Available online at www.sciencedirect.com
SCIENCE DIRECT®
Journal of Insect Physiology 51 (2005) 243–266
Journal of Insect Physiology
www.elsevier.com/locate/jinsphys

Review

The spatial resolutions of the apposition compound eye and its neuro-sensory feature detectors: observation versus theory

Adrian Horridge*

Research School of Biological Sciences, Australian National University, P.O. Box 475, Canberra, ACT 2601, Australia

Received 22 September 2004; received in revised form 18 November 2004; accepted 22 November 2004

Abstract

For 100 years three ideas dominated efforts to understand the apposition compound eye. In Müller's theory, the eye viewed the panorama through an array of little windows without overlaps and without gaps, with no details within windows. Spatial resolution then depended on the interommatidial angle ($\Delta\phi$) and the number of ommatidia. In the second proposal, the insect detected the temporal modulation of the light, which was limited by the aperture of the lens and the wavelength, assuming good focus. Modulation is the change of intensity in the receptor, usually caused by motion of a spatial contrast in the stimulus. Thirdly, motion was detected from the successive temporal modulations at adjacent visual axes. Recently, two more principles arose. The light-sensitive elements, called rhabdomeres, project through the nodal point of the lens to the outside world, and the resolution was limited by their grain size, like the pixels in a digital camera. Finally, detection of contrast and colour was limited by the signal/noise ratio (SNR) which was improved by brighter light and more visual pigment.

These five physical principles provide satisfying explanations of eye function but they all originated from theory. Actual measurements of resolution depend on the operation of the test. The visual system of the honeybee recognizes a limited variety of simple cues, but there is no evidence that the pattern of ommatidial stimulation is re-assembled, or even seen. The known cues are: the temporal modulation of groups of receptors, the direction and angular velocity of motion, some measure of the spatial disruption of the pattern or the length of edge (related to spatial frequency and contrast), colour, the intensity, the position of the centre and the size of large well-separated areas of black or colour, the angle of orientation of a bar or grating, radial or tangential edges, and bilateral symmetry. Neurons connected to more than two adjacent ommatidia collaborate in the detection of cues, and the resolution depends on the neuro-sensory feature detectors at work at the time. Although some behavioural and electrophysiological measurements give a spatial resolution similar to the interommatidial angle, different spatial properties of neuro-sensory detectors predominate at different light intensities and with a diurnal rhythm. During the long history of this topic, the belief that the resolution ought to be $\Delta\phi$ has frequently been overturned by experimental measurement.

Keywords: Insect; Visual; Resolution; Cues; Parallel pathways

Contents

*Fax: +61 2 6125 3808.
E-mail address: horridge@rsbs.anu.edu.au (A. Horridge).

0022-1910/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jinsphys.2004.11.018

1. Measurements of various resolutions

1.1. Definitions of $\Delta\phi$

Most insects, including bees, have horizontal rows of hexagonal facets side by side at the front of the eye (Fig. 1b), but flies have vertical rows at the front (Fig. 1a) and horizontal rows at the side. Accordingly, the term interommatidial angle ($\Delta\phi$) must be defined in a way that accommodates these differences. Many authors use $\Delta\phi$ for the angle between adjacent optical axes irrespective of the direction on the eye, which is convenient for eye maps of $\Delta\phi$. The convention followed here will be to use $\Delta\phi$ in this way, and less frequently, $\Delta\phi_H$ and $\Delta\phi_V$ as shown in Figs. 1c and d, as commonly found in the literature, reminding readers to ascertain the convention used in each case. An eye like that of the honeybee has very different values of $\Delta\phi_H$ and $\Delta\phi_V$, and their ratio varies with the eye region, but it is not commonly appreciated that in the honey bee the array of axes remains isotropic in angular co-ordinates (Fig. 4). Lacking data, some authors take an average for the whole eye. For example, when comparing species of bees, Jander and Jander (2002) used a formula worked out by Land (1997a), the average $\Delta\phi = \sqrt{(23818/n)}$ where n is the number of ommatidia.

To avoid confusion, the receptor array is best represented as a two-dimensional eye map with every visual axis (Dahmen, 1991) or every five axes (Horridge, 1978) in angular co-ordinates, but this presents problems of drawing a sphere on a flat sheet (see Figs. 4 and 10). Most compound eyes are not spherical, and the radius of a horizontal row is usually different from that of the vertical row at the same place. Further, the optical axes are often not perpendicular to the cornea. These complications spoil the measurement of $\Delta\phi$ except by optical methods. As we will see, a study of eye maps (Figs. 1e, 4 and 10) and the experimental tests of resolution suggest that the number of visual axes per unit solid angle is a better measure of eye performance than $\Delta\phi_H$ and $\Delta\phi_V$.

1.2. Early observations

Philosophers of scientific method, from Aristotle to Kuhn, discussed how scientific advances are made from the mutual interaction of theory and observation. Some topics, however, provide a miscellaneous collection of efforts, unsteady progress, re-inventions of the wheel, and ignored contributions that are eventually revealed as progress. The resolution of the insect eye is a splendid example of circuitous advance. As often as not, errors persisted for decades but good observations were not absorbed, because the accepted story appeared to be the way that it ought to be, and was in the text books.

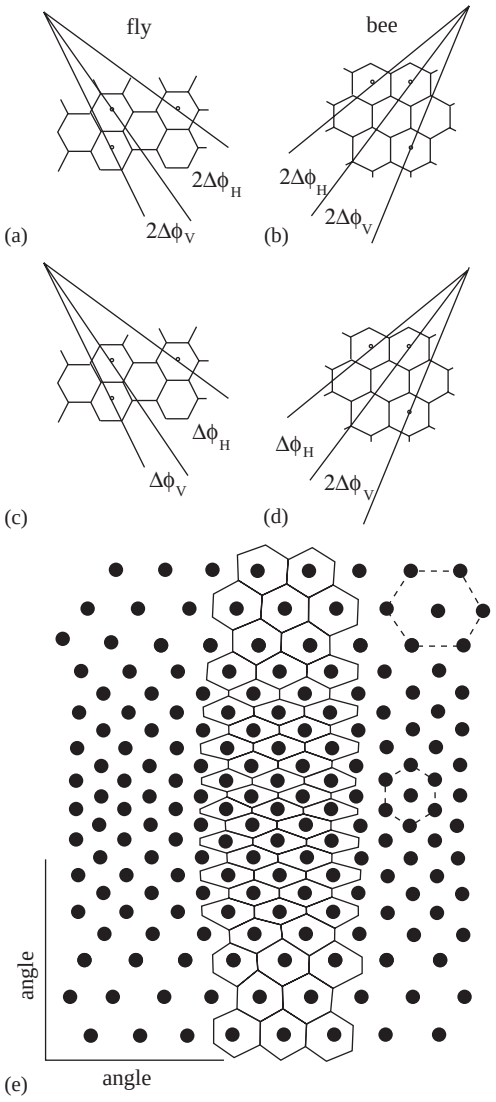

Fig. 1. Ommatidia at the front of the eyes in fly and bee. (a,c) Fly eyes have vertical and diagonal rows of facets. (b,d) Bee eyes have horizontal and diagonal rows, in linear co-ordinates. (a,b) Conventions for measuring $\Delta\phi$ adopted by Stavenga (1979), Land (1997a). (c,d) Conventions commonly found in the literature, which should be carefully examined in every case. (e) The arrangement of visual axes of a bee in angular co-ordinates, showing in principle how the vertical compression along the horizontal midline creates vertical rows of axes and distorts the hexagonal facets in angular co-ordinates, but the array of visual axes is almost isotropic everywhere (Fig. 4). For details of the fly, see Stavenga (1979), for *Gerris*, see Dahmen (1991), for others, see Horridge (1978).

Robert Hooke (1665, page 179) inferred, but did not observe, a minute reversed image behind each eye facet of a drone fly. He realized the difficulty of smoothly uniting an array of reversed images and assumed that only the central rays of each image contributed to vision. The repeated images behind each facet of the corneas of several insects were vividly described in 1695 by van Leeuwenhoek (Bernard, 1966, p. 4). They are most easily seen in flies and butterflies. They did not divide the view like small panes in a window, but had the same image in each facet, which has often confused popular writers.

The images were repeatedly described during the following centuries (refs. in Grenacher, 1879; Wehner, 1981). In 1826, Johannes Müller, although aware of them, did not even try to accommodate the available observations. Like Hooke, he assumed that the light passing through a single facet was concentrated to a narrow receptor, so each facet must look in a single direction (Fig. 2a) but that the panorama is divided without overlaps and without gaps (Fig. 2b). The theory was a primary school simplification of the truth, but, like Hooke, Müller was an outstanding, versatile, respected scientist of his day, and his text book carried sufficient authority to inhibit alternatives even to the present time.

The first substantial descriptions were made by a histologist, Grenacher (1879), who described small refractile inclusions, each called a rhabdomere, that he inferred to be sensitive to light. Some groups of insects had 6, 7 or 8 separate rhabdomeres in the right place to receive the inverted image, so there could be several directional sensations in each ommatidium. These open rhabdomere eyes, overlooked by Exner (1891), are found in a large variety of common insects, notably the bugs, flies, many beetles, and in the primitive wingless insect *Lepisma*, but, apart from the fly, are not given their fair share of attention in modern accounts.

Grenacher also confirmed that in some groups of insects the rhabdomeres were fused to a single rod, called a rhabdom, that extended inwards from the tip of the cone. As Exner noted later, Grenacher inferred that these eyes could have only one directional sensation for each ommatidium, but possibly more than one sensation of colour. The fused rhabdom is found in many of the

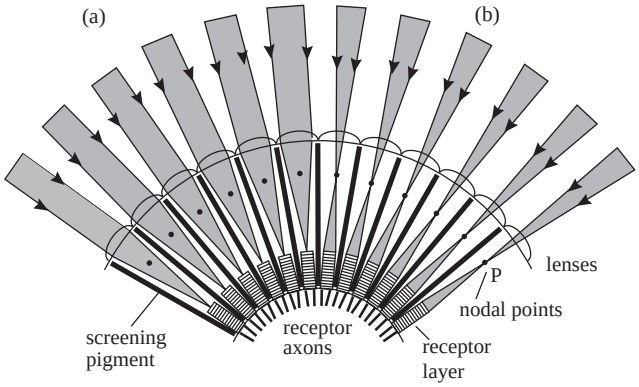

Fig. 2. Representations of Müller's theory. (a) A parallel beam is focused to a point in each ommatidium, as many authors supposed, with increasing gaps between the beams further from the eye. (b) A more realistic representation with the receptor projected through the nodal point and with sampling independent of range.

common large insects that fly by day, notably bees, wasps, butterflies, locusts, crickets, mantids, dragonflies and in the primitive wingless insect *Machilis*.

Grenacher argued that ommatidia with separate rhabdoms would be able to detect 6 or 7 separate parts of the image. He also inferred that the field size would depend on the size of the rhabdomere, that broad rhabdomeres would function at lower light levels than narrow ones, and that ommatidia with large apertures would be more sensitive than those with small apertures. These important compromises between sensitivity and resolution were neglected for a century.

In his paper (1876) and book (1891), Sigmund Exner assumed that the light is concentrated upon the end of the rhabdom rod by the curvature of the cornea and refraction in the cone. A check of the species that he examined reveals one, the fly *Eristalis*, that has separate rhabdomeres, but he did not illustrate them. He described the rhabdom in apposition eyes as a single light guide that absorbed light along its length, which was a good approximation for large day-flying insects but it omitted the others in the majority.

At the end of the 19th century, it was well known that the resolution of an optical instrument is limited by the aperture (D) and the wavelength of the light (λ). At the best focus, parallel rays are concentrated to a blur circle of minimum $2.4\lambda/D$ radians in full width, or λ/D radians at the 50% intensity contour (Fig. 3a). Mallock (1894) took the next step, which is quite separate from the calculation of the best focus. The bee was supposed to "see" the panorama. Mallock argued that the inter-ommatidial angle ($\Delta\phi$) should be matched to the full width of the blur circle ($2.4\lambda/D$) so that the image of a distant point will just touch the receptor of one ommatidium as it leaves the adjacent one, so $\Delta\phi = 2.4\lambda/D$, and $D\,\Delta\phi = 2.4\lambda = 1.2\,\mu m$ for green light. Since $\Delta\phi = D/R$ radians, where R is the radius of the compound eye, the radius should be proportional to the square of the facet diameter. A survey of 18 insects of different sizes gave a reasonable match between $\Delta\phi$ and λ/D. This theory was neglected for 60 years. It assumed a single rhabdom of negligible width on axis, an inverse relation to the wavelength, contrast sensitivity similar to a human eye, and a suitable test with two lights, none of which were realized.

The generally accepted view that insects actually see things was in some ways a block to progress. For example, Exner's (1891) photograph of a letter R on a window, taken through the cornea of a firefly, demonstrated the image in an unusual eye. In standard texts it was used to illustrate insect acuity as 1/60th that of the human eye (Wigglesworth, 1965).

In the early years of the next century, Vigier (1907, 1909) in France, Cajal (1909) in Spain, and Dietrich (1909) in Germany, described the separated rhabdomeres of the fly and inferred that they looked in different directions through every facet. There are six (1–6) in a peculiar pattern that is not quite a ring surrounding two (7 and 8), one above the other, that form a thinner central rod (see inset, Fig. 6). Vigier carefully described how the nerve fibres from the six outer ones that run in different directions below the neighbouring ommatidia could bring together the six views in the same direction, as seen through six separate facets. This amazing inference was overlooked for 50 years.

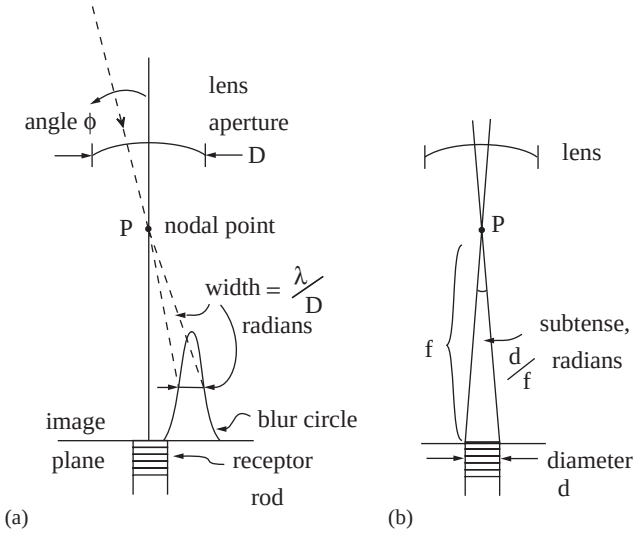

Fig. 3. The match between optics and anatomy in the formation of the receptor field. (a) The diffraction component. With a point source, a lens of aperture D forms a diffraction image (called a blur circle) of angular width λ/D radians at the 50% level of intensity in the focal plane of the lens, subtended at the nodal point, P. As a point source is moved outside the eye, the blur circle moves across the receptor profile. (b) The receptor subtense component. The rhabdom of width d μm in the focal plane of the lens subtends an angle of d/f radians at the nodal point. The receptor field, of angular width $\Delta\rho$ at the 50% contour, is the product of the blur circle and the absorption profile of the receptor. For narrow receptors, when d/f is negligible, this reduces to $\Delta\rho = \lambda/D$ but the sensitivity is sub-optimal. For wide receptors, when λ/D is negligible, $\Delta\rho \approx d/f$.

Unaware of Mallock's work, Barlow (1952) assumed a match between the minimum field size (λ/D), and a minimum interommatidial angle ($\Delta\phi$). He considered three ommatidia in a row, with $\Delta\phi$ such that two distant point sources excite the two outer ommatidia sufficiently more than the central one. He predicted that $\Delta\phi$ should be less than λ/D but greater than about $0.5\lambda/D$. Again there were two separate principles, namely the best focus and the optimum separation of neighbouring inputs. Barlow was unaware of measurements by Baumgärtner (1928) and assumed an isotropic eye. Although the data were incorrect, in a number of eyes of Hymenoptera of different sizes, the average eye radius was proportional to D^2, which was compatible with the theory. There remained the problem of devising a test with two lights.

