

04 PERCEPTION OF PATTERN, FROM 1950 ON¹

There were many earlier descriptions of how particular insects responded to lights or ran towards dark holes or contrasting edges, and several useful summaries of this kind of behaviour, categorised into taxes, kineses and tropisms (Fraenkel and Gunn 1940). The movements that insects make when stimulated by light, however, say almost nothing about the mechanisms of processing. Similarly, the outstanding work by Baerends (1941) and van Beusekom (1948) in Holland showed that wasps recognised their nest site by the memorised configuration of landmarks in different directions relative to each other, but this was about performance, not mechanism. In the second half of the twentieth century, starting with Bernard (1966), various symposia on insect vision were published. Wigglesworth's classical work on insect physiology, revised in 1965, gave a summary of many factual details but no mechanisms were in sight until the extensive compilation by Autrum (1979–81)—and even that was incomplete. Understanding was confused by the statements of Exner, Hertz, Autrum and Reichardt that insects distinguished shapes through motion, although there were plenty of observations that many insects hovered to take a better look.

When research started up again, the prewar (mostly German) effort was scarcely mentioned, even by the Germans themselves. From the autobiographical sketch of Karl von Frisch (1957), we can infer that National Socialism played a part in the suppression of the work of some of his students, and certainly after 1945 there was a strong tendency to deliberately turn away from all the events and literature of the 1920s and 1930s.

More fundamental reasons for ignoring the earlier results—except for a summary of Hertz—were numerous. One was a push towards quantitative data, with empirical mathematical relations to support a theory, as advocated by teachers of scientific method at the time (Chapter 2). Second, there was the cybernetic movement that sprang from the operational research groups of World War II, as illustrated by Reichardt's group at Tübingen and the journal *Kybernetik*, which

he founded. There was also the destruction of libraries, a wish to forget the past, a new generation of students in a hurry, a general thrust away from natural history towards mechanisms and the particular interests of the key players.

In 1965, a view through Russian eyes was translated and edited by Timothy Goldsmith at Yale. Georgii Mazokhin-Porshnyakov, a professor of entomology at the Institute of Information of the Academy of Sciences of the USSR, had published numerous papers on the compound eye and trained bees to discriminate patterns. Mazokhin-Porshnyakov (1969) thought that bees responded to the 'the totality of the object's characteristics and not—to individual parameters such as shape, size, and so on'. He observed that '[t]he fact that insects can distinguish shapes is taken for granted by the majority of contemporary authors'. He ignored the fact that every researcher up to that time had found that trained bees detected parameters such as disruption, area, colour and radial symmetry, not shape.

Let me quote further:

Insects, in particular honeybees, are able to distinguish shapes and recognize simple figures, such as circles and triangles, and complex figures like stars. Highly decomposed figures are perceived by insects through the flickering of light produced by motion of the retinal image over the receptors...Insects are even able to distinguish solid objects from plane ones, and can estimate depth. They distinguish colors and make large use of color vision in their normal patterns of behaviour. (Mazokhin-Porshnyakov 1969)

There is a very telling translator's footnote:

The reaction to various figures exciting the eye to a different extent is not proof that insects really distinguish shapes. Insects can move back and forth along the edges of black bands and distinguish these bands simply as a darkening in their visual field and not as a field decomposition (shape). (Mazokhin-Porshnyakov 1969)

There is also an interesting footnote on page 123: 'Hertz's (1929–31, 1933) analysis of figure perception and identification in bees is not substantiated, and we will not consider it here.' Hertz was of the opinion that her bees did not see shapes that were laid flat.

Mazokhin-Porshnyakov himself accepted that earlier authors had sometimes failed to train bees to distinguish different shapes, but he believed that they had used patterns that were too large. His successful patterns contained the same shape on two spatial scales. From a distance, his 1965 patterns looked like an empty triangle, square or circle, but the edges as seen from a distance were composed of many small triangles, squares or circles that could be resolved close up. He convinced no-one because there were none of the necessary controls against the many possible cues. The emphasis was on what insects could see—

that is, successes in training—but successes alone leave us with the impression that ‘insects really receive and make use of a variety of visual information and accordingly behave more or less like vertebrates do’ (Mazokhin-Porshnyakov 1969). This is terrible stuff—mostly guesswork.

A related observation was made 30 years later by Campan and Lehrer (2002), who successfully trained bees to distinguish a filled triangle, square and circle, and who mentioned that ‘*A. mellifera* tended to scan mainly those contours whose direction differed between the two shapes’. They concluded that the shape discrimination ‘is based on the use of local parameters situated at the outline of the shape, such as the position of angles or acute points and, in particular, the position and orientation of edges’. These proposed parameters, however, were also guesswork, and there were no tests to identify them. Even into the new century, the majority of authors apparently continued to believe that insects saw shapes, despite the lack of evidence for the idea, and plenty of evidence against it.

A virtue of the condensed little book by Carthy (1958) was an account of some of the German, French and English literature on reflexes and other behaviour. Even so, while some of the findings of von Frisch, Hertz, Opfinger and Wolf on trained bees were mentioned in English, the crucial ones by Baumgärtner, Friedlaender (see Figure 1.6) and Wiechert were missing. It provided a partial impression of what was available in the mid-twentieth century, but no explanations. There was no useful theory at that time and little to assist students with their essays.

This was the sorry state of the art when Scholes, Tunstall, Bennett, Shaw and I started recording from insect retina and optic lobes of the locust at the Gatty Marine Laboratory, Scotland, in 1962. Besides showing that the field sizes of the receptor cells were nothing special, we found groups of large neurons with large fields that responded in a variety of ways to the motion of edges or black spots. The neurons were excited by very simple stimuli, but the large field sizes precluded the separation of features and the responses could not be related to different patterns presented to the eye. Insect vision remained a puzzle.

At the time, it was commonly stressed that recording the properties of neurons would eventually explain or even predict simple reflexes or even complex behaviour—and many still believe this. Our introduction to the problem of explaining insect vision by this route was so disappointing, however, that for 25 years we abandoned high-level neurons and tackled the retina first. In a system of pathways in parallel, it is impossible to know which neuron relates to which behavioural response or what is happening in pathways other than the one that is recorded. At the time, we did not understand that the behaviour could explain some properties of the neurons, not the other way round, so the behaviour must be analysed first.

