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Honeybee: Design of the Visual System

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Abstract
The compound eye of the bee collects a composite image of the panorama in radial coordinates over about 200° horizontally (and $\pm 90°$ vertically) with about 10,000 ommatidia (analogous to pixels). The photoreceptors are of three color types, with a peak in the green, blue, or ultraviolet. As each contrast in the panorama passes, small motion detectors spanning two or three ommatidia sense the angular motion relative to the eye from the sequence of intensities. The units of pattern or place recognition with excellent resolution are: a) modulation detectors one ommatidium wide; and b) edge orientation detectors three ommatidia wide. In the deep optic lobe, there are large-field neurons with tonic or phasic antagonistic inputs from two or three color types of receptors. All detectors respond to passing edges as the bee scans in the horizontal plane. Irrespective of the actual pattern, the responses of the detectors are summed by type and position to form 7 or 8 different cues in each local region of the eye. If rewarded, the cues are remembered in an order of preference, and the coincidence of different cues in a local region may be remembered as the label on a retinotopic landmark. The panorama is represented as a low-resolution sparse map of landmark labels. Bees learn a combination of one or more labels to identify a place and find the reward. To a bee, a color or pattern or even a mixture of modalities is just another landmark.

INTRODUCTION

Most animals have some sensitivity to light, and eyes have evolved at least 10 times, but many are at the level of an automatic door that responds to the approach of anything that moves. It is quite a different matter to design and make a visual system that can be programmed to recognize a particular place, follow a track, explore an unfamiliar terrain, and return home from anywhere within it. Bees can do these tasks. Honey bees are readily trained to come to a target for a reward of sugar and so are the invertebrate of choice for the study of natural visual mechanisms of medium complexity. They can be trained to recognize many different objects, patterns, colors, and locations, and follow a sequence of them through a maze. Furthermore, the visual system of the bee is at about the level of complexity that can be analyzed in a formal model and implemented in silicon for testing in the natural world, then used to guide an autonomous vehicle by land, underwater, or in the air.

PRINCIPLES

Like any other efficient, versatile seeing system, the insect eye is adapted to give the maximum spatial and temporal resolution and sensitivity range in three-dimensional space, discrimination of the polarization plane, color and direction of light, angular velocity and direction of motion, speed of action, and the economical use of weight and fuel in a flying vehicle, which can be compressed into a small eye. The sensory processing is done in several kinds of parallel channels drawing from the same set of receptors, and then converging with progressive reduction of redundancy. The mechanism produces sparse maps linked to time of day for recognition of a route to a place. Every detail in the bee is adapted for particular behavior patterns, so the exact data are not of much practical use, but we can copy the principles to make our own seeing gadgets for similar tasks.

THE DESIGN OF THE OPTICS

Receptor Spacing

In the human eye, the external panorama is projected in three-dimensional angular space through one lens, and the two-dimensional image is inverted on the retina (Fig. 1A). In the bee, in each facet, a narrow beam is focused on a small group of receptors. The result is effectively the same, a composite projection for the whole eye (Fig. 1B). Behind the retina in the bee there are about five successive layers of retinotopic projection with several kinds of processing in parallel, with synapses at each stage and progressively wider lateral interactions. The retinotopic projection becomes confused in the deeper layers where memory, recognition, decisions, and motor control are supposed to be formed.

The interommatidial angle between the axis and the adjacent axis ($\Delta\varphi$ in Fig. 2) is about 1.4° in the center of the bee eye. The convex corneal surface of each facet projects a narrow field of view upon the receptor organelle, called the rhabdom, which is formed by a group of nine columnar receptor cells in each ommatidium, that share a common angular sensitivity field. In the bee, the field is about 2° wide at the 50% sensitivity level ($\Delta\rho$ in Figs. 2 and 3). Each ommatidium is an optical instrument like a camera with a single pixel, so the resolution is limited by the
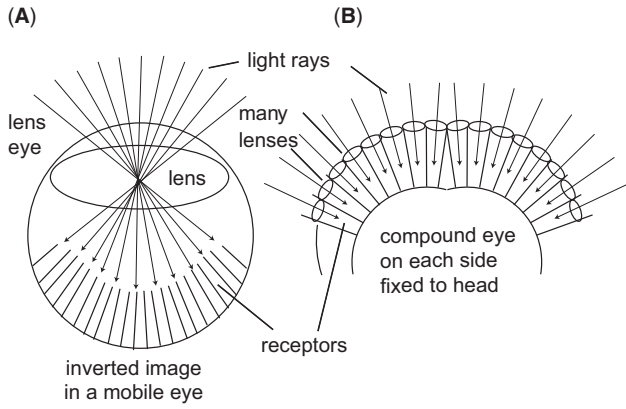
Fig. 1 In the human eye (A), the projection of the external panorama on the receptors of the retina through the nodal point (np) is inverted but not in the bee (B). The compound eye has a wider field of view but poorer spatial resolution.
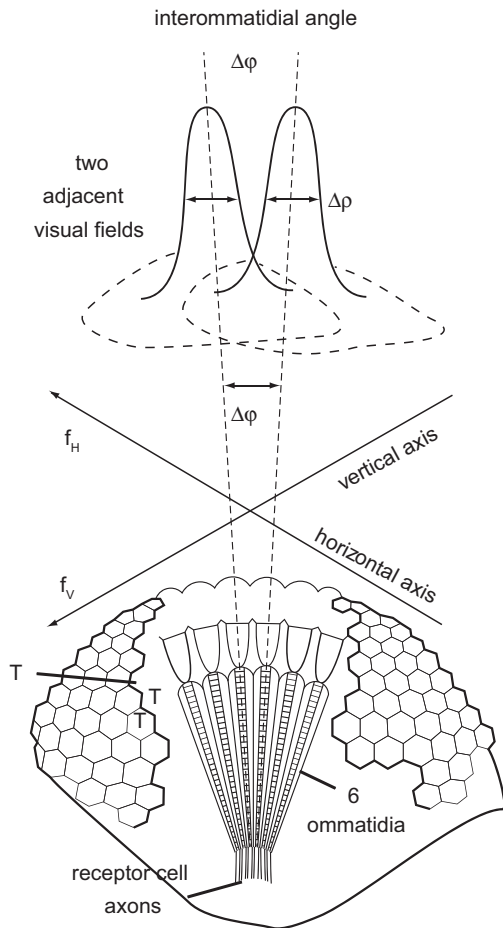

Fig. 2 The optical units of the eye are the ommatidia. There is a trade-off between the smallest detectable black spot and the minimum separation of spots (receptor resolution versus spatial resolution). The optimum is when the neighboring fields intersect at about the 50% level of sensitivity. More facets (smaller $\Delta\varphi$) implies smaller facets, which implies wider $\Delta\rho$. Each axis has a separate lens, so the principles are not like those in the human eye, where receptor size and receptor spacing are roughly equal.

aperture (D) and the wavelength of light (λ). The F number of 2–6 (f/D in Fig. 3) is typical of cameras and eyes that must be able to function in sunlight and deep shade.