1.3. Early experimental work on the bee

Measurements of resolution were slow to appear. From sections, Baumgärtner (1928) measured the anatomical $\Delta\phi$ of the honeybee eye, ranging from $\Delta\phi_H = 2.4^\circ$ at the front to 2° at the side and 4° at the back, and $\Delta\phi_V = 1^\circ$ (convention as in Fig. 1d). The whole eye was surveyed by Seidl (1982), who located the actual optical axes, showing the exact vertical compression, but Seidl's data remained unpublished until recently (Giger, 1996; Land, 1997a, b). Although the design of the bee eye was described in angular co-ordinates (Horridge, 1978, 1980, Fig. 3 therein), even today it is not realized that the vertical compression produces an array of axes that is nearly isotropic with $\Delta\phi \approx 1.65-1.7^\circ$ in all directions, and vertical rows of axes at the centre of the eye (Fig. 4).

Baumgärtner measured the minimum angular sizes of blue and yellow rectangles that were detected or discriminated from a distance by flying bees, and showed that a coloured rectangle is more easily detected if the long side is vertical rather than horizontal. He correlated this result with his measures of $\Delta\phi_H$ and $\Delta\phi_V$ (but see Fig. 4) and he inferred that the critical factor is the number of ommatidia involved (see Section 2.8). For decades, however, Baumgärtner's work was quoted as evidence that the resolution of the insect eye is limited directly by $\Delta\phi$.

Measurements in Hecht's laboratory at Columbia showed that the relative numbers of untrained bees that walked towards two lights were proportional to the flicker frequencies. The maximum frequency was about 55 Hz, similar to the human eye. The bees went to the flickering light of larger area, and lights of equal frequency were equally effective when they had the same area multiplied by intensity (Wolf, 1935). This result tells us that untrained bees do not look for frequency or area, only the total photon flux (Fig. 5).

The resolution was measured by allowing each bee to walk freely on an inclined glass plate beneath which a regular grating moved (Hecht and Wolf, 1929). The bees turned against the direction of the motion, so this was not an optomotor response. The minimum stripe period was near 2° in bright light, irrespective of orientation. They were aware that the minimum blur circle width was $\approx 1.14^\circ$. Referring to Baumgärtner, the authors inferred the limiting factor to be diffraction, not $\Delta\phi$, which was too large. In dim light the minimum period increased to 30°, so they postulated other receptors with wide fields and further directional motion detectors with a wide span. The actual mechanism is unknown, but Dubs et al. (1981) recorded extraordinary sensitivity in the fly lamina.

Early measures of the bee's contrast resolution are too large. By adjusting the contrast between the stripes in a moving grating, Wolf (1933) obtained a minimum

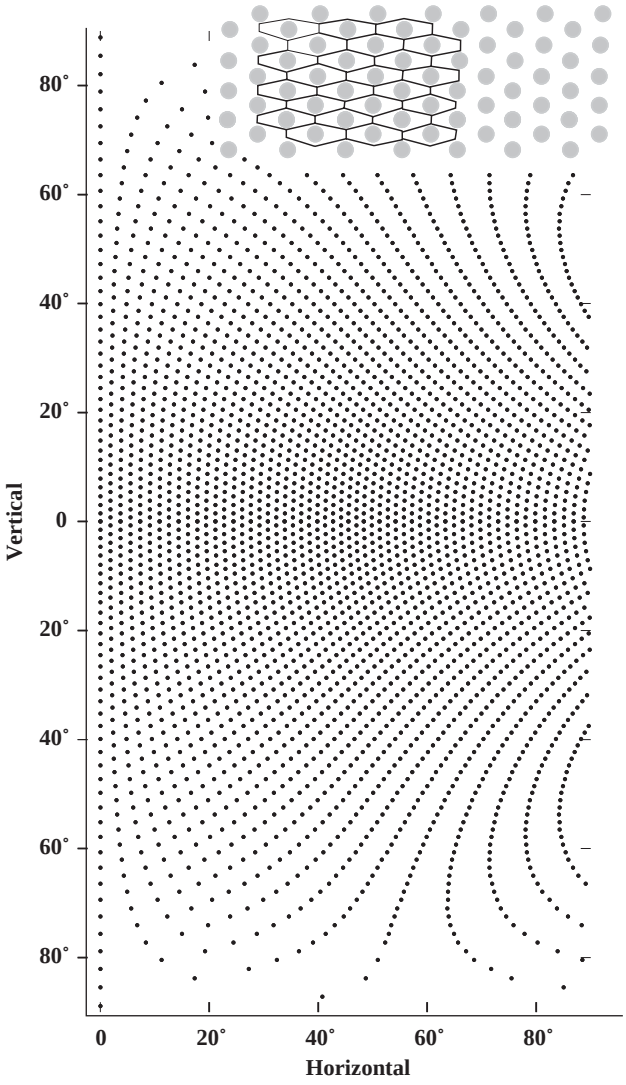

Fig. 4. Map of the front of the left eye of the worker honey bee, with each visual axis shown in angular co-ordinates on equal horizontal and vertical scales. The densest region is near the equator, about 45° from the front, which is towards the left. Near the centre, the rows of axes appear to be vertical, but the rows of hexagonal facets are actually horizontal, as shown in the inset at the top and Fig. 1e. Data from Seidl (1982), digitized by Giger (1996), see http://cvs.anu.edu.au/andy/beye/descript.html (Fig. 3).

$\Delta I/I = 0.24$ in bright light. Similar ratios were obtained with the optomotor response of fixed flying bees (Kunze, 1961). These strange results suggest to me that the honey bee has quite different sensitivities for separate detector systems. Later results (Pinter, 1979; Giurfa and Vorobyev, 1998) suggest that they might have been caused by the use of large targets. $\Delta I/I$ can be as small as 0.5% in the optomotor response of the fly *Musca* in bright light (Fermi and Reichardt, 1963; Eckert, 1973), 0.3% in the locust (Thorson, 1966), and $<1.0\%$ in motion-sensitive neurons of the bee (Bidwell and Goodman, 1993). An absolute limit of 0.5% in bright light is a reasonable assumption.

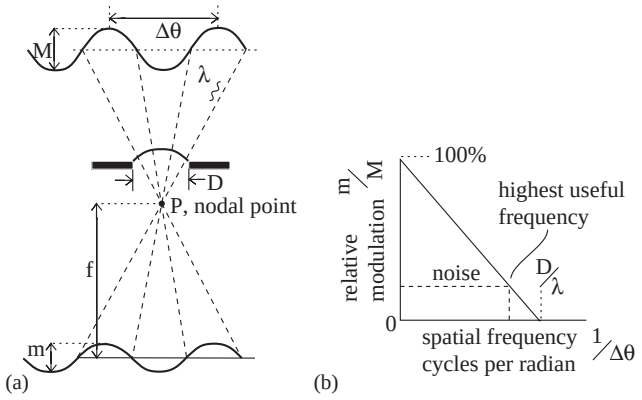

Fig. 5. The diffraction limit with an extended grating as object. (a) A sinusoidal grating of modulation M is focused by a lens of aperture D to an image with relative modulation m, given by m/M in (b). The relative modulation m/M is zero at $\Delta\theta = \lambda/D$, but the practical limit is set at a larger period by the noise level. Note that modulation detection does not involve perception of the pattern.

To allow rapid measurements of threshold intensity to prevent adaptation, the bee was held with its head projecting from the end of a tube. When a grating was moved in front of the eyes, the antennae pointed towards the direction from which the motion came. After 30 min in the dark, there was a 1000-fold increase in sensitivity to a coarse grating (Wolf and Zerrahn-Wolf, 1935). This result tells us that the bee is remarkably insensitive to light by day, and may have a sensitivity switch for work in the hive. There is rapid adaptation of the diurnal receptor potential (Baumann, 1975), but the anatomical changes in the retina appear to be confined to movement of intracellular granules towards the rhabdom in the light and away from it in the dark (Kolb and Autrum, 1972).

Temporal modulation frequency has long been considered a factor in pattern perception. Quite early, Hertz (1929–1931, 1933) discovered that bees are able to discriminate between otherwise similar stationary patterns that differ in length of edge. It was one of the first parameters discovered, but it was a long time before the parts played by motion and colour were elucidated (see Section 2.1).

The preferences of untrained bees for different sector wheels, checkerboards or parallel stripes were the same when there was the same total length of edge. Motion of the pattern increased the attraction. By adjusting the area visible, a fine grain pattern with many edges could be equal to one with a coarser grain (Wolf, 1935). These experiments tell us, all other factors being equal, that naïve bees measure something related to spatial frequency but ignore the actual pattern.

For the bee, $\Delta\phi_H$ varies between 3.0° at the front of the eye, 2.1° at the side and 3.8° at the back (convention as in Fig. 1d), but behavioural measures were inconsistent. As said above, Hecht and Wolf (1929) found a minimum period of 2° in the directional detection of motion of a black and white grating by freely walking bees. In an optomotor drum the bee's response fell to zero at a period of 4–5° (Hertz, 1933). The maximum separation of two windows through which motion was detected was 7–8° (Kunze, 1961). For discrimination between horizontal and vertical gratings in bright light, a threshold period of 2.8° was measured for trained bumblebees by Macuda et al. (2001). In the honey bee, Warrant et al. (1996) found a large minimum period of 4°, with an increase to near 8° at low light levels. Assuming a constant value of $\Delta\rho = 2.6°$ (the width of the angular sensitivity curve at the 50% sensitivity level), and constant $\Delta\phi_H = 1.9°$ (Fig. 1d), they inferred spatial and temporal summation in dim light.

Recently, Warrant et al. (2004) have turned to the same problem in nocturnal bees, which return in extremely low light levels through the tropical forest to their nests in the ends of hollow sticks. The ommatidia are relatively normal, except that the rhabdom is 350 μm long and 8 μm wide, giving a dark-adapted $\Delta\rho = 6.3°$. The response to a short flash is also more drawn out. The bees clearly detect small contrasts at the ends of sticks. At the ambient illumination, the calculated photon capture by a single receptor cell is about one hundredth of that required to detect a contrast by the brightness difference between adjacent areas, because the signal/noise ratio is so low. Accordingly, the authors infer a spatial summation, but on the other hand, there must be a narrowing of the fields at lamina level by lateral inhibition, as for example in *Velia* (Meyer, 1971), to account for the resolution of the nest entrance. They give no measurements of spatial resolution of landmarks or the detection of white cards of various areas, or tests with coloured cues, and rely upon a formula that omits the size of the response to single photons. Maybe the nocturnal bee is like the night-flying locust or mantid, with huge responses to single photons (Horridge et al., 1981), and the pertinent question is why the honey bee is insensitive, with minute responses to individual photons (see Vorobyev et al., 2001).

When trained honey bees were tested for discrimination of horizontal and vertical gratings separately against a plain grey target of the same average intensity, the minimum period in daylight was near 2.5° in both cases (Srinivasan and Lehrer, 1988), and the limit was inferred to be temporal modulation, not $\Delta\phi$.

The diversity of results may be due to different criteria of success. Also, bees differ, patterns are not perfect, and factors such as temperature and the age of the bees have an effect. The undersampling by the bee eye did not show up because the gratings are discriminated at the limit by temporal modulation cues, not by separation of

the bars or orientation cues. Accordingly, $\Delta\phi$ is not the limiting factor.

Further analysis confirmed a limit near 2.5° on horizontal and vertical gratings tested separately against a plain grey. When orthogonal test gratings are oblique, they show no temporal modulation difference and the bees discriminate the orientation cue, in which case the inputs are only the green receptors, and the minimum period is near 3° (Horridge, 2003c). The modulation generated by a grating is summed over a large solid angle, a point often missed by those who regard the resolution of a grating as a limiting factor in foraging ability.

1.4. Early work on the fly

With the same technique as used for the bee, Hecht and Wald (1934) measured the resolution of *Drosophila*, where the ommatidia are in vertical rows (Fig. 1), and found that the response in bright light fell to zero at a period of 9.3°, unlike the bee where the limit was 2°. The discrepancy caused some comment, of which more later (compare different insects, Fig. 7).

In a pioneering study, nowadays forgotten, the responses of *Drosophila* to moving gratings at different periods were plotted by von Gavel (1939) at different light intensities. The central region of the eye had the highest resolution. At a period near 9° the response reversed, but in low light levels the reversal occurred at a larger angle, as if the spatial tuning of the motion detectors had increased. The reversal was correctly explained as a Moiré effect between $\Delta\phi$ and the grating.

By 1950, it was still not known whether the angle between functional visual axes in the fly was the angle between receptor axes or between ommatidial axes. In any case, the anatomical angle measured from sections was not the correct angle between optical axes. To explain why the minimum period increased so much at low light levels, Hecht had championed the improbable idea of a wide variety of receptor field sizes and sensitivities. The few behavioural measures of resolution in bees or flies before 1964 had all cast doubt on Müller's theory, one way or another, but they were ignored.

1.5. Modern analysis

In the late 1950s a Dutch physicist, de Vries and his student Kuiper (1966) re-discovered and improved upon Mallock's (1894) theory. Kuiper calculated the receptor field width from the diffraction at the lens, the angular width of the fly rhabdomeres (subtended at the nodal point) and the properties of rhabdomeres, which, up to 2 μm in diameter, act as absorbing light guides. Beyond 2 μm, where ray optics applied, Kuiper predicted that the receptor field width ($\Delta\rho$) would be the angular subtense of the rhabdomere at the nodal point. Most rhabdomeres and rhabdoms have a significant width and so $\Delta\rho$ is larger than λ/D, even if the focus is good. $\Delta\rho$ would be independent of the wavelength, because at short wavelengths more modes of vibration would be caught by each rhabdomere, compensating for the narrower blur circle caused by shorter λ. Conceptually brilliant because it included diffraction, light guides and anatomy, it said nothing about $\Delta\phi$.

A burst of pioneering work followed the post-war improvements in technology. First, the spatial resolution of the fixed flying fly (Götz, 1965), locust head rotation (Thorson, 1966) and fixed flying bee (Kunze, 1961) was measured in the optomotor response with gratings. The Hassenstein/Reichardt model assumed that the detection of the motion of a contrast was done by adjacent visual axes, and the true situation was never properly published (see Fig. 7). Secondly, the angular sensitivity of individual receptors was directly measured by intracellular recording in the blowfly (Burkhardt and Streck, 1965), the locust (Tunstall and Horridge, 1967), and the bee (Laughlin and Horridge, 1972). The angular sensitivity curve approximated to a Gaussian curve that had a width $\Delta\rho$ at the 50% level of sensitivity. $\Delta\rho$ was called the acceptance angle or half-width. As illustrated below (Section 1.8), in these early recordings $\Delta\rho$ was usually too large because the optics was damaged by the electrode.

The Gaussian shape of the receptor fields was used by Götz (1965) to calculate the temporal modulation in the receptors directly from the contrast in a moving grating, cutting out the optical transfer function. As the grating period decreases, the temporal modulation falls to threshold roughly when the grating period equals $\Delta\rho$. The optomotor response falls to zero sooner and reverses direction, because the fly detects the correlation of the temporal modulations caused by the moving edges interacting with the array of ommatidia in a Moiré effect, not the layout of the grating. The cross-over point gives an inferred value of $2\Delta\phi_H$, and the shape of the response curve gives $\Delta\rho$. For *Drosophila*, the cross-over point was at 9.2° and calculated $\Delta\rho$ was 3.5°. There cannot be an accurate measure of $\Delta\phi$ because at cross-over there is not a zero response, but a balance between opposing directions from different eye regions. An optimum $\Delta\phi/\Delta\rho = 1.61$ was based on the Reichardt theory of motion detection in bright light (Götz, 1965); or, with consideration of low light levels, $\Delta\phi/\Delta\rho = 1.67$ (Srinivasan and Dvorak, 1980).

