

How Bees Exploit Optic Flow: Behavioural Experiments and Neural Models [and Discussion]

Author(s): Mandyam V. Srinivasan and R. L. Gregory

Source: *Philosophical Transactions: Biological Sciences*, Vol. 337, No. 1281, Natural and Artificial Low-Level Seeing Systems (Sep. 29, 1992), pp. 253-259

Published by: Royal Society

Stable URL: <http://www.jstor.org/stable/57057>

Accessed: 18-04-2018 03:55 UTC

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://about.jstor.org/terms>



JSTOR

Royal Society is collaborating with JSTOR to digitize, preserve and extend access to *Philosophical Transactions: Biological Sciences*

How bees exploit optic flow: behavioural experiments and neural models

MANDYAM V. SRINIVASAN

Centre for Visual Sciences, Research School of Biological Sciences, Australian National University, P.O. Box 475, Canberra, A.C.T. 2601, Australia

SUMMARY

Over the past thirty or so years, motion processing in insects has been studied primarily through the 'optomotor response', a turning response evoked by the movement of a large-field visual pattern. More recently, however, evidence is accumulating to suggest that, in addition to the optomotor pathway, there are other pathways which use motion information in subtler ways. When an insect moves in a stationary environment, the resulting optic flow field is rich in information that can be exploited to estimate the distance to a surface, distinguish between objects at different distances, land on a contrasting edge, or distinguish an object from a similarly textured background. This article reviews recent behavioural studies in our laboratory, investigating how honeybees accomplish such tasks.

1. INTRODUCTION

The visual systems of insects are exquisitely sensitive to motion. When placed in the middle of a rotating striped drum, most insects exhibit a tendency to turn in the direction of the drum's rotation. This response, termed the optomotor response, serves to stabilize the insect's orientation with respect to the visual environment, helping it maintain a straight course and simplifying the detection of objects moving within the environment.

The properties of the motion detecting system underlying the optomotor response are now well documented. Motion is detected in a direction-selective way, by comparing the visual signal arising from a small patch of visual space with a delayed (or otherwise filtered) version of the signal from a neighbouring patch (for a review, see Reichardt (1969)). The comparison takes the form of a nonlinear interaction which, in functional terms, resembles multiplication. Such an 'elementary movement detector' (EMD) will produce the strongest response when a visual pattern moves in a specific direction (the 'preferred direction') and the weakest response when the pattern moves in the opposite direction (the 'null' direction). A characteristic feature of this motion-detecting system is that its response to a moving striped pattern (grating) depends primarily upon the contrast frequency of the intensity fluctuations that the stripes produce as they move across a photoreceptor's field of view (Reichardt 1969; Borst & Egelhaaf 1989). The response does not depend directly upon the angular velocity of the grating, or upon its angular period. In

many insects, the lobula complex contains direction-selective movement-detecting neurons with large visual fields, typically covering one entire eye. It is almost certain that these neurons are involved in the optomotor response, because the characteristics of their responses closely resemble those of the optomotor response (Hausen & Egelhaaf 1989). The neural pathways subserving the optomotor response are thus becoming increasingly well defined.

Recently, however, it has become apparent that, in addition to the optomotor pathway, there are other pathways which use motion information in subtler ways. Owing to the small interocular separation (in comparison with humans and other vertebrates), most insects cannot rely on stereo vision to measure the range of objects at distances greater than a few centimetres; they need to exploit cues derived from optic flow. It has been proposed that locomoting insects perceive the distances of objects in terms of the speeds of their images on the retina, a higher image speed being associated with a smaller range (Collett & Harkness 1982; Horridge 1987). Indeed, the 'peering' head motions displayed by locusts, grasshoppers and mantids prior to jumping, or reaching out for a nearby twig, appear to be a means of judging the distance of objects in the visual environment by inducing motion of their images on the retina (Wallace 1959; Collett 1978; Eriksson 1980; Horridge 1986; Sobel 1990).

This paper reviews behavioural research in our laboratory, where we have recently demonstrated for the first time that flying insects – honeybees – use optic-flow cues to gauge the distances of surfaces,

discriminate between objects at different distances, land on a contrasting edge, and distinguish an object from a background.

