

Bee vision of pattern and 3D

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Summary

Insect vision is nothing if not active. The regular head movements, called saccades, enable the fly *Drosophila* to keep a straight path in flight despite inequalities in the thrust of the wings. Using their own motion, bees in flight measure the ranges of nearby objects. A long history of research shows that bees discriminate visually in ways that depend on their activity or task, so we must distinguish between vision during flying, fixating or hovering and landing.

Bees return again and again for a reward of sugar solution and use their eyes to find their way. In an apparatus that makes them discriminate between two simultaneously visible but regularly interchanged targets, seen at a distance of 27 cm, bees are able to distinguish a remarkable number of simple patterns, but they fail in certain critical cases. The results can be explained with the hypothesis that bees have several broadly tuned overlapping filters with large fields that respond to the predominant orientation in a region of the image, and others for radial and circular patterns. Together with colour, these filters are independent of range. Bees prefer to use landmarks where they can, then global pattern at the largest scale, and lastly the detail around the goal. The way that discrimination of one visual feature is independent of other variables can be explained by models analogous to the colour triangle in colour discrimination.

Introduction

Insect vision is an interesting topic in itself, studied for a century⁽¹⁾, but only recently have we progressed from descriptions of interesting performance towards the elucidation of mechanisms as the components of a machine that might one day be copied into computer hardware. Inevitably, someone with a knowledge of insect vision 'saw' a possible contribution to robot vision. Insect vision is now at the right level of complexity to be made comprehensible by experiment. The question is, how can we understand the vision of an insect sufficiently well for engineers to be able to copy the prin-

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ciples into artificial vision? This question assumes that we know what kinds of principles to look for and that we are then able to design useful experiments. This is no easy task, and the basis of two-dimensional (2D) pattern recognition is a central problem for artificial as well as natural systems. Also, the whole philosophical basis of vision research is currently being overturned by new ideas based on exactly the kind of active vision, using the motion of the eye, upon which insects rely in flight.

At the outset, it is essential to say what I mean by 'seeing' and 'discrimination' with reference to insects. The evidence that insects 'see' is that they avoid obstacles in flight, and have many other responses in which they use their eyes. Experiments have partially revealed some aspects of their on-line visual processing. 'Discrimination' is the selection of one rather than another of two or more targets, irrespective of their location, as a result of innate preferences or previous experience. In each case, two practical problems are: how to break into the natural system by discovering where the performance fails, not where it succeeds, and how to design experiments that do not obscure the essentials that we seek. Perhaps the greatest problem is to escape from the bondage of the currently accepted ideas. The advantage of bees for the study of vision is not their sun compass, visual memory or homing ability, though these are relevant, but that they avoid obstacles under visual control, recognise and steer towards a goal, and learn to return repeatedly for a reward of sugar solution. Over the past decade, the topics of visual control of straight flight in insects and pattern vision in bees have been revised by the discovery of several new visual mechanisms and the realization that the visual processing itself depends on the activity at the time, i.e. *walking*, *flying*, *fixating* or *landing*. The new approach is to seek the properties of the filters that abstract motion, range, landmarks and pattern.

Apparently peculiar vision

Even though his own eyes generated flicker in every receptor as they swept across the visual image, in 1875 Exner⁽¹⁾ had proposed the preposterous idea that form vision of insects is limited by the sequence of flicker in each facet as the insect moves, an idea that for *flying* bees has been replaced by 2D pattern vision, but has still not been disproved for *landing* bees. Sixty years ago, Mathilde Hertz^(2,3) concluded from numerous experiments that the flicker induced by the bees' own flight is actually the main factor in the bees' spontaneous preferences, and in their frequent failures to discriminate between black and white patterns *laid flat* that look obviously different to us. She also found that certain aspects of the pattern, related to flower-like symmetry and the form as a whole, are important for discrimination.

Progress was limited by the technique, which was to score the bees when they *landed* upon one of several targets placed on a flat table. This method has several disadvantages. The bees appear to be unable to relate their flight lines to the orientation of contours, which would explain why they are forced to depend on flicker, why they confuse patterns that look quite different to us, and why they favour patterns with rotational symmetry. The image of the target expands contin-

usually as the bee approaches, so there is no way to estimate what features of it the bees use, and when landing the bees can see only the local detail around them. This early stage of gathering data that could not be interpreted was followed by a long pause before a change in the experimental design allowed an advance.

