

02

THEORIES OF SCIENTIFIC PROGRESS: HELP OR HINDRANCE?

We expect to have a problem in understanding what honeybees see because they have a tiny brain combined with a very wide view of the world: *multum in parvo*. We must draw conclusions from the way they behave. We reasonably expect that they detect only relatively simple parts of the scene, but at first we are unable to imagine how they see anything in a moving panorama. To make progress, we have to devise ways of asking questions of the bees so that logical conclusions can be made from the way they react. This chapter is about making firm conclusions.

Unlike most experimental science, there is no need for equipment, purified chemicals or electricity. Anyone with some patterns and sugar solution could have inferred most of what we know about bee vision at any time in the past centuries. That did not happen. Progress was excruciatingly slow, although the bees were eager for lessons once they learnt that sugar was available at school. Why the delay?

At each step, progress was limited by error and the slow development of ideas, so it took a long time to formulate each next appropriate question. At first, the questions put to the bees never produced sensible answers. The bees were observed, their responses to experimental change were a mystery and the proposed explanation was just a guess. There were many unsuspected factors and guesses that were not tested became facts. The errors blocked the imagination of those who followed. As a result of this patchy acceptance of a mixed bag of insight and error, there was no acceptable answer to the interesting question ‘What does this insect actually detect?’ The question was not asked.

Let us examine the development of scientific theories to see whether the ways of thinking about explanations—what we call the philosophy of science—have been of any help.

Early theories of scientific advance

There is a long and fascinating road that winds through history and explores how the natural world was elucidated. The problem faced by the great innovators of the philosophy of science in the past 3000 years was to find a general method that would apply to any problem, although as things turned out, this was a bad place to start. The process is not direct because the best questions to ask become obvious only when the answers are anticipated. The process starts with collecting facts of interest long before any moment of truth arrives. We have to observe and think at the same time, followed by a dissection of the subject into components, an effort at analysis to see what causes what, and then we must assemble the tentative mechanisms into a coherent story.

Aristotle,¹ an ancient Greek philosopher, taught that we should accumulate facts and look for generalisations about them. In coming to his own conclusions, however, he was usually short of facts and relied on the primitive assumptions of the day. As a result, he was knowledgeable but often mistaken. He was unwilling to abandon his general principles, although, on the topic of the reproduction of bees, he admitted that there were insufficient facts to warrant any conclusion at all.

Although real experiments had been done for millennia—for example, helpful and fatal trials with medicinal herbs—the idea of the experimental approach and the concept of an *experimentum crucis* was first systematised by Francis Bacon² at the end of the sixteenth century. The idea was to invent a crucial experiment that allowed the observer to decide between two alternatives. We now know that it is a rare piece of luck to find such an experiment that is conclusive. It can be wrongly conceived, so that the result cannot be interpreted, or there might be more than one explanation, or new facts emerge later. Bacon stressed that the gathering of facts must be steady and progressive, with conclusions at each stage, and this advice was followed by great scientists such as Charles Darwin, but Bacon had no idea how a scientific concept or theory was formed in the first place. He advised us to be suspicious of first principles (meaning Aristotle's principles), but we still find them getting in the way today, such as the belief that there is something special about symmetry or the idea that insects see things, even if blurred.

Bacon was aware of the danger of proposing a theory and then inventing experiments to prove it, but he could not stop the practice. You have an idea out of the blue, then enthusiastically rush around proving it. Sadly, it was equally useless to rely on Bacon's pet method: induction. This is the formation of a general principle that is consistent with a number of separate facts. Induction depends on regular occurrences and the uniformity of natural events. It is, however, boring to collect facts without knowing why. The opposite of induction is deduction, in which the observations are logically deduced from data and general principles.

Alone, or even together, deduction and induction are not strong enough, or even sufficient, to generate useful experiments. The two missing ingredients are imagination and a caution about multiple causes. Like Aristotle, Bacon argued as though a phenomenon could have only one cause. The visual system—with numerous receptors in parallel, multiple pathways to the brain and numerous superimposed arrays of nerve cells, always changing with time—would never be understood if single effects always had single causes.