2. EXPERIMENTS, RESULTS AND INFERENCES

Four kinds of experiments are described below, each designed to address a specific aspect of visually mediated behaviour that relies on cues derived from optic flow. In all of these experiments the procedure consisted of marking groups of *ca.* six bees and training them to fly into a laboratory, enter an experimental apparatus, perform a specific visual task, receive a reward of sugar solution and return to their hive. On a warm summer's day, a trained bee will continue to visit the apparatus every 5 min throughout the day.

(a) *Flying through a gap*

This series of experiments was inspired by the casual observation that when a bee flies through a hole in a window, it tends to fly through its centre, balancing the distances to the left and right boundaries of the opening. How does it gauge and balance the distances on the two sides? One possibility is that it balances the speeds of image motion on the two eyes. To investigate this, we trained bees to enter an apparatus which offered sugar solution at the end of a tunnel formed by two walls (Kirchner & Srinivasan 1989). Each wall carried a pattern consisting of a vertical black-and-white grating (figure 1). The grating on one of the walls could be moved horizontally at any desired speed, either toward the reward or away from it. After the bees had received several rewards with the gratings stationary, they were filmed from above, as they flew along the tunnel. When both gratings were stationary, the bees tended to fly along the midline of the tunnel, i.e. equidistant from the two walls (figure 1a). However, when one of the gratings was moved at a constant speed in the direction of the bees' flight – thereby reducing the speed of retinal image motion on that eye relative to the other eye – the bees' trajectories shifted toward the side of the moving grating (figure 1b). When the grating moved in a direction opposite to that of the bees' flight – thereby increasing the speed of retinal image motion on that eye relative to the other – the bees' trajectories shifted away from the side of the moving grating (figure 1c). These findings suggest that when the walls were stationary, the bees maintained equidistance by balancing the apparent angular speeds of the two walls, or, equivalently, the speeds of the retinal images in the two eyes. A lower image speed on one eye was evidently taken to mean that the grating on that side was further away, and caused the bee to fly along a trajectory closer to it; a higher image speed, on the other hand, had the opposite effect.

Were the bees really measuring and balancing image speeds on the two sides as they flew along the tunnel, or were they simply balancing the contrast frequencies produced by the succession of dark and