Apparently normal vision

In 1967, Rudiger Wehner^(4,5) introduced the idea of having a tube at a fixed distance in front of each pattern, which was

presented on a *vertical* surface and subtended an angle of 110° at the point of choice at the tube entrance (Fig. 1A). This arrangement had the effect of making the bees face the pattern from a hovering position as they entered one of the tubes. The two patterns were regularly interchanged during the training to make the bees use their eyes and not learn the location of the reward. We now call these *fixating* bees, and they were able to discriminate between large black and white discs with different numbers of sectors, two orientations of a single edge differing by 45° , or the rotation of a disc with 8 black and 8 white segments by 22.5° ⁽⁵⁾. This wave of discov-

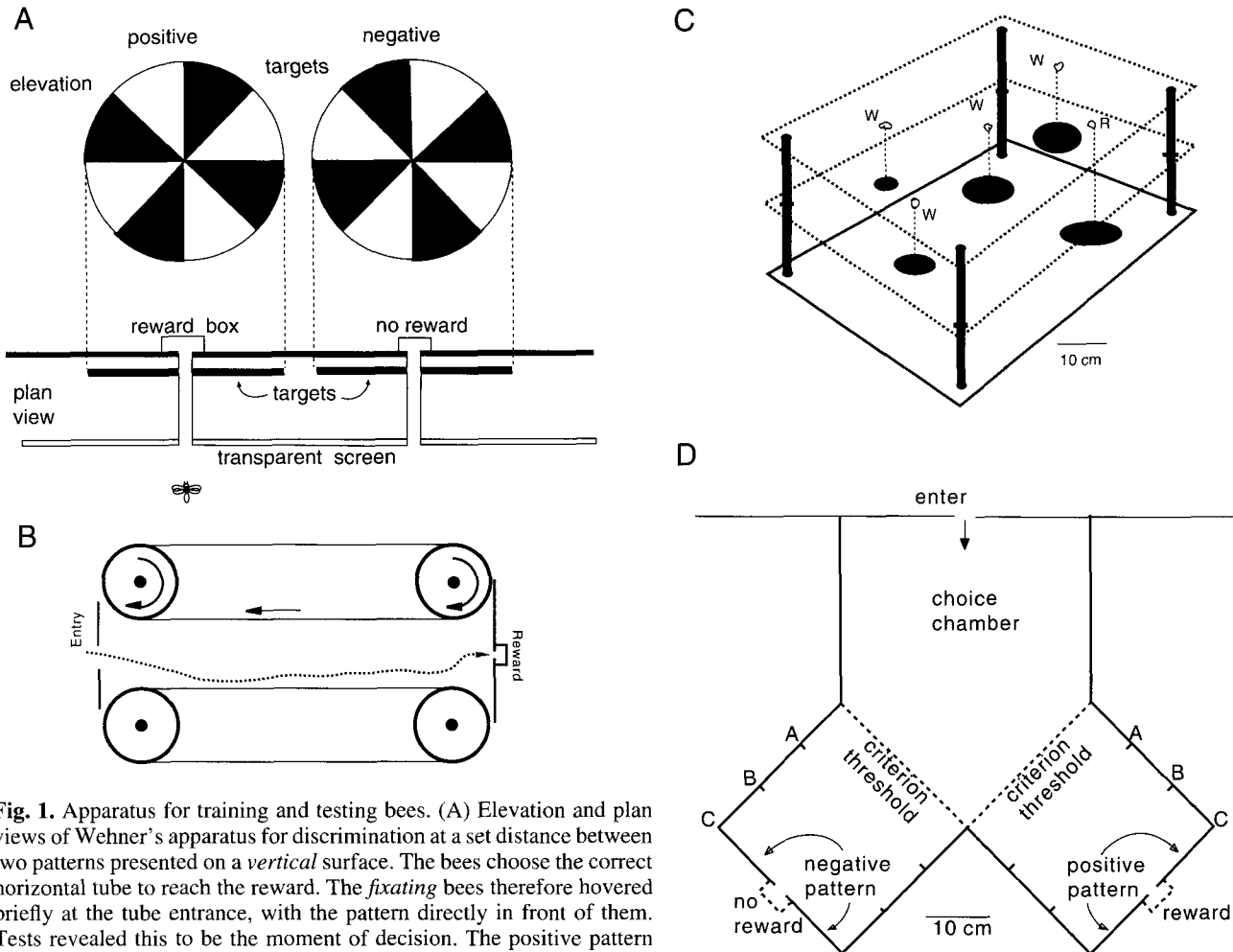


Fig. 1. Apparatus for training and testing bees. (A) Elevation and plan views of Wehner's apparatus for discrimination at a set distance between two patterns presented on a *vertical* surface. The bees choose the correct horizontal tube to reach the reward. The *fixating* bees therefore hovered briefly at the tube entrance, with the pattern directly in front of them. Tests revealed this to be the moment of decision. The positive pattern was rewarded, the other not, and the two patterns were interchanged regularly during the training. The bees could detect the rotation of a sector pattern by 22.5° ⁽⁵⁾. (B) The Canberra tunnel apparatus with moving walls. As the bees flew along the tunnel to obtain a reward at the other end and then returned, their flight paths were recorded by a video-camera placed above. The bees fly along paths which equalize the apparent angular velocity on their two sides, irrespective of the direction of the relative motion (which can be upwards, downwards or even forwards relative to the bee)^(13,14). (C) The Canberra apparatus to demonstrate the discrimination of range irrespective of size or position by *flying* bees. The three sheets of Perspex are separated by 5 cm spaces. The targets were black discs of paper which were randomized in position and size, but there was always one disc at the range selected for training. The reward (R) was a drop of sugar solution placed over this disc. A drop of plain water (W) was placed over each of the other discs. Marked bees flying in a restricted space over the apparatus could choose one of the drops. The same apparatus can be used to train bees to one angular size or one absolute size of the disc, irrespective of its range or position⁽¹⁶⁾. (D) The Canberra Y-choice apparatus with two targets presented on *vertical* surfaces that can be seen simultaneously from the central choice chamber. The *flying* bees enter the hole and their choice is scored when they fly across the threshold of one of the two arms. The percentage scores of the bees (as given in Figs 2 and 3) appear to be a reasonable measure of the outputs of their visual filters⁽¹⁸⁾.

eries suggested that bees discriminate the orientation of edges with 2D pattern vision rather like our own, but with poorer resolution.

Vision based on motion

Meanwhile advances were being made with the analysis of fly vision, also with a constrained experimental design. The optomotor response is the relatively predictable reflex turning of the eyes or the whole body, observed in many animals when a patterned drum is rotated around them. In the 1950s, Hassenstein⁽⁶⁾ and Reichardt⁽⁷⁾ pioneered the idea that the on-line *directional* motion perception, which is obvious in the optomotor response, is entirely a bottom-up process (i.e. one starting with very local interactions) that can be modeled with simple filters. Not much in modern studies of vision can be understood without this idea of an array of local filters as components.