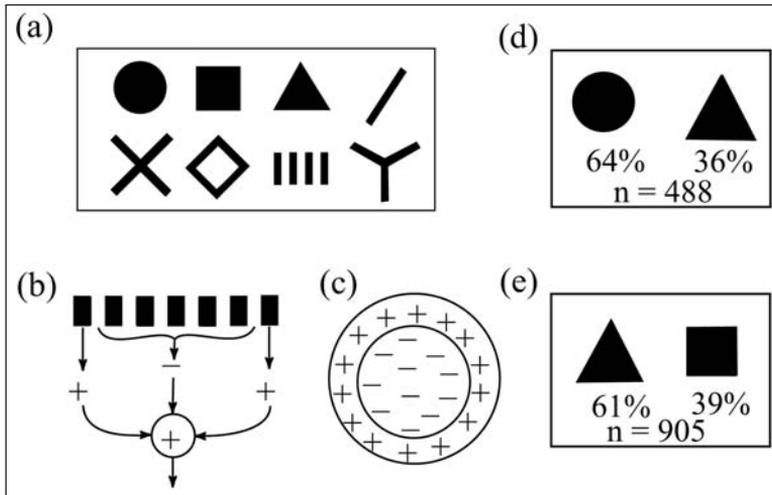
The mobile eyestalks of the shore crab were also ideal objects to study, because the responses to motion were reliable and informative. In 1966, I published a series of papers with Peter Shephard and then with Malcomb Burrows showing that the shore crab *Carcinus* had a peculiar sort of memory when placed in an illuminated arena with a few vertical black bars. After the crab has seen the stationary bars for a few minutes, the light is put out and the crab's surroundings are rotated by a few degrees while it is in the dark. When the light is switched on again, the crab's eye moves until it points towards the same position as before, relative to the bars, showing that there is a memory of their former positions on the eye. The precision was much better than the angle between receptor axes (2°). Some individual crabs respond as though they remember only the former positions of black areas, but others remember the former positions of edges irrespective of which side of the edge is black. Later, the separate memories of positions of edges and black areas turned out to be similar in ants and bees.

The meaning of these observations surfaced only when it was found that crabs were aware of the direction of their burrow at all times, and insects stabilised their walking or flight positions by exact memories of the positions of surrounding contrasts.

A promising new start

In von Frisch's busy institute in Munich, Rudolf Jander, Una Jacobs-Jessens (1959) and several students assiduously studied the navigation and visual system of the red wood ant (*Formica rufa*), which recognised some landmarks visually. They measured spontaneous preferences to various black shapes on the sides of a white arena and trained the insects to discriminate between the same shapes. Whereas a protozoan or a barnacle might have a single detector and gives the same response to almost any visual stimulus, the vision of ants and bees was treated by Jander and colleagues as a collection of simple detectors guiding a variety of responses. By 1963, Jander and his student Christiane Voss at Freiburg inferred that ants had detectors for: a) a dark area, b) horizontal versus vertical stripes, and c) disruption of the pattern. Untrained ants prefer solid black, closed figures to disrupted patterns, which can be reversed by training, and they prefer vertical stripes to horizontal ones, which is unaltered by training. A black triangle was distinguished from a black disc or square (Figure 4.1e), but possibly the centres of gravity of the figures were at different heights.

Figure 4.1 a) Patterns frequently used to illustrate edge length or modulation as a cue. It was supposed that each pattern (laid flat on a white table) could not be discriminated from those in the same row, but any pattern in one row could be discriminated from those in the other row. This does not apply if they are presented vertically. b) and c) The feature detector proposed for ants and bees. d) and e) Pairs of patterns that were discriminated, but note that the centres are at different heights.



Source: (b) and (c) Jander (1964); (d) and (e) Jander et al. (1970).

In 1964, Jander proposed that insects had modulation detectors that acted as filters and that ants and bees learned features that they later detected in unfamiliar patterns. The feature detector proposed for insect vision was symmetrical, with a centre/surround structure (Figures 4.1b and 4.1c) that would detect a spot or an edge irrespective of which side was black or white. The responses of trained wasps to the orientation of edges were explained by strings of these detectors (Jander et al. 1970). Such detectors, however, would be useless for areas of black or colour. The concepts and terminology could be traced back to seminal papers of 1950–62 by Barlow and Levick, Kuffler, Lettvin, Maturana, Mittelstaedt, Hubel and Wiesel and others who found that arrays of single neurons in the peripheral visual system of vertebrates responded to simple visual features such as edges or spots.

In Frankfurt, Voss (1967) also showed that wood ants detected the orientation of black and white gratings with a minimum period of 1° although the interommatidial angle was $9\text{--}10^\circ$. This remarkable sub-pixel resolution, also found in several carnivorous insects that hunt for prey, must rely on modulation differences, not pattern. The ants distinguished between areas of black and edges, irrespective of which side was black. They also detected the difference between a sharp black/white edge and one that had the edge orientation spoiled by cutting it into square steps. Voss demonstrated that the ants measured

the height above the horizon of a black spot of constant size (14° diameter), with a maximum spontaneous attraction at 30° up. There was no hint of shape discrimination. Although these findings were scarcely ever given due credit, they recurred in many later papers by others on ant and bee vision.

The quantitative approach

In a search for empirical laws, Schnetter (1968) at Würzburg used black patterns of four-pointed and six-pointed stars with circular symmetry, presented flat on a white table, as Hertz had done 40 years before. It was a mistake to start with such a complex image. He trained with one star that was duplicated many times and then tested the trained bees with the training star versus a series of similar stars of the same area that differed in one measurement: the length of edge. He found that the greater the difference, the better the discrimination. The score in the discrimination was related to the relative differences in the lengths of edge $(d_1 - d_2)/(d_1 + d_2)$ —that is, *an empirical law*. It was not surprising, really, because the edge length was already known to be a parameter and it was the only variable that the bees could use. The results for four-pointed stars fitted a single curve but the curve for six-pointed stars was different. Later, the tests were repeated with other values of the diameter, the number of points, the angle at each point and relative length of the points (Schnetter 1972)—again, with no useful conclusion. There was no test of what the trained bees really detected or whether they could distinguish the stars from other patterns.

Schnetter's quantitative measurements served only to confuse the issue for decades. There was in fact no need for this cumbersome search for the best correlation. The relation between the length of edge and the number of correct choices is neither interesting nor informative. The effect of area was omitted and there should have been a logical identification of the cues by testing the trained bees.