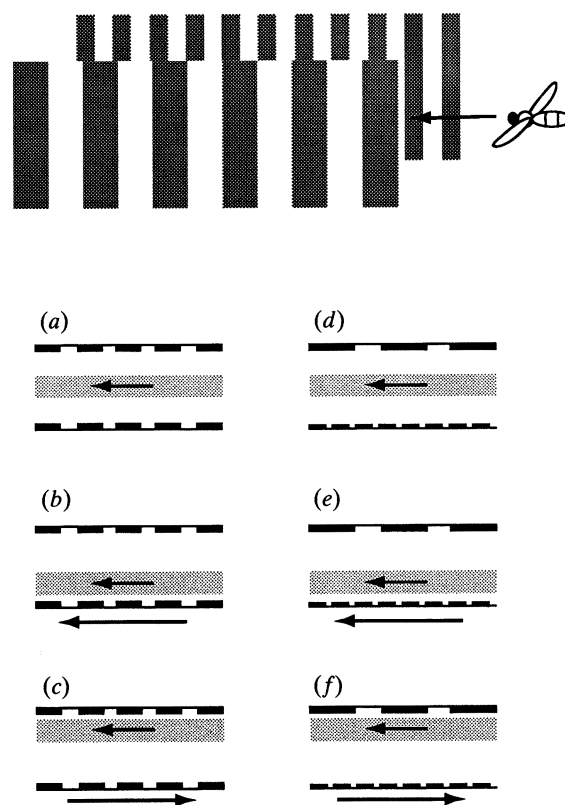


Figure 1. Illustration of experiment demonstrating that flying bees infer range from apparent image speed. Bees flying through a tunnel (40 cm long, 20 cm high) with walls 12 cm apart lined with vertical gratings (period 5 cm, top illustration) tend to fly along the midline of the tunnel when both gratings are stationary (a). However, when one of the gratings is in motion, bees flying in the same direction as the grating fly closer to the moving grating (b), whereas bees flying in the opposite direction fly further away from the moving grating (c). Similar responses are obtained when the experiment is repeated using gratings of different spatial periods (10 cm, 2.5 cm) on the two walls (d,e,f), indicating that the distances to the two walls are estimated in terms of the apparent angular speeds of their images, and that the bee's visual system is capable of computing the angular speed of a pattern irrespective of its spatial structure.

The shaded areas represent the means and standard deviations of the positions of the flight trajectories, analysed from video recordings of several hundred flights. Modified from Srinivasan *et al.* (1991).

light bars of the gratings? This question was investigated by analysing the flight trajectories of bees when the two walls carried gratings of different spatial frequencies (Srinivasan *et al.* 1991). When the gratings were stationary, the trajectories were always close to the tunnel axis, i.e. equidistant from the two walls, even when the spatial frequencies of the gratings on the two sides – and therefore the contrast frequencies experienced by the two eyes – differed by a factor of as much as four (figure 1d). When one of the gratings was in motion, the trajectories shifted toward or away from the moving grating (as described above) according to whether the grating moved with or against the direction of the bees' flight (figures 1e,f). These

results indicate that the bees were indeed balancing the speeds of the retinal images on the two eyes, and not the contrast frequencies. The above findings are true irrespective of whether the gratings possess 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 are equal, or considerably different (Srinivasan *et al.* 1991). Further experiments have revealed that – knowing the velocities of the bee and the pattern – it is even 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 (Srinivasan *et al.* 1991).

Taken together, the above findings suggest that the bee's visual system is capable of computing the apparent angular speed of a grating more or less independently of its contrast or spatial-frequency content. It is worth noting that if movement cues are to be exploited to estimate the range of a surface, it is necessary to use a mechanism that measures the speed of the image independently of its geometrical structure. This is evidently what the bee seems to possess, and is the kind of system that would enable an insect to fly through the middle of a gap between, say, two vertical branches, regardless of the textural properties of the bark on the two sides.

More recent work suggests that range perception is mediated by movement-detecting mechanisms that are largely insensitive to the direction of motion of the image on the eye. In other words, it is the speed of the image that is measured, not its velocity. The non-directionality of the underlying motion-detecting process, and the finding that angular speed, rather than contrast frequency is the relevant parameter, suggest that the motion-sensitive systems involved in computing range may be substantially different from those that mediate the optomotor response.

A non-directional speed detector offers a distinct advantage over a detector that measures speed along a given axis: the latter can produce large spurious responses when the orientation of an edge is nearly parallel to the detector's axis. For example, a detector configured to measure speed along the horizontal axis will register large horizontal velocities if it is stimulated by a near-horizontal edge moving in the vertical direction. This 'obliquity' problem can be avoided by using either a two-dimensional velocity detector, or a non-directional speed detector; of which the latter offers a simpler, more elegant solution (Srinivasan 1992a).

A simple model of a non-directional speed detector consists of four functional stages of processing (Srinivasan *et al.* 1991; Srinivasan 1992a). The moving image is first converted to a binary image composed of two levels ('black' and 'white'), by an array of neurons which possess high sensitivity to contrast and saturate at low contrasts. This neural image, which moves at the same velocity as the original image, is then spatially low-pass-filtered by a subsequent array of neurons, resulting in a moving neural image in which the abrupt edges of the binary image have been

converted to ramps of constant slope. The speed of the image can then be monitored by measuring the rate of change of response at the ramps. Accordingly, the neural image at this level is temporally differentiated by an array of physically responding neurons, giving a moving neural image composed of a train of pulses, one located at each edge of the binary image. The amplitude of each pulse will then be proportional to the rate of change of intensity at the corresponding ramp, and therefore to the instantaneous speed of the image at that location. A subsequent stage of rectification ensures that the response is positive, regardless of the polarity of the edge or the direction of movement. Thus, we have a scheme which measures the local speed of the image, independently of structure, contrast or direction of movement.