A filter is defined as a place on the visual pathway that allows only a selected part of the information in the image to pass. Anatomically, the filters reside in groups of neurons, but the performance of the filter is modeled as a mathematical operation which need not be related to possible neural mechanisms. As contrasts in the outside world move across the eye, they excite the receptors in succession across the retinal array, and the performance of the whole insect is related to the moving stimulus in a single intervening stage. The fundamental conclusion of the early work on a beetle, and on flies in tethered flight with fixed head, was that the neural mechanism of motion detection is very local and can be modeled by multiplication of the filtered outputs of adjacent pairs of receptors⁽⁷⁾. Such a system has severe limitations. A coarse grating moving rapidly gives the same response as a fine grating moving slowly, so that pattern as such cannot be separated from velocity or range. With a single set of homogeneous filters, such a system cannot measure range using its own motion, as was later shown to occur in bees.

This advance, away from the anecdotal approach towards the representation of the system as an array of mathematical operators across which the image is scanned, with its influence on the development of artificial vision, was followed in the 1970s by a similar analysis by Reichardt, Poggio and others, of the fly's response (also in tethered flight with the head fixed to the thorax and with recordings averaged) to a patterned vertical stripe moving horizontally on a moving patterned background – called the figure/ground stimulus⁽⁸⁾. The flies could separate the one-dimensional motions of the object in the foreground from those of the patterned background. These results were difficult to apply to the wide variety of visual behaviour of other insects in flight, and even to the behaviour of freely flying flies. As first demonstrated by Mike Land⁽⁹⁾, it turned out that fixing the head to the thorax and averaging the responses had obscured the most important mechanism in visual flight control, namely the spontaneous movements of the head. In tethered flight in a wind tunnel, large flies repeatedly turn their head in all three body axes under the influence of visual and other cues. As Stange and Hengstenberg now say⁽¹⁰⁾, 'the repertoire is far larger than previously thought' and 'this system is of considerable theoretical interest'.

In a new approach in the early 1980s, Martin Heisenberg and Reinhard Wolf⁽¹¹⁾ found that *Drosophila* in tethered flight, now with its head free to move, at regular intervals makes small head movements (called *saccades*) that enable it to calibrate its flight on a straight course. By continually sampling the visual feedback obtained from head saccades in each direction, the fly is able to steer its course and to compensate for asymmetry in the wings. Mutant flies (the double mutant *reduced optic lobe: small optic lobe*) are able to steer on a straight course by use of saccades towards alternate sides, although they have no optomotor response⁽¹¹⁾. Active vision, in particular the feed-back from the self-initiated saccades and locomotion, is essential to normal flight in *Drosophila*. These results threw into question all the earlier work in which the fly's head was fixed and the recordings averaged.

