01

EARLY WORK BY THE GIANTS

Palaeolithic humans—with excellent vision and endless opportunity—must have examined honeybees busy at their work and wondered what the insects saw and what they were doing, just as somebody else, watching the humans in turn, wondered what on earth they were doing studying bees. For a social animal, it was important to know who was watching what.

The powerful obstacle to understanding what bees see—and they obviously see something—is that the human mind reads itself into the minds of others, even into bees. We call it anthropomorphism. We imagine that the bees are seeing things. We see the bee and the bees see us, which becomes obvious if we steal their honey. So, for about two millennia since Aristotle, the general opinion seems to have been that the bees see things and organise their affairs very much as we do. They see flowers; they collect honey; they fly home; they defend their store; the drones pursue the virgin queen. It is like a play based on the human world, just as Shakespeare described:

> For so work the honeybees,
> Creatures that by a rule in nature teach
> The act of order to a peopled kingdom.
> They have a king and officers of sorts,
> Where some like magistrates correct at home,
> Others like merchants venture trade abroad,
> Others like soldiers armed in their stings
> Make boot upon the summer's velvet buds,
> Which pillage, they with merry march bring home.[1]

We now know much more, but a veil will always obscure our understanding of what bees see because we are not in a position to observe it ourselves. The collapse of confidence in the reality of human perception began with René Descartes (1596–1650) and proceeded through Bishop George Berkeley (1685–1753) and the French rationalists of the eighteenth century.[2] Now it is the turn of the bees. The interest now lies in how the bees manage to do so much with a tiny brain, how humans have evolved scientific techniques to investigate them and how and what they see.

Nineteenth-century beginnings

The giants—or rather, gentlemen of leisure—on whose shoulders we stand began systematic observations and the experimental approach only in the nineteenth century. Sir John Lubbock (1834–1913), a polymath, who invented, among other things, bank holidays and the term 'Palaeolithic', published his own careful observations of the behaviour of ants, bees and wasps about 1873.[3] He found that ants detected ultraviolet (UV) light and that blue was their preferred colour. When he carried bees away from the hive and gave them honey, they rarely returned for more (they were probably not foragers). When he fed them in an upstairs room, they failed to recruit other bees (they could not remember heights above ground). His writing illustrated his difficulties because he could not refer to a body of reliable observations and there were no relevant theories.

Auguste Forel (1848–1931), a remarkable medical professor in Zürich and best known as a psychiatrist and expert on Hymenoptera, aimed to eliminate anthropomorphic ideas from the study of insect behaviour.[4] One of his targets was Felix Plateau (1841–1911), the Professor of Zoology at the University of Ghent, Belgium, who had the misfortune to be the son of a very famous mathematician. Between 1885 and 1899, Felix studied how bees found flowers and published many papers.[5] Unhappily, he repeatedly produced the wrong answers, so they caught the eye of one or two critical scientists.

Plateau tried to attract the bees with paper flowers that were carefully painted with natural colours. He also hid dahlia flowers behind paper but the bees went under the paper, so he concluded that the shape and colour did not attract them. Because the bees ignored his flowers, he concluded that bees recognised flowers by their odour, not by vision of shapes or colours. He was unwilling to concede that the bees remembered the place of the reward by use of landmarks.

On the numerous works of Plateau, Forel (1908) lamented:

> It is with reluctance that I have decided to undertake the criticism of this author, not, indeed, that it will be difficult, but because of the space which it demands, and because it is painful to me to have to bring to light the false conclusions of a colleague whose patience, work, honour and good faith I esteem.

Forel then launched without mercy into 50 pages of objections, supported by his own experiments.

Plateau worked with large artificial flowers that were scarcely distinguishable from real flowers. The bees passed them by, so he supposed that the match of the colours was unsuited for the bees. Forel repeated the experiment with crude artificial flowers, laced with honey and found that bees would not visit them unless they found the honey by chance, or had it pushed at them. They would then return repeatedly to the same artificial flower. Plateau persisted with his contention that the bees used their sense of smell, but other published work had shown that bumblebees returned to their flowers when their antennae, palps, mouth and pharynx (that is, the seat of the sense of smell) had been removed.

After 50 pages of fierce criticisms, Forel accepted the correct data but not the false conclusions:

> I must make an excuse for my long criticism and my long series of controls, as much to M. Plateau as to the reader. But it was necessary. In using the experiments of M. Plateau himself to show the errors of judgement that he draws from them, I fully render homage to his scientific honesty. And it is precisely this honesty which has allowed us to follow the author step by step, and to pick up, by the help of his faithful narration of facts, the thread of their actual connections [how the facts relate to each other] and their agreement [that they are mutually consistent]. Thanks to this, our study will not have been a sterile polemic, for it has brought us to see more and more clearly into the very question which occupies us. (Forel 1908)

Modern science has lost this art of pulling the rug from under one's opponent.

The main obstacle to this research was that the bees had already arrived at their destination, with a memory of what they expected to find, so, in any experiment, they were likely to be frustrated by any change and would either start to relearn the place of the reward or simply go away.