Thanks to the revival of the methods of staining nerve fibres, Braitenberg (1967) and Kirschfeld (1967) confirmed the pattern of summation of the receptor axons (Fig. 6), such that the angle between receptor axes is the same as that between ommatidial axes, as Vigier (1909) had described. The summation increases the sensitivity.

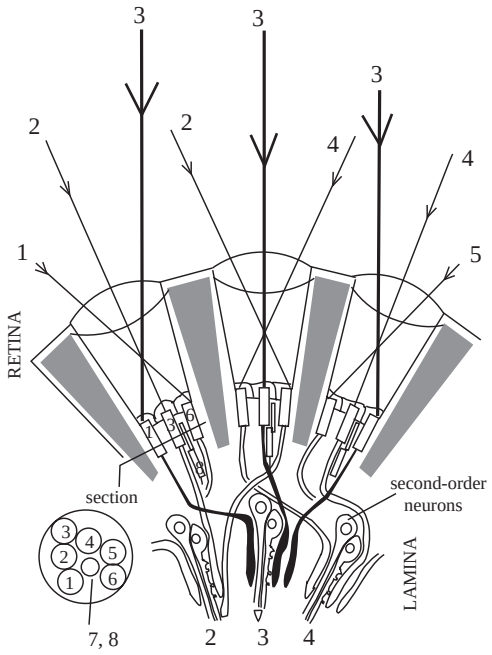

Fig. 6. The optics in higher Diptera, and perhaps some other open rhabdomere eyes. Behind each facet is a tiny fixed retina. The rays that are parallel outside the eye (with the same numbers) are directed to different receptors in adjacent ommatidia. They are recombined at the level of the second-order neurons by the appropriate paths of the retinula cell axons. Cells 7 and 8 lie on the central optical axis and their axons bypass the lamina.

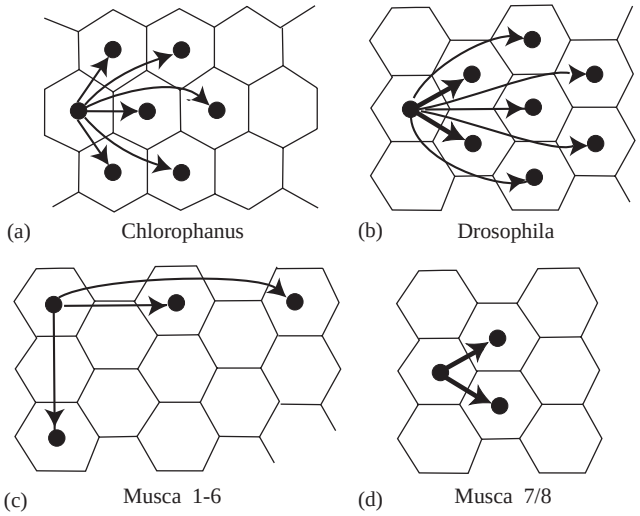

Fig. 7. The interactions between neighbouring visual axes in directional motion detection. (a) The beetle *Chlorophanus*, (b) *Drosophila*, (c) Receptors 1–6 in the housefly *Musca*, (d) Receptors 7/8 in *Musca* (after Buchner, 1976).

An interesting addition that appeared later is often neglected; at very low intensities, with a grating stimulus, the excitation of the second-order neurons of the lamina is 18–20 times that in the receptors, measured by counting bumps, but this extra summation disappears at high intensities (Dubs et al., 1981).

Further complications soon appeared. The fly optomotor response peaks near 2 Hz and cuts off near 20 Hz (3 Hz in roll and lift) and so is much too slow to account for the behaviour in free flight. The flicker fusion frequency of the receptors is near 200 Hz. The function of the spare capacity is presumably for other responses, such as piloting, escape or chasing in flight. Over the temperature range 19–34 °C, the speed of response doubles and motion perception is faster, which gives an advantage to insects, such as the bee and hoverfly, that warm the eyes (Tatler et al., 2000). The discovery of the temperature effect means that many measurements on fixed animals were made at unphysiological temperatures.

In the fly *Musca*, the acceptance angle inferred from the optomotor response increases from 1.7° minimum in bright light to at least 4.1° at low intensities, and the spectral sensitivity becomes less blue (Eckert, 1973). The central rhabdomeres of cells 7–8 in each ommatidium are thinner than in cells 1–6, and are blue or UV sensitive, while 1–6 have spectral peaks in the green and UV. The interpretation that thinner central rhabdomere of receptors 7–8 contribute less to the optomotor response at low intensities was later questioned (Hardie, 1979) and subsequently attributed to the movement of the pigment particles in the pupil within receptor cells 1–6 (Stavenga, 2003).

The optomotor experiments were improved by presenting sinusoidal gratings with a range of periods along and across the rows of facets of *Drosophila* (Buchner, 1976). In bright light the main contribution for horizontal motion comes from the two nearest ommatidia in the adjacent vertical row, with a smaller component from the next ommatidium in the horizontal direction in the sub-adjacent vertical row (Fig. 7b).

A direct determination of the interaction in horizontal motion detection was made by stimulating selected individual receptors in the fly *Musca* with small localized lights (Franceschini, 1975; Kirschfeld, in Buchner, 1976). Receptors 7/8 correlate with the adjacent axes (Fig. 7d) but receptors 1–6 (Fig. 7c) correlate with the axes 2 and 4 rows away (and probably the adjacent ones as well, but this is obscured). Cells 1 and 6 inside each ommatidium make a directional motion detector, the response of which is reduced by stimulation of cells 7 or 8 in surrounding ommatidia. Cell 7 and cell 8 inhibit different sets of 1:6 motion detectors in other ommatidia (Kirschfeld and Lutz, 1974). The experiments with this degree of refinement are tedious, but they demonstrate the variety of motion detectors with different spatial tuning.

The resolution is further complicated by regional specialization in the fly eye (Hardie, 1985, 1986). In

Drosophila, $\Delta\phi_H$ ranged from 4 to 8° (Hecht and Wald, 1934; David, 1979). In *Musca*, cells 1–6 are a homogeneous population with two spectral peaks in UV and green, but there are four types of cells 7 and 8. In the dorsal frontal region of the male *Musca*, cells 7 and 8 have the same visual pigment as 1–6. This region, which detects the female in flight, has a smaller $\Delta\phi$. Over the rest of the eye, two types of 7, 8 are scattered, one with peak shifted towards the yellow. Along the equator is a band where 8 axons of receptors 1–6 converge on each cartridge of the lamina. Along the dorsal rim of the fly eye is a region specialized for detection of the plane of polarization of the sky, with broader but flatter rhabdomeres (Hardie, 1985).

The span of the motion detectors in low illumination still remained a problem. In the beetle *Chlorophanus* (Fig. 7a) and the honeybee (Kunze, 1961) the correlation in the optomotor response in the horizontal direction was between adjacent and sub-adjacent ommatidia, no further. The optomotor response of the fly *Musca* was measured at different light intensities. In bright light the response fell to zero at a period equal to the separation of vertical rows, defined as $\Delta\phi_H$ (Fig. 1a), and there was also a strong component involving the sub-adjacent vertical row (Pick and Buchner, 1979). In low light levels the spatial tuning increased and three adjacent vertical rows were involved almost equally, with inhibition from a fourth row. There was no long-distance correlation as Hecht had proposed, but the method could not distinguish between enhanced contributions from motion detectors of different spans, or pooling at other levels (Dvorak and Snyder, 1978).

Subsequent research demonstrated many large-field directional motion-detector neurons in the deep optic lobe, with fields that are far from homogeneous. In varied and changing proportions in parallel, they generate the optomotor response, so that the functions of each cannot be inferred from the single optomotor output.

In retrospect, instead of the limit in motion detection being fixed by the interommatidial angle, we find that the only insects properly tested by the optomotor response, the beetle *Chlorophanus*, the honeybee and higher Diptera, have a spatial resolution that depends on the mix of spans of different motion detectors, and the reversal of the response shows that the insect does not see the layout of the grating, and that $\Delta\phi > \Delta\rho$, called undersampling.

As a test of the theory of ommatidial optics (Snyder, 1975), we measured the angular sensitivity of large numbers of receptor cells of two flies *Calliphora* and *Eristalis* at 11 different wavelengths (Horridge et al., 1976). As Kuiper (1966) had predicted, $\Delta\rho$ was independent of wavelength in each cell. For receptors 1–6 of *Calliphora*, with $D = 30\,\mu m$ and rhabdomeres $1.9\,\mu m \times 1.7\,\mu m$ in cross-section, the average $\Delta\rho_V$ was $1.66° \pm 0.22$ s.d., $n = 25$, and average $\Delta\rho_H$ was $1.44° \pm 0.31$ s.d., $n = 25$. These values are not close to the diffraction limit, which would be 1.0° at $\lambda = 540\,nm$ or 0.63° at $\lambda = 333\,nm$, but are compatible with the theory of Kuiper (1966). Snyder (1975) illustrated the modes (Figs. 9.7 and 9.8 therein). We postulated that at $\lambda = 540\,nm$ only one mode is admitted, but at $\lambda = 333\,nm$ the first three modes enter, and $\Delta\rho$ is independent of λ. With direct measurements of $\Delta\rho$ available, the theory was improved in such detail (Snyder, 1979), that substantial argument was replaced by the study of biological diversity. Subsequently, Smakman et al. (1984) measured $\Delta\rho$ cells 1–6 of *Calliphora* and offered more curve fitting, with a similar result.

The measured values of $\Delta\phi$ are greater than $\Delta\rho$, which the experts in optics say is required in open rhabdomere eyes to provide gaps between the rhabdomeres to avoid optical cross-talk. So, the minimum $\Delta\phi$ appears to be determined by unexpected factors, the light power of modes outside the rhabdomeres, and the crowding of the transduction apparatus, not by λ/D. In *Drosophila*, with a smaller head, $\Delta\phi_H \approx 5°$ and $\Delta\rho \approx 3.5$–4° (Götz, 1965); in a nocturnal mosquito, $\Delta\phi \approx 7°$, and calculated $\Delta\rho \approx 37°$ in the dark (Land et al., 1999).

Cells 7/8 with a rhabdomere near 1.0 μm in diameter had narrower measured fields, of width near $\Delta\rho = 1.15°$ in *Eristalis*. For white-eyed *Musca*, where the optics is not complicated by pigment cells acting as a stop, Hardie (1979) gives $\Delta\rho = 2.3°$ for cells 1–6 and $\Delta\rho = 1.5°$ for 7/8. This is similar to the new theoretical $\Delta\rho$ for cell 7, near 2.0°, assuming reasonable values of the refractive indices (Stavenga, 2003). Theory and measurements suggest that rhabdomeres of cells 7/8 are near the minimum diameter to capture the first mode. Values of $\Delta\phi$, the focal length, and the differences between cells 7/8 and 1–6, are designed around this limit.

Recently more theory appeared, again vindicating Kuiper's general ideas. Interestingly, $\Delta\rho$ is not sensitive to the exact focus of the lens, and the total light power is not very sensitive to the F number (Stavenga, 2003). The F number (f/D) determines the photon flux available from the ambient light, as is illustrated in bumble bees of different sizes (Spaethe and Chittka, 2003).

The directly measured values of $\Delta\rho$ were less than those inferred from the optomotor response in all the studies mentioned above. The receptor resolution is therefore degraded in the processing of motion, probably because many local circuits are combined across the eye. Moreover, regional differences in $\Delta\phi$ and $\Delta\rho$ are hidden in the optomotor response, which turns out to be poor way to measure anything.

A similar analysis was made by recording from the large neurons of the fly lobula that responded to horizontal motion. Intensity thresholds are incredibly low in this system, down to a few photons per receptor per second at the peak of the spectral sensitivity. The

results were consistent with a model in which the large neuron is fed by numerous small-field temporal modulation detectors preceding the motion detection. Each small unit was inferred to have an excitatory centre (see Fig. 13a) of width $\Delta\rho = 2.0^\circ$ at 50% sensitivity, and lateral inhibitory flanks extending horizontally (perhaps from cells 7/8, see above). The effective $\Delta\phi$ was near 1.25° in bright light and near 1.7° in dim light (Srinivasan and Dvorak, 1980). These small angles again reveal that temporal modulation is better resolved than motion. The field of the detector is controlled by the ambient intensity via inhibitory lateral interactions, and not equal to $\Delta\phi_H$. At low light levels, the inhibitory flanks of the input units disappear and the inferred $\Delta\rho$ is 2.6°. The inhibitory flanks were predicted by Marčelja (1979) and recorded by James (1992).

The reports must be examined carefully to see whether so-called dark-adapted insects were kept in the dark during the day or whether they were in the correct phase of their diurnal rhythm. Over the years, I taught my students to work with day eyes or night eyes, not a hybrid. Recent work is now showing that besides the changes in the retina, neurons change size, the dendrites sprout and synaptic frequencies change with the diurnal rhythm (Meinertzhagen and Sorra, 2001; Pyza and Meinertzhagen, 2003).

1.6. Other open rhabdomere eyes

An enormous variety of arrangements of separated rhabdomeres and corresponding optics occurs among the eyes of various groups of beetles, lower Diptera, Isoptera, Dermaptera, and Hemiptera. Quantitative data are scarce, probably because the eyes of this huge range of insects have been neglected since Exner (1891) and subsequent authors have omitted them from their reviews. We cannot assume that they are organized like the higher Diptera. Two major differences are already known. First, the axes within a single ommatidium can co-incide with axes of facets beyond the adjacent ones. Secondly, in the commonest type, with a mobile cone, the rhabdomeres are separate and usually move away from the cornea in bright light and towards it in the dark (not in flies). Almost no measurements of resolution have been made. Electrophysiology of mobile receptors is difficult, but recordings from higher-order neurons and behavioural analyses are possible.

In male bibionid flies, the angular separation of the optical axes of the rhabdomeres is greater than $\Delta\phi$, and each axis co-incides with others several ommatidia away (Zeil, 1983). In the very large open-rhabdomere eye of the giant water bug *Lethocerus*, the rhabdomeres are enormous, 10 μm × 15 μm. In the dark-adapted eye, $\Delta\rho$ is 10°, the optical axes of the receptors within a single ommatidium, measured optically or electrophysiologically, are 10° apart, and co-incide with axes 3–4 facets away (Ioannides and Horridge, 1975). The cone is fluid and changes shape, being pressed flat between the cornea and the rhabdomeres in dim light (Fig. 8a). Whether the neuronal summation in the lamina corresponds with the wide spacing of axes is not yet clear, but in some cases probable, e.g., in the water strider, *Gerris* (Dahmen, 1991).

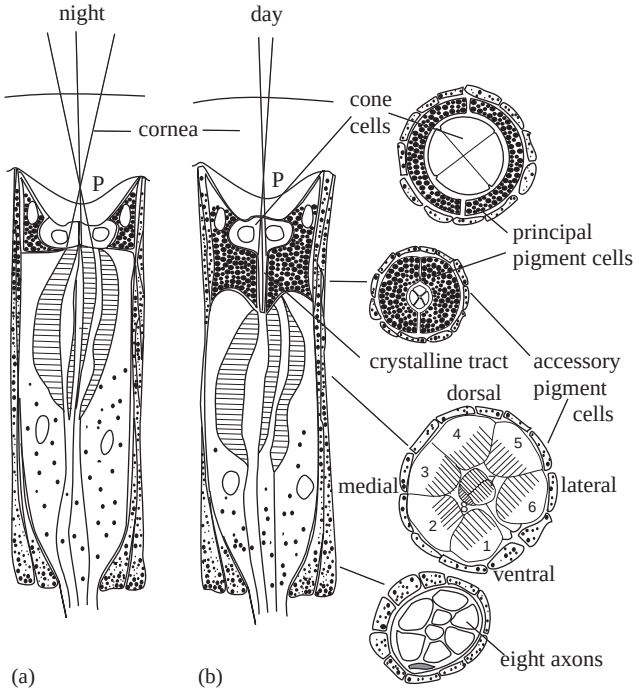

Fig. 8. Mobile cones and separate rhabdomeres in the bug *Lethocerus*, as found in many lower Diptera, Hemiptera, and Coleoptera. (a) In the night eye, the fields and the angles between them are wide. (b) In the day eye, the cone is extended to a thin transparent tract between pigment cells, giving narrow and less sensitive fields on the same axis (partly after Walcott, 1975).