Active vision

With this interesting background, in the mid-1980s in Canberra, we started to analyse how *freely moving* bees see the 3D world by means of the 2D image on the retina, taking our ideas from the active head movements of mantids⁽¹²⁾ and grasshoppers when they measure range. These two groups of insects make a sideways peering movement that gives them sufficient visual feedback to reach for a twig or jump at a target. The way that flying bees measure the range of nearby objects in order to steer was demonstrated in a simple tunnel with moving paper walls (Fig. 1B). The bees had to fly along the tunnel to obtain a reward, and they were filmed while the motion of the walls was controlled. It turned out that the bees take the average track which equalizes the angular velocity on their two sides, irrespective of pattern^(13,14). The angular velocity is useful because its reciprocal is proportional to the range. The bees show us how they obtain the minimum necessary representation of the 3D world to steer through it. Later, it was found that the velocity detectors are *non-directional* and function up to 100 Hz, so they are quite different from the directional optomotor response⁽¹⁴⁾. This system, that measures angular velocity for range estimation, steering and flight control, was previously unsuspected.

In other experiments, Srinivasan, Lehrer and I⁽¹⁵⁾ found that flying bees can learn to come to a target at a certain range irrespective of its position or apparent size (Fig. 1C), or absolute size⁽¹⁶⁾, so they clearly have adequate cues from their surroundings in 3D. They *discriminate* the ranges of objects irrespective of background. Another cue that bees use is the parallax, as nearer objects slide over the pattern of more distant ones. Like all visual behaviour dependent on motion, this performance is colour blind⁽¹⁷⁾.

Orientation detectors

The next problem was to discover the nature of the bees' filters for 2D pattern vision, as revealed by the way that they discriminate patterns. With a new apparatus, the Y-choice maze (Fig. 1D), in which the *flying* bees have to choose between two targets seen at the same time, Van Hateren and Srinivasan⁽¹⁸⁾ showed that they discriminate between two

different predominant orientations of bars or gratings, irrespective of other features (Fig. 2A). The trick was to repeatedly change the spacing between the stripes during the training, but keep their orientation constant. This introduced the technique of randomizing those features of a pattern that the bees were not to learn, and rewarding only the feature in question.

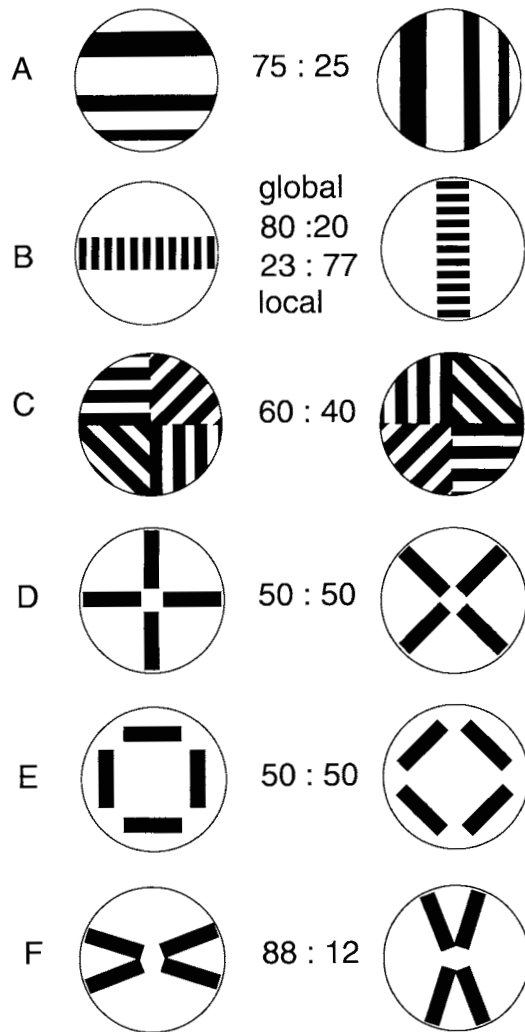


Fig. 2. The performances of flying bees, as shown by the ratios down the centre, with some patterns in the Y-choice apparatus in Fig. 1D. Positive (rewarded) patterns are on the left, although in the training and tests the two targets were regularly interchanged. (A) Bees readily learn strong differences in orientation^(18,21) irrespective of bar position (which is randomized in the training and tests). (B) With this pair of test patterns, the bees trained on A use the global orientation when the test distance is set at 27 cm (Fig. 1D), but the local and opposite orientation when the criterion is at 9 cm⁽¹⁹⁾. (C) When the training and test pattern is strong but does not fit the global filters, the bees can use regions of it to discriminate its rotation by 180°⁽²⁰⁾. (D and E) Bees cannot discriminate these patterns⁽²¹⁾, which excite global symmetry filters irrespective of orientation, but they discriminate the patterns in D and E from each other⁽²²⁾. (F) Bees trained and tested on these patterns discriminate rotation when there is a predominant orientation of the pattern as a whole⁽²¹⁾.