The classical and medieval minds tended to work in terms of rather rigid categories with sharp boundaries. Something was either this or that. They respected categories as though they had been created with the universe and had an independent existence. Classifications also had a value of their own. The categories ruled the discussion without being questioned themselves, directed the next venture and diverted attention away from unexpected but significant novelties. Observations were suspect, as Galileo was firmly told by the Church. We still see the pleasure enjoyed in an armchair argument about concepts and the definitions of terms.

More recently, we have been urged to think not only of alternative causes, but of all the intermediate stages between them. Categories also become blurred. I prefer to assume that the visual system operates with parallel pathways, each with a definite function. As a first approximation, I assume that each type of component and pathway can be analysed separately with yes/no answers if the appropriate tests can be devised. So far, it has worked.

In the late seventeenth century, John Locke (1632–1704) traced the origins of knowledge, while David Hume (1711–76) analysed ideas about causation in the mid-eighteenth century. Bishop Berkeley doubted the evidence of the senses but still relied on learning and commonsense. These English philosophers were more empirical than their continental colleagues and, in the early nineteenth century, the differences were sharply intensified in the battle between John Stuart Mill (1806–73) and Sir William Hamilton (1788–1856), who in general accepted as valid anything that was intuitively obvious, especially the rules of reasoning and the evidence of the senses. Hamilton imported these ideas from Germany. For centuries, induction had also been relied on, with little criticism. As already mentioned, induction is the method of inferring the general rule from the particular instances. The more general statement that applies to many situations is derived from a number of less general statements that apply to only some cases. Induction is based on two principles: that nothing can happen without a cause, and that the same combination of causes is always followed by the same effect.

The methods of scientific induction—noted mainly because they were effective in the industries developing in the foundries, potteries and factories, and were indispensable for progress in physics and chemistry—were summarised by William Whewell (1794–1866) in an influential book *The Philosophy of the*

Inductive Sciences (1840).³ With one foot still in the past, Whewell accepted the ancient view that the rules of thought, including the intuitive recognition of categories in visual perception, were built innately into the human mind. They were not to be questioned. This was in line with German philosophers, of whom Immanuel Kant (1724–1804) was the most influential in the early nineteenth century. Kant assumed that reason was not subject to space or time. Basically, a reasonable cause that was proposed on intuitive grounds was accepted until further observations made it untenable.

In the early nineteenth century, accompanying the further development of mathematics and the exact sciences, empirical philosophy was strongly promoted by an intellectual prodigy, John Stuart Mill. Mill put the arguments of the English empiricists of the previous century—Berkeley, Hume and Locke—into a systematic framework. He replaced intuition with learning from experience, particularly by relying on numerous observations and deducing their logical consequences. A lack of independent checks infuriated Mill, who, in 1865, wrote a long condemnation of Kant’s support for intuition. To Mill, the combination of induction and intuition was the way to errors of thought, and the German philosophers were a threat to right thinking.

Apart from governing India from a distance, writing a stream of articles in favour of freeing slaves, the liberation of women and guiding the social conscience, Mill’s contributions were crucial for the development of experimental science, especially biology.⁴ In his book the *System of Logic* (1843), Mill laid down the rules for the inference of causes from effects. I recommend them as a guide to any budding investigator. Mill distinguished between necessary causes, sufficient causes and possible causes. He accepted multiple causes operating in parallel and repeated Newton’s advice that ‘no more causes of natural things are to be admitted than such as are both true and sufficient to explain the phenomena’—a principle that is usually called ‘Occam’s razor’. A necessary cause is one that is logically required. A sufficient cause is one that is adequate but there might be more to be said.