In the early stages of processing in the insect visual pathway – the lamina and the medulla – there is an abundance of neurons which exhibit phasic responses that saturate at low contrasts (Laughlin *et al.* 1987; D. C. Osorio, personal communication). However, it remains to be seen whether such neurons are indeed involved in the speed-based computation of range.

(b) *Discriminating objects at different distances*

Given that honeybees are eminently trainable – they can be trained to discriminate colours or shapes (for a review, see Wehner (1981)) – one can ask whether bees can be trained to distinguish between objects at various distances. We trained bees to fly over an artificial 'meadow' and distinguish between artificial 'flowers' at various heights (figure 2). The training was carried out by associating a reward with a flower at a particular height (Lehrer *et al.* 1988). The sizes and shapes of all 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, its distance from the eye), and not its position, or angular subtense, with the reward. Using this approach – details of which are described in Srinivasan *et al.* (1989) – it was possible to train bees to choose either the highest flower, the lowest flower, or even one at intermediate height. These findings indicate that distance preference in the honeybee is not necessarily a 'hard-wired' process geared to find the nearest object, i.e. the object whose image moves most rapidly on the retina. Rather, it is a process which is flexible and trainable.

The ability of bees to discriminate flower height is disrupted severely when the flowers are presented within a rotating striped drum (Lehrer & Srinivasan 1992). The optomotor response evoked by the rotating drum introduces strong distortions into the optic flow that the flowers would have otherwise induced as the bees flew over them. This indicates that optic flow cues are important in discriminating object range. However, rotation of the arena does not affect the bees' capacity to carry out other tasks, such as colour discrimination. Thus, rotation of the arena disrupts movement-related cues selectively; it does not 'confuse' the bees in a non-specific way.