The light-adapted receptors have totally different optics (Fig. 8b). The cone is pulled down to form a transparent thread that leads between pigment cells to the rhabdomeres below, with a single shared axis, with $\Delta\rho = 3.5^\circ$ and sensitivity only 0.1% of that in the dark (Walcott, 1975). Lower Diptera, and many Hemiptera and Coleoptera have similar cell movements, but in this extensive descriptive literature spanning a century the dark-adapted eyes were usually dark-adapted during the day, rather than during the night when they would be in synchrony with the diurnal rhythm. The effects on resolution are quite unknown.

Small insects are forced to desperate compromises. In several species of mosquitoes the corneal lenses are almost hemispherical, but D remains more than 20 μm. Diurnal species (*T. brevipalpis*) have F number ≈ 1.66, $\Delta\phi \approx 3^\circ$, and calculated $\Delta\rho \approx 3.2^\circ$. Nocturnal species (*A. gambiae*) have F number ≈ 0.5, $\Delta\phi \approx 7^\circ$, and calculated $\Delta\rho \approx 18^\circ$ in the light and 37° in the dark (Land et al., 1999). Better to have poor resolution than not to see at all.

1.7. Eyes with small $\Delta\rho/\Delta\phi$

Some insects have large $\Delta\phi$, few facets but narrow receptor fields. For example, in the light-adapted beetle *Chlorophanus*, Hassenstein (1951) found that $\Delta\phi$ is 6.8° and Varjú (1959) calculated $\Delta\rho/\Delta\phi = 0.18$, making $\Delta\rho = 1.2°$. The red wood ant (*Formica rufa*) can distinguish the orientation of a grating of period 1° (maybe not a very accurate grating) but $\Delta\phi$ is about 10° (Jander and Voss, 1963; Voss, 1967). Similarly, the stick insect *Carausius* discriminates between vertical and horizontal gratings with a period of 4° although $\Delta\phi$ is near 6° (Jander and Volk-Heinrichs, 1970). In the water strider, *Gerris*, $\Delta\phi$ is up to 20 times λ/D (Dahmen, 1991). These remarkable measurements have never been followed up. In the light of other findings, they suggest that the improved detection of small prey or the direction of orientation of edges is a priority in these insects, but the direction of the stimulus is less important (see Sections 2.2 and 2.3).

An outstanding example is the water strider, *Velia*, which lives on the flat world of the surface of ponds. The preferred size of a black disc that imitates prey is 4°, with negligible response at 3° or 5°, but $\Delta\phi$ is about 10° (not measured optically). Increasing the length of edge reduces the response. Flicker at 1.6–8 Hz enhances but 0.4–3 Hz reduces the response. Co-incidences with water surface vibrations are essential. Two horizontal rows of ommatidia in the middle part of the eye are the most effective. When a black 4° disc is moved to higher positions there is a periodic rise and fall in sensitivity with a period of 8°, with four periods up to 30° towards the top. Similarly, when a second spot is added at a controlled angle in the horizontal direction there are falls and rises in sensitivity with a period of 11° (Meyer, 1971, 1974). The author infers an array of detectors, each with an excitatory centre and four adjacent inhibitory centres corresponding to ommatidia, with strong interactions that narrow the excitatory fields, and calls these detectors the units of vision (Seheinheiten). Clearly they, and not $\Delta\phi$, determine the resolution. Similar detectors presumably exist in a host of predatory insects such as Mantoidea, Odonata, and Asilidae.

1.8. Anomalous resolution of the locust

Some insects, or some of their neurons, respond to a movement in either direction of a black/white edge by as little as 0.1°. This stimulus illustrates the high sensitivity to temporal modulations that are summed across several ommatidia, but is not suitable for a test of lens resolution, which requires strict control of the maximum period presented (Fig. 5), best done with an accurate grating with a fuzzy outer boundary.

In the common large locusts, the facets are relatively small, near 20 μm. At a small fovea at the front of the eye the minimum $\Delta\phi$ is 0.8° horizontally at the front of the eye, and $\Delta\phi = 1.3°$ vertically (Horridge, 1978; Land, 1997b). At the side of the eye, Catton (1998) gives $\Delta\phi = 1.7°$. In earlier work (Tunstall and Horridge, 1967), the values of $\Delta\rho$ were too large because the optics was damaged. Wilson (1975) found $\Delta\rho = 2.2°$ at the side of the light-adapted eye. In 405 measurements of $\Delta\rho$ at the front of the eye, the average minimum $\Delta\rho$ was 1.16° in bright light in mid-afternoon and the maximum was 2.64° when dark-adapted at night (unpublished work in Canberra by Dr. Wu). The optomotor response of the locust falls to zero at a grating period near 3° (Thorson, 1966), which implies a light-adapted $\Delta\rho$ less than 3° and $\Delta\phi$ near 1.5°. Again, the optomotor response is a poor measure of $\Delta\rho$ or $\Delta\phi$.

A large neuron (the DCMD unit) of the locust ventral cord responds to movement of a grating of period 0.3° (Burtt and Catton, 1962; Catton, 1999), which is 10 times smaller than expected from the diffraction limit. Critics pointed out that when a small square grating is moved, there is a shift in the position of the average brightness (Barlow, 1965; Palka, 1965). Indeed, when the frame around the grating was rotated by 45° to remove this edge effect, the resolution returned to that expected from diffraction theory (Palka and Pinter, 1975). However, Burtt and Catton (1969) persisted with a rotating wheel of black and white sectors, and again found the limiting period at the edge of the wheel to be 0.3°. Palka and Pinter were unable to replicate this. However, Northrop (1975) reported the high resolution and inferred a summation of temporal modulations in several receptors, with no peculiar optics. Northrop's data were also questioned by Palka and Pinter.

A serious criticism is that targets larger than 10° inhibit the response so that extended sources cannot be used (Pinter, 1979). There is summation in large-field neurons that shuts off the response, rather than a single filter with balanced excitation and inhibition that fails to see a large target (compare Giurfa and Vorobyev, 1998, and Section 2.5).

There is significant sharpening of small targets, but no narrowing of the measured $\Delta\rho$ of the receptors themselves. Responses to On or Off of a single bar are different from those for a pair of bars close together, down to separation limit of 0.4°, for dark on light or light on dark bars (Catton, 1998), and are stronger for horizontal than for vertical bars. Responses to a single bar increase with narrowing of the bar, with a lower limit of 0.1° (Catton, 1999). If these results can be repeated, there must be strong lateral inhibitions as in *Velia* (Meyer, 1974), and summations that produce the extreme sensitivity to modulation by a line stimulus (compare vernier acuity in man). Good resolution of small movements of small contrasts, and possibly to other patterned co-incidences of temporal modulations, is probably a feature of many insects not yet tested.

1.9. The eye parameter

The Raleigh criterion (limit $= 1.22\lambda/D$ radians) was a measure of whether two stars could be resolved as separate points of light. At the limit there is about 19% drop in intensity between the two peaks in the image. This criterion is not applicable for extended sources. In the case of a moving regular grating (Fig. 5), the temporal modulation at the focus of the lens falls to zero at a period approximated by $\Delta\theta = \lambda/D$ radians, where $\Delta\theta$ is the fundamental period of the grating, λ is the wavelength, and D is the aperture of the lens. As quite a separate issue, the bars of the grating cannot be re-assembled by any eye when $\Delta\theta$ is less than $2\Delta\phi$ (Shannon's criterion). At the physical limit, in bright light and assuming no noise, $\Delta\theta = 2\Delta\phi$, therefore $D\,\Delta\phi = \lambda/2 = 0.25\,\mu m$. On the other hand, the Raleigh criterion gives a value of $D\,\Delta\phi = 0.6\,\mu m$ at the human observational limit.

The product $D\,\Delta\phi$, called the eye parameter, has been acclaimed as demonstrating that the evolution of various compound eyes has led to an optimum compromise between the aperture and the number of ommatidia (Snyder, 1979). For vision in dim light, D and $\Delta\phi$ and the rhabdomeres are large, giving fewer sampling points. For living in bright light, D, $\Delta\phi$ and the rhabdomeres can all be small, giving a small $\Delta\rho$ maximum number of sampling points (pixels), and small $D\,\Delta\phi$. For example, in one homogeneous group of insects, diurnal bees, $D\,\Delta\phi = 0.6$–$0.8\,\mu m$, and nocturnal bees have $D\,\Delta\phi = 0.95$–$1.15\,\mu m$ (Jander and Jander, 2002).

Although $D\,\Delta\phi$ is a very general indicator of life style, this topic is another house of cards constructed from theory. Complications abound. There is no evidence that insects re-assemble a grating. The evidence from bees is that in a grating they detect only the temporal modulation, motion and edge orientation, so Shannon's principle does not apply. Resolution depends on $\Delta\rho$ ($\approx$rhabdom subtense, not λ). None of the known cues are detected purely by interaction of adjacent ommatidia. Natural contrasts are low, so the highest priority is temporal modulation above the noise level. Most diurnal insects have similar values of $D\,\Delta\phi$ near $0.5\,\mu m$, and rely on fast receptor and lamina cell adaptation and slower screening pigment movements to operate in and out of direct sunlight. $D\,\Delta\phi$ may or may not be constant across the eye (Fig. 9). Resolution is usually limited by the rhabdomere size, not the aperture, and resolution is often independent of wavelength. Rhabdomere sizes are adapted to life styles, and differ in different regions of the eye. In many insects the rhabdom rod is tiered, as if to widen the dynamic range. Many insects have mobile cones and large movements of the rhabdomeres. Many examples are known with rhabdomeres of different sizes or at different levels in the same ommatidium, as if high and low intensities are separated. In others, such as the

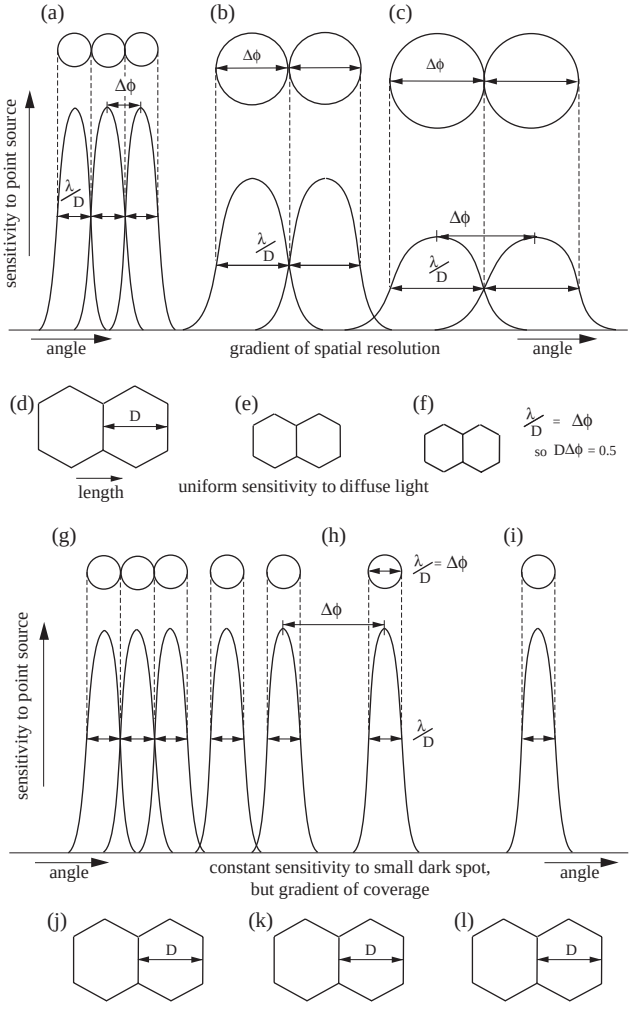

Fig. 9. Two naturally occurring ways to build an acute zone in a compound eye. (a–f) In dragonflies, the acute zone is a flatter part of the eye with (a) smaller interommatidial angle and (d) larger facets. At the side of the eye (c), the interommatidial angles and receptor sizes are greater and (f) facets are smaller. The sensitivity to an extended source, which is the volume in the Gaussian field, could be constant across the eye. (g–l) The corresponding situation in an eye with uniform sensitivity to a small dark spot, i.e., uniform D and $\Delta\rho$ but a gradient of $\Delta\phi$.

locusts, mantids, and many arthropods that are active by night and by day, there is a diurnal rhythm of the width of the rhabdomeres, which grow by a factor of 10 at night. In a nocturnal bee, the eye parameter is $0.9\,\mu m$ (Warrant et al., 2004), which looks ridiculous, and reminds us that the lower limit of absolute sensitivity depends on the receptor response to individual photons as well as calculations from theory. Conversely, $D\,\Delta\phi$ for diurnal *Velia* is about $4\,\mu m$ (Meyer, 1971). The biology is too rich and varied to be summarized by a single value of $D\,\Delta\phi$.

The eye parameter is a measure of undersampling if we ignore rhabdomere size. However, there is no evidence that a minimum $\Delta\phi$ is the first consideration.

If we consider the task of discriminating cues, the number of ommatidia per solid angle looking at the cue is obviously important (see Meyer, 1974; Land, 1997a, Fig. 7; Spaethe and Chittka, 2003). In summary, we need a new inclusive parameter for the comparison of different insects, maybe even an experimental test.

1.10. Regional differences of $\Delta\phi$

In the 1970s it became obvious that there are many examples of divided eyes and regional differences in D and $\Delta\phi$, focal length, spectral sensitivity or arrangement and size of rhabdomeres, for particular behaviour patterns. Use of the pseudopupil led to the making of eye maps of $\Delta\phi$ in a hoverfly (Collett and Land, 1975), many insects (Horridge, 1978) and other flies (Land and Eckert, 1985). The values of $\Delta\phi$ and minimum $\Delta\rho$, calculated from the apertures or the rhabdomere subtense, can be plotted on the same map (Fig. 10). Much detail about $\Delta\phi$ is summarized by Land (1989, 1997a, b) and previous reviewers.

The commonest regions of high resolution (foveas) have greater density of visual axes per unit solid angle, larger D focal length and eye radius, and longer rhabdoms (Horridge, 1980). The larger facets imply that other regions of the eye have a reduced resolution.

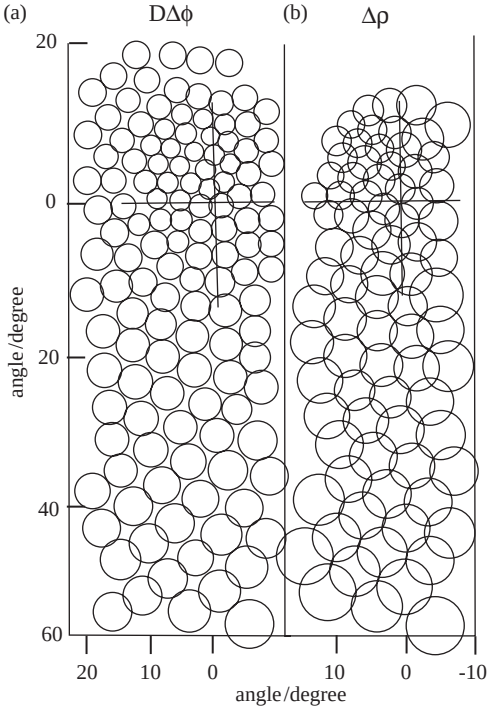

Fig. 10. Maps of the front of the eye of the dragonfly *Austrogomphus*, plotted in angular co-ordinates. (a) The circles of diameter $5\lambda/D$ are centred at the axis of every fifth facet. (b) The same region, with circles of diameter $5\Delta\rho$, plotted on the same axes as before. From this map it is possible to calculate the temporal modulation caused by the motion of any moving pattern of illumination (from Horridge, 1980).