Second, Mill did not accept anything just because it appeared to be intuitively so or was a reasonable guess. Even Mill’s most abstract works were aimed against the German a priori school, called ‘Intuitionism’ and best known in the works of Kant. Mill denied any ability or performance that was reckoned to be ‘innate’ and instead derived all human knowledge from human experience: ‘The notion that truths external to the mind may be known by intuition or consciousness, independently of observation or experience, is, I am persuaded in these times, the great intellectual support of false doctrines and bad institutions’ (Mill 1843). To him, all causes, inferences, conclusions or categories were obtained by making bare observations, noticing regularities and then deducing the causes. A century before Jean Piaget, therefore, the development of the human mind was an exercise in self-education by trial and error.

Mill was well known and influential among the scientific community in London, where he became Secretary of the India Office and later MP for Westminster. Mill, once said to be the cleverest man in the world, also demonstrated that there was more to science than observations, empirical laws and rules for scientific investigations. As a result of his efforts, the teaching of philosophy in England was deflected from the path led in Europe by Kant and saved England from the Gestalt and holistic psychologists of Vienna and Zürich.

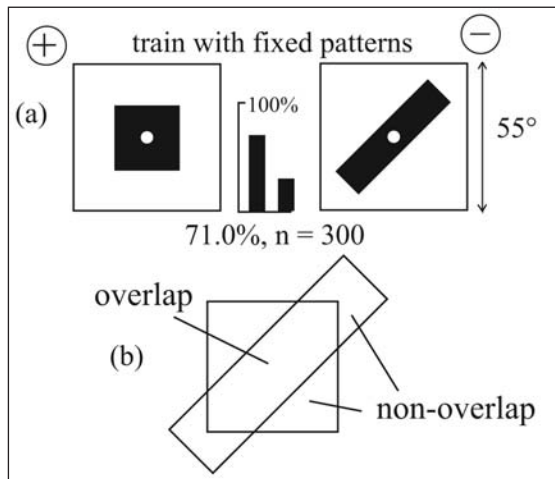
At the time, these ideas had no effect on research on the vision of the bee. Instincts were proposed and accepted as innate as explanations of behaviour. An experiment was an observation, followed by a guess about the cause. Most of the philosophers of the nineteenth century and more recent times were of no further help, being engrossed with the meanings of words and the theoretical basis of physics, astronomy, mathematics and the relation between mind and matter. Towards the end of the century, however, Mill's methods were taken up in the United States by C. L. Morgan (1890), Edward Thorndike, Margaret Washburn and J. B. Watson, who opened the subject of experimental psychology, but little of this spread back to Continental Europe. We can detect Mill's influence in the work of Herbert Spencer Jennings (1868–1947), who concluded that the detailed behaviour of lower organisms was controlled largely by learning by trial and error (Jennings 1906).

Mill's rules allow us to make deductions from observations and experiments, provided we do not ignore some hidden cause. Unfortunately, we can never list all possible causes. Another difficulty has always been to arrange sufficient examples so that a common cause is established. A third difficulty is that a number of facts might be totally unrelated but we might still derive a theory from them. A fourth difficulty is that we might be totally ignorant of the type of system being studied—for example, whether memory is a solid-state molecular transformation, a wet chemical reaction or a rearrangement of connections between nerve cells—so no lasting conclusions can be made. Perhaps the most common error is to waste time on facts that prove useless. The most dangerous error is to postulate a hidden cause, give it a name, raise it to the status of reality and then validate it by devising an experimental proof, while still missing the real cause. This is called 'misplaced concreteness'. These potholes produce errors of deduction and account in part for the hesitant and meandering progress in every branch of science, but especially in vision and analysis of the nervous system, where we start with multiple causes in parallel but no map.

For experimentalists, Mill's best contribution was originally Newton's idea that a postulated cause must be capable, realistically and mechanically, of producing the effect that was observed. He went further and advised that the nature of the postulated cause should be demonstrable by an independent means. We can

translate this as 'list the components and find out how the mechanism works, then confirm it experimentally'. How few students of animal behaviour even bother to list the components! How easy to label the performance 'cognitive'!