Like the rods in vertebrate eyes, each rhabdom is a rod-shaped light guide about 70 μm long, packed with the visual pigment, rhodopsin. To catch rays optimally, it points directly at the nodal point of its lens, and absorbs about 0.7% of the light per micron along its length. When light guides are about 1–2 μm in diameter, their capture cross-section for light can be approximated by a Gaussian distribution of diameter d at the 50% level of sensitivity, where d is the diameter of the guide (Fig. 3).

The nodal point is defined as the point through which rays pass as straight lines through the optics. An eye acts as a one-sided lens (Fig. 1A), and the power of the insect lens lies in the curvature of the cornea, so that the nodal point lies near the center of curvature of the facet surface (Fig. 3). The focal length (f) is measured from the nodal point to the focus. To achieve optimum spatial sampling to detect contrast, the angle $\Delta\varphi$ between each ommatidium and its neighbor should be about equal to the field width $\Delta\rho$ at the 50% level of sensitivity:

$\Delta\varphi = \Delta\rho = 1.4\lambda/D$ radians (Figs. 2 and 3)
Then, $D\Delta\varphi = 1.4\lambda = 0.7$ μm
In the bee, $\Delta\varphi = 1.4°$
and $D = 25$–30 μm,
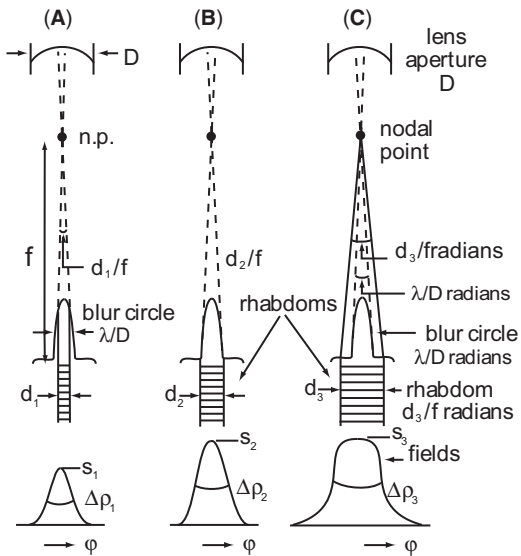which fits the theory very well.

Fig. 3 The design of the ommatidium as an optical instrument. Axial rays are focused through the nodal point (np) to form a blur circle of width d/f radians on the distal end of the receptor (the rhabdom rod). If the rhabdom is too narrow, sensitivity (s) is reduced, but if too broad, resolution is lost. The angular sensitivity field, of width $\Delta\rho$ radians at 50%, is generated by the convolution of the blur circle moving across the receptor cross-section for light capture. (A) Narrowest rhabdom. (B) Typical 2 micron wide rhabdom. (C) Wide low-light rhabdom.

The smallest black spot, like a queen bee that the drone can detect against the sky, is about $1°$, twice the apparent size of the moon.[1] Larger receptors (Fig. 3C) subtend a larger angle in the outside world and therefore catch more light, but they waste the lens resolution, exactly as happens with large pixels in a cheap camera that make the image grainy however sharp be the camera lens. Receptors subtending less than λ/D radians in diameter (Fig. 3A) throw away sensitivity with no gain in resolution.

Cameras and eyes that operate in daylight have similar F numbers, and silver grains in film are similar in diameter to biological receptor organelles because the optics is governed by the laws of physics, the wavelength of light, and the noise in the signal. To match the resolution of the lens to the capture cross-section of the receptor, we have $\lambda/D = d/f$ radians (Fig. 3B). We can calculate the rhabdom diameter in two ways. From the optics (Fig. 3B), d/f is approximately equal to λ/D, and $f/D = F$ (the F number of the lens), so $d = F\lambda$. Because F ranges from 2 to 4 for sensitive eyes, and λ is $0.5\,\mu m$ for green light, a rhabdom between 1 and $2\,\mu m$ wide makes full use of the resolution of light. In practice, most photoreceptor rods that operate in daylight are about $2\,\mu m$ in diameter. On the other hand, a rhabdom between about 1 and $2\,\mu m$ wide is exactly the right size for the light within to be controlled by pigment migration outside that acts as a tubular diaphragm. The width of $\Delta\rho$ is approximately proportional to d/f radians (Fig. 3C) and is therefore fixed, but the sensitivity can be adjusted. These changes are outweighed by changes in gain in the transduction process between the absorption of light and the generation of the receptor potential, and by the changes in sensitivity at the synapses upon the second-order neurons.

The receptor cells are of three types, with peak sensitivity in green, blue, or ultraviolet (UV). The rhabdom rod has a sector contributed by each receptor cell with the result that each sector absorbs its own component of the light along its length. The rhabdom acts as a whole to absorb about 50% of the light but color separation is sharpened and self-absorption has little effect.

The ommatidia are not all the same; the dorsal ones contain more blue and UV-sensitive cells while ventral and lateral ones are more green sensitive. Types of retinula cells differ according to spectral sensitivity and direction of their optimum sensitivity to polarized light. Bees have specialized UV-sensitive ommatidia along the dorsal rim of the eye that detect the polarization pattern of the sky for navigation. For more extensive accounts of insect retinas and optics, see Vallet,[1] Horridge,[2,3] and Snyder.[4]

MOTION DETECTION

Piloting and flight are controlled visually, and neurons that respond to motion are abundant in the optic lobes. There are two main systems plus a few other responses important in flight control. Each passing contrast in the panorama stimulates adjacent or subadjacent receptors. The shift of the modulation from one receptor to the next is detected by local circuits containing directional inhibition (Fig. 4). They are necessarily sensitive to the frequency of passing contrasts and therefore cannot measure angular velocity. In practice, this does not matter, because the vision is dominated by the insects' voluntary motion, including head movements and scanning. Separate large-field neurons detect the cardinal directions on the eye. Their directional sensitivity is very effective in the optomotor response that counteracts unintended displacement from a steady position relative to the panorama, enabling the bee to hover or fly steadily through disturbed air. No neural mechanisms of motion detection have yet been demonstrated for the bee, and the formal circuits for the fly (Fig. 4) inferred from the behavior are nothing like the anatomical circuitry.