The results show that flying bees discriminate the average or predominant global orientation (i.e. at the largest scale over the whole target, see Fig. 2B), as if they have a family of broadly tuned filters with large fields that are sensitive to the rotation of a bar or edge⁽¹⁹⁾. Such a filter would look like a fence with large elongated slits. *Global* vision is here interpreted as vision with filters that cover the whole target. In these tasks, bees discriminate the approximate orientation of parallel gratings with bars only 4° apart, but there is no suggestion that they remember the individual bars. The bees use local orientation only when forced to do so. By dividing the target into quadrants with different orientations of a grating in each, Zhang and I⁽²⁰⁾ found that the area over which the angle of the tilt is summed is about 15-20° across (Fig. 2C). Unexpectedly⁽²¹⁾, the orientation detectors appear not to distinguish between edges or bars that cross (Fig. 2D), although other experiments show that they can detect short bars (Fig. 2B,C). There are signs that the size of the filter's field is under control, with priority given to the global pattern rather than to local details^(20,22). The filters have broad orientation-tuning curves and large fields, or they would not fail with the patterns obviously different to us in Fig. 2D and 2E.

Symmetry detectors

When this work had separated out the orientation detectors⁽²¹⁾, Lehrer, Zhang, Gadagkar and I investigated whether bees distinguish patterns that contain no predominant orientation, namely those with pairs of bars at right angles (Fig. 2E), and radial or circular patterns (Fig. 3). First, we trained bees to come to a chequered pattern of randomized check size and orientation, and then presented them with a great variety of sectors, circles and combinations of bars and other patterns that they had not seen before⁽²²⁾. They innately prefer radial patterns of bars and especially sectors, and they select against circular patterns and random patterns. They learn to discriminate very well (Fig. 3A) between radial sectors and concentric circles (both with a randomized period of the pattern), and they distinguish either of these equally well from a chequered pattern (Fig. 3B,C). As there is no predominant or average orientation in any of these patterns, the results suggest that the bees have additional filters, of which the minimum number is two types in polar co-ordinates that resemble radial sectors and concentric circles⁽²³⁾. These filters with circular symmetry explain many of the results in earlier work, e.g. Hertz^(2,3) and Free⁽²⁴⁾ found a preference for flower-like shapes, bees recognize holes, and radial symmetry can be learned. Again, the filters with larger fields that detect the global features have a higher priority than those of the same type that respond to local features. If the large-field or global detectors of polar symmetry inhibit the orientation detectors, this would explain why bees cannot discriminate between a St George's cross (+) and a St Andrew's cross (x), even when they both subtend 40° at the eye (Fig. 2D). Similarly, rotation of the pattern in Fig. 2E is not discriminated because it already excites the global circular filter.

Putting all these new results together, we see that *flying* bees use filters for the degree of disruption of a pattern⁽²⁾, filters for predominantly global orientation^(18,19,21) and for

global radial symmetry^(23,25). If these global filters are not excited, then the bees discriminate more local regions with similar filters with fields down to about 15° across⁽²⁰⁾. Together with colour, these filters are independent of range, and being broadly tuned and overlapping they are able to respond to various intermediate patterns in various ratios⁽²⁶⁾. Orientation filters detect orientation contrast and are unaffected by moving the image along a line; filters with circular symmetry detect some contrasts of symmetry and are independent of rotation. With these filters, a coarse orientation difference on a background of other orientations, and flower-like symmetry or straight bars on a background of irregular texture, would stand out. Psychophysical observations suggest, and recent single neuron recordings reveal⁽²⁷⁾, the presence of neurons in the visual cortex of primates with fields responding to radially symmetrical patterns similar to