Figure 2.1 a) Two patterns of similar area and position on the targets that are easily distinguished by bees in the apparatus shown in Figure 1.1d. The patterns are fixed, not shuffled in position, but are interchanged every five minutes to ensure that the bees look at them. The square is the rewarded pattern. b) The intuitive idea that the bees 'compare the stored image with the current image of another shape' by the areas of overlap and non-overlap when they are superimposed.



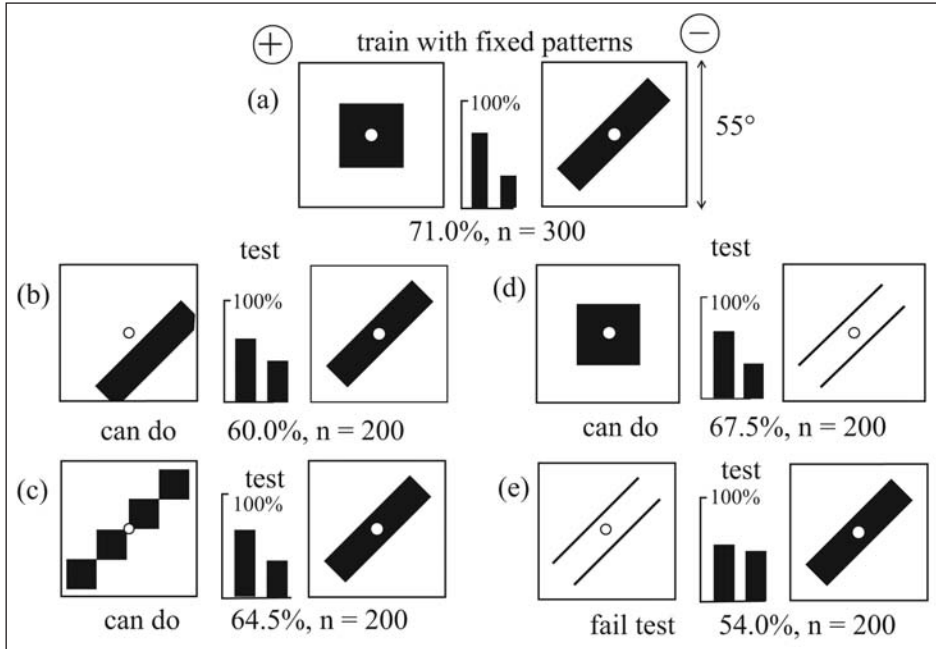
Source for (b): After Wehner (1981:Fig. 86).

How Mill's logic was applied to bee vision

Now we come to the part that requires a little concentration. Figure 2.1a shows the success rate when bees are trained to select the rewarded black square, but those choosing the oblique rectangle receive nothing. The two patterns were in the apparatus in Figure 1.1d, of the same size at the same centre, to give the bees a fair choice. The two targets were interchanged every five minutes to teach the bees to look at them and not simply learn to go left or right. The bees clearly learned this task, but the real score means little because it depends on the length of the training, the hunger of the bees, and so on.

Until recently, the success of the bees would have been explained by the difference in shape of the square and the rectangle. It was proposed that the bees measured the region of overlap and the regions of non-overlap (Figure 2.1b). This is a general explanation that could apply to all patterns, but we have no indication that it is the correct explanation. In fact, it was a misleading guess.

Figure 2.2 a) Training patterns; the bees avoid the bar. b) The trained bees avoid the bar when displayed versus a bar that is moved down. c) They avoid the bar when displayed versus a bar with modified edge orientation. d) They distinguish the edges of the original bar from the square. e) They confuse the edges alone with the original bar, which they fail to recognise. These results show that the trained bees recognised only the orientation of the bar edges in the expected position. They say nothing about the square. They



Now turn to Figure 2.2, where the trained bees are given four tests to reveal what they have actually learned. They distinguish the original bar in the training from the same bar moved down (Figure 2.2b), so they are sensitive to bar position. They distinguish the bar from a similar shape with stepped edges (Figure 2.2c), so they detect the orientation of the edges. They distinguish the square from a hollow bar (Figure 2.2d), which by itself tells us little; however, the trained bees have equal preference for the hollow bar and the original bar (Figure 2.2e). In this case, whatever makes the bees avoid the oblique black bar is displayed on both targets in Figure 2.2e, so in the training they have learned to avoid the orientation on the edges of the oblique bar.