A second system of the bee, with an unknown mechanism, detects the angular velocity of the local image irrespective of the direction on the eye.[8] This measure is integrated over the length of the outward foraging path and is conveyed to other bees by the number of abdominal waggles in the dance of the forager when back home in the hive. As they near the target, landing bees keep the optic
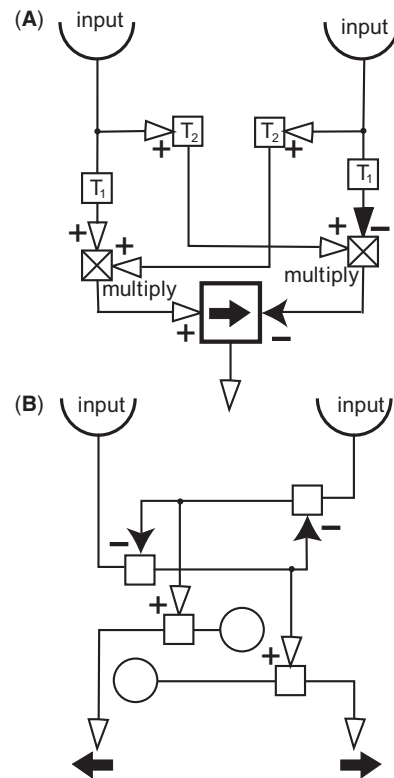

Fig. 4 In principle, motion is detected by a nonlinear lateral interaction between adjacent and subadjacent input channels. (A) The 1969 Reichardt model.[5] (B) Circuit proposed in 1971 for the fly[6] based on a 1965 model for the rabbit.[7] Neither of these models was validated.[42]

flow ahead constant by reducing the approach speed over the ground as the altitude diminishes.[9] Bees use relative motion of the eye to estimate the absolute size of a contrast irrespective of its angular size or range.[10] Motion detection is also effective for detection of danger, and UV light directs the direction of escape. Bees in flight also detect opening parallax, which they identify as an open passage, and closing parallax, which they identify as a place to land.[11] As the bee in flight approaches textures or objects ahead, the convergence and expansion at nodes in the optic flow could theoretically be useful for measuring the time to contact, for avoiding a collision or deviation by the wind during flight.

A visual mechanism based on the piloting of the bee has been implemented several times in silicon for small autonomous helicopters and planes, but it is unlikely that a system using reflected sunlight will be useful for large fast machines. The scaling factors suit the small size, power, speed of action, and inertia of the bee in daylight, but large, heavy, fast machines use accelerometers, radar, ultrasonics, satellite navigation, and radio control at long range.

PATTERNS IN BEE VISION

The Training Method

Early workers trained bees with a number of patterns, and the bees learned to land on the one that rewarded them with sugar solution. The pattern was therefore large but of unknown size at the moment of choice. After 1988, individually marked bees were trained to fly into an experimental choice chamber and select one of the two smaller patterns of known size displayed vertically on the back walls (Fig. 5A). At the center of each pattern was a hole but only one led to a small chamber with the reward. The two patterns (and the reward) changed sides every 5 min to make the bees look at them, rather than simply learn the rewarded side. The trained bees were then tested with a large variety of unfamiliar test patterns that were intercalated so that the bees could not learn them in the tests.

Early Results

A century of training and then testing the trained bees revealed that the bees measured a few parameters; namely, the total length of edges in the pattern, the area, and color, as if they had feature detectors for edges and also for the amount of blue in a local area, region by region. They also detected certain properties of the whole pattern, namely, whether it was circular or had radial spokes or sectors, and whether it was smooth or highly disrupted.[13] With a very large rectangle subtending >100°, tests against the same rectangle at different angles suggested that the bees had learned the positions of areas of black, not the angles of the edges.[14] Until recently, no one considered that the >100° patterns (Fig. 5B) were divided into local
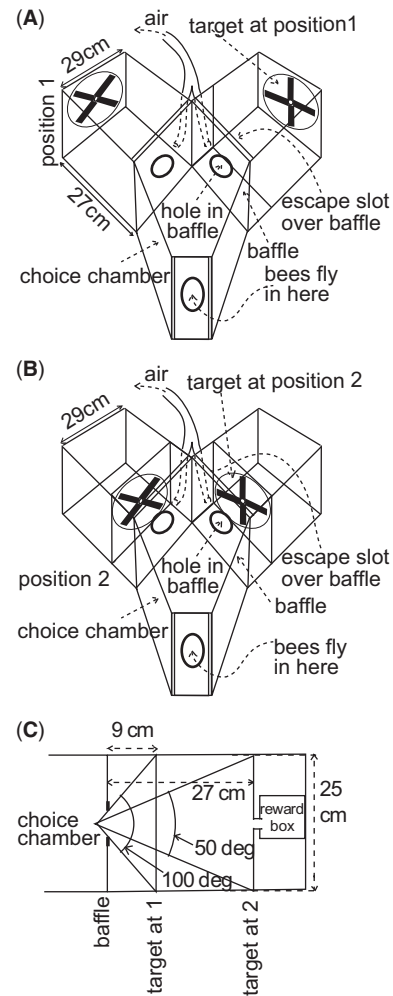

Fig. 5 (A) The Y-choice apparatus for training bees with the target at a controlled angular size from the point of decision. The bees choose a target and pass through one of the two transparent baffles. The targets, with the reward box behind one, are interchanged every 5 min. (A, B) Two different positions 1 and 2 of the target to control the angle subtended. (C) Plan view.[12]

regions by the bee visual system to make a few separate labels, or that a 50° pattern (Fig. 5A) was a single artificial landmark for which the bees used only a few cues. Repeated tests of bees trained on patterns of 50° targets eventually revealed the local feature detectors and the cues.

Feature Detectors: The Basic Units of Vision

In each ommatidium, bees have three color types of ordinary photoreceptors, with their spectral sensitivity peaking in the UV, blue, and green. Little is known about pattern vision in the UV. The features or parameters of a pattern are outside the bee; the feature detector responses are inside the bee. Blue and green receptors feed into feature detectors with balanced excitatory and inhibitory inputs that are so arranged that they detect contrast at edges but are
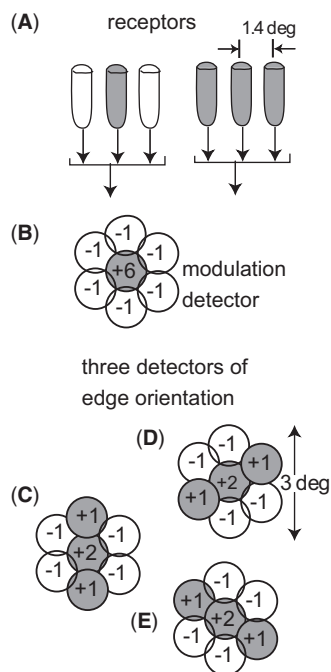
Fig. 6 (A) Four types of feature detectors for edges are formed by convergence of receptor responses. (B) The radially symmetrical modulation detector. (C–E) The detectors of edge orientation are green-sensitive and bilaterally symmetrical, therefore unable to discriminate a difference between the two sides of an edge. The numbers show a token excitation and inhibition of the receptors so that they are insensitive to intensity changes.

insensitive to changes in brightness (Fig. 6). Those with a center and a symmetrical surround (Fig. 6B) detect spatial modulation in the signal as the bee scans in flight, with peak sensitivity for sharp edges. Those with bilateral symmetry are sensitive to the edge orientation (Fig. 6C–E). For a bee, "an edge" turns out to be anything that excites the edge detectors.[15] Each feature detector has a line label that specifies the type of signal, an amplitude, a position on the eye, a signal duration, and inputs and outputs. These are also the properties of a neuron.