Among many intermediates, two extreme types of regions of high acuity have been defined, with constant sensitivity to a diffuse source or to a spot (Fig. 9). The large mantid *Tenodera* has a facet aperture D ranging from 35 μm peripherally to 50 μm at the centre of the fovea, and a gradient of increasing focal length (cone length), with thinner rhabdoms and decreasing $\Delta\phi$ equal to $\Delta\rho$ from 2.6° laterally, to 0.6° at the centre (Rossel, 1979). In dragonflies, also, the width of the rhabdom is matched to the width of the blur circle (Fig. 10b), and the gradient of $\Delta\rho$ that of $\Delta\phi$ towards the centre of the fovea (Horridge, 1978).

A large variety of insects have a band of smaller $\Delta\phi_V$ along the horizontal midline, looking towards the horizon, especially those that live on flat surfaces. The effect is to emphasize the vertical rows of visual axes and reduce the sampling density elsewhere on the eye (Figs 1e and 4). An extreme example is the water strider, *Gerris*, where $\Delta\phi$ between nearest neighbours is 1.1° at the front of the band, but 4–8° over most of the eye (Dahmen, 1991).

Regions of smaller $\Delta\phi$ (called a fovea) evolved together with special behaviour patterns when a predator catches prey or a male pursues a mate. Examples of the former are the dorsal foveas of many dragonflies (Horridge, 1978), forward-looking areas of dragonfly larvae, mantids (Rossel, 1979), many wasps, notonectid bugs and asilid flies. An example of the latter is the forward-looking area on the eyes of male houseflies (Land and Eckert, 1985). Many male mayflies and bibionid flies have an upward looking area. The drone bee (Seidl, 1982; Land, 1997b) detects a target of 0.32° with $\Delta\rho = 1.2°$ (Vallet and Coles, 1991). The male simuliid fly *Wilhelmia equina* detects a female subtending only 0.2° against blue sky, for which a 10% temporal modulation would imply an acceptance angle near 0.6° for blue light (Kirschfeld and Wenk, 1976). The resolution must be measured during the appropriate activity, and is not necessarily related to $\Delta\phi$.

The selective advantage of the reduced $\Delta\phi$ in the fovea is not immediately obvious. It is not necessary for pursuit of a target in flight, as is usually assumed. When radar was first put on fighter planes for use at night, it was discovered that the target plane could easily be found although the directional error was 20°, because the approach was progressive. For an explanation of foveas let us consider the cues. The predator must distinguish moving prey from useless black spots. The smaller $\Delta\phi$ helps detect length and orientation of edges, colour and colour distribution, size, symmetry and angular velocity, all of which require a group of ommatidia, the more on the target the better.

1.11. Signal/noise ratios

A measure of any kind is not complete until the precision is known, but this aspect of insect visual

responses has been neglected until recently. At very low light levels there is more noise than signal in insect receptor cells, and threshold is sometimes defined as the point where they are equal. Thirty years ago, Laughlin began to measure signal/noise ratios (SNRs), at first by hand, but measurements are now made on line. About half the noise is due to random arrivals of photons, and about half arises from the different amplitudes of responses to single photons (transducer noise). Increase in the number of rhodopsin molecules, and therefore the size of the rhabdomere, improves the SNR (Howard and Snyder, 1983). No matter how bright the illumination, noise is still the limiting factor in the detection of achromatic contrast (Laughlin, 1994).

In the fly, receptors 7/8 catch fewer photons and are more noisy than cells 1–6, but the slope of the response curve is steeper, so they have similar sized signals. The LMCs are general-purpose filters that optimize the signals before they are fed into arrays of the various detectors in parallel. Analysis so far has concentrated on the gain and temporal properties in the receptors, and the large lamina monopolar cells (LMCs) with which they connect (Anderson and Laughlin, 2000). Most studies relate to the detection of temporal modulation on the colour-blind pathway. Since bees, and probably other insects, detect cues but ignore the rest of the image, SNRs will have to be measured for each cue.

In the bee, the noise levels of the three receptor types together with their colour opponency predicts very well the shape of the photopic spectral sensitivity curve measured behaviourally (Vorobyev and Osorio, 1998). Following on after this, an outstanding piece of work showed that noise measured directly in the receptor cells sets an absolute limit on the accuracy of the discrimination of colour cues of different wavelengths (Vorobyev et al., 2001). This study combined the skills of different specialists on behaviour, physiology and computation, as a foretaste of what must be done throughout the whole subject, including detection of motion and all visual cues. Interestingly, for a bee to discriminate a colour in a field of 60 ommatidia requires a photon flux per receptor cell about a thousand times that required by a fly to detect directional motion in a large field (Dubs et al., 1981). The honey bee really does have an insensitive eye by day (Wolf and Zerrahn-Wolf, 1935).

2. Tests of resolution of the cues in honeybees

One might suppose that the discovery of what bees see preceded the measurement of their resolution in tests, but it was not so. Although in some cases we can use a reflex response to measure a resolution of a stimulus, bees can be trained to discriminate several visual cues that assist them to recognize a place. Measuring the resolution of each cue is a convincing demonstration that the bees detect cues, but provides no evidence that the bee remembers anything else about the training pattern. Even so, good resolution signifies functional importance.

2.1. The temporal modulation cue

As mentioned above, Hecht and Wolf (1929) inferred that in bright light a grating period of 2° was detected by the temporal modulation of single honey bee receptors, as expected for a diffraction limited receptor, but they thought that $\Delta\phi_H$ was at least twice $\Delta\phi_V$. Srinivasan and Lehrer (1988), found a limiting period near 2.5° for both vertical and horizontal gratings versus grey, and argued that because the eye was astigmatic, the limit was set by the temporal modulation, not by $\Delta\phi_H$ and $\Delta\phi_V$. Actually, the array of axes is almost isotropic in angular co-ordinates (Fig. 4). With vertical versus horizontal gratings composed of coloured papers, they found that with blue receptors only (with no green contrast) the limiting period was near 3.5°.

Later Giger and Srinivasan (1996) found that orientation is detected by the green receptors only. If orthogonal gratings are oblique and without green contrast, they cannot be discriminated even when stationary (Horridge, 2003c). Therefore, with the finest vertical versus horizontal gratings with no green contrast, the cue must be the difference in induced temporal modulation of blue receptors as the bees yaw in flight, irrespective of measurements of $\Delta\phi$.

Bees will not fly near a target generating more than 8 Hz. They discriminate between a rotating sector wheel and a similar wheel rotating faster than the flicker fusion frequency (fff = 200 Hz), with an optimum in the range 60–90 Hz. This response has nothing to do with pattern perception because the bees did not discriminate between a stationary sector wheel and a grey one (Perhaps only for large targets, see below). Discrimination requires the actual motion of the target, and is colour blind and green sensitive (Srinivasan and Lehrer, 1984a). Other authors found a cut-off at 55 Hz in response to motion (Wolf, 1935). In the optomotor response, with appropriate gratings, bees respond directionally to angular velocities between 0.1°/s and 2000°/s with a contrast frequency peak at 10 Hz and cut-off at 100 Hz (Kunze, 1961).

The bees' discrimination of isotropic textures, such as two different checkerboards, is not very sensitive. It requires a difference of 30% in period or linear scale (Horridge, 1997). Bees are unable to discriminate between a steady light and a flickering one at any frequency if they are the same colour and average intensity, no matter what the colour. Therefore, pure flicker frequency is not the cue for discrimination

between patterns of different spatial frequency. They discriminate very well, however, between a steady light and a flickering one of the same average composition if the flicker is between two colours, called heterochromatic flicker, for which motion or green contrast is not essential. They respond up to 10 Hz if blue is absent and to 40 Hz if blue is present (Srinivasan and Lehrer, 1984b). This neglected result shows that the temporal modulation detectors function in colour (as later confirmed) and suggests that learning of landmarks and places can use heterochromatic spatial modulation (not tested).

Lateral inhibition generated by flanking cells in the lamina narrows the receptive fields of the lamina cells in most insects examined and increases the bandwidth (see Fig. 13a). With an extended lateral network, the theoretical optimum $\Delta\phi/\Delta\rho$ reduces towards 0.6 (Marčelja, 1979). A more sophisticated approach subtracts a weighted mean from neighbouring receptors from the signal at a central receptor. At lower light levels the inhibitory flanks must be weaker and wider to balance the increase in noise and reduced signal/noise ratio. Taking into account the distribution of spatial frequencies in the natural panorama also improves the signal/noise ratio. The theory was extended to the time domain to include post-response inhibition, which improves the response to high temporal frequencies at the expense of low ones. This model of redundancy reduction fitted the data on the modulation of the large lamina ganglion cells (Srinivasan et al., 1982). The mechanism codes the temporal modulation signal to protect it against subsequent synaptic noise and has nothing to do with reconstructing the scene or abstracting specific features.

2.2. The edge orientation cue

Bees discriminate between two targets on a vertical surface that differ strongly in the average orientation of edges (Turner, 1911). When there are several thin parallel bars, they can be shuffled on the target during the training. The bees learn to discriminate the averaged orientation cues in the range of places where they were during the training (Horridge, 2003a, e).

The edge orientation detectors appear to be summed over large fields, but not over the whole field of vision of an eye. Edges with the same orientation in different parts of the target add together, but edges at right angles on the same side of the target subtract from them (Srinivasan et al., 1994), so that the orientation cue is cancelled when there are equal lengths of edges at right angles (Fig. 11b and c). One set needs to be about 25% longer than the other for the average orientation to be detected (Horridge, 2000a).

There is evidence that neighbouring large regions of differing strong orientation cues are separately discriminated (Zhang and Horridge, 1992; Stach et al., 2004).

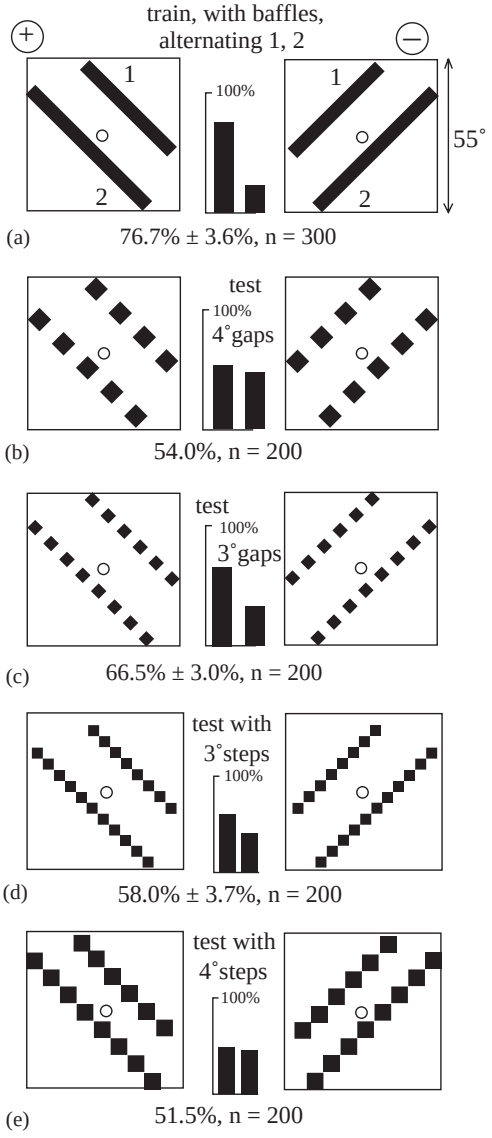

Fig. 11. Evidence for the maximum length of the orientation detectors of the honey bee. (a) Bees were trained with oblique black bars that were shifted in position every 5 min. (b,c) In tests with rows of squares, gaps of 4° or more were not spanned. (d,e) In tests with stepped edges, steps of 4° spoil the orientation (after Horridge, 2003b).

Nevertheless, the summation of local orientation cues places a serious restriction on the bees' ability to discriminate patterns or textures, except for parallel, radial or circular edges. This point is ignored in all recent studies of shape discrimination.

The mutual cancellation of the local edge orientation cue by equal lengths of edges at right angles can be used to measure the maximum length of the orientation detectors. As an example, the global orientation of a straight line of squares is not discriminated if the squares are separately resolved, as they are when the gaps between squares are larger than about 3.5° although the edges are in line on each side of the gaps

(Horridge, 2003b). Similarly, the orientation of an edge is not discriminated if it is broken up into square steps greater than about 3.5° (Fig. 11d and e). Unlike humans, bees have no detectors that span global orientations of either edges or areas.

The summation of parallel orientation cues was used to measure the minimum length of edge required to discriminate orientation, in tests with patterns of many short bars or lengths of edge in parallel (Fig. 12a and b). The minimum length, near 3°, is similar for vertical, horizontal and oblique edges, and is insensitive to exchange of black and white (Horridge, 2003f).

When bees were trained to discriminate between oblique black/white gratings at 45° versus 135°, of the same period, the minimum grating period is near 3.5° (Horridge, 2003c), showing that there is no temporal or spatial modulation difference and the edge orientation alone is the cue.

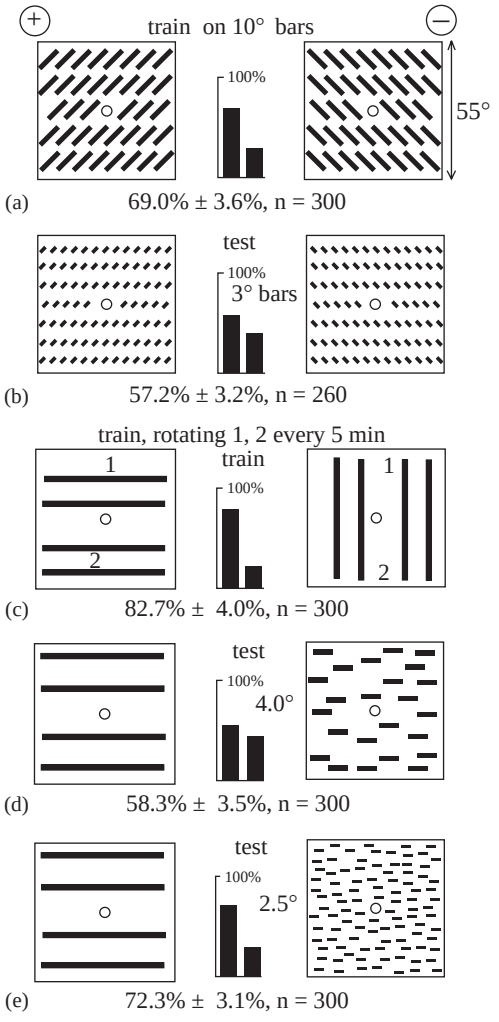

Fig. 12. Two experimental measures of the minimum length of the orientation detectors of the honey bee. (a) Train with oblique black bars. (b) Test with shorter bars, until discrimination is lost with bars of 3°. (c) Train with long black bars. (d,e) Test with long bars versus short bars with the same orientation. When the orientation of the short bars is resolved, they are not discriminated from the long bars (after Horridge, 2003f).

When bees were trained to discriminate an orientation cue and then tested with fuzzy (graded) edges, the shallowest intensity gradient in which they can detect the orientation is less than 2% per degree (Horridge, 2000a). This remarkable performance suggests that the function of the edge orientation detectors is the detection of the orientation of large blurred edges, which must be important in bee vision.