Figure 2.3 a) Training patterns, as before. b) The trained bees fail to distinguish the square from a horizontal bar; or c) from a bar with stepped edges. d) They also fail when the square and the bar are both moved; and e) when a black spot is added. They do not recognise the square in any of the tests.

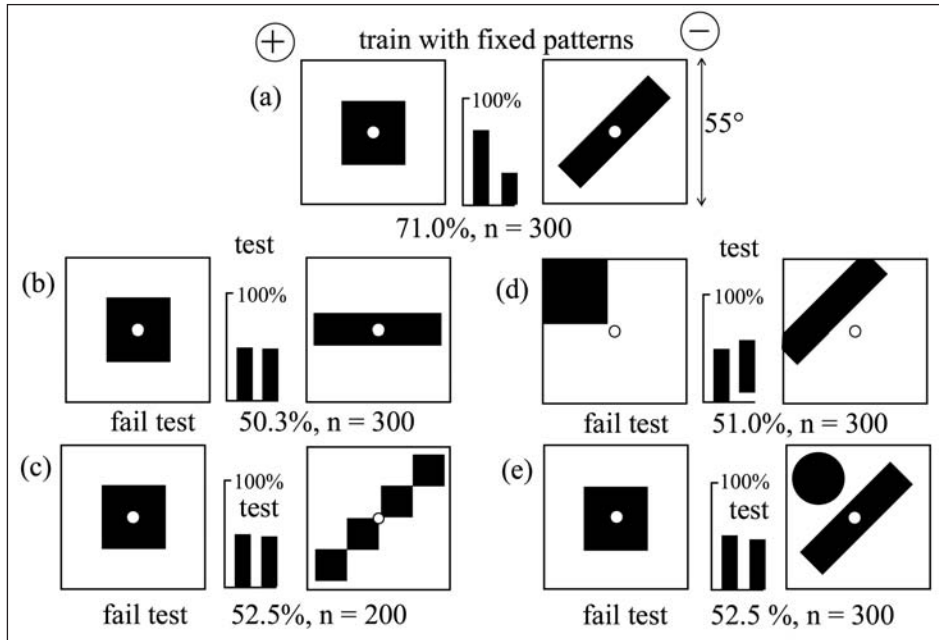


Figure 2.3 shows what they did not learn. The trained bees were tested with the original black square in the training versus other patterns. The square was chosen equally with the rotated bar (Figure 2.3b), or with the bar with stepped edges (Figure 2.3c), because the orientation cue was not displayed on either target. The square was chosen equally to the bar when both were moved (Figure 2.3d) because the expected parameter was not in the expected place. Finally, the original patterns were chosen equally when a large black spot was added (Figure 2.3e), because this additional parameter was not expected, so the bees failed to recognise the place. Clearly, the bees had not learned to recognise the square or the bar, only a simple cue in the expected place. This experiment does not exclude the possibility that bees can recognise some patterns that were untested.

In my search for the cues that bees use, I tried a large number of pairs of patterns. Some they discriminated, others they did not. Between every pair of patterns that bees are able to discriminate there is obviously a difference, or more than one, which the trained bees detect. When we find a number of successfully discriminated pairs of patterns (Figure 2.2), and the pairs have only one common factor or common difference, we have probably found the common cause—that

is, the cue that they detect, if we have persisted in looking at enough examples. This is Mill's 'Method of Agreement' in the search for factors. In the above example, the parameter was the edge orientation at the expected place.