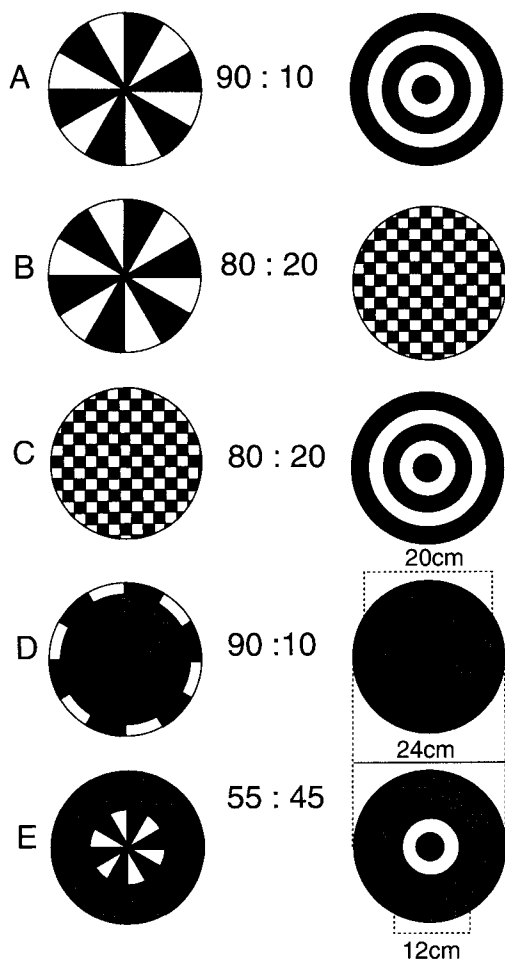


Fig. 3. More discrimination tests in the Y-choice apparatus in Fig. 1D. (A) Radial and circular patterns are readily discriminated⁽²³⁾, irrespective of contrast reversal or number of rings or sectors. (B) The rewarded (positive) pattern in A is preferred to a previously unseen chequered pattern⁽²³⁾. (C) The previously unseen chequered pattern is preferred to the previously negative pattern. (D) Covering the centres with a grey area has little effect, but (F) covering the periphery of the patterns with grey removes the discrimination⁽²⁵⁾. For the tests B to F, the bees had been trained on the patterns in A. The ratios show the percentage performances.

those proposed here. They are presumably useful for the same reasons. Mathematically, these filters are related to the well-known Lie set of spatial operators⁽²⁸⁾.

A model of visual discrimination

We need a convenient and economical way of thinking how the outputs of several broad-field filters can act together to yield pattern discriminations. But in vision we already have such a model which has long been in use, namely that for colour discrimination in man and bee (Fig. 4A). Each point within a triangle (projected to the three sides) represents the ratios of the inputs at the three corners. The *colour signature* of a region of a target is represented in Fig. 4A by a circle within the triangle, which has the three spectral sensitivities at its three corners. The triangle is not arbitrary because the spectral sensitivities are measured properties of the receptors. The minimum sizes of the separate areas within the triangle depend on how closely the signal can be defined relative to noise. Because alternative sources of light are not distinguished within the broad spectral sensitivities, many different mixtures of *wavelengths* can yield the same *colour*, as shown by discrimination tests, and the exact mix of the stimulus wavelengths is not recovered at a discrimination. Colour signatures, not wavelengths, are distinguished.

Similarly, we can represent 2D pattern discrimination in the bee by ratios of the responses of broad-field filters for features in 2D. The *orientation signature* of a region of the target lies in a triangle which has three broadly tuned orientation filters at 60° to each other at its corners (Fig. 4B). Three equally spaced preferred orientations are sufficient⁽²¹⁾, although we have recorded from neurons with other tilts. As for colour, many different mixtures of orientations within the same area can yield the same orientation signature, and the separate orientations are not recoverable. Similarly, the *symmetry signature* lies in a triangle with radial, circular and random (flicker or disruption) filters at its corners (Fig. 4C), and it relates to the ratios of the responses of filters which preferably detect global rather than local features. The innate responses to flicker and flower-like patterns⁽²²⁾ show that these three circularly symmetrical filters are not entirely arbitrary.

This central representation by *signatures* is a model with economical coding that enables numerous discriminations to be made with few filters, roughly independent of range. With only three visual pigments, we humans can distinguish a thousand colours. The bee presumably has cruder circuitry, but the six 2D filters in Fig. 4B and C would allow numerous patterns to be distinguished.

Advantages of global vision

In all the discrimination tests, the patterns subtend a very large angle at the eye of the bee at the moment of decision; in landing bees the angle is near 180°, in fixating bees (Fig. 1A) it is 110°, and in our experiments (Figs 1C, 2 and 3) it is 40°. As in man⁽²⁹⁾, global form has a higher priority for the bee than local features. When we removed the central part of the

target (Fig. 3D) we found that the bees could discriminate as well as before⁽²⁵⁾, but removal of the outer region of the pattern completely spoils the discrimination (Fig. 3E).