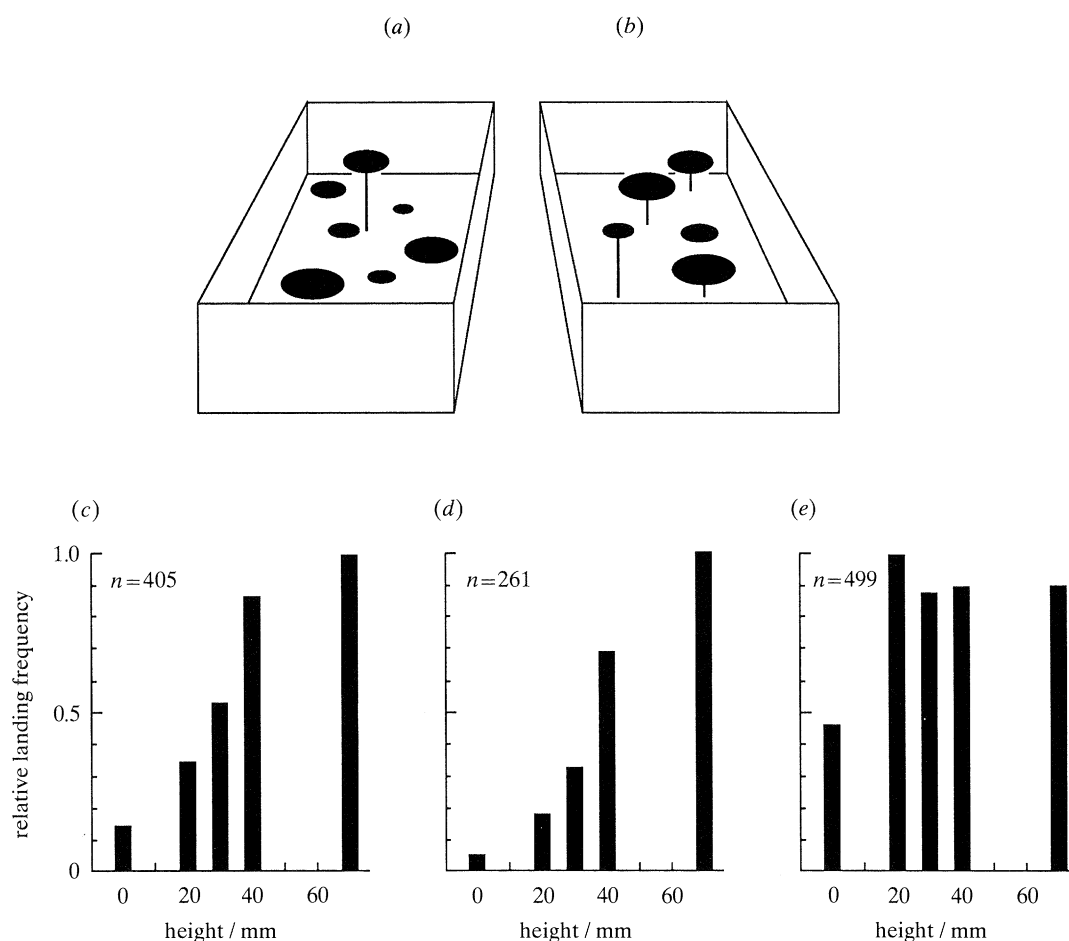


Figure 2. Experiment demonstrating that bees can be trained to distinguish between artificial 'flowers' at various heights in a 'meadow'. The training configuration (a) consists of one 'high' flower, carried on a 70 mm stalk, offering a reward of sugar water and six 'low' flowers on the floor of the meadow, carrying no reward. The test configuration (b) consists of five flowers of different diameters (ranging from 20 mm to 70 mm) and heights (ranging from 0 mm to 70 mm). The charts show the relative choice frequencies with respect to the flowers at various heights (normalized to a maximum value of unity) for (c) black flowers on a white background; (d) a colour combination that offers green contrast at the flower boundaries; and (e) a colour combination that offers blue contrast at the flower boundaries. n = total number of landings analysed. After Srinivasan *et al.* (1989).

We went on to examine the chromatic properties of distance perception by repeating the artificial-flower experiments using a fixed colour for the flower and varying the colour of the background. It turned out that distance discrimination was good even when the flower-background boundaries provided no contrast to the blue-receptor channel of the bee's visual system (figure 2d). Distance discrimination was very poor, however, when these boundaries provide no contrast to the green-receptor channel (figure 2e). Thus, it is the green channel, and not the blue one that plays a crucial role in this task. This suggests that the visual subsystem that deals with this type of distance perception is 'colour-blind', using inputs only from green receptors; although the bee's visual system as a whole possesses excellent trichromatic colour vision. Since motion perception in the bee is already known to be colour-blind (see Kaiser (1975) for a review, and Srinivasan (1992b)), the above finding is consistent with the notion that the bees were using motion cues to gauge the distances of the flowers.

The colour-blindness that is displayed by bees in

detecting motion, and in extracting depth from motion, has some interesting parallels with vision in primates, although the precise status of colour in primate motion perception is controversial (e.g. Livingstone & Hubel 1987; Papathomas *et al.* 1991). The emerging picture of insect vision is that the green-sensitive receptors drive a primordial, 'workhorse' subsystem which serves many of the primary visual functions such as maintaining a steady course via the optomotor response, deriving range information from motion cues, and segmenting objects by detecting their boundaries (as we shall show below). In bees, the blue and uv receptors probably feed into a separate system that is specialized for colour vision, which evolved more recently after the emergence of flowering plants.

(c) *Landing at a contrasting edge*

Bees can be readily trained to find, say, a black disc placed on a white background in the horizontal plane, by associating the disc with a reward of sugar solution.

