel inputs for different features, but there is no evidence that they recognise separate objects by anything other than simple feature detectors.

Figure 7.12 Demonstration that bees detect the foreground moving over a patterned background when the bee itself moves. a) A sheet of perspex is raised above a 50/50 black-and-white background of random pixels at an adjustable height (h). A small target of random pixels is placed on the perspex sheet. The target is rewarded with a drop of sugar solution and drops of water are placed elsewhere on the perspex sheet. The target is moved at intervals and can be found by the flying bees only when raised above the background. b) As the target is lowered towards the background, bees trained to a target at a height of 5cm progressively lose it, but performance returns when the target is again raised to 5cm.



Source: After Srinivasan et al. (1989).

## Mechanisms of piloting

Two things can be said about mechanisms. First, we are nearing the stage when the different behaviour patterns are sufficiently well distinguished for us to restrict experiments about mechanisms to one or another of them, so that we have some chance of separating the parallel inputs and solving them one at a time.

Second, like all the rest of the insect visual inputs, the piloting mechanisms are likely to be simple feature detectors that operate independently but in parallel. I expect that angular velocity at a place on the eye will turn out to be measured separately from the direction of motion at the same place, that the optic flow at each place on the eye, range and flight speed will be measured as scalars, not as vectors; that direction of motion is likely to be a direction, not a vector; that all the measurements will be irrespective of the pattern and they will be correlated by coincidences, not by reassembly. Time will tell.

## Endnotes

1. A large part of the results in this chapter will be found in the publications of Srinivasan and also of Martin Egelhaaf. For information about the practical applications to flying vehicles, see Javaan Chahl on 'Google'.