Forel was one of the first to use individually marked bees effectively in a variety of experiments. Confirming earlier work by Lubbock, he stressed that the bees did not follow an experienced bee, but they were attracted to a number of bees feeding and they remembered the place where they found food. To Forel, these observations showed that feeding bees made little use of their sense of smell. Forel also concluded that bees distinguished the contours of objects poorly and that they returned to any shape that offered them honey at the expected place. 'Vision of form, colour, dimension and distance…guides the bees by means of visual recollections associated to those of taste and smell' (Forel 1908).

In the nineteenth century, public criticism was more robust than we enjoy today. Serious scientists flung identifiable mud at one another's conclusions and sometimes at the experiments themselves. For example, Forel again:

> The publications which have appeared on the subject before us are very numerous, but they consist for the most part of theoretical dissertations only, of hypothesis, and, as Lubbock (Linn. Soc. Journal vol 12, Observations on bees and ants) has very well remarked, of oft-told tales of ancient experiments, borrowed, through more than a century, from one 'authority' to another, without attempt at control or checking. (Forel 1908:5)

The philosopher of scientific method, Karl Popper, would have appreciated this approach: not advancing on the shoulders of others, but shooting them down. In the end, Rabaud (1928) covered the literature in French but did not refer to Plateau's numerous works.

Professor Albrecht Bethe (1872–1954), father of Hans, the physicist, was a versatile physiologist and anatomist of the nervous system, sometimes called the 'conscience of German biological science' of the time because he brought attention to the errors of the other professors—not a bad idea, actually. For Bethe, all comparative psychology of animals was an absurdity. His paper of 1898 illustrates the conflict between the general belief in bees' cognitive powers versus the experimental evidence of their extreme stupidity. He replaced his beehive with an empty hive with an open back, so that returning bees flew out through the back and continued repeating this manoeuvre. When he moved a normal hive back by a metre, the bees stopped at the former position of the entrance as a cloud in the air, failing to recognise the hive. These observations were old hat to beekeepers, illustrating the isolation of professors from artisans.

Bethe's belief in mechanistic analysis guided him to do experimental tests. His experiments proved to him something beyond the science of the day: the bees did not locate their hive by scent and could do so after their antennae were cut off. When a hive was closed at night, and opened the next day in a new place far away, at first the released bees made short exploratory flights and returned to the hive. They remembered the new position of the entrance with great precision and appeared to be guided by something external to the hive. Similarly, when carried in a box for up to two kilometres, either they flew upwards and headed in the direction of home or they flew in a circle and returned to the box. After many such experiments, Bethe logically concluded that the bees obeyed a force, absolutely unknown to us, that carried them back to the place in space from whence they came. At that time, radioactivity, radio waves and x-rays were in the news and Bethe must have been disappointed with the hilarious reception of his hypothetical force.

Accounts of insect behaviour of the nineteenth century had pages of detail of how the flowers were arranged or how the bees appeared to do this or that, repeated with variations in other papers and whole books. We find voluminous accounts later in the works of Karl von Frisch (1886–1982) and others, but from 1920 onwards the professional journals gave only bare accounts of experiments and tables of results. Finally, the detailed measurements disappear also and we moderns are left with boring summaries of methods, results, condensed diagrams and long reference lists. Unfortunately, the loss of innocence—and incidentally, disproving the other fellow—was not replaced with a better design of experiments, greater significance of the results, more critical polemics or lucid logic in the conclusions.

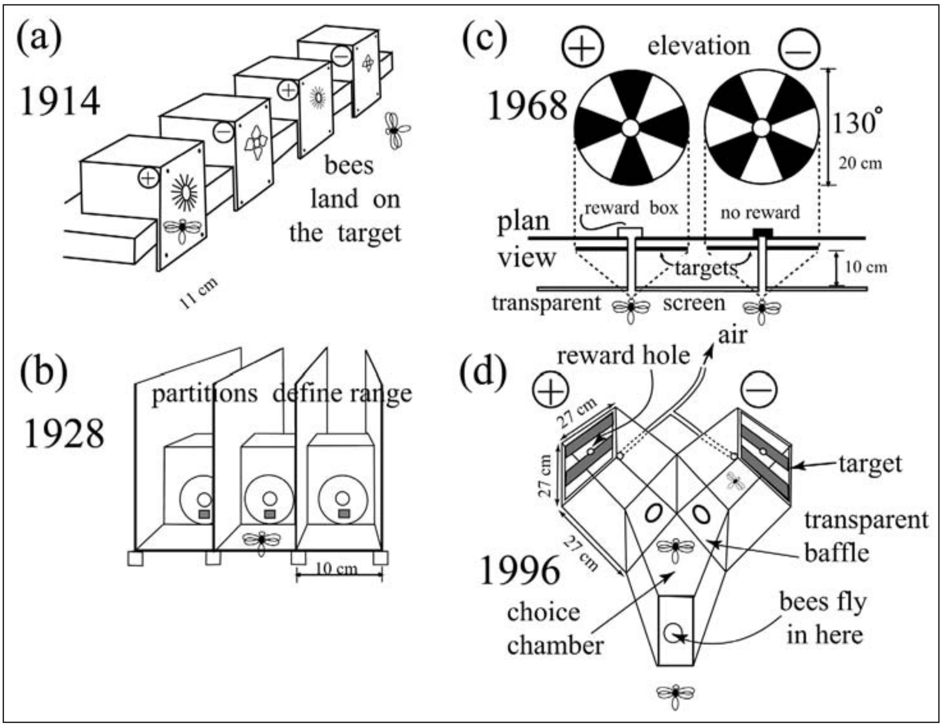
Scientists of the nineteenth century, such as Lubbock and Romanes, who understood the experimental method, struggled to separate the mechanistic analysis from the descriptions of performance. They tried to interpret their observations on the vision of honeybees, ants and wasps, but sought in vain for explanations. They had no idea of peripheral processing by connections of neurons in parallel. Anyway, the neurons were only just being discovered by new techniques. We find the same in every science, every sphere of activity. At first, understanding is slow to start because there is no map to guide us through the jungle of unrelated observations. In the case of honeybee vision, the early analysis was documented by Lubbock, Romanes, Plateau, Bethe and Forel, provided with an anatomical substrate in the histological works of Grenacher and Exner, and the arrays of neurons in parallel were described by Cajal, Sanchez and Zawarzin.