In a new type of resolution experiment, a group of bees were trained to discriminate between horizontal versus similar vertical bars. The trained bees were tested with the horizontal bars versus a scatter of small horizontal bars of the same total length (Fig. 12c). Bars more than 4° in length are not distinguished from the full length bars. As the small bars are made shorter, so that their orientation is not resolved, the discrimination from the long bars improves (Fig. 12e). The bees ignore the differences in temporal modulation because they were not trained to that cue, and they fail to detect a difference between the long bars that they were trained on and other bars longer than 4° that have the same orientation.

So we find that the orientation detectors are short, cannot collaborate to span gaps, and are not strung together to detect longer lengths. When bees discriminate orientation, they do not detect whether individual edges are long or short. There is a measure of the dominant orientation but no local separation of different orientations, which makes re-assembly of the pattern or shape recognition problematical. Discrimination of orientation is colour blind and done via the green receptors, but in parallel there is also discrimination of the temporal modulation or total length of edge in colour.

2.3. The mechanism of orientation detection

Bees discriminate the orientation of gratings presented in flashes of 2 ms every half second (Srinivasan et al., 1993), and also moving gratings up to a contrast frequency of 50 Hz, irrespective of velocity or spatial frequency (Giger, 1996), showing that the orientation cue is the detection of modulation of receptors with a temporal resolution of co-incidences in the range 2–20 ms.

The discrimination of orientation requires edges subtending 3.5° in length, which is approximately twice the angle between adjacent ommatidia in the eye map (Fig. 4). We can infer that behind the retina are at least three arrays of primary edge detection units, similar to those used in machine vision, at orientations of 120° to each other. The fields extend over 3.0–3.5°, and probably are $2\Delta\phi$ or three receptors long (Fig. 13b–d). They appear to detect a gradient of intensity as well as the edge orientation (Horridge, 2003b and f).

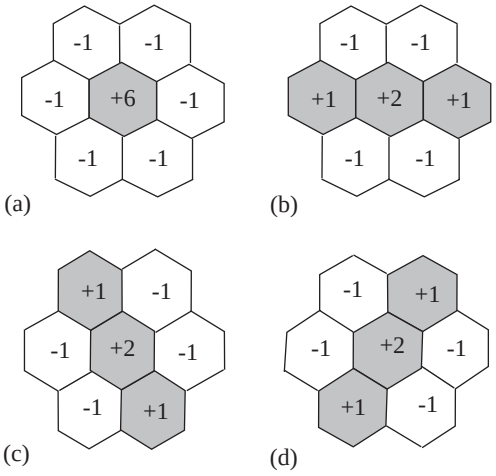

Fig. 13. Local filters for models of insect vision. (a) A hypothetical temporal modulation detector based on a hexagonal grid, as in the bee. (b–d) A set of three hypothetical orientation detectors that are compatible with data from the honey bee. These filters are similar to Canny detectors as used in machine vision.

The short baseline of the orientation detectors of the bee (Fig. 13) explains why their angular sensitivity curve is very wide. Larger $\Delta\phi$ means improved orientation discrimination. Indeed, in the stick insect *Carausius*, where $\Delta\phi$ is near 6° and $\Delta\rho$ is near 4°, the detectors are aligned with the rows of ommatidia, with three directions of detectors for attraction at 120° to each other, and three orthogonal directions of inhibitory detectors, all more sensitive to orientation than in the bee (Jander and Volk-Heinrichs, 1970). The red wood ant had $\Delta\phi$ near 9° but resolved gratings down to a period of 2° and detected an orientation shift of 10° from the vertical (Voss, 1967). This performance has never been found in the bee, where angular sensitivity fields are 90° wide at the 50% sensitivity level (Srinivasan et al., 1994). Each array of primary orientation detectors with the same orientation axis is separately summed at a deeper level, so preserving the resolution of angle.

2.4. Distance flown and range of nearby contrasts

The honeybee visual system measures the angular velocity across the eye of the optic flow generated by flight and calculates the range of nearby contrasts. The optic flow also controls the speed, landing and turning in flight, all of which depend on motion detection and are colour blind. The optic flow is integrated over time to measure the distance flown. There is an interesting mix of error and accuracy in these tasks. The standard deviations approach half the mean values, and statistical significance is obtained by observing numerous bees, so it is hard to understand how individual bees cope so well. Changes in the environmental variables, such as contrast, ambient illumination, surrounding pattern, and length of journey, have little effect. These measurements are not so robust against changes in the flight height or the range of nearby landmarks (Aung Si et al., 2003).

Many experiments show that bees return to a reward at the correct range from the landmarks (Cartwright and Collett, 1979), even when using the side of the eye (Lehrer, 1990). They learn the range on leaving a landmark (Lehrer and Collett, 1994). Bees learn to use a cue at a given range versus a similar cue at a different range (Lehrer et al., 1988) or in the Y-choice apparatus with the targets on vertical surfaces (Horridge et al., 1992). The detection of direction and range of each cue in training experiments implies that the bees make a sparse projection of cues in their surroundings, as indeed they must to recognize a place. The maximum and minimum ranges that are measured, however, and the precision of different range measurements, are not known.

2.5. Size

Many insect behaviour patterns require the measurement of angular size, especially when hovering to feed, to keep a fixed range from a landmark, or to recognize food, prey, a mate or a predator. Most workers on bee vision have been careful to control against differences in pattern size, so that they could study other cues. When the bee had to land on the reward hole or pattern, the angular size increased continually as the bee approached, but size (or something) could still be learned. Bees can be trained to discriminate the size of spots presented horizontally (Hertz, 1926), but they confuse area and photon flux. A 30% difference in area is required. When trained on two black discs of different sizes, the trained bees confuse a small black disc with a larger grey one (Ronacher, 1979), although able to re-learn the new task. When trained on a spot of one size and tested with the training pattern versus a spot of another size, the discrimination tends to follow Weber's Law. As Wolf (1935) and others found, they measure the area times intensity as a minimum cue, and ignore shape.

Bees learn to discriminate the absolute size of a black spot on a target at a variable range from another that has the same angular size but at a different range, even when the positions are regularly shuffled (Horridge et al., 1992). Green contrast is not necessary, except to stabilize the eye on the target, and size is measured as area, not as vertical or horizontal extent.

Although there are plenty of descriptions of size discrimination of spots, bees fail to detect a single dark grey spot greater than about 15° on a light grey background (Giurfa and Vorobyev, 1998). The proposed explanation is that the field of the detector is a difference of two large Gaussians, with balanced excitation and inhibition, so that detection of a small spot is enhanced but a spot that covers the field is cancelled out. This model would confuse edges with

spots, however, and fails to cater for most of the related data on the discrimination of black spots, bars and sectors in different positions. To detect a coloured spot down to 5°, green contrast is required as well as chromatic contrast (Giurfa et al., 1996), but the explanation may be that the green contrast is required to detect motion and stabilize vision in the yaw plane, to keep the target on the same region of the eye (Horridge, 1999).

2.6. The radial/tangential cue

Bees learn to discriminate between a radial pattern of sectors or bars and a pattern of concentric circles, both shuffled in position and 50% black, 50% white. When two different patterns are rotated at random during the training, the cues of position and orientation are removed, but radial or tangential cues are discriminated. Detection is via green receptors only. There is evidence for detectors of radial patterns with six axes at 60° and non-specific filters that detect any radial arrangement (Horridge, 2000c). The resolution of symmetrical patterns appears to be enhanced because they stabilize the eye on the target. As yet we have insufficient data and no theory concerning thresholds.

2.7. The position of the centre

The bees appear to be unable to distinguish separate positions of individual black areas on the same side of the target, and learn the position of the common centre of black irrespective of pattern. When bees have learned to discriminate between two fixed black patterns, they may fail to discriminate if a part of the pattern is moved up or down on the target. The memory is not lost until they begin to retrain; they simply fail to recognize the displaced black area. They learn the retinotopic position of the common centroid of black areas in the vertical direction, with resolution of 6–8°, irrespective of the pattern (Horridge, 2003d and e). We do not know exactly where the bee places the centroid. The areas must be quite broad; positions of thin black bars are less important. The vertical and horizontal dimensions are ignored unless that is the sole difference. The resolution of position in tests depends on the constancy of position during the learning process, so fixation on the target is an advantage. Two coloured areas on each target can be separately located (von Frisch, 1914) by the positions of their centres (Horridge, 2003d), but as yet we have insufficient data on the resolution.

2.8. Resolution of position

Despite the simplicity of the task, we find no useful experimental measurements until Baumgärtner (1928) found that trained bees make a relatively poor discrimination between two different coloured patches. He concluded that the number of ommatidia stimulated influenced the resolution of colour and its position. The recognition of the colour of a patch depends on the signal-to-noise ratio, and therefore on the photon flux per receptor and the way that receptor responses are summed. The contrast at the edges is not necessarily a good measure of the colour inside. The photon flux depends on the F number of the lens, so small facets are not necessarily bad for this task. The results are also influenced strongly by the stabilization of the eye on the target (Horridge, 1999). When the vision is not stabilized by green contrast, the bee starts to relearn afresh each time that a colour is presented, because the target is at a different place on the eye at each visit. When the eye is stabilized by green contrast, the minimum diameter for the discrimination of a blue spot on one target from a yellow one on another target in indirect sunlight is about 4° for the honeybee (Lehrer and Bischof, 1995). A single coloured flower must subtend an angle of 5° to be detected against green foliage (Giurfa et al., 1996; Giurfa and Lehrer, 2001). Recently, Spaethe and Chittka (2003) found that in large bumble bees (thorax width 4.4 mm, $\Delta\phi_V = 0.6°$, $\Delta\phi_H = 1.8°$, $D = 29\,\mu m$, at the front of the eye; convention Fig. 1d) a single ommatidium is sufficient to detect a yellow disc of minimum subtense near 3.5° on a white background, but in small bees (thorax width 3.5 mm, $\Delta\phi_V = 1.4°$, $\Delta\phi_H = 3.3°$, $D = 19\,\mu m$) seven ommatidia are required to detect a 7.8° disc. The difference could not be attributed entirely to the calculated photon flux, but a constant $\Delta\rho = 2.5°$ was assumed. However, this is not the size limit because when honey bees have learned a minimum colour cue, a group of smaller spots may be detected as a whole. It appears to be a matter of photon flux, not edge contrast.

A fixed pattern is one that is fixed with reference to the choice point of the bee. Bees easily discriminate between many fixed patterns that differ in location of a coloured or black area, but they fail to discriminate the left/right interchange of a large black and a large white rectangle unless the vision is stabilized in the yaw plane, and trained bees fail in tests when a part of a black area is moved in the vertical direction (Friedlaender, 1931; Horridge, 2000d). When a fixed pattern is learned, to discover the cue requires a large number of positive and negative tests, because the bees could have learned the position of just one part relative to the reward hole, as they had done in some earlier experiments (Baumgärtner, 1928).

An interesting example is a pair of black and white sector patterns that differ by half a period in rotation (Fig. 14). When the targets are stationary the position of an area appears to be the cue; different black and white spot or sector patterns cannot be discriminated if they are shuffled by rotation (Horridge, 2000c) and

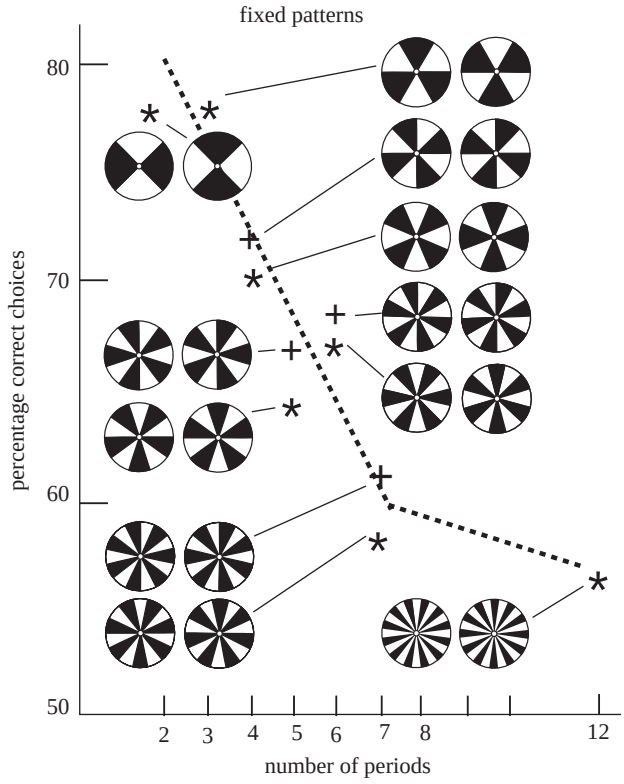

Fig. 14. Honeybee discrimination of the rotation of fixed black and white sector patterns by a half-period. The limit is near 7 periods, where the maximum width of a black segment subtends 9° at the bees' eye (after Horridge, 2000c).

discrimination between different sector patterns does not require green contrast (Horridge, 1999).

The limit in this task was 16 periods in the pattern when the target subtended 130° (Wehner, 1981, p. 477). In a similar task (Gould, 1985) the limit was 16 parts. These tasks look spectacular but they are well within expectations because the targets were large enough to give sufficient difference in position at the edge of the perimeter. With fixed targets subtending 55°, the limit of 7 or 8 sector periods (Fig. 14) corresponds to a position difference of 8–9°, which is within the detectable resolution of the position of a single patch of black in the vertical direction, or relative to the reward hole. Exchange of two colours in the horizontal direction is discriminated if the frame of reference is stabilized by green contrast. With isolated bars of black or colour, the resolution of position is better than 8° in the vertical direction even with no green contrast (Horridge, 1999, 2000d).

2.9. Combining the cues

The cues are detected by coarsely tuned filters or channels (Horridge, 2000b), and the different kinds of cues are summed separately in large fields, so most of the information load is ignored and the final representation is sparse. Cues can be repeated across the target to improve the performance. Numerous results have shown that the bigger the area of colour or grating, or the greater the number of cues, the better the discrimination by bees. Wehner (1972) made a detailed study showing that the cues from different positions of areas of black were added together.

To recognize a place, bees use the co-incidence of a few cues in a few different directions (Horridge, 2005). Recognition is based only on the region-by-region co-incidences of summed cues, which are inadequate to assemble the image. They also make use of co-incidences with other modalities, and multimodal neurons are the rule, even in the deep optic lobe. Co-incidences and sequences of cues have been sufficient for these animals during a long evolution. There is no internal image that requires picture analysis or elaboration of the brain, and the small brain has no way to put together a pixel by pixel image of the panorama.

3. Observation versus theory

3.1. Theory-led development of the subject

For all the past century, it was assumed that insect vision is limited by the optics and spacing of receptors. Of these two strands of theory, the first has been very successful, the other less so. Direct observations of the optical pathway led to further understanding of the diffraction-limited blur circle, the capture of the light by the rhabdom, its progressive absorption by the visual pigment, signal/noise ratios, and the measurement and calculation of $\Delta\rho$. In all aspects of the capture of light, measurements were successfully related to theory. Each stage of processing appears to be optimized to give a maximum signal/noise ratio in the temporal modulation of the lamina cells (Laughlin, 1994). The behavioural detection of small temporal modulations, which is the simplest cue for the bee, depends on the number of ommatidia stimulated, but not directly on $\Delta\phi$.

The second main strand, the sampling principle, that the ommatidial array detects the lay-out of a pattern, has not fared so well, because there is no evidence of re-construction of pattern nor a test with two points or lines. When bees detect gratings, they use either the temporal modulation or the orientation of edges, and in either case there is plenty of evidence that they are not interested in the lay-out, and that resolution is not $2\Delta\phi$. Elsewhere, the measurement of $\Delta\phi$ led to catalogues of regional differences of different types of eyes, some of which can be related to behaviour but tell us little about visual mechanisms.

The theory of the detection of directional motion at first assumed that the lateral interaction is between

adjacent ommatidia (Hassenstein, 1951; Götz, 1964), but experimental analysis eventually showed that measurement of the resolution is complicated by receptor and regional diversity, by sub-adjacent interactions, and by pooling of channels in low light. Moreover, undersampling is the rule, so the direction of motion is not detected in the finest patterns that the insects can discriminate by temporal modulation differences.