Bees have difficulty in finding again a small black and white target if it's location is moved, even though it remains clearly visible; this is understandable if they use landmarks and colour rather than 2D pattern. There is no need to look at detail along the route if landmarks⁽³⁰⁾ will do, no need to look at the pattern of the goal if lateral marks lead the way towards it⁽³¹⁾, and no need to remember the form of the goal if the outer parts of the target act as landmarks as the bee approaches⁽²⁵⁾. By relying on large landmarks, the eye resolution is less important, the signal/noise ratio is increased⁽³²⁾, and simple geometry⁽³⁰⁾ shows the advantage of being guided by the largest and most separated contrasts.

The milk run

Putting ourselves in the place of the bee, we follow our sun compass⁽³³⁾, to lead us to the locality of the reward, aided by a few large distant landmarks⁽³⁰⁾. By placing ourselves relative to the local landmarks in the vicinity of the goal, we point ourselves towards the right direction⁽³¹⁾. As we approach it, the target grows in size and we use its outer edges in the same way⁽²⁵⁾. Our radial and circular filters respond to flower shapes^(22,24) and centre our track, but there is little need to look forwards. In fact, the region dead ahead is not very informative because it moves little and expands too slowly. Only at a close approach, might we actually use the two-dimensional pattern around the goal. On the other hand, when attracted to the Y-choice apparatus by a stronger sugar solution, we are forced to pay attention to two separate targets with 2D patterns because they are continually inter-