Forel ejected the nineteenth-century 'astrologers with their ancient rubbish' (von Uexkull 1908) with many trenchant comments of his own:

> As we have seen, the causes of the erroneous judgements with which Plateau has obscured the question at issue are errors of interpretation, inadmissible and continual generalisations, and the almost total omission of the psychical faculties of the insect, especially with regard to memory and association. (Forel 1908:193)

He found that the bees learned to return to the place, not to the flower, and shape was of no significance, but he could take the analysis no further. Later, in 1910, he noted that bees would return at a time of day when they were regularly given a reward, and so started the study of their time sense. The reward for the bees was marmalade at breakfast time—a novelty in Switzerland, adopted from the first English mountaineers.

Figure 1.1 Apparatus with vertical presentation for visual discrimination experiments with honeybees. a) Patterns on boxes that are shuffled in position. b) Defining a range by partitions. c) The apparatus introduced in 1967; before they enter, the bees hover with the pattern subtending an angle of about 130° directly in front of them. d) The Y-choice maze, with baffles; the bees enter at the front into a choice chamber from which they see both targets; they select one side, reach the reward hole, then when satisfied, exit by the way they came; the targets and the reward change sides every five minutes.



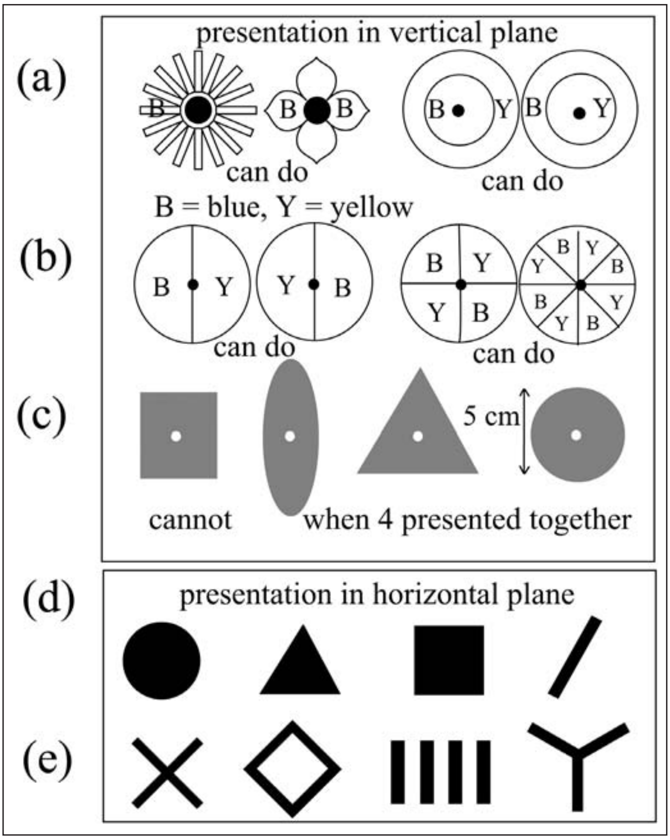
Sources: (a) after von Frisch (1914); (b) after Baumgärtner (1928); (c) after Wehner (1981).

The early twentieth century

In 1914, when von Frisch published his results with trained bees, he had been working at his family's country house in the Austrian Alps on the colour vision of freshwater fish, but he turned to bees to give a demonstration of learning when fish were not available.[6] He used Sigmund Freud's principle of association by simultaneous presentation. On the balcony of his alpine summer house, von Frisch copied from a remarkable African-American naturalist Charles Henry Turner (1867–1923) the method of putting a reward in one of several small cubical boxes, with a different pattern on the vertical front of each box (Figure 1.1a). Access to the inside was through a hole in the middle of the pattern (Turner 1911). von Frisch put a reward of odourless sugar in the box that displayed the pattern to be learned and nothing in the other boxes. The positions of the boxes were shuffled in a row all facing the same way, so that the bees could not learn where to go, but were obliged to look at the patterns to find the reward. Without realising it, von Frisch (and all others after him who interchanged the targets) trained the bees to ignore the landmarks that indicated the exact place of the box. This was an important ingredient in the experimental design because it made possible the acceptance of unfamiliar patterns that displayed the same combination of cues.