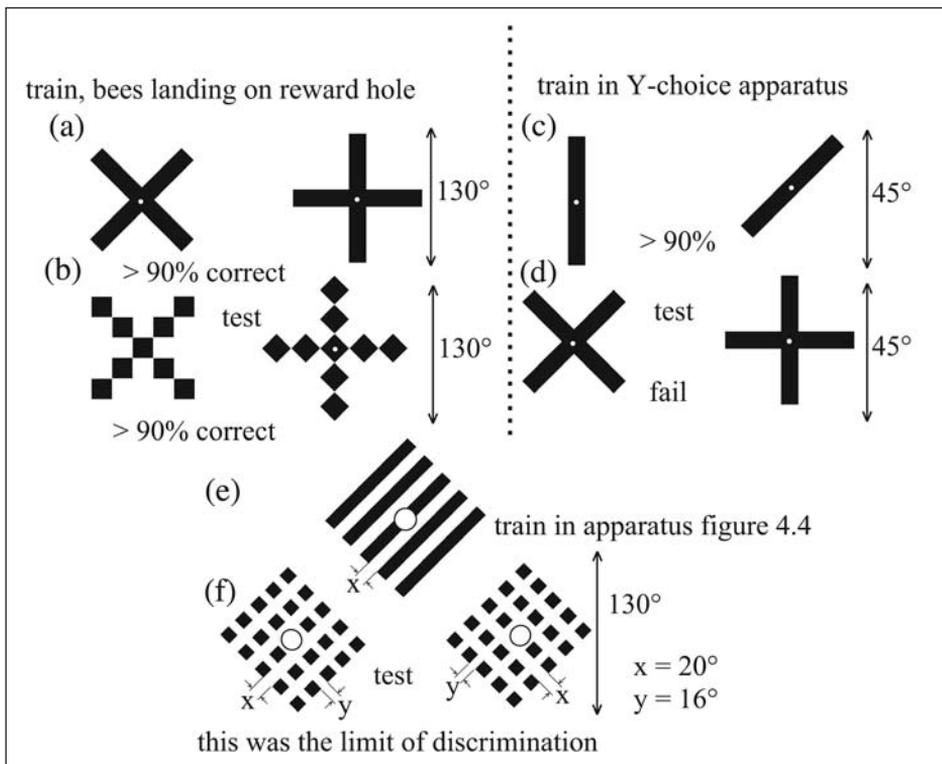
Large patterns at Frankfurt

In 1958, von Frisch retired from München and, following custom, his staff and students moved to new positions and left space for Hans Autrum, his successor. Martin Lindauer became the professor at a new department in Frankfurt and soon found a student, Rudiger Wehner, who worked on pattern perception in honeybees.

I am sorry that, at this stage in the history, comprehending the next group of findings will need all your attention and constant referral to the illustrations. In their new effort in Frankfurt, Lindauer and Wehner presented the targets on a vertical plane, as in most of the prewar work. At first, they used two targets side by side, alternated in position to make the bees look and learn which target to visit. The patterns were centred and fixed and at first the criterion

was landing on the reward hole, so the patterns subtended a large unknown angle at the point of decision. In Wehner and Lindauer (1966a), the bees were trained to discriminate between two patterns, in which case we now know that they ignored cues that were the same on the two targets. Wehner and Lindauer (1966b) trained with a single pattern versus a blank white target and later said that the results were similar, which showed that they were unaware of what the bees had learned.

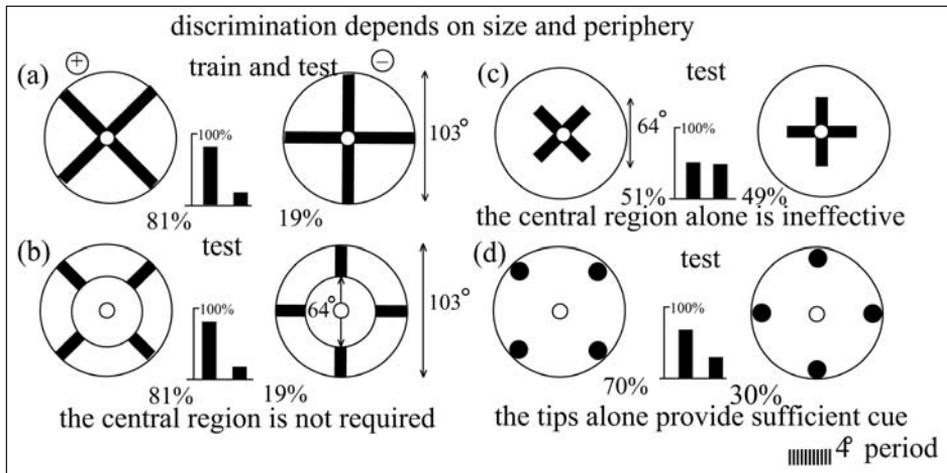
Figure 4.2 a) Large crosses were discriminated when the criterion was landing on the target. b) Bees trained on (a) were able to discriminate (b) with the same score. c) Bees easily discriminated between two orthogonal bars with angular size of 45° . d) The same bees could not discriminate between the cross with angular size of 45° and the same rotated by 45° . e) Bees trained on the large grating (period 32°) were able to discriminate the two patterns of large squares (f), but it was not clear what they detected.



Source: (b) after Wehner (1967); (d) Srinivasan et al. (1994); (e) after Wehner (1971).

Bees trained on a square cross of two bars (18cm by 3.6cm), or to discriminate between two crosses at 45° to each other (Figure 4.2a), could discriminate crosses with edges that were stepped to destroy the edge orientation (Figure 4.2b), and did not distinguish between the plain cross and the same cross with stepped edges. So, '[t]he stripe contours may be dissected in a sawtooth-like pattern without affecting the [bees'] orientation to the inclination of the long axes of the black stripes' (Wehner and Lindauer 1966a). The edge orientation was clearly not a factor. They could discriminate a square cross of two bars (18cm by 2cm) versus the same cross rotated by 45° (Figure 4.2a) with a remarkable minimum difference in angle of only 4°, which was impossible for edge-orientation detectors, so it was finetuned to whatever feature was detected (the shift in black areas).

Figure 4.3 a) Bees were trained to discriminate the large crosses. b) They easily discriminated the peripheral parts but (c) not the central parts. d) Spots in the correct positions were adequate for the discrimination.



Source: After Horridge (1996c).