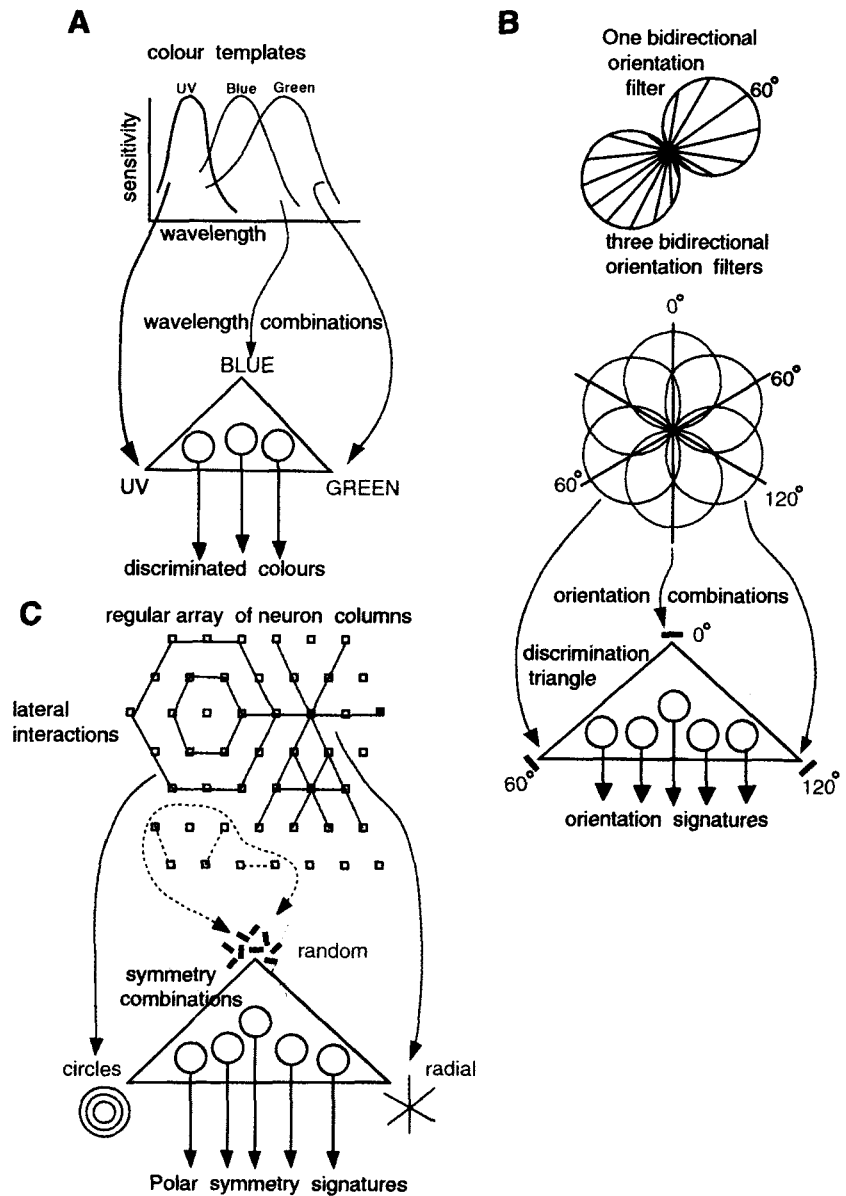


Fig. 4. The representation of discriminations with the proposed input filters. (A) The way that colour discrimination is modeled as a triangle with a broad spectral filter at each corner. The different regions within the triangle then represent different ratios of the responses of the three receptor types. (B) Orientation discrimination can be modeled as a triangle with three broad filters 60° apart. Different ratios within the triangle then represent different orientation signatures⁽³⁴⁾. A possible derivation of how these filters arise as neurons (that are not hypothetical) in the hexagonal pattern of medulla columns, is illustrated. (C) Flower-like patterns in polar co-ordinates. Three filters for radial, circular and disruption (flicker) or random texture patterns originate in hypothetical neurons that run across the columns of the medulla. These particular filters are the simplest in polar co-ordinates and they fit the performance of the bee. As before, three types of feature detectors feed into a discrimination triangle. This symmetry signature would work together with the orientation signature in Fig. 4B, so that all of the available black and white pattern discrimination is represented in six-dimensional space⁽²⁸⁾ for each region of the image.

changed during the training. We are obliged to discriminate them from a distance of 27 cm (Fig. 1D), but we still pay little attention to the region around the goal (Fig. 3E).

Task-oriented vision

So, summing up, there is no evidence that the bees put an undigested copy of the image into memory for consultation later, even if they see it. To retain a mass of visual information that is mostly irrelevant is hopelessly inefficient. Even if we have accounted for all the visual filters feeding into the memory of the bee, we can still say nothing about what bees actually *see*, but we can say that they *remember* what excited or passed these filters in different proportions. While on-line vision without memory controls flight manoeuvres, the bees remember abstracted signatures of the target that are based on colour, orientation of edges, radial and circular filters, angular size and amount of flicker caused by self-motion. Engineers call this a 'reduced instruction set'. Significantly these filters have an interesting selectivity, and all are independent of exact range. If we model such filters, we can predict the performance, test new patterns, and work towards an artificial seeing system that performs as well as the bee. The inconvenient fact is, however, that this kind of vision is task-oriented, and to be useful the filters have to fit the task, especially in their tolerance, or widths of their tuning curves. Only certain robots, like rice planters, fruit or mushroom pickers, have visual tasks similar to those of bees. A useful principle, however, is that natural visual systems are built with broadly tuned, overlapping filters *in parallel* (Fig. 4), and the remarkable invariances and versatility of discrimination vision comes from combinations of simultaneous responses^(26,34). As in colour vision, the use of signatures in 2D-form vision eliminates the stimulus variables that influence the input filters equally, and stores just the significant extract in an economical code.

Prospects

Some of the gaps in our knowledge have stuck out like sore thumbs for years. Firstly, almost all the performance of the insects' on-line flight control has been measured in the horizontal plane only, but the serious problems of artificial vision are in 2D and 3D. Examples are: separating the directions of motion from the orientations of edges, global discrimination mechanisms of symmetry and texture, recognizing pattern in irregular motion or instant avoidance of looming. Retinal images are in 2D and visual processing is a struggle to grasp the 3D world. Engineers are not much interested in 1D vision. When Srinivasan⁽³⁵⁾ invented a new rapid algorithm for extracting angular velocity on-line in 2D, and therefore range on-line, it was snapped up by a computer company and used for generating the apparent motion of objects in 3D worlds for virtual reality games.

Secondly, saccades are hardly studied except in man, crabs and *Drosophila*, and processing by scanning is barely studied. The hottest topic is now the eye movement of flies. Thirdly, although many of the neurons have been described in the optic lobes of fly and some in other insects, the relation

between behaviour and the weightings within combinations of neurons in successive arrays within the optic lobe and brain is really a maze of hypothetical circuits. At every point in that account, performances must be quantified, circuit details need substantiating, multiple-electrode data is in very short supply, ideas about separate pathways must be broadened to more species, and whether the hypothetical neuronal models are adequate needs to be checked by simulations. For lack of suitable experiments, no neural mechanisms have been found for insect discriminations and learning. There is plenty to do, and we now have a quest for robot vision that generates the research funding with enormous profits in mind. The point of this article is that you don't have to be cellular or molecular to be at the cutting edge of fundamental and technologically useful biological advances. You don't even need a grant! A little sugar and some patterns on paper, with the willing help of some honeybees, are sufficient to build upon and perhaps disprove the existing theories.

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