The criterion of success was the bee landing on the correct reward hole, and therefore the angular sub-tense of the target was not known at the moment of the bee's decision, but could be very large. As later demonstrated by Baumgärtner (1928) and Friedlaender (1931), the bees took special notice of the region immediately below and around the reward hole.

Figure 1.2 Results of early experiments. The pairs of flower-like patterns in (a) and (b) were discriminated from each other in the vertical plane, but those in (c) were not when presented together. The patterns in (d) laid out flat were not discriminated, similarly those in (e), but those in (d) were discriminated from those in (e).



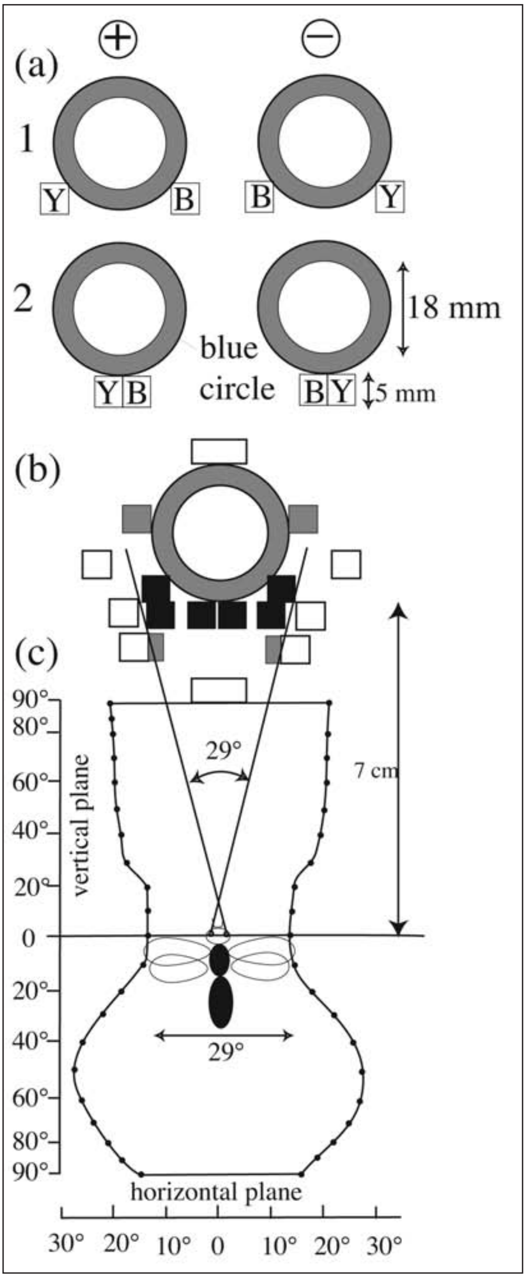
Sources: (a–c) after von Frisch (1914); (d–e) after von Frisch (1965).

In the first half of the twentieth century, bees were trained to discriminate between two or more patterns. von Frisch found that bees easily learned the difference between a flower shape with many small petals and one of the same size and colour with a few large petals (Figure 1.2a). Also, bees easily discriminate between pairs of flower-like shapes in which an area of blue and one of yellow have different positions in the two training patterns, even a left/right reversal (Figure 1.2b). He demonstrated that bees distinguished yellow and blue from all shades of grey. He was interested mainly in the bees' abilities and he had no particular theory in mind to guide his experiments.

von Frisch proposed that bees were able to distinguish flower-like patterns because their vision was adapted to their normal repertoire. The idea of pattern processing being adapted to the normal function was not examined further until the 1990s. von Frisch's bees, however, could not learn to discriminate between a blue square, triangle, disc and a diamond shape (Figure 1.2c) although trained for five days. This failure would have caused confusion in the literature but for some reason it was almost ignored for 90 years. Much later, in the decade between 1995 and 2005, it was discovered that bees learned quite quickly to discriminate between pairs of these shapes. Probably von Frisch failed with four shapes because he displayed too many in one task, but that excuse needs further testing.

von Frisch's students and younger colleagues found that bees discriminated between pairs of many varied patterns, but there were other pairs they confused for no apparent reason. His student Baumgärtner (1928) found that bees could distinguish between flowers (taken in pairs) with three, four, five or six petals, if one but not the other had a petal immediately below the reward hole. He was interested primarily in how well bees detected the place of a coloured patch relative to the reward hole, and in the angular resolution in behavioural tests compared with the angles between the receptor axes. Bees could distinguish between a blue and a yellow 20mm by 20mm square in bright light if they subtended at least a minimum of 3^o at the eye—a result that was ignored for 70 years. Two 5mm by 5mm squares of different colours could be discriminated from the same squares that were exchanged in position only if they were located immediately below the reward hole. This was the region that would be visible to both eyes and outside this area this particular task was impossible (Figure 1.3). In 1999, I showed that the discrimination of the exchange of positions of two coloured spots in the horizontal direction was possible only when there was contrast with the green receptors, which was essential to stabilise the position of the eye in the horizontal direction.

Figure 1.3 Discrimination between small yellow (Y) and blue (B) squares, with vertical presentation and landing on the reward hole as the criterion of success. a) Two examples of the targets. b) The region around the lower lip of the reward hole where discrimination of the colours is successful (black squares) and unsuccessful (white squares). c) The overlap between the two eyes in angular coordinates.