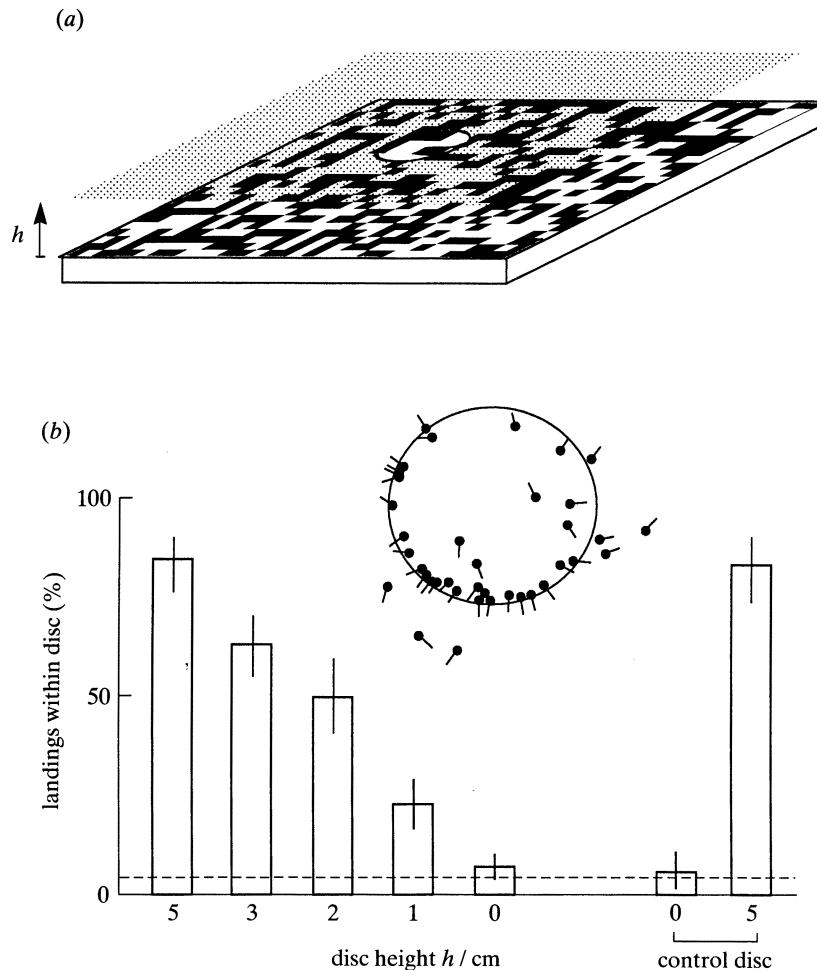


Figure 3. (a) Apparatus for training and testing the ability of bees to detect a textured disc (diameter 6 cm) presented at a height of h cm above a similarly-textured background (size 42 cm \times 30 cm, texture pixel size 5 mm \times 5 mm). (b) Results of tests using the apparatus. The bars on the left show the percentage of landings occurring within the disc, for various heights (h) of the disc above the background. The two bars on the right depict the results of a control experiment in which the disc was replaced by one of the same size but carrying a texture of one-third the original density. The dashed horizontal line depicts the level corresponding to random choice (2.3%). The results were obtained by analysing 1121 landings. The inset shows a sample of the distribution of landings of trained bees on a 6 cm diameter textured disc at a height $h=5$ cm. Most of the landings occur at the boundary between disc and background. Adaptive from Srinivasan *et al.* (1990).

When landing on the disc, it is striking that the bees do not land within the disc or near its centre – where the reward is located – but at the boundary of the disc (Lehrer *et al.* 1990). This preference for the boundary disappears, however, when there is no green contrast at the boundary (Lehrer *et al.* 1990), suggesting that motion cues are important in detecting the boundary. Evidently, the landing response is triggered by a rather specific pattern of optic flow: a rapidly approaching edge in the ventral field of view.

(d) Figure-ground discrimination

In all of the work described above, the ‘objects’ in the environment were readily visible to the insects, as they presented a strong contrast – in luminance or colour – against a structureless background. What happens if the luminance or colour contrast is

removed and replaced by ‘motion contrast’? To the human eye, a textured figure is invisible when it is presented motionless against a similarly-textured background. However, the figure ‘pops out’ as soon as it is moved relative to the background. This type of relative motion, termed ‘motion parallax’, can be used to distinguish a nearby object from a remote background. Is a bee capable of distinguishing a textured figure from a similarly textured background purely on the basis of motion parallax?