Modulation

Light absorbed effectively by a receptor cell causes an electrical response in the form of a depolarization, which adapts slowly, and is carried to the synaptic terminals in the next neuron layer, the lamina. Here, the response is a hyperpolarization and there is some narrowing of the field by lateral inhibition. More importantly, the second-order neuron adapts rapidly so that it responds to the (phasic) rate of change of light intensity, not to the (tonic) photon flux. The response, called the modulation, is now measured as the power over the range of effective frequencies in the signal. In each channel, there is also noise, which becomes significant at low light levels near moonlight. Modulation is summed in each local region of the eye to form a local

modulation cue irrespective of the local pattern, which is lost. The modulation cue in a local eye region is a measure of the total length of edge and its average position in the corresponding part of the panorama. The local summation reduces the information load in the image. The angular size of the feature detectors for modulation was measured in the following way. Bees were trained to discriminate between a horizontal and a vertical black grating, or between a grating of any orientation and a gray paper of matched brightness. The minimum period that was resolved was $2°$, irrespective of the orientation of the rewarded grating. The modulation feature detector is therefore defined by its size which is a little less than the interommatidial angle ($1.4°$ in the bee).

Edge Orientation Detectors

The feature detectors for edge orientation are symmetrical about their axis of orientation (Fig. 6C–E), as shown by the inability of the bee to distinguish which side of an edge is dark and which is light. To measure their minimum size, bees that had been trained to discriminate between orientations of edges at $45°$ on one pattern and $-45°$ on the other pattern, presented on a vertical surface, were tested with a large number of short parallel edges that were each reduced in length (with the same total length of edge) until the orientation on each pattern was no longer resolved. The minimum edge length for resolution of orientation was $3°$.[16] This is remarkably small. The detector size can also be measured by testing the discrimination between a stepped edge at $45°$ (a staircase going up to the right) and one at $-45°$ (similar, going up to the left) presented on a vertical surface. When the step size is less than $3°$, the orientations are discriminated, but larger steps are resolved with the result that the orthogonal orientations cancel out. All feature detectors have a similar size, which is about three ommatidia in diameter. The orientations of edges are discriminated only by the green receptors,[17] but the resolution of vertical versus horizontal gratings was little changed by removing green contrast,[18,19] so the cue was blue modulation. When the bees were trained on a black and white grating at $45°$ versus the same at $-45°$ (Fig. 7A), there was no difference in modulation so the bees were obliged to use the less preferred difference in edge orientation, with resolution near $3°$. Having inputs only from the green receptors, the orientation detectors are color blind and detect no edges or boundaries when green contrast is lacking (Fig. 7B). For humans who see the oblique edges in color, this is anti-intuitive, but the bee clearly fails because the remaining blue contrast and the total color are the same on the two targets. However, when green contrast is absent, bees can discriminate horizontal from vertical gratings with their blue-sensitive modulation detectors (Fig. 7C and D). The bees do not reassemble the gratings, but they measure the sum of the modulation as their first preference.[19]
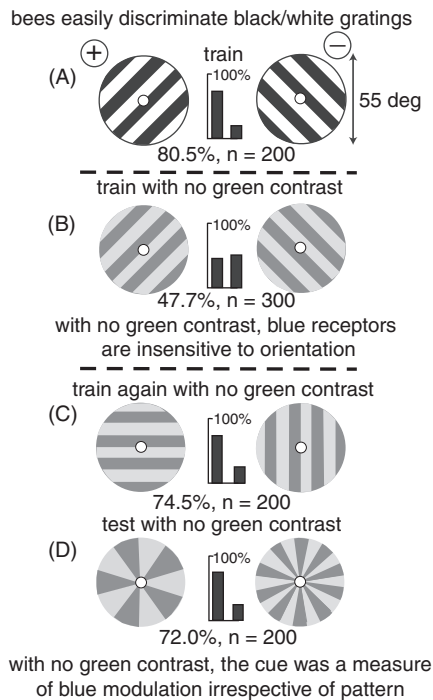
bees easily discriminate black/white gratings

(A) train

80.5%, n = 200

train with no green contrast

(B)

47.7%, n = 300

with no green contrast, blue receptors
are insensitive to orientation

train again with no green contrast

(C)

74.5%, n = 200

test with no green contrast

(D)

72.0%, n = 200

with no green contrast, the cue was a measure
of blue modulation irrespective of pattern

Fig. 7 (A) Oblique black-and-white gratings are easily discriminated. (B, C) These targets display no green contrast to the bee, so the bees cannot use the orientation to discriminate the two targets, but they discriminate when there is a difference in the measure of blue modulation. (B) At 45° versus 135°, no discrimination because green contrast and a blue modulation difference are lacking. (C) A horizontal grating versus a vertical one is easily discriminated with no green contrast. (D) Bees trained on (C) recognize the blue modulation difference irrespective of the pattern. Dark grey = blue, light grey = buff color.

The Cues Related to Edges

The bees look toward the center of the target or pattern and the eyes operate separately.[20] The cues are the units of recognition and discrimination within the bee. They are formed by summation of responses of each kind of feature detector within the local region on each side (Fig. 8). Just as the receptors sum responses to photons, each cue detector totals the coincident responses of its own local array of feature detectors (Fig. 8).

The summation explains why only one cue of each type is learned in each local region of the eye at the range of positions where it was displayed during the training. The absence of a cue is itself a cue.[21–23] The bees do not learn the pattern or the panorama; they learn only the coincidences of cues that enable them to find again the place of the reward. Although simple and sparse, a few cues are usually sufficient to identify a place with certainty.

Summation of feature detectors into cues has some counterintuitive effects on what the bees can detect. Most significant of these, the layout of the features is lost at this point in the processing (Fig. 9), but the modulation, average
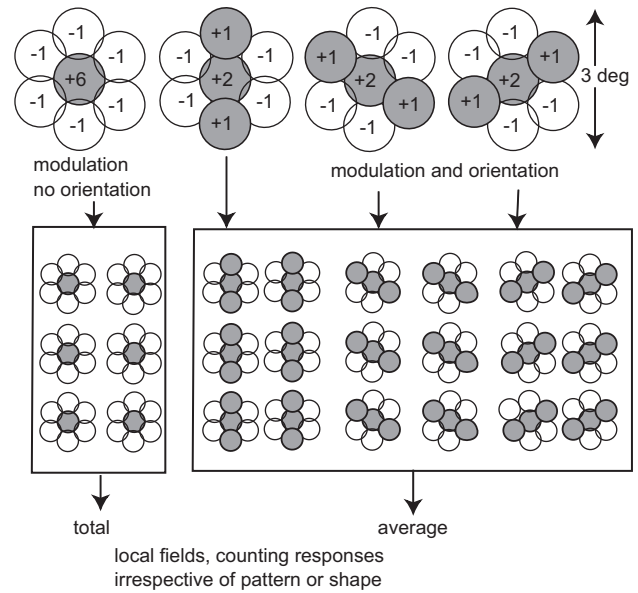