Although thoroughly criticised by later writers, Mill's rules are still useful in the crucial design stage of experiments and in making inferences from them. When there are groups of pairs of patterns that bees cannot be trained to discriminate, there is likely to be a common factor that is missing from all of them (Figure 2.3). This is Mill's method of 'Agreement in Absence', which is very decisive if the number of instances is large. In all cases where an effect is missing and one possible cause is consistently absent, there is a strong presumption that these two circumstances are cause and effect in spite of possible multiple causes. There might, however, be several reasons why the bees fail. We saw this in the failure caused by the addition of a spot, which was in fact a strong salient parameter that was easily recognised by bees.

When bees fail to learn to distinguish a pair of patterns, or trained bees fail to discriminate in tests (Figure 2.3), we call it negative evidence. It is good evidence of the inability to perform, which is not the same as absence of evidence. Although it can be observed and confirmed, the bees' failure to discriminate still gives us a problem. We have to be careful that the same bees can discriminate other similar pairs of patterns, so that we are sure that they are not failing for some trivial reason. The bees might be unable to learn to discriminate because they fail to notice the patterns or the cues displayed, the two patterns might display the same cues or the bees might be unable to stabilise their eyes on the targets. Similarly, when trained bees are tested, they might fail because they detect an unfamiliar cue on the test targets or because the preferences for the available cues are balanced on the two targets (Figure 2.3e), so it cannot be assumed that one cue has been omitted. The ambiguity makes the research harder and longer but the situation can be resolved with a sufficient number and variety of tests. The solution to the difficulty is to take two patterns that bees prefer equally despite extensive training—that is, that they cannot learn to distinguish (Figure 9.12)—then add a parameter that bees recognise. The resulting learning is then a positive demonstration that the parameter is effective when the patterns are not.

Similarly, when the bees succeed, we must devise control experiments to show that there is not some other irrelevant cue, such as an odour, a difference in size, range, position or illumination, which enables the bees to 'cheat'. When we find two patterns that bees easily discriminate, but with no known cause, we can suspect that there is a previously unknown parameter.

In the study of bee vision, I assume that the bees detect certain features in the patterns—called parameters—to which their feature detectors are innately adapted. They remember something in the brain derived from the feature detector responses—called a cue—that is a small part of the whole pattern. There

is no evidence that the bee brain is able to reassemble the visual inputs to make a more complete picture. This is 'absence of evidence' and not conclusive. There are many pairs of patterns that look different to humans, however, which bees are unable to discriminate in training experiments (Figure 2.3 and Chapters 9 and 11), so I infer that they generate no cue or no difference in cues. Clearly, the bees do not distinguish or recognise them. This is 'evidence of absence of recognition' in these examples. Now, to emphasise the effectiveness of the empirical method to investigate the matter further, look again at Figure 2.1b. The intuitive idea of overlaps and non-overlaps of shapes never surfaced in the exposure of the parameters. It was just a guess.

Problems of applying theory

With logic defined, why was progress so slow?

In the late nineteenth century, apart from the efforts related to Darwin's theory of evolution by natural selection, biology produced almost entirely what we now call 'natural history'. It was a period of belief in the progressive improvement of understanding, but the biological sciences were mostly descriptions of species, anatomy, development, fossils, geographical distributions, physiological systems and the chemistry of some processes in animals and plants. At the very end of the century, detailed anatomy, histology and the physiology of the nervous system became established. The analysis of insect vision took off in Germany with the works of two giants, Grenacher (1879) and Exner (1891), who studied stained sections of the insect retina with newly invented compound microscopes and provided the basis of our modern knowledge of the compound eye (Chapter 5).

The advances in the nineteenth century were made, for the most part, by men who were thoroughly conversant with the knowledge of their time and who made more than one outstanding advance. Romanes was famous for his work on the nervous systems of primitive animals. Forel was a distinguished entomologist. von Frisch dedicated his whole scientific career to the study of the honeybee. At the time, the interest lay in describing and making sense of the performance. Bees were trained and the brain of the bee was recognised as adequate for its own dedicated tasks, but there were no techniques to reveal mechanisms. Possible mechanisms were not mentioned until the late twentieth century. The scientists knew how to plan an experiment, and the experimental equipment was available, but there was no fund of knowledge of what tests the bee had previously passed or failed. The early experiments show that the early scientists simply did not know what to do.