Sources: (b) after Baumgärtner (1928); (c) after Seidl and Kaiser (1981).

Mathilde Hertz (1891–1975), daughter of the physicist Heinrich Hertz and acquainted with many German scientists, studied bee vision from 1925 to 1936 at the Institut für Bienenkunde in Berlin (where von Frisch worked). She caused more puzzled brows among reviewers and students than any other bee researcher in the twentieth century. Her method was to lie a number of patterns on a white table and place a reward of sugar solution in a glass dish next to the rewarded pattern. She stressed that the bees could use different parts of their eyes to discriminate correctly. The patterns were shuffled in position at intervals to make the bees look for the rewarded one. The bees were therefore trained to ignore the exact place. On the flat table, with shuffled target positions, the bees did not discriminate edge orientations or relative locations. Later, we found that only patterns that were salient for the bees would be learned in these conditions. Examples are areas of spots, coloured patches, radial patterns, concentric circles and patterns rich in black/white edges (Chapter 9).

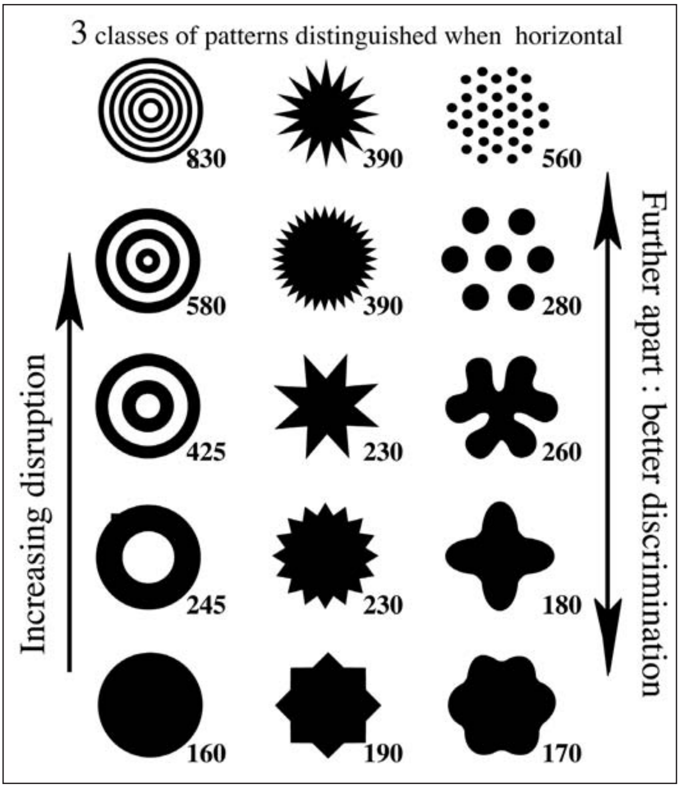
Knowledge about any visual system was in a sorry state at the time. Hertz used a great variety of training and test patterns, following any idea that the results suggested and, from 1926 to 1933, discovered many interesting details, most of which have been neglected for three reasons. First, she wrote in an obscure style that was difficult to translate. Second, the bees did not correlate edge orientations with the directions of their sun compass as they flew in all directions over them, although Wiechert (1938) later showed that bees used edge orientation on patterns laid flat when restricted in their direction of approach. Third, having no general paradigm outlining how insect vision operated, Hertz interpreted everything in terms of the Gestalt theory[7] for human vision, as in Wertheimer (1923), which was briefly expressed as:

> There are wholes, the behaviour of which is not determined by that of their individual elements, but where the part-processes are themselves determined by the intrinsic nature of the whole. It was the hope of Gestalt theory to determine the nature of such wholes. (Wertheimer 1924)

As will be seen, the idea of 'global' vision had great influence on later research on bees.

On the one hand, Hertz analysed patterns into low-level parameters, such as area, length of edge and circular versus radial contours, which looked as though they were fundamental—much of which was later verified. On the other hand, patterns were classified by arbitrary global characters such as symmetry, disruption, isotropy, smoothness, texture, variability of patch size and separation into parts. There was, however, no demonstration that these categories really had any meaning for bees.

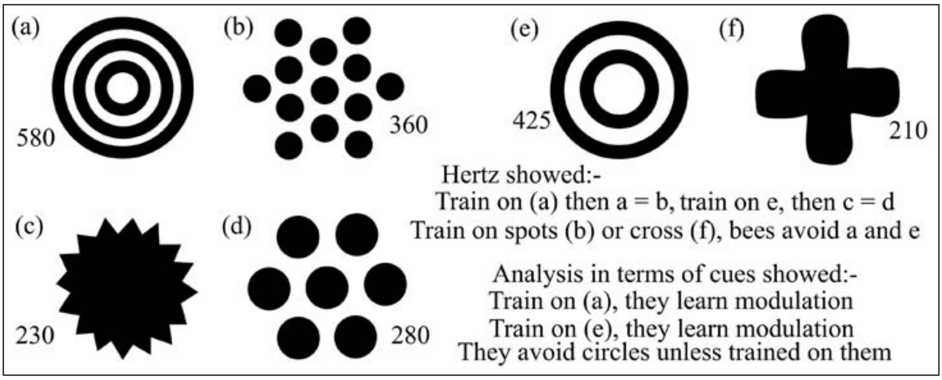
Figure 1.4 The basic separation of figural intensity (disruption) in columns and figural quality (shape) along rows, when patterns are laid flat. Bees easily discriminate the patterns on the top row from each other, and with greater difficulty within each row going downwards. The further the patterns are apart within each column, the better the bees discriminate them. The numbers indicate the relative lengths of edge.