We probed this question by examining whether bees could be trained to find a textured figure when it was presented raised over a background of the same texture (Srinivasan *et al.* 1990). The figure was a disc, bearing a random black-and-white texture, carried on the underside of a transparent Perspex sheet that could be placed at any desired height above the background (figure 3a). It was found that bees were

indeed able to locate the figure and land on it, provided the figure was raised at least 1 cm above the background (figure 3*b*). A series of control experiments demonstrated that the cue used to locate the figure was the relative motion between figure and 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 (figure 3). These experiments show that bees are capable of using motion parallax as a cue to detect an object against a more remote background. They also reveal that the boundary between the object and background – where the abrupt change of range causes an abrupt change in the speed of motion of the image on the retina – is of special visual significance. Further experiments, using various kinds of striped patterns for the figure and the background, have shown that the bee's visual system is capable of detecting covering as well as shearing parallax at these boundaries. Models of neural mechanisms that would be sensitive to such forms of parallax are discussed in Srinivasan *et al.* (1990).

Curiously, the visual mechanism that detects motion boundaries does not seem to communicate with the part of the visual system that deals with learning and recognizing shapes. Thus, we find that while bees can easily learn to distinguish between, say, a dark rectangle and a dark circle presented against a white background in the vertical plane, they cannot be trained to distinguish between a textured rectangle and a textured circle, presented in relief against a similarly-textured background (M. V. Srinivasan & S. W. Zhang, unpublished results). This is despite the fact that the bees clearly approach the textured figures, showing that they definitely see them and distinguish them from the background. Evidently, the visual mechanisms involved in detecting motion boundaries are used for locating the edges of objects prior to landing on them, but not for memorizing or recognizing the objects' shapes.

The ability to detect objects through the discontinuities in motion that occur at the boundaries is likely to be important when an insect attempts to land on a leaf of a shrub. This is a situation where it may be difficult to distinguish individual leaves or establish which leaf is nearest, because cues based on contrast in luminance or colour are weak. That visual problems of this nature are not restricted to insects can be readily appreciated by anyone attempting to distinguish individual trees in a dense forest (Helmholtz 1866).

3. CONCLUDING REMARKS

The research summarized here shows that flying bees, and probably many other insects, use optic-flow cues in ways that are far subtler than those indicated by an analysis of the optomotor response. Their visual systems are capable of measuring the range of a surface or an object in terms of its apparent angular velocity, independently of the object's size, shape or

texture. Specific cues derived from optic flow are used to land on a contrasting edge, to distinguish an object from a similarly textured background, and to delineate the figure's boundaries by detecting motion discontinuities. While we can propose plausible neural models to account for the behavioural observations, the next challenge is to discover the neural circuits that actually engender these capacities.

This work was carried out in collaboration with Miriam Lehrer of the University of Zurich, Wolfgang Kirchner of the University of Wurzburg, and Shao-Wu Zhang and Adrian Horridge of the Australian National University.