When it was thought that resolution was a question of separating two points of light, Raleigh's criterion was accepted as the limit. $D\,\Delta\phi$ is then 0.6 μm. When it was generally believed that insects "see things," the idea of pictorial coding was based on sampling the lay-out of contrasts and re-assembly of the image, at first with no noise. $D\,\Delta\phi$ is then 0.25 μm. When it was thought that the limiting factor in motion detection was the temporal modulation at adjacent green receptors, the detector architecture predicts that $\Delta\rho/\Delta\phi = 1.67$ and $D\,\Delta\phi = 0.3$ μm (Srinivasan and Dvorak, 1980).

In each effort to find what was optimized, the most efficient flow of information was sought by excluding redundancy, i.e., the useless signals. There was a major problem in defining the useless signals before the useful ones were identified. When information theory and photon shot noise was applied (Snyder et al., 1977), the optimum $D\,\Delta\phi$ was greater for eyes adapted to less light. Later, it was found that the limiting factor in bright light is intrinsic receptor noise and synaptic noise in the lamina (Howard and Snyder, 1983). Mechanisms were sought and found, some that reduce noise by smoothing, and narrowing the bandwidth, others that amplify the most useful parts of the signal before the synaptic noise is generated (Laughlin, 1994). In the late 1980s the idea was developed that eyes are designed to detect contrasts with the statistics of natural scenes (Field, 1987) so the bandwidth of the response was matched to the expected stimuli. The receptors were optimized to detecting contrasts or motion in the scene, i.e., looking out to lifestyle and habitat.

There has recently been a change in attitude away from analysis based on general theories, towards actually noticing the experimental measurements. Let me quote "the difference in resolution limit of the drone bee's detection of the queen in flight (0.3°) and the workers resolution of a coloured patch (5°), emphasizes the need for caution in extrapolating from one task to another" (Land, 1997b). This comment shows how recent was the realization that the resolution depends on the task, and in neither of the examples is the limit $\Delta\phi$.

It now seems likely that insects detect only simple cues that excite a small local group of neurons, and rely on co-incidences between them or with other inputs. The bandwidth of the incoming signal can now be further reduced, because everything except the cue is redundant. With the orientation detectors (Fig. 13), we are now at a similar stage to that achieved by Hassenstein in 1956 with the motion detector. We know that the orientation detectors are short (3–4°), independent and colour blind. We know that they are averaged in such a way that parallel edges are summed but orthogonal edges cancel. They detect large fuzzy edges but exclude isotropic textures. With other cues, we need more measurements before the noise analysis can proceed.

The most carefully studied insect behaviour can be explained by detectors of cues; and we have no evidence of image reconstruction; in fact, much against it (e.g., Figs. 11b,c and 12d,e). If the lay-out of the bars of a grating is not seen by the bee, it is not relevant that the limiting period is $2\Delta\phi$. The compound eye has not evolved to optimize the sampling of the image for reconstruction of as much detail as possible, as proposed by Snyder et al. (1977). However, the cues are quite diverse and at each place on the eye $\Delta\phi$ must be a compromise influenced by all of them. The result may resemble an eye designed to make the most of all the information in the environment, but in other insects one detector and its cue may dominate, so we find unusual values of $\Delta\phi$ and $\Delta\rho$ (Section 1.7).

Right up to the present time, all the best authorities have assumed that the angular resolution of the compound eye is limited by the interommatidial angle. Some actually defined acuity as $1/\Delta\phi$ and use the term "resolution" in a loose way to mean "ability to resolve fine detail" (Land, 1997a). Most assumed that the smallest grating that could be assembled by adjacent ommatidia measured the resolution (Kirschfeld, 1976; Snyder, 1979; Wehner, 1981; Wehner and Srinivasan, 1984). It was all theory-driven; it looked as if it ought to be so, but experimental observations point to a different conclusion, that $\Delta\phi$ is one component of some of the neuro-sensory feature detectors.

The persistent statement that the acuity is $1/\Delta\phi$ had two sources. The first was anthropomorphism. When we thought that the insects see the panorama, it followed that the eye divided up the scene as an array in which each receptor summed its field of view. The spacing between sampling stations was then half the period of the minimum regular grating that was reconstructed. However, bee vision and perhaps all insect vision is economically explained by innate detectors of cues that are quite insufficient to reassemble the image. The idea that insects actually see a picture in pixels, that has persisted since Müller (1826), is a human illusion.

Secondly, in the model of the optomotor response, it was assumed that directional motion was detected from the successive temporal modulations of adjacent visual axes (Exner, 1876; von Gavel, 1939; Götz, 1965), but it was later found that they do not see the lay-out and the span changes with the ambient intensity.

4. Conclusion

Where the measured resolution is near the physical limit we can infer that the task is important for survival. Examples are the sensitivity to single photons, contrast and small movements, the discrimination of wavelength, modulation, orientation, and intensity gradients, all separately averaged over large fields. Where the resolution is moderate, as for the sensitivity to optic flow, positions of movements and black areas or relative positions of two colours, we can infer that the task is less important. Where resolution is poor, as for discrimination of size, contrast frequency, or light intensity, we should look elsewhere for vital behaviour.

The theory here is that nothing but cues are detected. At present the advances lie in showing how cues are processed. Clearly, we can re-consider the optimum $\Delta\phi$ for the most efficient detection of each cue, but not for the whole eye. Although measurements have been made for nearly a century, I can find none where the measured spatial resolution is actually fixed at $2\Delta\phi$. The performance of each cue depends on the density of sampling points and the number collaborating.

There is no valid evidence that an extended grating generates temporal modulation better than expected from the diffraction limit set by the individual ommatidial aperture. This conclusion is now an irrelevant limit only, because cues are never extended gratings. With lateral inhibition there can be improvement at high spatial frequencies to help detect small targets with a loss at low frequencies. Of course there are other limits; the signal/noise ratio must be adequate, and the statistical distribution of contrasts in the particular cue can be matched. ''The resolution depends on what the bees use for the visual cue. That each cue has its own resolution is the operational view, based on measurements in the tests, not on theory'' (Horridge, 2003c).

Finally, I quote two great visual scientists with reference to *Drosophila*, ''This difference between the physiologically achieved and anatomically expected resolving power may mean that the neural paths of the ommatidia are interconnected, and that therefore they cannot act as individuals but as connected groups'' (Hecht and Wald, 1934).

Acknowledgement

I am much obliged to two ardent referees who, with their contrasting conceptions of their duty, cast light and heat into this debate.

References

Anderson, J.C., Laughlin, S.B., 2000. Photoreceptor performance and the co-ordination of achromatic and chromatic inputs in the fly visual system. Vision Research 40, 13–31.

Aung Si, Srinivasan, M.V., Zhang, S., 2003. Honeybee navigation, properties of the visually driven ''odometer''. Journal of Experimental Biology 206, 1265–1273.

Barlow, H.B., 1952. The size of ommatidia in apposition eyes. Journal of Experimental Biology 29, 675–684.

Barlow, H.B., 1965. Visual resolution and the diffraction limit. Science 149, 553–555.

Baumann, F., 1975. Electrophysiological properties of the honey bee retina. In: Horridge, G.A. (Ed.), The Compound Eye and Vision of Insects. Oxford University Press, Oxford, pp. 53–74.

Baumgärtner, H., 1928. Der Formensinn und der Sehschärfe der Bienen. Zeitschrift für Vergleichende Physiologie 7, 56–143.

Bernard, C.G. (Ed.), 1996, The Functional Organization of the Compound Eye. Pergamon Press, Oxford.

Bidwell, N.J., Goodman, L.J., 1993. Possible functions of a population of descending neurons in the honeybee's visuo-motor pathway. Apidologie 24, 333–354.

Braitenberg, V., 1967. Patterns of projection in the visual system of the fly. I. Retina-lamina projections. Experimental Brain Research 3, 271–298.

Buchner, E., 1976. Elementary movement detectors in an insect visual system. Biological Cybernetics 24, 85–101.

Burkhardt, D., Streck, P., 1965. Das Sehfeld einzelner Sehzellen—eine Richtigstellung. Zeitschrift für Vergleichende Physiologie 51, 151–152.

Burtt, E.T., Catton, W.T., 1962. A diffraction theory of insect vision. Part I. An experimental study of visual acuity in certain insects. Proceedings of the Royal Society of London B 157, 53–82.

Burtt, E.T., Catton, W.T., 1969. Resolution of the locust eye measured by rotation of radial striped patterns. Proceedings of the Royal Society of London B 173, 513–529.

Cajal, S.R.y., 1909. Nota sobre la estructura de la rétina de la mosca (*Mosca vomitoria*). Trabajos de la Laboratorio de Investigaciones, Madrid 16, 109–139.

Cartwright, B.A., Collett, T.S., 1979. How honey-bees know their distance from a near-by visual landmark. Journal of Experimental Biology 82, 367–372.

Catton, W.T., 1998. A test of the visual acuity of the locust eye. Journal of Insect Physiology 44, 1145–1148.

Catton, W.T., 1999. The effect of target orientation on the visual acuity and the spatial frequency response of the locust eye. Journal of Insect Physiology 45, 191–200.

Collett, T.S., Land, M.F., 1975. Visual control of flight behaviour in the hoverfly, *Syritta pipiens* L. Journal of Comparative Physiology 99, 1–66.

Dahmen, H., 1991. Eye specialization in waterstriders: an adaptation to life in a flat world. Journal of Comparative Physiology 169, 623–632.

David, C.T., 1979. Optomotor control of speed and height by free-flying *Drosophila*. Journal of Experimental Biology 82, 389–392.

Dietrich, W., 1909. Die Facettenaugen der Dipteren. Zeitschrift für Zoology 92, 465–539.

Dubs, A., Laughlin, S.B., Srinivasan, M.V., 1981. Single photon signals in fly photoreceptors and first order interneurones at behavioural threshold. Journal of Physiology 317, 317–334.

Dvorak, D., Snyder, A., 1978. The relationship between visual acuity and illumination in the fly, *Lucilia sericata*. Zeitschrift für Naturforschung 33c, 139–143.

Eckert, H., 1973. Optomotorische Untersuchungen am visuellen System der Stubenfliege *Musca domestica* L. Kybernetic 14, 1–23.

Exner, S., 1876. Über das Sehen von Bewegungen und die Theorie des zusammengestzten Auges. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe. Wien, 72, 156–190.

Exner, S., 1891. Die Physiologie der facettirten Augen von Krebsen und Insecten. F. Deuticke, Vienna. Transl. Hardie, R.C. (1990), The Physiology of the Compound Eyes of Insects and Crustaceans. Springer, Heidelberg.

Fermi, G., Reichardt, W., 1963. Optomotorische Reaktionen der Fliege *Musca domestica*. Kybernetik 2, 15–28.

Field, D.J., 1987. Relations between the statistics of natural images and the response properties of cortical cells. Journal of the Optical Society of America 4, 2379–2394.

Franceschini, N., 1975. Sampling of the visual environment by the compound eye of the fly: fundamentals and applications. In: Snyder, A.W., Menzel, R. (Eds.), Photoreceptor Optics. Springer, Berlin, pp. 98–144.

Friedlaender, M., 1931. Zur Bedeutung des Fluglochs im optischen Feld der Biene bei senkrechter Dressuranordnung. Zeitschrift für Vergleichende Physiologie 15, 193–260.

von Frisch, K., 1914. Der Farbensinn und Formensinn der Biene. Zoologische Jahrbucher, Abteilung für allgemeine Physiologie 35, 1–182.

von Gavel, L., 1939. Die kritische Streifenbreite als Mass für die Sehschärfe bei *Drosophila melanogaster*. Zeitschrift für Vergleichende Physiologie 27, 80–135.

Giger, A.D., 1996. Ph.D. Thesis, Australian National University, Canberra.

Giger, A.D., Srinivasan, M.V., 1996. Pattern recognition in honeybees: chromatic properties of orientation analysis. Journal of Comparative Physiology A 178, 763–769.

Giurfa, M., Lehrer, M., 2001. Honeybee vision and floral displays; from detection to close-up recognition. In: Chittka, L., Thomson, J.D. (Eds.), Cognitive Ecology of Pollination. Cambridge University Press, Cambridge, pp. 61–82.

Giurfa, M., Vorobyev, M., 1998. The angular range of achromatic target detection by honey bees. Journal of Comparative Physiology A 183, 101–110.

Giurfa, M., Vorobyev, M., Kevan, P., Menzel, R., 1996. Detection of coloured stimuli by honeybees: minimum visual angles and receptor specific contrasts. Journal of Comparative Physiology A 178, 699–709.

Götz, K.G., 1965. Die optischen Übertragungseigenschaften der Komplexaugen von *Drosophila*. Kybernetik 2, 215–221.

Gould, J.L., 1985. How bees remember flower shapes. Science, New York 227, 1492–1494.

Grenacher, H., 1879. Untersuchungen über das Sehorgan der Arthropoden, insbesondere der Spinnen, Insecten und Crustaceen. Göttingen, Vandenhoeck und Ruprecht.

Hardie, R.C., 1979. Electrophysiological analysis of fly retina. I. Comparative properties of R1-6 and R 7 and 8. Journal of Comparative Physiology 129, 19–33.

Hardie, R.C., 1985. Functional organisation of the fly retina. In: Ottoson, D. (Ed.), Progress in Sensory Physiology, vol. 5. Springer, Berlin, pp. 1–79.

Hardie, R.C., 1986. The photoreceptor array of the dipteran retina. Trends in Neurosciences 9, 419–423.

Hassenstein, B., 1951. Ommatidienraster und afferente Bewegungsintegration. (Versuche an dem Rüsselkäfer *Chlorophanus viridis*). Zeitschrift für Vergleichende Physiologie 33, 301–326.

Hecht, S., Wald, G., 1934. The visual acuity and intensity discrimination of *Drosophila*. Journal of General Physiology 17, 517–547.

Hecht, S., Wolf, E., 1929. The visual acuity of the honeybee. Journal of General Physiology 12, 727–760.

Hertz, M., 1929–1931. Die Organisation des optischen Feldes bei der Biene. Zeitschrift für Vergleichende Physiologie 8, 693–748. Hertz, M., 1929–1931. Die Organisation des optischen Feldes bei der Biene. Zeitschrift für Vergleichende Physiologie 11, 107–145.Hertz, M., 1929–1931. Die Organisation des optischen Feldes bei der Biene. Zeitschrift für Vergleichende Physiologie 14, 629–674.

Hertz, M., 1933. Über figurale Intensität und Qualitäten in der optische Wahrnehmung der Biene. Biologische Zentralblatte 53, 10–40.

Hooke, R., 1665. Micrographia or some Physiological Descriptions of Minute Bodies made by Magnifying Glasses. J. Martyn, J. Allestry, London.

Horridge, G.A., 1978. The separation of visual axes in apposition compound eyes. Philosophical Transactions of the Royal Society of London B 285, 1–59.

Horridge, G.A., 1980. Apposition eyes of large diurnal insects as organs adapted to seeing. Proceedings of the Royal Society of London B 207, 287–309.

Horridge, G.A., 1997. Pattern discrimination by the honeybee: disruption as a cue. Journal of Comparative Physiology A 181, 267–277.

Horridge, G.A., 1999. Pattern vision of the honeybee (*Apis mellifera*): the effect of pattern on the discrimination of location. Journal of Comparative Physiology A 185, 105–113.

Horridge, G.A., 2000a. Pattern vision of the honeybee (*Apis mellifera*) What is an oriented edge? Journal of Comparative Physiology A 186, 521–534.

Horridge, G.A., 2000b. Seven experiments on pattern vision of the honeybee, with a model. Vision Research 40, 2589–2603.