A number of properties of the visual system contributed to these difficulties.

Systemic hurdles

1. *Diversity*

A drag on the advance of ideas was the enormous diversity of insects with miraculous behavioural patterns. The fascinating descriptions concealed the lack of analysis. The first stage was the assumption that sign stimuli were used in the recognition of mates, food or predators. The sign stimuli, however, are the consistent signals such as colours, movements or markings, which humans intuitively assume the animals detect. This work is still going on. It is far more difficult to identify the real features that enter the nervous system. They are much smaller than the sign stimuli and are probably common to all insects. When the feature detectors have been identified from behavioural experiments, they can be sought by electrophysiology.

2. *Parallel processing*

As Grenacher, Exner and Ramon y Cajal showed in great detail about the turn of the century, the insect retina has thousands of photoreceptors in parallel and feeds into several arrays of pathways in parallel that pass through successive layers of neurons. The first requirement is to list the anatomical components—a formidable task not yet complete even in the most studied insect, the fruit fly. Finding the rules of action requires hundreds of tedious physiological recordings of the individual nerve cells during the continuing behaviour, as well as decades of obsessive study of their connections. Having done all that, there is still a long way to go, because the nervous system functions by the coincidences between activities of neurons in arrays and they learn, so they are not constant.

To analyse a system of elements in parallel it is useful to know what the mechanism cannot do or what is not there. For example, if a genome is known not to contain a particular gene, it is known that that gene is not essential for any remaining process in the living animal, and this fact helps the analysis of the gene's function elsewhere. Whether or not he had a motive, if the suspect proved his absence, he could not have been the agent. This is the correct use of the evidence of absence. In law, it is the theory of the alibi. Further, if there was no motive to kill grandma, no sign of violence and there was no-one around at the time, grandma probably died of natural causes, so a positive deduction might be made. Positive evidence of absence is perfectly valid and is essential when there are many possible causes that can be eliminated one by one. Critics of negative evidence, please note.

There are other ways to separate multiple causes. In the 1920s, R. A. Fisher (1935) developed novel experiments randomising different treatments of agricultural crops with different amounts of fertilisers, soil types and water, to separate the effects of possible multiple causes. Right from the beginning of our work with trained bees, we eliminated some possible causes by randomising those aspects of the stimulus that we wanted the bees to ignore, as in the papers

by Lehrer et al. (1988) on the measurement of range irrespective of size or position and van Hateren et al. (1990) on the discrimination between horizontal and vertical bars irrespective of bar width or position. The method appeared pathetically late in the analysis of insect vision.

From 1909 on, bees were trained to discriminate a pattern or between a pair of patterns displayed on movable targets that were shuffled in position to prevent the bees learning their locations (Figure 1.1d). This had the unexpected consequence that the bees ignored local landmarks outside the training targets (Chapter 12).

From 1926 onwards, the trained bees were also tested with patterns that were related to the training pattern or various parts of it. The method was progressively refined after 1990 as more cues within the bees were recognised and their limits found. It was essential that some of the test patterns contained the necessary cues and others did not. Results obtained using all the methods, in the hands of many researchers using a variety of training and testing techniques, were eventually all explained by the same few simple cues in parallel, as listed in Chapter 9.

3. Feedback loops

One of the great hurdles that had to be surmounted in the analysis of the nervous system was the control of the action by a part of the action itself. The feedback loop makes the system look purposeful. In the nervous system, a feedback loop can be within the animal—for example, the sensors at our joints and in the muscles keep our limbs in constant positions under a varying load. We would not be able to stand up without these feedback loops. The loop can be outside the body. We guide our hands and feet with our eyes. We hear our own voice and adjust it under control. Feedback loops were not really understood until cybernetics became popular in the 1960s, and it took decades before the experimentalists found even poor methods of analysis by breaking or clamping the loops, or more refined methods by replacing the natural loops with artificial ones.