Source: After Hertz (1933).

Although the language and terminology were frequently obscure, the actual data were not so bad. Hertz discovered that the bees discriminated area or size and total length of edge (Figure 1.4). The last is sometimes called the disruption of the pattern and has been mistakenly identified with spatial frequency. The bees detected radial symmetry about a centre and some major types of pattern such as blobs, groups of spots, gratings of parallel bars, concentric circles and radial patterns of bars. In the first 60 years of experiments, only one other parameter was discovered: the orientation of edges (Turner 1911; Wiechert 1938).

Figure 1.5 An example from Hertz (1933). Bees trained on (a) accepted (b) equally well. Bees trained on (e) accepted (c) and (d) equally well. Bees trained on (d) or (f) avoided (a) and (e). These results were a puzzle until it was realised that the bees learned the modulation and avoided rings and crosses unless trained on them.

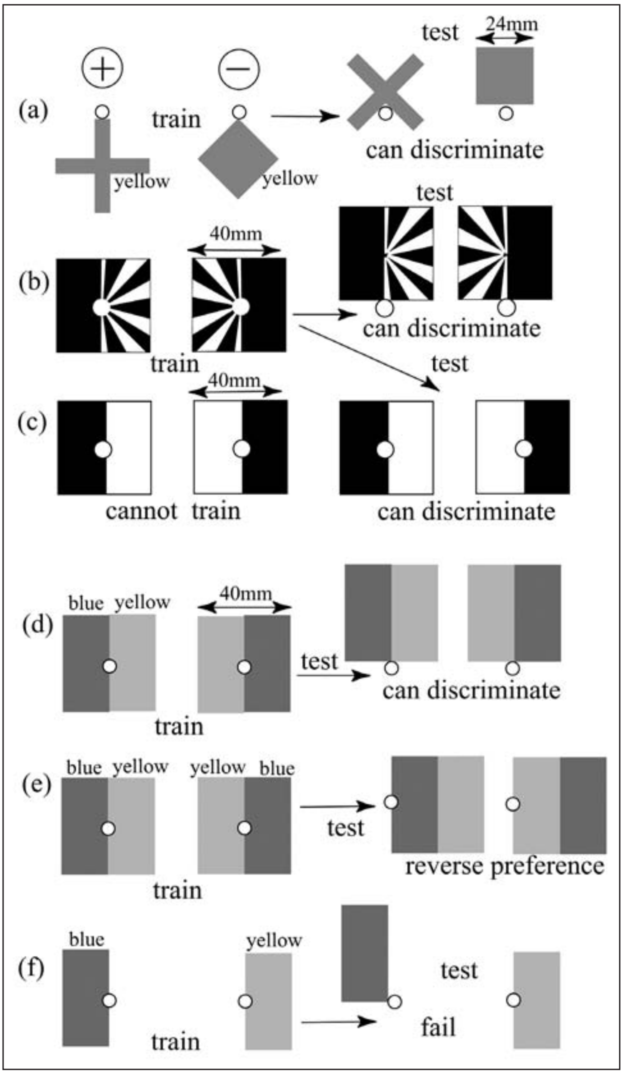


Gertrud Zerrahn (1933), working in Heidelberg but obviously in touch with the contemporary work in Berlin and Münich, also presented flat patterns on a white table. Although the patterns were different, Zerrahn's conclusions duplicated some of Hertz's work, and Zerrahn also showed that the preferences of untrained bees for patterns of various types mirrored their ability to learn to discriminate them.

A student of Professor Otto Koehler in Königsberg, Marianne Friedlaender (1931) used the same type of reward boxes as von Frisch. Bees were trained to discriminate between a rewarded yellow square cross (with bars 40mm by 8mm) and a square (24mm by 24mm) of the same colour and area, both on a white background (Figure 1.6a). In a significant advance, the trained bees were given several tests. Both the cross and the square were accepted as the original when turned through 45°. Movement of either shape within the target had little effect on the discrimination. The radial pattern of the square cross had salience for the bees because they detected it even when it was moved a short distance or rotated. It was 60 years before the next steps were taken (Chapter 9).

Friedlaender found that bees could not discriminate between a target with a rectangle of grey on the left of the reward hole and one with the rectangle on the right (Figure 1.6c). When the bees had been trained with radial spokes adjacent to the rectangles, however, they could do this task and they retained the discrimination of the locations without the spokes (Figure 1.6b). Moreover, patterns that included radial spokes could be moved up or down on the targets without spoiling the discriminations. Her explanation was that the position of the centre of symmetry of the spokes provided a salient reference point. The bees in flight scanned continually in the horizontal plane and they failed to remember the position of an image that was not stabilised on the retina.