modulation
no orientation

modulation and orientation

total

average

local fields, counting responses
irrespective of pattern or shape

Fig. 8 Retention of averaged features but rejection of redundant detail. Modulation is measured separately as the total responses in a local region of the eye (within the field of an optic lobe neuron), but orientation detector responses are summed and counted irrespective of orientation. Detailed pattern that is dependent on the orientation of edges is therefore lost, but the measures of the amount of edge are remembered.
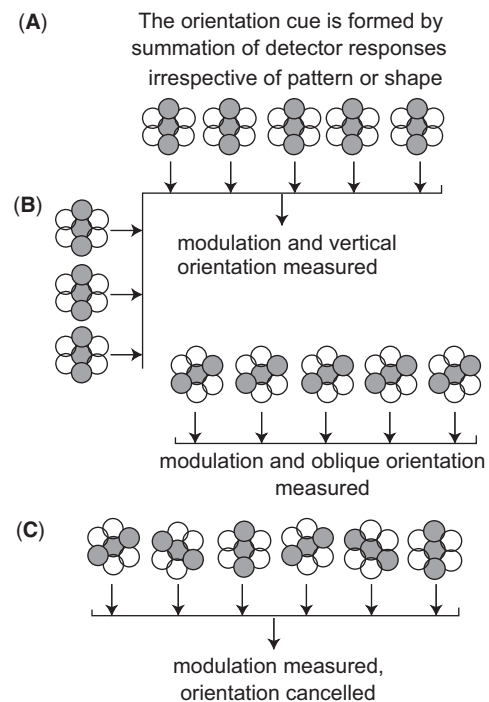

(A) The orientation cue is formed by summation of detector responses irrespective of pattern or shape

(B) modulation and vertical orientation measured

modulation and oblique orientation measured

(C) modulation measured, orientation cancelled

Fig. 9 Summation of responses of feature detectors for edge orientations in various positions in a pattern in the formation of cues. The average orientation in the local region is measured but the pattern is lost. (A) Detectors with vertical axes. (B) A line of detectors with oblique orientation. This would add up to a scalar quantity, not a line. (C) Mixed orientations cancel leaving a residue.

orientation, positions of hubs, and centers of cues are preserved and used as cues.

The trained bees are interested only in the detection of the cues that together identify the place of the reward. They detect and learn the cues but they retain no information about the pattern of the individual feature detectors that lie within a single local region. Consequently, trained bees cannot distinguish 50° training patterns from unfamiliar patterns that display the same cues. In tests, the trained bees detect familiar cues in the corresponding retinotopic positions in unfamiliar patterns but the actual patterns are of no interest.[24,25] To a bee, the orientation cue is an average of the orientations of edges in a local region of the eye (Figs. 8 and 9). For example, in a small circle, square, or square cross, the orientation cue is zero because of the cancellation of the orthogonal edges.[26] Similarly, the orientation is destroyed when an edge or bar is broken up into squares, or cut into square steps that are resolved by the feature detectors for edge orientation.[27] The greatest gap that can be spanned in a row of small squares is 3°, which is a measure of the maximum size of the feature detectors for edge orientation.[27] As a result of the loss of the pattern, trained bees respond to quite different patterns that display similar cues (Fig. 7D), and frequently the bee's error is wrongly called a generalization of two patterns.

Radial and Tangential Edges

The edge detectors also collaborate together to detect the hubs of radial or circular patterns (Figs. 10 and 11). The type of pattern, radial or tangential, and the position of the hub to within 5°, can be learned, but again the actual layout of the pattern is lost in the summation of the responses of the feature detectors.[28]
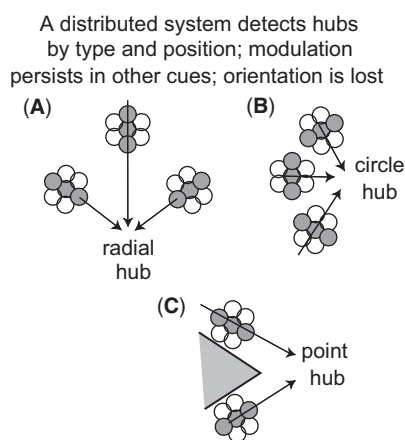

Fig. 10 The positions of the hubs are detected at the centers of radial patterns by summation along the orientation axes of the feature detectors, and centers of circular patterns by summation along the orthogonal axes. The orientation cue is canceled in the edges of a square but weak hubs are detected at corners with smaller angles. These cues are detected in parallel by the distributed network in Fig. 11.

Cues Related to Areas

The unit detectors for areas of black or color appear to be small groups of blue receptors that are separately totaled within the local areas on each side of the target. As in all natural and artificial seeing systems, but unlike a camera, the detectors and cues for an area are separate from those for its edges. In tests,[29] isolated areas were discriminated by their angular size, or [(number of receptors) times (brightness)], or the vertical position of the center, but nothing about shape.[1,30] The positions of large, colored areas are separately discriminated if they fall in two separate local eye regions,[31–33] especially when the criterion is the landing of the bee on the target, so that the areas are separated by large angles. Separate areas are not necessarily all learned, a blue patch being the preferred and sometimes the only position and color of interest. The positions of two areas of the same color or black are not separately remembered when they are close together, but the bees learn the position of the common center. The merging of two spots diminishes as they move apart, from an angle subtending 5°, until at 15°, they are quite separate.[30]

Learning the Cues

The bees do not learn the visual task for future reference; they learn a few cues, and when they return, they have
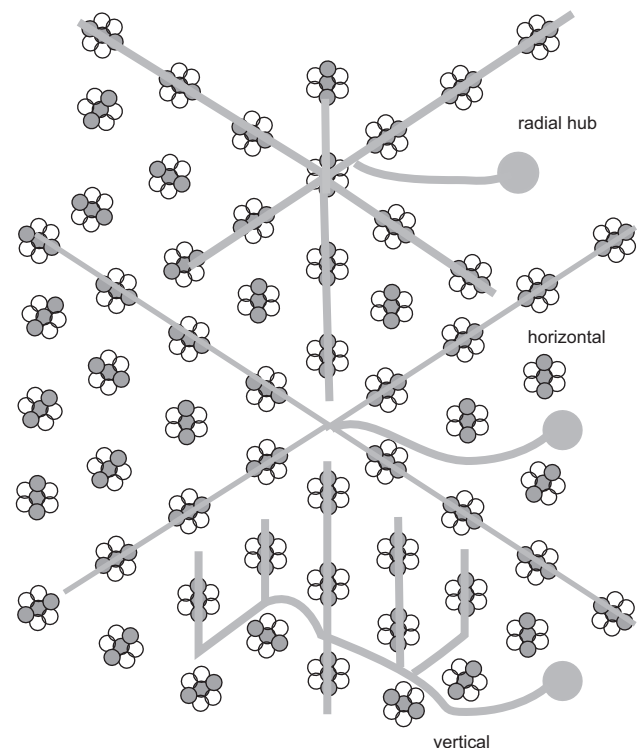

Fig. 11 A notional distributed network that would detect a radial hub and a horizontal or vertical orientation (Fig. 10). Representative candidate output neurons are suggested.