This result is of interest because later it was flatly contradicted. Using the Y-choice maze with smaller targets and simultaneous viewing of two patterns, Srinivasan et al. (1994) found that a square cross with angular size of 40° was not discriminated from the same cross rotated by 45° (Figures 4.2c and 4.2d). On this result, they based a notable theory that relatively insensitive orientation detectors were very coarsely tuned to edge orientation. Also, edges were summed in local fields within which orientation cues from neighbouring edges at right angles to each other were cancelled. In a reinvestigation of this disagreement, with simultaneous viewing and two targets, it was found that with very large bars the bees learned the positions of the black areas at the tips (Figure 4.3). The discrepancy between Wehner and Srinivasan was therefore due to the difference in the angular sub-tense of the training patterns (Horridge

1996b). The excellent resolution of the rotation of large patterns came from the sensitivity to the shift in position, not the edge orientation. Later, this result gave us the clue that adjacent regions of the eye remembered the positions of parts of large patterns separately and opened up the explanation of all the data collected when the criterion of success was the landing of the bee on the target.

In Wehner's other experiments, the training pattern was a large black bar, a square cross of two orthogonal bars or a grating of several parallel bars on a white background—all huge patterns. The criterion of success was landing on the reward hole. In tests, as the test pattern was rotated, the discrimination of it from the training pattern improved. The percentage of correct responses was plotted as a function of the angle of rotation. The empirical law relating the response to the angle of rotation was similar for a bar, cross and grating, although with a regularly spaced grating the position of black on the target did not change in the same way as the others. Wehner spotted this discrepancy and, having already excluded edge detectors by using stepped edges (but only for the cross), he postulated that the parameter 'is the orientation of the long axes of the black stripes, but not the direction of the black and white contours'. Although wrong, this was an interesting idea because it shifted the emphasis from edges to positions of areas in the pattern.

In the light of later work, the rotation of the regular grating must have been detected by the change in edge orientation, but Wehner could not accept that idea because he had already shown that edge orientation was not the cue for a rotated cross. He missed the point that there are two separate cues in parallel and the bees prefer to learn the position of black rather than the edge orientation.

To control the angular size of the training pattern during training, Wehner (1968) introduced a transparent screen 25cm in front of each training pattern and made the bees walk through this to the reward via a tube (Figure 4.4). Behind the screen, the pattern (with cues) was visible in a similar position on the bee's eye each time it arrived during the training. The patterns were huge (130° by 53°) as seen from the bees' point of decision, and were not viewed simultaneously, except perhaps from far away.

Shortly after, Wehner (1969) trained bees to come to a single, huge black bar, subtending 130° by 53° at a fixed range, versus a blank, and tested the trained bees with the same bar versus one that had been rotated through various angles about its centre—again looking for an empirical law. The percentages of correct responses at different angles fitted the idea that the bees distinguished better when there was less area of overlap (multiplied by a fudge factor) and more area of non-overlap (also multiplied by a fudge factor) between the positions of the training bar and the test bar (Figure 4.5). With the help of two arbitrary constants, the overlaps of training and test areas could easily be made to fit the data. The bee would then have a measure of the similarity of the training and test patterns. Apparently, it could not fail.

Figure 4.4 The apparatus for training bees with the target at a known range. Bees were trained on a single large bar of angular size 130° by 53° versus a white target. The trained bees were tested with the original bar versus a similar bar at various angles. Results in Figure 4.5.

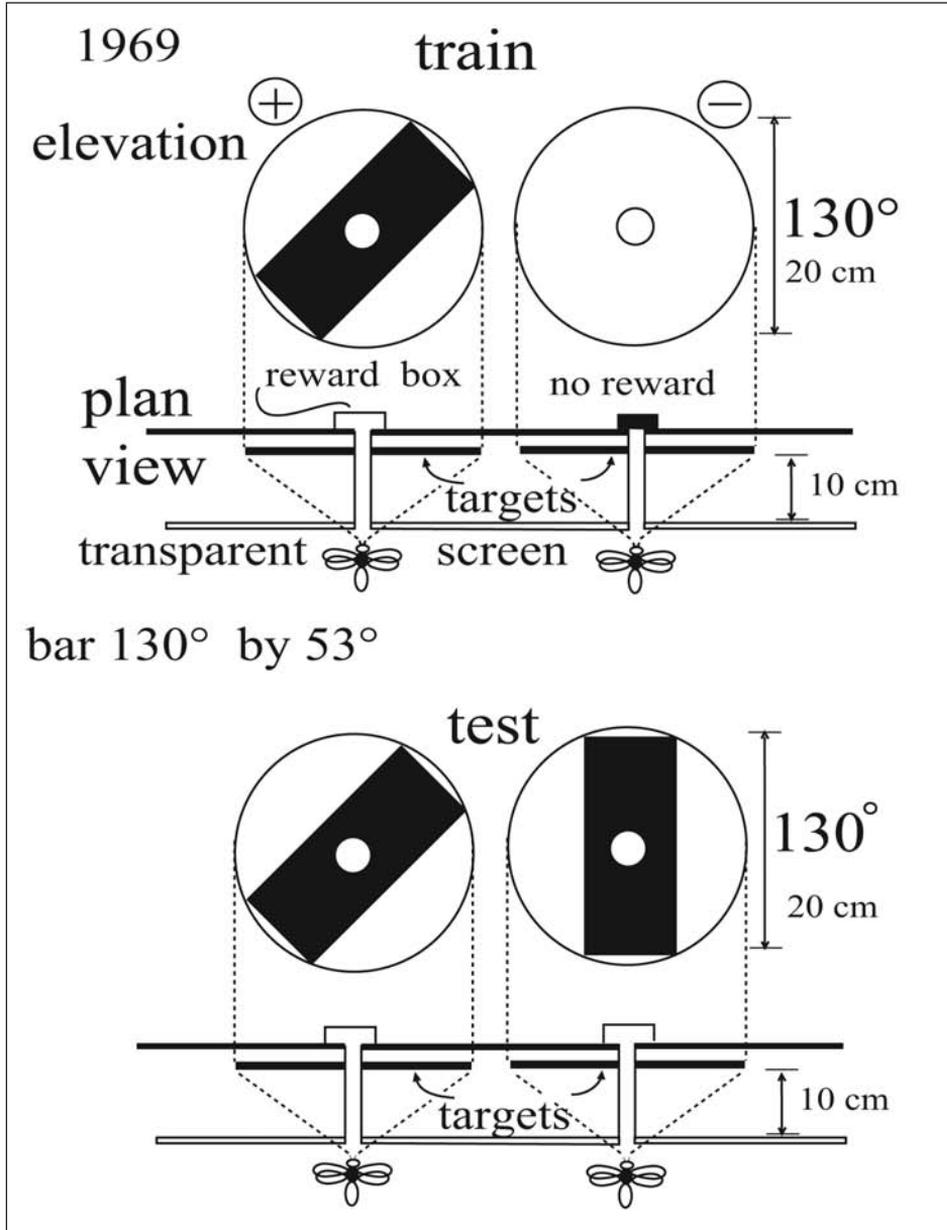
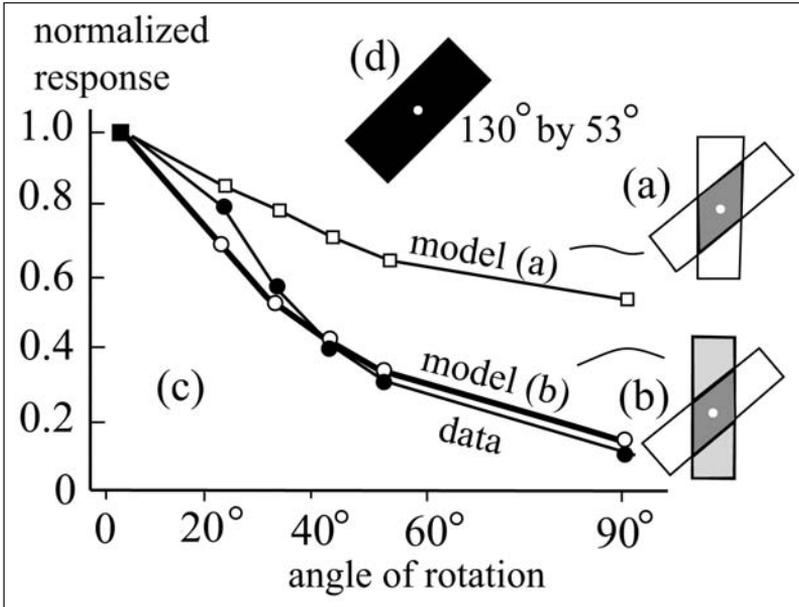


