CHAPTER SUMMARY

1. Early work by the giants

In the nineteenth century, progress on what insects saw was slow and contentious, with fierce argument about whether bees found places by odour or by sight and how they navigated to places, identified them and returned home. The pioneering experiments were done in Germany from 1896 to 1940. None of this research has been previously summarised in English for the scientifically interested layperson. The chapter concludes with a discussion of the young bee's transfer from using odours in the dark hive to vision outside as she matures.

2. Theories of scientific progress: help or hindrance?

Science is validated by logic, experimental observations and commonsense, starring Aristotle, Francis Bacon, J. S. Mill, T. S. Kuhn and Karl Popper, with discussions of empirical laws, mechanistic analysis and computer modelling. The visual system presents us with a special problem because there are arrays of processing channels in parallel, and many layers of these arrays, but no identifiable end point in the brain. There are also multiple causes for every observed effect. One reason why bee vision was only slowly understood was the lack of methods of analysis of a multidimensional system without an existing map.

3. Research techniques and ideas, 1950 on

New postwar electronic techniques for the study of the nervous system gave a fresh lease on life to a topic ideal for the age of laboratory experimentation. Persistent research in a small number of labs produced detailed information about the functioning of the retina and optic lobe neurons. The modelling of motion perception of the fly in Tübingen, Germany, was upset by the discovery of rapid eye movements that controlled piloting—much as they do in humans.

4. Perception of pattern, from 1950 on

Returning to his job after the defeat of the Nazis, Karl von Frisch appointed a youthful group of researchers in Münich, and when he retired, they began afresh in Frankfurt, with new techniques for the behavioural study of pattern vision in trained bees. They worked with huge patterns and obtained entirely new results that dominated the topic but could not be integrated into the rest of the literature. This led to much argument about images in the brain of the bee and a hiatus until new work started again in 1987.

5. The retina, sensitivity and resolution

An account of the structure and function of the retina of the bee is filled out with some material from the more detailed work on the fly. The eye catches light and processes the image, the signals are transmitted to the neurons below and vision is limited by the noise in the signals. There are simplifications for the non-specialised reader, but it is not a primary school account.

6. Processing and colour vision

Tedious probing with sophisticated equipment has revealed how nerve cells respond and collaborate. Based on the recent electrophysiology of identified single neurons with microelectrodes, this chapter continues the description of how the visual image is processed, transformed and summarised as it passes from the retina to the memory and initiates behavioural responses. The insect visual system is one of the best-known parts of the central nervous system in the animal kingdom. There is no evidence of reassembly of patterns in the brain. This technical account is essential for understanding the machinery of vision.

7. Piloting: the visual control of flight

This chapter is a description of how insects fly by visual control—a topic that was expanded by work in Canberra in 1987. There are accounts of keeping a straight course, avoiding collision, how to turn without getting in a knot, how to counteract sideswipes from gusts of wind, how to measure altitude, range, speed over the ground and distance travelled, and how to make use of the parallax caused by one's own movements. This work has led to significant practical applications for self-guided flying vehicles.

8. The route to the goal, and back again

The work of Karl von Frisch, from 1914 until the 1960s, slowly brought together the previously unimagined navigation and dances of the honeybee. The use of the sun as a compass in the sky—already known from detailed work on ants—required an internal clock, also known previously. Aristotle knew about the bees' dance, but its function in directing foragers was discovered in two stages by von Frisch in the 1920s and 1940s. The pattern of polarisation of blue in the sky also acted as a compass. Bees can learn to negotiate a maze, which involves the use of a sequence that is stored in memory—like the recognition of landmarks along a track.

9. Feature detectors and cues

New people, new apparatus, a new research theme, new ideas and generous funding spawned a hive of activity in Canberra from the mid-1980s, when the world's best bee trainer, Miriam Lehrer, arrived as a seasonal visitor. We brought Zhang Shaowu from Academia Sinica and started on pattern perception. First, the orientation cue was isolated. Later, the feature detectors for edge orientation were shown to act independently and were only 3 degrees long. The cues from modulation, radial and tangential edges, bilateral symmetry, position of the centre of black and position of hubs of radial and circular symmetry were also demonstrated and placed in an order of preference by the bees.

10. Recognition of the goal

To a bee, a panorama or a very large target displays parameters that overlap several local eye regions, so several landmark labels are learned and recognition of the place is relatively certain. The simultaneous responses of numerous small feature detectors form a cue, of which there is one of each kind in each local region of the eye. A coincidence of cues in a local region forms a label that identifies a landmark. The label is the unit of memory like a signpost on a route. The local regions are distributed around the eye, so that a place is recognised by the expected coincidence of a few labels at large angles around the head. As the bee nears the destination, she heads in the direction that changes these angles towards their expected values. This task makes good use of the 300^{o} coverage of the compound eye.

11. Do bees see shapes?

From the beginning there has been contention about this question. Some think that bees see separate objects distributed in the panorama, with corresponding spatial representations in memory in the brain. They propose that bees recognise abstract properties such as triangularity, squareness or shape in general. These ideas originated from earlier theories of human vision. Careful testing of trained bees reveals no evidence for spatial representation, object or shape recognition, but only the recognition of coincidences of the cues already described. This idea is supported by the neuron responses, by efforts to make artificial vision and by numerous recent training and tests of bees.

12. Generalisation and cognitive abilities in bee vision

There has also been disagreement for a century as to whether bees can learn one pattern and then accept other patterns because they have a concept of a general likeness or difference, called generalisation. However, they also accept many quite different patterns. The explanation is that when trained on targets that are moved about to make the bees look, the bees learn insufficient cues to enable them to distinguish all other patterns. When they generalise, they are simply confused. There have been many claims that bees detect generic categories such as symmetry, topology and categories such as faces, but when the trained bees are carefully tested, it turns out that they have learned the particular cues required for the single task at hand. Trained bees accept an unfamiliar pattern if it displays the cues that they learned to expect—and no extra ones. The idea that they generalise in a cognitive way is founded on poor data, an inadequate variety of tests, failure to consider the cues and intuitive use of terminology borrowed from the cognitive sciences.