Q1

feature	weak	strong	action of blue receptor input	action of green receptor input
modulation			active when green is not available	preferred input, retinotopic
area			tonic blue input summed, measured and located	not sensitive to areas or colors
width and height			retinotopic	measures and locates angular width to 90 deg. retinotopic
polarity	blue↓angle	blue		locates and measures angular width from tonic blue to green mod, and polarity in horizontal direction
radial	*	✱	not sensitive	active
bilateral symmetry			not sensitive	active
orientation	/	////	not sensitive	active
tangential	○	◎	not sensitive	active

Fig. 12 The cues in approximate order of preference in the learning process. In the bee, cues are coupled with time of day and nonvisual modalities, so the visualization of them for humans is only a convenient fancy.

only these cues to locate the place of the reward. In discrimination training with two targets, a cue that occurs on the rewarded target and also on the corresponding side of the unrewarded one is not learned; or rather, it is learned on one target and unlearned on the other. Having learned a cue on one side of the target, the bee does not recognize it outside the area where it occurred in the training or on the other side, as if the bee looks at the center and each eye learns its own side. The preferred cue is learned first, and often the bees learn only the unrewarded target.[23] When cues are learned, they become coupled with the time of day and detection of one leads to expectation of the others. Preferences change when an expected cue is omitted, or an unfamiliar cue is added, and the bees immediately start to relearn the new situation.

There is an order of preference for learning the cues in the training situation, with blue color and green modulation the most preferred, then position of the center, a black spot, area, radial edges, bilateral symmetry, average orientation, and finally tangential or circular edges, which are avoided.[23] At first, the bees learn only the strongest signal and most preferred cue, but may learn more with further training. In spite of many searches, no more cues have been found. This is a small but obviously adequate collection of cues for the varied life of a bee. Natural panoramas display a variety of orientations of edges with a strong modulation cue for bees, but within each local region of the eye, most orientation cues may cancel out, so only the location and measure of modulation of green and blue receptors remain. Features are abundant but the outstanding cues

are sparse to match the size of the memory. Here and there, however, the bee encounters a significant cue such as the color and symmetry of a flower. The neural processing is not done by simple bits in a time series. Many simultaneous multidimensional packets run in parallel in labeled lines. Each cue is line-labeled with the qualities and amplitude of the signal, a position on the eye, a signal duration, and outputs. Again, these are also the properties of a neuron.

Color

Careful consideration of Fig. 7 reveals that in Fig. 7C, the bees learned the measure of modulation of the blue receptors, not the color. Therefore very careful tests are required whenever color appears to be the cue. Bees prefer to learn the black/white or the amount of blue around and below the reward hole (Fig. 13), not yellow if blue is present.[34] Critical research on the discrimination of colored patterns, and especially textures, is notably lacking in the literature, probably because the results would upset the accepted view that the bees see the flowers in color. Recent work shows that when the bee learns from a colored pattern, the location and amount of blue and its spatial relation to a strong green contrast is learned retinotopically. The separation can be up to $50°$. The coincidence of the two cues acts as a landmark with polarity, like a signpost indicating direction. Green contrast is essential for discriminating colors or
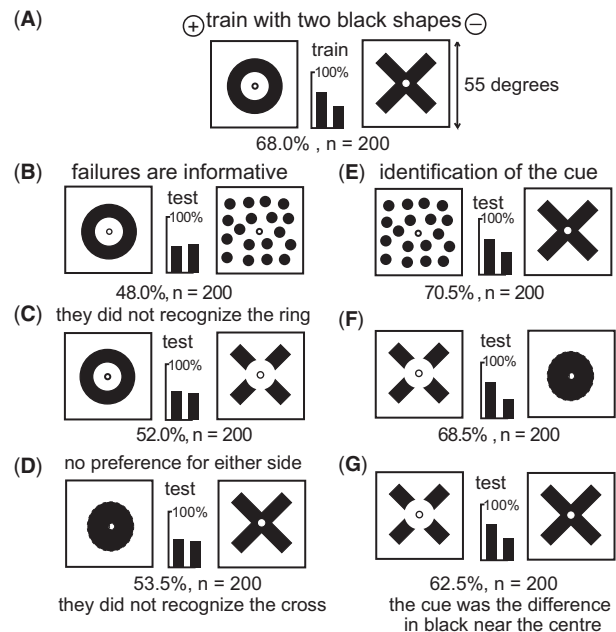
(A) ⊕train with two black shapes⊖
train
100%
55 degrees
68.0% , n = 200

(B) failures are informative
test 100%
48.0%, n = 200

(C) they did not recognize the ring
test 100%
52.0%, n = 200

(D) no preference for either side
test 100%
53.5%, n = 200
they did not recognize the cross

(E) identification of the cue
test 100%
70.5%, n = 200

(F)
test 100%
68.5% , n = 200

(G)
test 100%
62.5%, n = 200
the cue was the difference in black near the centre

Fig. 13 Shape discrimination is explained by the use of simple cues. (A) Training patterns. (B, D) In these tests, the trained bees did not recognize either the ring, or a disk, or the cross. (E–G) They avoided black around the reward hole, irrespective of pattern. The training performance alone would lead to the wrong conclusion.

colored patterns, but there appears to be no tonic input from the green receptors.

Shape Discrimination

When presented with learning a shape or discrimination between two simple shapes subtending less than 40° in a target of 50°, bees use the features and cues described (Fig. 13). In small targets, they learn the preferred cue on whichever side it is displayed,[2,35] not the global form of a closed boundary, which is lost in the formation of cues (Figs. 8 and 9). When the shape subtends more than about 60° at the eye (Fig. 5B), it can be broken up into regions, each of which can display a landmark (Fig. 14), so new cues appear and the gross layout of the display can be discriminated. When the criterion of success is the landing on the target, the display becomes huge and acts like a panorama. The score of successful recognitions then rises toward 100%, and the trained bees will not accept other targets.
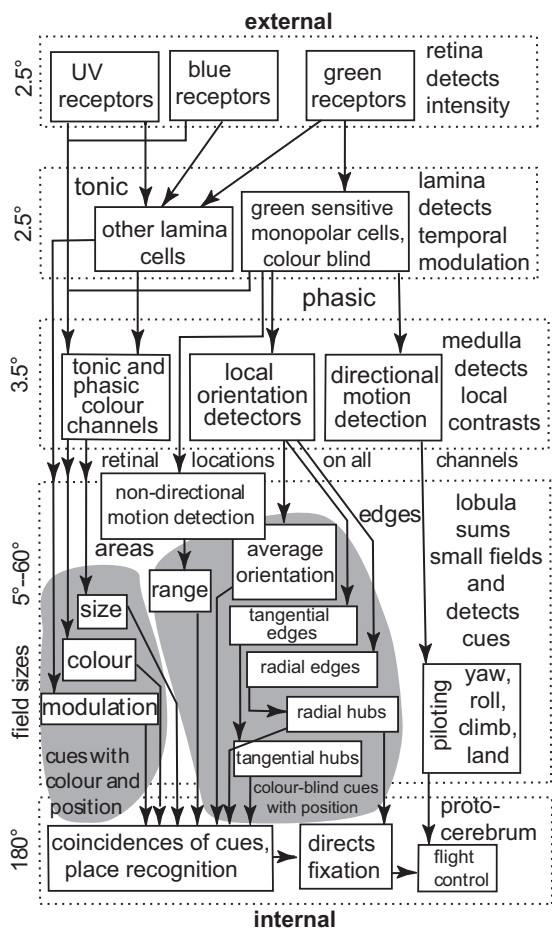

Fig. 14 A map of the formal interactions between the different processing channels in a single local region of the eye. The receptors at the top feed through the lamina to feature detectors and then to cues. Approximate field sizes are shown on the left. Any resemblance to the bees' optic lobe is not accidental.