Figure 4.5 Data from the experiment in Figure 4.4. a) Calculated from the overlap only. b) Calculated from the overlap and non-overlap. d) The real shape of the bar.



Source: (b) from Wehner (1969).

It was not mentioned that the measure of overlaps would be different for different initial orientations, but the bees would not know the angle of rotation. Therefore the overlaps were not useful as an indicator of shape. Also, the measure of the overlaps as a function of angle would be different for different shapes, so would be even less useful as an indicator of shape. It was not realised that the result applied only to targets that subtended very large angles. There were no scales on the illustrations.

This theory of matching positions of black areas was taken to imply that the bees remembered the *shape* of the training pattern and compared it with each test pattern, although that conclusion went far beyond what the data really showed. The retinotopic eidetic image in memory became accepted in the literature, but there are two twists in the story. First, in 2001, my bees trained on a small oblique black bar versus a blank white target learned neither the shape nor the orientation (Figures 9.3b and 9.3c), only the position and modulation (Figures 9.3d–f) because there was an order of preference for the different parameters. Second, in the discrimination of the rotation of a sector pattern, on which bees fixated, I found that they in fact used the position of the most horizontal sectors but failed to recognise the pattern (Figure 11.11). With very large targets, the bees detected the change in distribution of black over several local regions of the eye differentially (Figure 4.3). It was the parameters, not the pattern, that were retinotopic.

When trained with a single large target, the bees' preferred cue was always the position of areas of black (Figure 4.5). If the changes made in large targets to test the trained bees were too great, the bees refused to choose and simply went home. They had lost the black areas that were moved—that is, the expected landmark was missing.

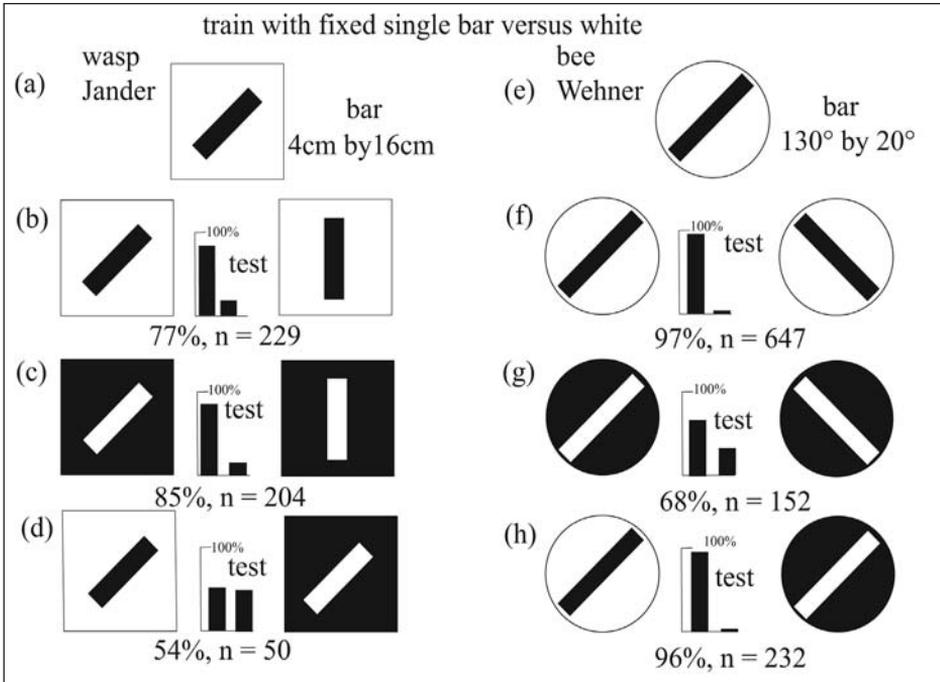
In all the earlier work, from von Frisch (1914) onwards, in which bees were trained to land on vertical targets, orientation was scarcely mentioned. The reported parameters were the position, the area and length of edge, because the patterns subtended a large angle at the choice point and edge orientation was not preferred.

According to Schnetter (1972), 'Wehner succeeded in isolating the position of the black areas as the relevant parameter for direction information.' That was true, but by accident, because he chose to work with bars 130° long and 53° wide that overlapped several local eye regions. This story illustrates the belief that the bees see the patterns and how the unsuspected effect of pattern size has influenced the progress of the research. From this work, I drew a new conclusion. When the bees discriminated very large targets, they used the coincidences of features in well-separated parts of their eyes, as though they were viewing several landmarks in a scene.