Figure 1.6 Early analysis of the effect of a change of location. Each new group of bees was trained with the pairs of targets on the left and tested with the pairs on the right. The targets were fixed in position and the criterion of success was landing on the reward hole, so the patterns were huge at the moment of choice. a) The cross and square are discriminated although they are changed in orientation and moved relative to the reward hole. b) Radial rays stabilise the eye and the discrimination persists although the patterns are moved relative to the reward hole. c) These patterns were not discriminated. d) A blue panel on the left and a yellow one on the right, with green contrast where they meet, are discriminated from the mirror image. In tests with the panels moved up, discrimination persists. e) Preference is reversed when the panels are moved to the right. The cue is the colour adjacent to the reward hole. f) Single coloured panels on opposite sides of the reward hole are discriminated, but not in tests with the reward panel moved up.



Source: Redrawn from Friedlaender (1931).

Next, bees were trained to discriminate a pattern with a blue patch on the left of the reward hole and a yellow on the right versus another pattern with the colours reversed (Figure 1.6). The bees failed in tests when the position of the reward hole was shifted or one of the patches was omitted. When the bees were trained with a yellow patch on the left of the reward hole versus a similar patch on the right of it, moving a patch in the horizontal direction relative to the reward hole in tests had little effect, but moving a patch in the vertical direction spoiled the discrimination (Figure 1.6c). These important clues to the bee's spatial world were forgotten for 70 years (Chapter 9).

Elsbeth Wiechert (1938), another student of Koehler, showed that relative positions of two rectangles of different colour were discriminated when displayed in the horizontal plane as well as in the vertical plane, if natural obstacles restricted the direction of approach of the bees.

Conclusions by mid-twentieth century

By 1950, the training patterns had been selected at the whim of each experimenter and there was still no general idea of bees' visual mechanisms or how to design useful experiments. With the aid of hindsight, we can draw out a few useful generalisations that have been clarified since that time.

One parameter that the bees detected was the disruption of the pattern or the total length of edge in it. In the oft-copied Figure (1.2d) from the work of Hertz (1929–31), bees could distinguish between any of the figures in the top row only with difficulty, but all figures in the top row were easily distinguished from those in the lower row. The explanation was that the bees learned the modulation of illumination of the receptors as the eye moved across the figure. In fact, this result does not apply when the eye is stabilised on very large targets (as illustrated in Chapters 4 and 9).

It was never asked what was the area in which the length of edge was measured. The training patterns were always isolated simple shapes, so it seems to have been believed that the bees first identified the rewarded shape and then measured its outline.

A second generalisation, also from Hertz, was the easy discrimination of radial patterns of edges and avoidance of circular patterns. Bees trained to go to a group of spots would not visit a pattern of concentric circles, but those trained to go to the circles would visit the spots (Figure 1.5). In addition, Friedlaender found that the centre of a square cross would act as a reference point (Figure 1.6a). Radial bars enabled the bees to discriminate a shift in the position of a black square (Figures 1.6b and 1.6c). Radial patterns of edges or a dark spot on a light background were salient to the bee's eye. Together with the spontaneous preference and ease of learning of radial patterns, the salience suggested that the bees' visual processing was adapted to flower-like forms, as von Frisch (1914) had suggested. The mechanism, however, remained a mystery.

Third, size was discriminated, so, when working with other parameters, patterns must be of similar size. Baumgärtner, with vertical presentation, had shown that if a coloured patch was to be discriminated, it must subtend a certain solid angle at the eye so that many facets were stimulated.

Fourth, bees discriminated easily whether a black spot was above or below the reward hole. Several authors had shown that bees could learn whether a yellow patch was to the right or to the left of an adjacent blue patch when both were close to the reward hole. The reward hole acted as a landmark. No-one, however, commented that when the reward box with the training pattern on it was regularly moved to make the bees search for the rewarded pattern, the bees were still able to discriminate the positions or relative positions within the training patterns. We now know that shuffling the positions of the reward boxes during the training causes the trained bees to ignore the local landmarks. They still used more distant landmarks and learned the range of relative positions of the parameters in the vertical direction at the places where they were displayed during the training.

By mid-twentieth century, it was well known that bees knew the approximate place to come for a reward by using landmarks at different distances and directions, so it was clear that they also learned the positions of areas of black or colour relative to a point of reference.

As part of the wider field of experimental psychology, it was thought at the time to be useful to plot the stimulus/response as a function of a variable in the tests, or a curve that showed the progress of learning. The percentage of correct responses, however, depends on the training conditions and duration. For the bee's visual system, many such empirical relations were published, but they were almost useless for the analysis of the visual system because there was only one experimental treatment and no tests of what the trained bees really detected.

Hiatus in Germany

All this early twentieth-century research on bee vision was done in Germany. Almost all the scientists were Jewish or had Jewish relatives. After 1938, research under von Frisch continued on navigation, route finding and colour and odour discrimination, but the work on pattern vision ceased until revived in the 1960s. Wolf and Zerrahn emigrated after 1933 and joined Professor Selig Hecht at Columbia, New York, from where they published many empirical relations about the vision of the bee and other animals. Again, they were hampered by lack of a sufficient body of bee neuro-ethology to interpret the measurements.

Others, such as Harald Esch and Rudolf Jander, later moved to the United States—not because of persecution by the Nazi regime, but because they were persecuted by German professors.