The Local Region for Processing a Landmark

Early work[36] showed that the endpoint in recognition, the detection of landmarks, was retinotopic, i.e., fixed in its local position on the eye. It follows that the whole detection system is retinotopic as well. The local region of summation is not necessarily the same for each cue. The size of the local region of summation has been inferred in some cases. Landmarks 20° apart were separately recognized.[36] Two black spots fuse into one when closer than 15° edges cancel their orientations, and two colors or two regions of modulation merge progressively over a similar angle. Putting together the formation of cues and landmark labels, we can envisage the stages of parallel processing in a column of the eye, either as excitatory pathways (Fig. 15) or as successive arrays (Fig. 16). These diagrams illustrate the inputs and outputs at each stage, the progressive convergence that reduces redundancy and the use of coincidences of the responses between lines in parallel.

At each level, as in all nervous systems, the coincidence of responses is the signal to excite the next level. The whole process from receptors through to feature detectors and then to cues and landmark labels (Fig. 15) is done region by region on the eye, and therefore in retinotopic coordinates related to the position of the head.[37] As foraging bees fly in familiar directions along known tracks and scan the scene in the horizontal direction, they detect landmark labels to find the place of the reward. In Skinner's terminology, learning the labels to recognize a place must be done by "operant" conditioning, which is part of "active vision" of animals flying freely, and difficult to analyze.

The Effect of Pattern Size

In the earliest discrimination experiments, it was thought that the bees learned the whole pattern because they recognized circles and radial sectors, apparently as a whole, irrespective of the exact size and number of radial arms. The intuitive inference was that the bees learned the abstract idea of the shape.[14,15,38] This conclusion was eventually disproved by experiments in which the trained bees were presented with the training pattern versus quite a different pattern, which also displayed the same cues and no unfamiliar cues. The trained bees could not distinguish the new pattern from the one they were trained on, showing that they were interested in the cues, not the patterns.[2,28,35] Very large patterns were used in the early work but 50° patterns after 1988. The effect of size was eventually demonstrated[39] in tests of trained bees with controlled target subtense (Fig. 14). Large patterns are discriminated by their peripheral parts.[20]

Landmark Labels; Place Recognition

The group of cues that are detected at the same time in a local region of the eye are bundled together to form the label
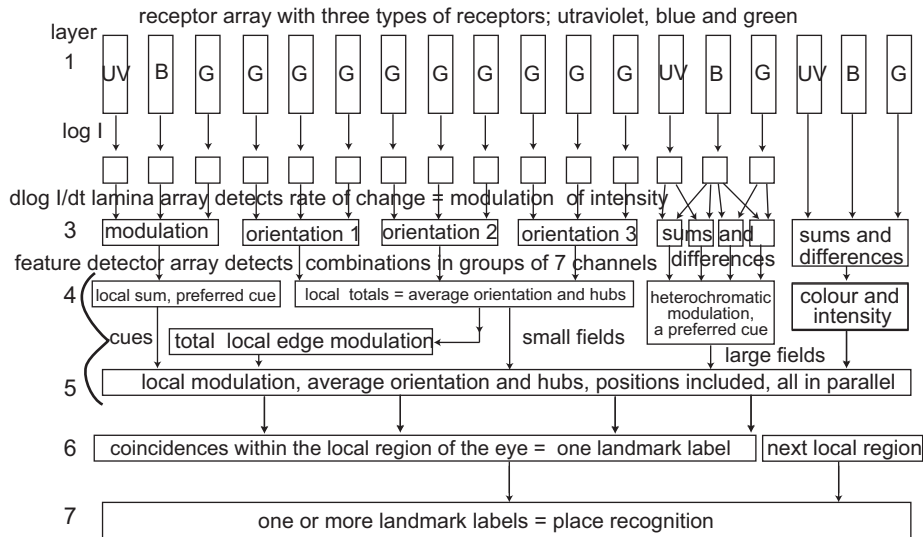
Fig. 15 A summary of the parallel processing in successive arrays. Starting with a region of most numerous receptors, it ends with the small array of landmark labels that detect a place.

of a landmark (Fig. 15), irrespective of the actual image in that part of the panorama.[23,40] When they detect one of the cues at the expected time and place, they expect to find the others, and if they do not, they fail to recognize the place. The resolution of landmarks is about 15–20° implying that the eye regions are about this size. The eye has a total angle of about 200°, so we can infer several local regions for the formation of cues (Fig. 17). This is sufficient to explain the angular resolution of landmarks, the summation of cues in local regions, and recognition of local cue

positions when the bee lands on the target.[41] The landmark labels at wide angles to each other that are detected at the same time by the whole eye are the key to the recognition of a place.[36,37] If there are several landmarks, it does not matter if one is missing.

Resolution in the Processing Hierarchy

Resolution depends on the angular subtense and shape of the field of the relevant active detector and on the separation between detectors. The size of the summation field that determines the resolution is not the same for each.[2,3] For
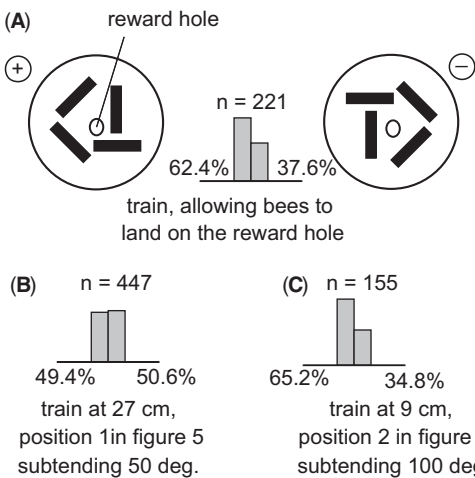

Fig. 16 The effect of pattern subtense. (A) The patterns are discriminated when the bees land on the target. (B) At a subtense of 40°, the orientation cue in this pattern versus the same pattern rotated by 180° cancels out. Neither the whole pattern nor the positions or orientations of individual bars are discriminated. (C) At a subtense of 100°, in the apparatus in Fig 5, the patterns are discriminated.
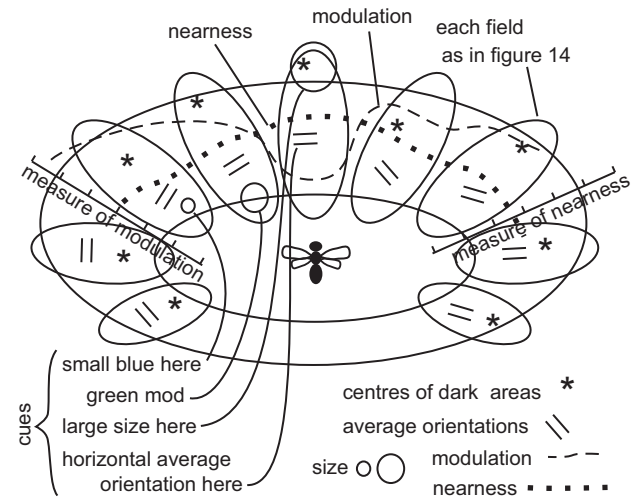**Source:** Modified, after Zhang and Horridge.[39]