An alternative theory

At the same time, Jander et al. (1970), working in the same institute at Frankfurt, found that wasps, trained to discriminate between a vertical bar and the same bar at 45°, were able to detect an oblique edge at 45° when tested with a black bar versus a black square of equal area, or even with white bars on a black background (Figures 4.6a–d). These striking results were interpreted in terms of strings of radially symmetrical local edge detectors, as found in vertebrate retina (centre-surround units). The authors pointed out three reasons why Wehner's theory of an eidetic image could not possibly be correct: it would require a different set of arbitrary constants for each shape, it could not apply to the discrimination of the orientation of a grating and Wehner (1968) had already shown that the response to rotation of a bar was relatively independent of the width of the bar. So, even as the new theory of overlaps emerged, it was attacked at the home base with arguments that still stand, based on a rival theory of feature detectors in parallel. At the time, there was a serious conflict but both ideas were in fact supported by data.

Figure 4.6 Contrasting results and conclusions. a–d) Wasps were trained with a single black bar versus a blank; the criterion of success was landing on the reward hole. b) The trained wasps discriminated the orientation, and (c) when black was exchanged for white. They failed to recognise the black bar when the orientation cue was the same on both targets, showing that they relied on the orientation cue. e–h) Bees were trained with a single large bar in the apparatus in Figure 4.4. f) The trained wasps discriminated the orientation. g) They discriminated weakly, when black was exchanged for white. They also recognised the black bar when the orientation cue was the same on both targets. They must have learned two cues: position and orientation.



Source: Reassembled from the original papers (see text).

As though galvanised by this competition, Wehner (1971) trained with a single, large oblique black bar, at 45° to the vertical, subtending 130° by 50°, versus a blank target. The trained bees discriminated correctly between the training bar and a similar bar at right angles. They discriminated rather poorly when both test bars were white on a black background, but very well between the training black bar on white at 45° and a white bar on black, also at 45° (Figures 4.6e–h).

To explain these new data, ‘analysers’ of generalised orientation were intuitively inferred and ‘an angle discrimination is more easily possible when the relevant analyser...is switched on by previous training’ (Wehner 1971). The bees ‘abstract from some special stimulus properties by generalizing the sensory input according to special cues, for example the direction of visual stimuli’ and ‘the information about the direction of the visual cue had been transferred to a

new pattern configuration never seen by the bees during the training situation' (Wehner 1971). The words 'direction of the visual cue' are ambiguous and could mean the direction of black as seen from the point of choice or the angle of orientation on a vertical surface as an abstract cue irrespective of the real pattern. As expected from the training with a single fixed bar, most of the test results can still be explained by memory of the location of black, but both Jander and Wehner found that some discrimination of orientation persisted after the exchange of black and white (Figure 4.6).

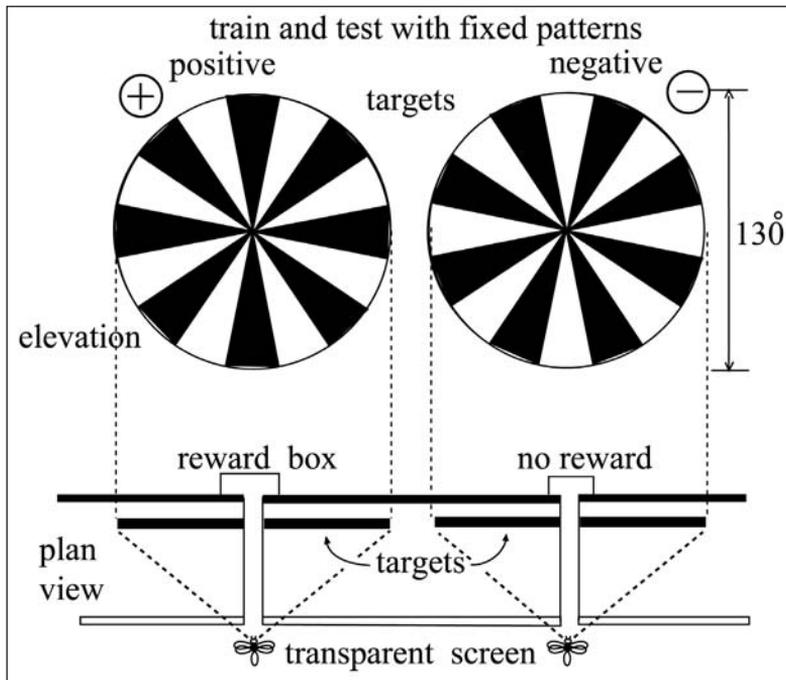
Wehner (1971) also trained on a large, coarse grating (period 20°) versus a blank white target and tested on patterns of squares that were prepared by adding white bars of various width at right angles over the grating (Figure 4.2e–f). The limit for discrimination by the trained bees was a width of 16° . From the results, he inferred 'a real transfer of the information about the direction of stripes on a complex pattern'. Whether the bees really detected the orientation in these patterns of squares is open to question, because a separation of 16° approaches the separation of local regions of the eye and is greater than the resolution of position. It is now clear, 30 years later, that Jander's wasps and Wehner's bees had learned several cues—the position of black, the area, the modulation and some edge orientation—but not the complete pattern.

It was known at the time that in ants and the shore crab the edges of shapes were processed separately from the areas in the centres, but 40 years ago this was a new and counter-intuitive idea. For bees, it was clear that edges and positions of areas of black were separate parameters, but a model with several pathways in parallel was not conceived. Analysis was delayed by the use of very large patterns that overlapped several local eye regions and so allowed the bees to detect some configurational layout of the patterns.

In all this, the preconceived ideas of the principal antagonists were illustrated by their terminology. Jander used the word '*Kantenrichtung*', meaning the 'orientation of the edge', but Wehner used words such as '*Winkelstellung*' and '*Winkellage*', meaning 'the place or position of the angle'. By 1971, however, Jander had left for the University of Kansas in the United States. For 20 years, there was no further mention of detectors that abstracted orientation irrespective of pattern, although the numerical parameters of total area and length of edge inferred by Hertz were redescribed several more times.

Up to this point, almost all of the work on training bees had been published in German; the theories were based on training performance and reached intuitively without extensive tests of the trained bees. There was no comprehensive review, so the details of the training, the results and the differing conclusions were scarcely known to English, French and especially American students.