Horridge, G.A., 2000c. Visual discrimination of radial cues by the honeybee (*Apis mellifera*). Journal of Insect Physiology 46, 629–645.

Horridge, G.A., 2000d. Pattern vision of the honeybee (*Apis mellifera*): the discrimination of location by the blue and green receptors. Neurobiology of Learning and Memory 74, 1–16.

Horridge, G.A., 2003a. Discrimination of single bars by the honeybee (*Apis mellifera*). Vision Research 43, 1257–1271.

Horridge, G.A., 2003b. The visual system of the honeybee (*Apis mellifera*): the maximum length of the orientation detector. Journal of Insect Physiology 49, 621–628.

Horridge, G.A., 2003c. Visual resolution of gratings by the compound eye of the bee (*Apis mellifera*). Journal of Experimental Biology 206, 2105–2110.

Horridge, G.A., 2003d. Visual discrimination by the honeybee (*Apis mellifera*): the position of the common centre as the cue. Physiological Entomology 28, 132–143.

Horridge, G.A., 2003e. The effect of complexity on the discrimination of oriented bars by the honeybee (*Apis mellifera*). Journal of Comparative Physiology A 189, 703–714.

Horridge, G.A., 2003f. Visual resolution of the orientation cue by the honeybee (*Apis mellifera*). Journal of Insect Physiology 49, 1145–1152.

Horridge, G.A., 2005. What the honeybee sees; a review of the recognition system of *Apis mellifera*. Physiol. Entomol., in press.

Horridge, G.A., Mimura, K., Hardie, R.C., 1976. Fly photoreceptors III. Angular sensitivity as a function of wavelength and the limits of resolution. Proceedings of the Royal Society of London B 194, 151–177.

Horridge, G.A., Duniec, J., Marcelja, L., 1981. A 24-hour cycle in single locust and mantid photoreceptors. Journal of Experimental Biology 91, 307–322.

Horridge, G.A., Zhang, S.W., Lehrer, M., 1992. Bees can combine range and visual angle to estimate absolute size. Philosophical Transactions of the Royal Society of London B 337, 49–57.

Howard, J., Snyder, A.W., 1983. Transduction as a limitation on compound eye function and design. Proceedings of the Royal Society of London B 217, 287–307.

Ioannides, A.C., Horridge, G.A., 1975. The organisation of visual fields in the hemipteran acone eye. Proceedings of the Royal Society of London B 190, 373–391.

James, A.C., 1992. Non-linear operator network models of processing in the fly lamina. In: Pinter, R.B., Nabet, B. (Eds.), Nonlinear Vision. CRC Press, Boca Raton, FL, pp. 39–73.

Jander, U., Jander, R., 2002. Allometry and resolution of bee eyes (Apoidea). Arthropod Structure Development 30, 179–193.

Jander, R., Volk-Heinrichs, I., 1970. Das strauschspezifische visuel Perceptorsystem der Stabheuschrecke (*Carausius morosus*). Zeitschrift für Vergleichende Physiologie 70, 425–477.

Jander, R., Voss, C., 1963. Die Bedeutung von Streifenmustern für das Formensehen der Roten Waldameise (*Formica rufa* L.). Zeitschrift für Tierpsychologie 20, 1–9.

Kirschfeld, K., 1967. Die Projektion der optischen Umwelt auf das Raster der Rhabdomere im Komplexauge von *Musca*. Experimental Brain Research 3, 248–270.

Kirschfeld, K., 1976. The resolution of lens and compound eyes. In: Zettler, F., Weiler, R. (Eds.), Neural Principles in Vision. Springer, Berlin, pp. 354–370.

Kirschfeld, K., Lutz, B., 1974. Lateral inhibition in the compound eye of the fly, *Musca*. Zeitschrift für Naturforschung 29c, 95–96.

Kirschfeld, K., Wenk, P., 1976. The dorsal compound eye of simuliid flies: an eye specialized for the detection of small, rapidly moving objects. Zeitschrift für Naturforschung 31c, 764–765.

Kolb, G., Autrum, H., 1972. Die Feinstruktur im Auge der Biene bei Hell-und Dunkeladaption. Journal of Comparative Physiology 77, 113–125.

Kuiper, J.W., 1966. On the image formation in a single ommatidium of the compound Eye in Diptera. In: Bernhard, C.G. (Ed.), The Functional Organization of the Compound eye. Pergamon Press, Oxford, pp. 35–50.

Kunze, P., 1961. Untersuchungen des Bewegungssehens fixiert fliegender Bienen. Zeitschrift für Vergleichende Physiologie 44, 656–684.

Land, M.F., 1989. Variations in the structure and design of compound eyes. In: Stavega, D.G., Hardie, R.C. (Eds.), Facets of Vision. Springer, Berlin, pp. 90–111.

Land, M.F., 1997a. Visual acuity in insects. Annual Review of Entomology 42, 147–177.

Land, M.F., 1997b. The resolution of insect compound eyes. Israel Journal of Plant Sciences 45, 79–91.

Land, M.F., Eckert, H., 1985. Maps of the acute zones of fly eyes. Journal of Comparative Physiology A 156, 525–536.

Land, M.F., Gibson, G., Horwood, J., Zeil, J., 1999. Fundamental differences in the optical structure of the eyes of nocturnal and diurnal mosquitoes. Journal of Comparative Physiology A 185, 91–103.

Laughlin, S.B., 1994. Matching coding, circuits, cells and molecules to signals: general principles of retinal design in the fly's eye. Progress in Retinal and Eye Research 13, 165–196.

Laughlin, S.B., Horridge, G.A., 1972. Angular sensitivity of the retinula cells of dark-adapted worker bee. Zeitschrift für Vergleichende Physiologie 74, 329–335.

Lehrer, M., 1990. How bees use peripheral eye regions to localize a frontally positioned target. Journal of Comparative Physiology A 167, 173–185.

Lehrer, M., Bischof, S., 1995. Detection of model flowers by honeybees: the role of chromatic and achromatic contrast. Naturwissenschaften 82, 145–147.

Lehrer, M., Collett, T.S., 1994. Approaching and departing bees learn different cues to the distance of a landmark. Journal of Comparative Physiology A 175, 171–177.

Lehrer, M., Srinivasan, M.V., Zhang, S.W., Horridge, G.A., 1988. Motion cues provide the bee's visual system with a third dimension. Nature, London 332, 356–357.

Macuda, T., Gegear, R.J., Laverty, T.M., Timney, B., 2001. Behavioural assessment of visual acuity in bumblebees (*Bombus impatiens*). Journal of Experimental Biology 204, 559–564.

Mallock, A., 1894. Insect sight and the defining power of composite eyes. Proceedings of the Royal Society of London B 55, 85–90.

Marčelja, S., 1979. Optimal lateral interactions in a compound eye. Journal of Comparative Physiology 132, 159–166.

Meinertzhagen, I.A., Sorra, K.E., 2001. Synaptic organization in the fly's optic lamina: few cells, many synapses and divergent microcircuits. Progress in Brain Research 131, 53–69.

Meyer, H.W., 1971. Visuelle Schlüssel reize für die Aulösung der Beutefanghandlung beim Bachwasserläufer *Velia capria* (Hemiptera, Heteroptera). Zeitschrift für Vergleichende Physiologie 72, 260–342.

Meyer, H.W., 1974. Geometrie und funktionelle Specialisierung des optischen Abtastrasters beim Bachwasserläufer (*Velia capria*). Journal of Comparative Physiology 92, 85–103.

Müller, J., 1826. Zur vergleichende Physiologie des Gesichtssinnes. Cnobloch, Leipsig.

Northrop, R.B., 1975. Information processing in the insect compound eye. In: Horridge, G.A. (Ed.), The Compound Eye and Vision of Insects. Oxford University Press, Oxford, pp. 378–409.

Palka, J., 1965. Diffraction and visual acuity of insects. Science, Washington 149, 551–553.

Palka, J., Pinter, R.B., 1975. Theoretical and experimental analysis of visual acuity in insects. In: Horridge, G.A. (Ed.), The Compound Eye and Vision of Insects. Oxford University Press, Oxford, pp. 321–337.

Pick, B., Buchner, E., 1979. Visual movement detection under light- and dark-adaptation in the fly, *Musca domestica*. Journal of Comparative Physiology 134, 45–54.

Pinter, R.B., 1979. Inhibition and excitation in the locust DCMD receptive field: spatial frequency, temporal and spatial characteristics. Journal of Experimental Biology 80, 191–216.

Pyza, E., Meinertzhagen, I.A., 2003. The regulation of circadian rhythms in the fly's visual system. Neuropeptides 37, 227–289.

Ronacher, B., 1979. Äquivalenz zwischen Größen- und Helligkeitsunterschieden im Rahmen der visuellen Wahrnehmung der Honigbiene. Biological Cybernetics 32, 63–75.

Rossel, S., 1979. Regional differences in photoreceptor performance in the eye of the praying mantis. Journal of Comparative Physiology 131, 95–112.

Seidl, R., 1982. Die Sehfelder und Ommatidien Divergenzwinkel von Arbeiterin, Königin und Drohne der Honigbiene (*Apis mellifera*). Ph.D. Thesis, Darmstadt Technische Hochschule, Darmstadt.

Smakman, J.G.J., Hateren, J.H., van Stavenga, D.G., 1984. Angular sensitivity of blowfly photoreceptors: intracellular measurements and wave-optical predictions. Journal of Comparative Physiology A 155, 239–247.

Snyder, A.W., 1975. Optical properties of invertebrate photoreceptors. In: Horridge, G.A. (Ed.), The Compound Eye and Vision of insects. Oxford University Press, Oxford, pp. 179–235.

Snyder, A.W., 1979. The physics of vision in compound eyes. In: Autrum, H. (Ed.), Vision in Invertebrates, vol. VII/6A, Handbook of Sensory Physiology, Springer, Berlin, pp. 255–314.

Snyder, A.W., Stavenga, D.G., Laughlin, S.B., 1977. Spatial information capacity of compound eyes. Journal of Comparative Physiology 116, 183–207.

Spaethe, J., Chittka, L., 2003. Interindividual variation of eye optics and single object resolution in bumblebees. Journal of Experimental Biology 206, 3447–3453.

Srinivasan, M.V., Dvorak, D.R., 1980. Spatial processing of visual information in the movement detecting pathway of the fly. Journal of Comparative Physiology 140, 1–23.

Srinivasan, M.V., Lehrer, M., 1984a. Temporal acuity of honeybee vision: behavioural studies using moving stimuli. Journal of Comparative Physiology A 155, 297–312.

Srinivasan, M.V., Lehrer, M., 1984b. Temporal acuity of honeybee vision: behavioural studies using flickering stimuli. Physiological Entomology 9, 447–457.

Srinivasan, M.V., Lehrer, M., 1988. Spatial acuity of honeybee vision, and its spectral properties. Journal of Comparative Physiology A 162, 159–172.

Srinivasan, M.V., Laughlin, S.B., Dubs, A., 1982. Predictive coding: a fresh view of inhibition in the retina. Proceedings of the Royal Society of London B 216, 427–459.

Srinivasan, M.V., Zhang, S.W., Rolfe, B., 1993. Is pattern vision in insects mediated by 'cortical' processing? Nature, London 362, 539–540.

Srinivasan, M.V., Zhang, S.W., Witney, K., 1994. Visual discrimination of pattern orientation by honeybees. Philosophical Transactions of the Royal Society of London B 343, 199–210.

Stach, S., Benard, J., Giurfa, M., 2004. Local feature assembling in visual pattern recognition and generalization in honeybees. Nature, London 429, 758–761.

Stavenga, D.G., 1979. Pseudopupils of compound eyes. In: Autrum, H. (Ed.), Invertebrate Photoreceptors. Handbook of Sensory Physiology, vol. VII/6A. Springer, Berlin, pp. 357–439.

Stavenga, D.G., 2003. Angular and spectral sensitivity of fly photoreceptors. Parts I, II, III. Journal of Comparative Physiology A 189, 1–17; 189, 189–202; 190, 115–129.

Tatler, B., O'Carroll, D.C., Laughlin, S.B., 2000. Temperature and the temporal resolving power of fly photoreceptors. Journal of Comparative Physiology A 186, 399–407.

Thorson, J., 1966. Small-signal analysis of a visual reflex in locust. I. Input parameters. Kybernetik 3, 41–53.

Tunstall, J., Horridge, G.A., 1967. Electrophysiological investigation of the optics of the locust retina. Zeitschrift für Vergleichende Physiologie 55, 167–182.

Turner, C.H., 1911. Experiments on pattern vision of the honeybee. Biological Bulletin, Wood's Hole 21, 249–264.

Vallet, A.M., Coles, J.A., 1991. The perception of small objects by the drone honeybee. Journal of Comparative Physiology A 172, 183–188.

Varjú, D., 1959. Anwendung der Systemtheorie auf Experimente am Rüsselkäfer *Chlorophanus viridis*. Zeitschrift für Naturforschung 14b, 724–726.

Vigier, P., 1907. Sur les terminations photoréceptrices dans les yeux composés des Muscides. Comptes Rendues Academie des Sciences Paris 63, 532–536.

Vigier, P., 1909. Mécanisme de la synthèse des impressions lumineuses recueilles par les yeux composés des Diptères. Comptes Rendues Academie des Sciences Paris 65, 1221–1223.

Vorobyev, M., Osorio, D., 1998. Receptor noise as a determinant of colour thresholds. Proceedings of the Royal Society of London B 265, 351–358.

Vorobyev, M., Brandt, R., Peitsch, D., Laughlin, S.B., Menzel, R., 2001. Colour thresholds and receptor noise: behaviour and physiology compared. Vision Research 41, 639–653.

Voss, C., 1967. Das Formensehen der Roten Waldameise *Formica rufa*. Zeitschrift für Vergleichende Physiologie 55, 225–254.

Walcott, B., 1975. Anatomical changes during light adptation in insect compound eyes. In: Horridge, G.A. (Ed.), The Compound Eye and Vision of Insects. Oxford University Press, Oxford, pp. 20–33.

Warrant, E., Porombka, T., Kirchner, W., 1996. Neural image enhancement allows honeybees to see at night. Proceedings of the Royal Society of London B 263, 1521–1526.

Warrant, E., Kelber, A., Gislén, A., Greiner, B., Ribi, W., Wcislo, T., 2004. Nocturnal vision and landmark orientation in a tropical halictid bee. Current Biology 14, 1309–1318.

Wehner, R., 1972. Dorsoventral asymmetry in the visual field of the bee, *Apis mellifica*. Journal of Comparative Physiology 77, 256–277.

Wehner, R., 1981. Spatial vision in arthropods. In: Autrum, H. (Ed.), Vision in Invertebrates, vol. VII/6C. Handbook of Sensory Physiology. Springer, Berlin, pp. 287–616.

Wehner, R., Srinivasan, M.V., 1984. The world as the insect sees it. In: Lewis, T. (Ed.), Insect Communication. Academic Press, London, pp. 29–47.

Wigglesworth, V.B., 1965. The Principles of Insect Physiology. Methuen, London.

Wilson, M., 1975. Angular sensitivity of light and dark adapted locust retinula cells. Journal of Comparative Physiology 97, 323–328.

Wolf, E., 1933. The visual intensity discrimination of the honeybee. Journal of General Physiology 16, 407–422.

Wolf, E., 1935. An analysis of the visual capacity of the bee's eye. Cold Spring Harbor Symposium Quantitative Biology 3, 255–260.

Wolf, E., Zerrahn-Wolf, G., 1935. The dark adaptation of the eye of the honeybee. Journal of General Physiology 19, 229–237.

Zeil, J., 1983. Sexual dimorphism in the visual system of flies: the compound eyes and neural superposition in Bibionidae (Diptera). Journal of Comparative Physiology 150, 509–515.

Zhang, S.W., Horridge, G.A., 1992. Pattern recognition in bees: size of regions in spatial layout. Philosophical Transactions of the Royal Society of London B 337, 65–71.