Fig. 17 The display in the panorama that is detected by the bee. Each oval subtending about 30° represents a local region or one landmark label. Within each region, no more than one cue of each kind combines to make a label. A place is recognized by the coincidence of the labels with those in memory.

modulation detectors, we have a resolution of a stripe period of $2°$. On account of the lateral inhibition, this is better than for a single receptor. The minimum length of edge for directional edge detection is $3°$, and the minimum detectible small black spot is $2–3°$ for a worker bee. At the level of cues, modulation is summed in regions about $20°$ across; orientation in regions of $15–20°$; position of areas of black or color, $12–16°$, and the vertical position of the center is located to within $5°$. At the level of coincidences of cues to form a landmark label, we have summation in areas up to $45°$ across, and a resolution of $15–20°$ for the separation between neighboring landmarks but a single landmark can be $50°$ wide. The three stages of processing (Fig. 16) have resolutions of approximately $2–3°$, $15–20°$, and $40–50°$. The discrimination of the angle of orientation of an edge is poor because the feature detectors are independent and very short (Fig. 6). A difference of $45°$ is the limit for a single bar and $30°$ for parallel grating.

Generalization of Patterns

Generalization is the acceptance by trained bees of an unfamiliar pattern in the place of the familiar training pattern. Bees can be trained with a variety of different squares or equilateral triangles that are presented simultaneously or in succession, called generalization in the training.[13] The bees learn a preferred cue common to all the patterns, such as the mere presence of black or a measure of modulation. The trained bees can sometimes recognize the training pattern at a different size and commonly accept other patterns with the familiar measure of modulation.[13]

The trained bees accept an unfamiliar pattern as long as the familiar cues are detected in the expected positions, and no unfamiliar cue is added. Generalization is therefore nothing to do with cognition or recognition of an abstract similarity. It is a consequence of learning the simplest cue in a single task, then recognizing the same cue if the display is changed. Errors of recognition are less likely when the training pattern extends over several eye regions (Fig. 17). Bees do not learn pictures or patterns; they learn the most preferred cue that is sufficient.

Misleading Terminology

Abstract nouns and phrases borrowed from the cognitive sciences, such as "perception of shape," "similarity," "triangularity," "recognition," and even "color," have long supported anthropomorphic ideas about mysterious cognitive abilities of bees. The bees had certainly learned the task in the training, so that they could choose correctly on their return, but careful analysis showed only feature detector responses, cues, and landmark labels within the bee. There was no data to demonstrate perception of colors, patterns, or shapes outside the bee, although that is how it seemed to the casual observer. An even less convincing strategy is to define cognitive behavior in terms suitable for man or

higher animals, and then discover behavior or performance in bees or even robots that fits the definition, so that cognition is demonstrated.

Design of the Bee Visual System

The extremely wide visual field of the compound eye detects approaching enemies and the direction of an open way in flight, with two additional functions. When bees forage, they make use of the wide visual field to remember the direction that the axis of the body and head points relative to the sun-compass, the landmarks, and the direction of home. They recognize landmarks at large angles to each other on the eye.[36] A landmark is not necessarily an isolated object, it can be parts of distributed branches, flowers or pebbles, a pattern on a target in the experimental apparatus, or in fact anything that displays sufficient coincidences of cues. Patterns were introduced in the early days of bee training and persisted as experimental tools for a century. Bees appear to distinguish between patterns but actually they detect only a difference in the cues. If you doubt me, please peruse Figs. 7 and 13 and think about the consequences of the data there. Bee vision is designed to measure the flow field in flight and the labels on landmarks when recognizing a place.[40]

CONCLUSIONS

A Straightforward Mechanism

This analysis of the formal interactions of the inputs and cues would be little more than elementary common sense in computer vision. Three successive stages of coincidences of inputs of filters are laid out in the angular coordinates of the inferred model. The edge and modulation detectors (Fig. 6) resemble Canny detectors and are only $3°$ in size. Individually, their positions are not remembered. Each type is summed to form one cue in each local eye region. The coincidence of a few cues in a local region is the only retained information about that part of the image. The coincidence of landmark labels is recalled for the recognition of a place. There is little sign of internal feedback, central control of field sizes, or top-down adjustment. That is only half the mechanism, however, because the visual processing is retinotopic and the eye is carried on the head on the body. The posture and movement is controlled by the vision itself and learning is operant, i.e., active or instrumental with instant visual feedback. The eye is useless without its control of its own moving platform. That is the next frontier.

What Insects Actually Detect

Some would say that we may never know what insects actually see; indeed, little can be said about most insects. However, large species can be observed in tethered flight

and stimulated in a controlled way, and many neurons can be recorded, so that we can observe what they detect. The honeybee is a special case because a great variety of tests can be given to bees trained to fly to the place of a reward, for which they use landmarks that can be experimentally controlled in texture, color, and pattern. The answers lead to further questions that can be refined as much as we please.

The results show that bees do not see anything in the sense that we see a marvelous panorama. When bees learn to distinguish between two faces or pictures, it is just the beginning of a long series of tests to discover what the trained bees really detect. The answer was always a small part of the pattern, perhaps just the black patch or a measure of modulation, or a difference in positions of spots in very large targets, or regional differences detected as the bees land on the target. In local eye regions, they detect features, cues, and landmarks, which participate in a multimodal recognition process without a reassembled image. Reassembly requires a very large brain but detecting coincidences of cues and landmark labels is relatively easy. Similarly, a blind person may recognize a place by its smell, vibrations, touch, and the directions of noises, wind, and warmth. A human condition, called "blind sight," caused by brain damage, has a similar effect. Bright lights and salient objects cannot be seen but their direction can be reported. That, with memory of coincidences, is sufficient for a bee. The significance for the design of simple, extremely rapid dedicated systems for pattern recognition is obvious.

Many further references will be found in a recent e-book[3] that is freely available for personal use.

Q2   Recent research has identified the features in color that honey bees actually detect when they identify a place in the feeding behavior. They distinguish between colors including black, grey and white,[43] and between a simple colored pattern and its mirror image,[44] but there is no evidence of trichromatic color vision.[45] They locate on the retina and measure the strongest source of modulation of green receptors and the strongest display of blue content. They also measure the angle between these two. When blue content is absent, bees locate and measure the spatial relation between two positions of green modulation, detected by scanning. When green contrast is absent, they measure the spatial relation between a blue patch and the strongest modulation of blue receptors. Flat colors are also identified by whether they display more or less blue than background.[45] There is no tonic input via receptors for green. A century of work on bee color vision will have to be revised.

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