Figure 4.7 With this apparatus, bees trained on a single sector pattern versus a white target were able to discriminate the training pattern from a similar one rotated by half a period, with the following results: two periods = 95 per cent; four periods = 90 per cent; eight periods (as illustrated) = 70 per cent; 16 periods failed.



Source: Derived from Wehner (1981:Fig. 59).

In August 1972, at a symposium on insect vision at the International Congress of Entomology, Wehner proposed that the bee had sets of feature detectors that responded to relevant stimulus parameters. The theory of 'feature space' was popular at the time. He referred to the work of Jander and colleagues on feature detectors: 'Whether these "features" however are really used as parameters in an n-dimensional classification scheme, can only be decided by appropriate training tests.' Of course, there was a shortage of tests because the bees would not respond. He reproduced some of his data but was extremely cautious: 'All attempts to define the criteria of classification used by bees—or any other insect species—having failed, Cruse (1972a, b) returned to the method of calculating overlapping and non-overlapping areas between two figures by using a two-dimensional cross-correlation' Wehner (1975). But then, '[i]t is unlikely from another point of view that pattern detection can be done merely by cross-correlation methods'. It was impossible to fit the successes after reversal of contrast into any scheme with memory of overlaps. Within three years of its arrival on the scene, the theory of shape discrimination by matching area for

area was considered unlikely by its originator, who had himself disproved it experimentally with gratings in 1967, yet later it turned out to be valid for very large patterns.

Wehner turned to work on the marvels of navigation by the desert ant *Cataglyphis*, but in his review (1981), he illustrated the discrimination of sector patterns from the same patterns that were rotated by half a period (Figure 4.7), with the comment: 'The only factor which can account for the bees' ability to discriminate between these gratings is the exact retinal position of black and white sectors.' This takes us back to square one, but is partially true. After 50 years of evidence of generalised parameters, however, it was a little confusing for the general reader, and it later turned out to be wrong anyway (Figure 11.11).

In this tangled period, the real data were excellent but clear conclusions failed to emerge because in the tests several parameters were changed at the same time, and few tests were done on the trained bees. The eidetic image was proposed but not proved. The fundamental difference between the parameters for areas and edges, and the order of preference for learning several parameters, were almost discovered. The topic was generally regarded as incomprehensible and intractable, as had been the case after the immense effort by Mathilde Hertz 40 years before. Even the large indiscriminate texts on comparative psychology and ethology omitted the known results.

What went wrong

In retrospect, the scientific method of the physical sciences of the time—varying the test pattern and plotting the responses in a search for an empirical law—was doomed to failure because several unknown parameters were changed together and the numerical relations said nothing about what the bees detected or the mechanism of vision. Not surprisingly, there was continual increase of correct choices as the test pattern differed more and more from the training pattern. The overlap of areas is a measure of similarity; the non-overlap is a measure of difference. The area of overlap (multiplied by a fudge factor) and the area of non-overlap (multiplied by a different fudge factor) were put into an equation that modelled the performance. For a single variable and one training pattern, this strategy could not fail.

For different kinds of patterns, however, it was necessary to have different constants in the equations and even different forms of the equations. Schnetter summed the edge lengths; Cruse added the two parameters together; Anderson multiplied them. It was all ad hoc curve fitting. There was no prediction of the performance from one pattern to another and few tests of trained bees on critical patterns. The broader criticism is that we are not very interested in the fraction of choices that are correct as a function of an arbitrary parameter or in an equation that fits the data, because there are many interacting cues.

What we need is an insight into the mechanism. These are perennial problems in biology, which needs to stick to what Forel called 'the intimate connections of the causality'.

The quantitative differences between scores depended on the length of training. In contrast, much of the recent work relied on yes/no decisions of whether or not the bees could learn to discriminate between two patterns that differed in a subtle way. If they could learn them, they were then given a large variety of yes/no tests.

That could not be the end of the eidetic image, because positions of natural landmarks were learned as positions on the eye. Also, there were still unexplained results when the criterion of success was landing on the pattern. Gould (1985), working at Princeton, showed that bees distinguished whether two flower-like patterns had different positions of coloured areas with a resolution down to about 10°. There was little popular understanding, however, despite 60 years of effort. There was no popular book, no signpost to the future or discussions of alternative theories. With good salesmanship, a final long review omitted any reference to Jander's work on orientation detection and concluded rather inadequately that 'some decisive pattern parameters such as contour density or area distribution have been unravelled' (Wehner 1981).

On second thoughts, none of the theories was satisfactory. A single summed parameter such as the total edge length is a stupid way to distinguish objects in the natural world, although it is used to classify fingerprints. Let me make an analogy. Suppose we remember the weights of 1000 people, then, when we meet someone, we identify them by their weight. We have introduced a totally unnecessary need for precision in measuring weights and also ambiguity because weights are not constant and many people have similar weights. A retinotopic memory is also not suitable for the detail in the natural panorama because the bee is always in motion, which is bad for collecting and comparing whole images. Changes in range, rotation or translation of the image relative to the head, or a view from a different direction, spoil the match. At any one time there is not one isolated shape in view. The idea of an eidetic image is also impossible to reconcile with the detection of a moving textured object on a textured background. Mechanisms of vision must avoid these problems.

A transatlantic revival

The long review by Wehner (1981) was in English, so it had the staying power to reach the New World, where it clearly inspired James L. Gould to experiment with bee pattern perception. Gould published an excellent book on ethology in 1982, with descriptions of his work on the dance language controversy and the sun compass of the bee, but unfortunately this was in press when Wehner's digest of postwar work appeared. Gould (1984) then published a review in the

Dahlem Conference report, with many references to bee pattern perception but no new findings, followed by a series of papers on the discrimination of coloured flower-like patterns, mirror images and inversions of the patterns. The conclusion was that the bees learned a retinotopic copy of the pattern, even if fuzzy, but in all of that work the criterion of success was the landing of the bees on the pattern, so the bees were able to detect parameters at very large angles to each other and obtain some information about the configurational layout of the patterns. Gould's student Adrian Dyer continues to use the same criterion to the present day.