REFERENCES

- Borst, A. & Egelhaaf, M. 1989 Principles of visual motion detection. *Trends Neurosci.* **12**, 297–306.
- Collett, T.S. 1978 Peering – a locust behavior pattern for obtaining motion parallax information. *J. exp. Biol.* **76**, 237–241.
- Collett, T.S. & Harkness, L.I.K. 1982 Depth vision in animals. In *Analysis of visual behavior* (ed. D. J. Ingle, M. A. Goodale & R. J. W. Mansfield), pp. 111–176. Cambridge, Massachusetts: M.I.T. Press.
- Eriksson, E.S. 1980 Movement parallax and distance perception in the grasshopper (*Phaulacridium vittatum*). *J. exp. Biol.* **86**, 337–340.
- Hausen, K. & Egelhaaf, M. 1989 Neural mechanisms of visual course control in insects. In *Facets of vision* (ed. D. G. Stavenga & R. C. Hardie), pp. 391–424. Berlin, Heidelberg: Springer-Verlag.
- von Helmholtz, H. 1866 *Handbuch der physiologischen Optik*. Hamburg: Voss Verlag. (Translated by J. P. C. Southall, 1924; reprinted Dover, New York, 1962.)
- Horridge, G.A. 1986 A theory of insect vision: velocity parallax. *Proc. R. Soc. Lond. B* **229**, 13–27.
- Horridge, G.A. 1987 The evolution of visual processing and the construction of seeing systems. *Proc. R. Soc. Lond. B* **230**, 279–292.
- Kaiser, W. 1975 The relationship between visual movement detection and colour vision in insects. In *The compound eye and vision of insects* (ed. G. A. Horridge), pp. 359–377. Oxford: Clarendon Press.
- Kirchner, W.H. & Srinivasan, M.V. 1989 Freely flying honeybees use image motion to estimate object distance. *Naturwissenschaften* **76**, 281–282.
- Laughlin, S.B., Howard, J. & Blakeslee, B. 1987 Synaptic limitations to contrast coding in the retina of the blowfly *Calliphora*. *Proc. R. Soc. Lond. B* **231**, 437–467.
- Lehrer, M. & Srinivasan, M.V. 1992 Freely flying bees discriminate between stationary and moving objects: performance and possible mechanisms. *J. comp. Physiol. A* (In the press.)
- Lehrer, M., Srinivasan, M.V. & Zhang, S.W. 1990 Visual edge detection in the honeybee and its chromatic properties. *Proc. R. Soc. Lond. B* **238**, 321–330.
- Lehrer, M., Srinivasan, M.V., Zhang, S.W. & Horridge, G.A. 1988 Motion cues provide the bee's visual world with a third dimension. *Nature, Lond.* **332**, 356–357.
- Livingstone, M.S. & Hubel, D.H. 1987 Psychophysical evidence for separate channels for the perception of form, color, movement and depth. *J. Neurosci.* **7**, 3416–3468.
- Papathomas, T.V., Gorea, A. & Julesz, B. 1991 Two carriers for motion perception: color and luminance. *Vision Res.* **31**, 1883–1891.
- Reichardt, W. 1969 Movement perception in insects. In

- Processing of optical data by organisms and by machines* (ed. W. Reichardt), pp. 465–493. New York: Academic Press.
- Sobel, E.C. 1990 The locust's use of motion parallax to measure distance. *J. comp. Physiol.* **167**, 579–588.
- Srinivasan, M.V. 1992a How flying bees compute range from optical flow. In *Nonlinear vision* (ed. R. B. Pinter). New York: CRC. (In the Press.)
- Srinivasan, M.V. 1992b How insects infer range from visual motion. In *Visual motion and its role in the stabilization of gaze* (ed. F. A. Miles & J. Wallman). Amsterdam: Elsevier Press. (In the Press.)
- Srinivasan, M.V., Lehrer, M. & Horridge, G.A. 1990 Visual figure-ground discrimination in the honeybee: the role of motion parallax at boundaries. *Proc. R. Soc. Lond. B* **238**, 331–350.
- Srinivasan, M.V., Lehrer, M., Kirchner, W. & Zhang, S.W. 1991 Range perception through apparent image speed in freely-flying honeybees. *Vis. Neurosci.* **6**, 519–535.
- Srinivasan, M.V., Lehrer, M., Zhang, S.W. & Horridge, G.A. 1989 How honeybees measure their distance from objects of unknown size. *J. comp. Physiol. A* **165**, 605–613.
- Wallace, G.K. 1959 Visual scanning in the desert locust *Schistocerca gregaria*, Forskal. *J. exp. Biol.* **36**, 512–525.
- Wehner, R. 1981 Spatial vision in insects. In *Handbook of sensory physiology*, vol. VII/6C (ed. H. Autrum), pp. 287–616. Berlin, Heidelberg: Springer-Verlag.

Discussion

R. L. GREGORY (*Department of Psychology, University of Bristol, U.K.*).

Would Moire patterns upset flight, and be useful experimentally?

M. V. SRINIVASAN. Yes, indeed: Moire patterns would provide a useful means of manipulating the relationship between the bee's motion and the apparent motion of the pattern of the retina.