As a Jewish scientist in Berlin, Hertz was ruined after 1933, and from 1936, she and her mother lived in Cambridge, England. She was befriended by Bill Thorpe, a Cambridge don (like Lorenz and Tinbergen, an intuitionist). In Thorpe's (1956) otherwise excellent and comprehensive book on insect behaviour, he scarcely mentioned the discrimination of patterns by trained bees, as though he could make no sense of what was available to him. His lectures in 1949 to a Cambridge zoology class revealed to me no insights into the mechanisms or methods of analysis of insect vision.

There was an enormous number of descriptions of insect taxes, kineses and tropisms in response to light, but almost all the experiments reported in the influential textbooks by Willi von Buddenbroch (1937, 1952) and the handy little book by Carthy (1958)—which was almost all that was available in English—were unrelated to each other or to a comprehensive theme. The details of the neurons of insect optic lobes, so beautifully described by Cajal and Sanchez (1915) or Zawarzin (1913), were ignored as possible substrates of visual behaviour. The growing knowledge of responses of neurons and the physiology of synapses was also ignored.

To each generation, honeybee vision simply did not make sense. The reason for the failures and the confusion that followed, we now see with the benefit of hindsight, was due only partly to the lack of abundant data and theories to guide new experiments. In particular, it was never asked whether bee learning was like wax—which could be moulded to any external shape or pattern—or like a set of innate boxes that could be ticked when a limited variety of parameters appeared. Consequently, the right experiments were delayed. There was also the dead weight of the anthropomorphic belief that bees really saw the things they looked at. There was no theory of how or what insects really saw. The main problem, however, was the criterion of success (landing on the correct pattern or reward hole) in the training of the bees, so the experimenter could not control or infer what parameters the bees were using.

The primacy of odour

Worker bees are helped out of their sealed cells by nurse bees and soon take up a task within the hive, feeding the grubs, filling storage cells with pollen or nectar, fanning to ventilate, cleaning out old cells or tending the queen. All this is done in the darkness of the hive, so in the busy life of the young bee every action is governed by the sense of smell. The bee's antennae have thousands of odour receptors and the main association areas of the brain serve olfaction. Bees also detect the direction of gravity. The whole world of the young bee is one of odour, up/down, touch and taste.

After two or three weeks of working in the hive, the young bees are like those unenlightened human beings living in a dark cave, as described by Plato in Book 7 of *The Republic*.

The mouth of the cave is open, but the unenlightened slaves see only shadows of themselves, like shadow puppets on the opposite wall, never their true nature. Similarly, the young bee has sensed the real world of flowers, pollen, foliage and the passage of the days only by odours. Reality for young bees is nothing but sequences, mixtures and memories of odours. If they communicate with each other, they must do so in a language of odour or touch.

One day, when about a month old, a bee finds itself with a load of rubbish that must be thrown outside the hive and there is no experienced bee to take it, so it approaches the entrance. In his book, Plato suggests that in the first stage of liberation, the bright light is distressing and nothing is understood from the unfamiliar visual sensations. Gradually, the young bee will use the familiar odours to educate the visual system and soon will find that it can detect another bee or a flower at a distance without relying on the odour. For a time, as Plato describes, the shadows (odours) appear more real than the visual world. At first, the bee detects best the motions of contrasts, then the motions and ranges of the objects themselves, until finally the bee gazes on the blue sky and the sun in the proper place for that time of day and learns that the sun and the sky move in a regular way from horizon to horizon.

In Plato's words, the enlightened bee does not return willingly to the drudgery within the hive but would rather explore the outside world and return to the hive loaded with food for the unenlightened ones left behind. So, an education for new roles is required. As Plato says, to function in the upper world, the upwardly mobile 'must use the motion of objects and astronomy':

> The spangled heavens must be used as a pattern, with a view to higher knowledge…The sun will be seen to be the universal author of all things beautiful and right, parent of light in the visible world, and this is the power upon which the eyes of the rational are fixed.

Two thousand years later, we have to confess that we know little more than Plato about the process of the transition of the young bee from the dark world of odours to the bright world of vision. It seems obvious, however, that the new visual memories must be correlated at some point with the existing odour memories. The mushroom bodies in the brain, which are thought to be the centres of memory, certainly take the majority of their inputs from the odour pathways, with smaller tracts from the optic lobes (Figure 6.4). It is likely that the higher-order optic neurons establish connections with the existing higherlevel odour centres before the new visual associations can be remembered. Similarly, the existing gravity detectors of the vertical, which are so essential for the ordered construction and business of the hive in the dark, are somehow associated with the new uses of vision to detect the orientation of an edge and the pattern of the sky and horizon in relation to the sun.

Endnotes

1. Quote from *King Henry V*, Act 1, Scene 2, speech by Canterbury on the strategy to defeat France.
2. Among many others, early ideas about human vision are summarised by Richard Gregory (1981).
3. Lubbock wrote *Prehistoric Times* (1865) and *The Origin of Civilisation and the Primitive Condition of Man* (1871), as well as many books and papers on natural history.
4. The points made by Forel foreshadow many of those in the rest of this book.
5. Plateau did some good work on the physiology and anatomy of insects.
6. This story is recounted in his autobiography.
7. Gestalt theory tried to solve the problem of the apparent wholeness of sensations by proposing that there was a corresponding representation in the brain. See Gregory (1981:Ch. 12) and a full account in Koffka (1935).