Burps from an undigested topic

Despite all that, retinotopic matching became fixed into the literature on place recognition and fitted well into the intuitive idea that a small brain had vision like a camera. In the 1990s, the memory of a wasp for the nest site (Baerends 1941) and of a crab (Horridge 1966a) or a bee (Cartright and Collett 1987; Cheng et al. 1987) for the positions of surrounding landmarks was carried over to pattern discrimination. Here are four views. First, 'bees store an eidetic (i.e. photographic, or template-like) image of the pattern. This image is stored in the memory prior to landing during a fixation phase in which the bee hovers in front of the pattern' (Dafni et al. 1999). Second, 'the insect evaluates the ratio between the overlap of an actual retinal image with the stored template, and the total area of the actual retinal image' (Ronacher and Duft 1996). Third, with reference to sector patterns (Figure 4.7), '[t]he ability to distinguish between such patterns suggests that the pattern has been stored retinotopically, with the pattern only recognised when its elements fall in the same region of retina that viewed it during learning' (Collett and Zeil 1998). And again, 'the stored image and the actual image would have to be somehow superimposed. How are these images stored? Are they "real" images or parametrizations?' (Heisenberg 1995). Antagonists on one side or the other in these arguments quote any supporting statements they can find in the literature, however unsubstantiated by data.

A further muddle was introduced when Dill et al. (1993) and Dill and Heisenberg (1995) noticed that differences in the position of black accounted for discrimination by the fly *Drosophila*, and that discrimination failed if there was a shift of the pattern by 9° in the vertical direction on the screen. Recognition depended on the overlap as a fraction of the area, with no recognition of shape. The eidetic image brigade took this up as a validation of their theory, although it was exactly the same kind of evidence that had been known for 60 years (Friedlaender 1931). I told Martin Heisenberg, at a dinner in Cambridge for the Society of Experimental Biology in 1995, that the eidetic image was nonsense, but later discovered it was not entirely so. Meanwhile, unknown referees quoted this *fly* result at me and damned my papers on *bees* because I inferred parameters and feature detectors.

Fortunately, a new student refuted his professor (blessed be Würzburg for the action of one good student) and excluded the eidetic image by showing that the fly could learn to discriminate a few simple cues irrespective of the pattern, but not the overlaps and non-overlaps. The flies discriminated the height of the common centre of gravity of the black areas taken as a group, differences in total area, vertical and horizontal extent and the separation of pattern elements (Ernst and Heisenberg 1999).

A new effort to distinguish between the generalised parameters and the eidetic image began by training bees to discriminate between a triangle and a disc, either filled or in outline, in various combinations. The trained bees were tested with a variety of pairs of filled or empty triangles or discs in most of the possible combinations. The results could mostly be explained by postulating arbitrary parameters such as the triangular point at the top, or not. Unfortunately, the same results 'can also be explained by a template matching mechanism' (Ronacher and Duft 1996). Why do people do it? Or allow it to be published?

Efler and Ronacher (2000) therefore made another effort, training with pairs of black triangular shapes that differed in size or in disruption presented on a vertical surface. They tested with a variety of patterns that differed in the positions of black. They observed successful discriminations that should not be distinguished by a retinotopic memory and preferences for patterns that showed no overlap. They concluded that 'the bees must have used additional mechanisms and cues'. Yes, indeed they must have, but what were they, and why turn a blind eye to the literature?

Recently, Campan and Lehrer (2002) published a paper entitled 'Discrimination of closed shapes by two species of bee...' and certainly the bees discriminated between a square triangle, inverted triangle and square, and so on, presented fixed on a vertical surface. The bees explored the patterns closely and the criterion was landing on the reward hole, although previous work had shown that this technique yielded no conclusions. The authors suggested that the bees succeeded by scanning the patterns in flight and remembering the differences in the positions of the corners or edges (contours), not by memory of the shape. Again, this was an example of successful performance and the conclusion was an intuitive guess that did not contradict the data, but was not further tested.

I must mention at this point a strange lapse of the communal memory. After 1939 and until about 1995, the findings of Lubbock, Forel, Turner and others at the turn of the century, and also the works of von Frisch, Baumgärtner, Friedlaender and Wiechert on discrimination of vertical patterns, were almost erased from the record. Another memory lapse appears to have started with Cruse (1972), who actually says that, *in contrast with other authors*, Wehner (1968, 1969) trained with patterns presented in the vertical plane. In his long

review, even Wehner (1981:533) states '[u]ntil then [referring to his own work] patterns had always been displayed on a horizontal screen'. The discussions and reviews from 1966 to 1990 show that they really believed this.

Retrospect

The paradigm for pattern vision changed from a qualitative description of performance in the first half of the century to one based on quantitative percentages of correct responses to selected parameters in the second half. The technique changed from groups of unmarked bees to individually marked bees, from training on a choice of patterns to training on a single pattern versus a blank, and from small patterns to very large ones. The most significant innovation was probably the apparatus that forced the bees to hover with the training or test pattern at a constant size in a constant position on the eye each time they inspected it (Figures 4.4 and 4.7), but the patterns still subtended very large angles. As time went on, however, it became obvious that the different techniques made little difference to the results with large patterns, from all of which the same four or five parameters were eventually inferred.

Another fundamental problem was caused by the use of targets that were fixed relative to the point of choice of the bees during the training. This detail did not change until 1990. The performance in the discrimination always increased as the mismatch between the training and test patterns was increased. This result gave the impression that the bees could really perceive the training pattern, implying the whole pattern. The retinotopic memory was a guess that was never corroborated, but there is an interesting twist to the story. Between 1996 and 2001, the retinotopic memory was disproved by direct experimental tests in a local region of the eye (as in Figures 2.2 and 2.3), but later it was realised that very large patterns would spread into two or more local regions of the eye and be detected as separate parts like separate landmarks. For 75 years, and even to the present day (Dyer et al. 2005), major advances were blocked by allowing the bees to examine fixed targets at a very large angular sub-tense, as though the target was a panorama.

The experimenter always imposed the training and test patterns, so the bees never had an opportunity to reveal their order of preference for different parameters. Almost every researcher started with a new set of patterns but found the same two or three parameters as the others. The misinterpretation of perfectly good experimental data was repeated over and over because some or all of the parameters in parallel were ignored. For the whole century, we have a collection of papers full of good data by excellent experimentalists who somehow did not do the right experiment and did not repeat the experiments of others or put their own theories to a critical test. Following the fashion, they refrained from open criticism and simply published and taught conclusions that

differed from those of their predecessors, leaving a paper trail that no student was able to turn into a rational account. To each generation, for a whole century, the collected results on honeybee vision simply did not make sense.

Endnotes

1. This historical background might be better understood if read again after reading Chapters 9–12.