4. Preconceived ideas

Despite Mill's efforts, a trust in intuition and acceptance of causes that looked reasonable were serious sources of error in every decade. Intuition was represented in every aspect of bee vision in the twentieth century—not only by the Gestalt psychology that influenced Mathilde Hertz and, through her, other studies of bee perception. We will find numerous examples in the coming pages, even though Morgan (1890) advised readers to 'endeavor to distinguish observed fact from observer's inference' and 'to apply Occam's razor, especially to proposals of cognition in animals'.

Almost universally, it was assumed that the behaviour of insects was genetically innate and that a sign stimulus initiated a predetermined act. Quite the contrary: if the insect is allowed to initiate its own movements, it quickly modifies them by rapid learning that eliminates errors and selects the effective responses. This was described by Jennings (1906) as ‘reaction by varied or overproduced movements, with selection from the varied conditions resulting from these movements’. We now know that this applies to simple motor movements and to relearning the effects on sensory inputs by all parts of the central nervous system, even in the posture of the legs and the supposedly fixed opto-motor response.

The most insidious preconception, damnably difficult to escape, is to read human sensations into animal systems—and in this case to assume that bees ‘see’. For most of the twentieth century, this anthropomorphism led to an assumption, derived from the study of primate brains, that in the brain of the seeing bee there was a structural layout of the image—a bad guess that was not excluded until 2005 (Chapters 11 and 12).

Backsliding into intuitionism

From about 1900 onwards, two theories of general application and wide influence appeared in studies of vision. First, Wertheimer (1912) found that the mechanistic concepts of his time failed to explain why human perception seemed to proceed from an assessment of the whole to the recognition of the parts. Nowadays, there is abundant evidence of human top-down processing, as in visual search and size constancy. Wertheimer was followed by Koffka (1924) and Koehler (1925) and the Gestalt theory spread—notably to bee vision. The word ‘Gestalt’ is translated as ‘configuration of a whole’. The modern equivalent is the recognition of configurational layout.

In human vision, the Gestalt theory included numerous laws and factors. The most important is that the human visual system transforms the stimulus into the most perfect that the situation allows—for example, a ring of dots becomes a circle. Characteristics such as regularity, inclusiveness, symmetry, simplicity and unity are detected intuitively, even if present in an imperfect form. Similar patterns or objects that move together are seen as groups and are classified into categories. An enclosed surface is seen as a shape. This was the accepted theory when Hertz researched bee vision. Mill would have suggested that Gestalts were all learned.

The second corrosive influence was the development of ethology by Konrad Lorenz and Niko Tinbergen, who used intuitive concepts such as ‘fear’ and ‘drive’. In the 1930s, Lorenz published numerous observations of the behaviour of free-living animals and, with Tinbergen, produced a comprehensive theory of instinctive behaviour. The responses were ‘innately controlled movements’

initiated by a 'specific releasing mechanism' (internal) or a 'sign-stimulus' (external). They were driven by 'reaction-specific energy' that could accumulate and also be 'depleted' by the activity itself. Actions were directed with an intention of obtaining food or a mate or driving away a rival. Behaviour was basically stereotypical and inherited, but could be modified by learning. The theory was developed into a hierarchical model with many layers and parallel pathways.

In my terminology, this was mostly detailed description of performance, however wonderful and colourful, followed by an intuitive guess about causes, followed by a redescription of the performance in terms of the supposed causes. There seemed to be an intellectual block to empirical analysis of mechanisms. In a biting critique, Lehrman (1953) found serious flaws:

It involves preconceived and rigid ideas of innateness and the nature of maturation. It habitually depends on the transfer of concepts from one level to another, solely on the basis of analogical reasoning. It is limited by preconceptions of isomorphic resemblances between neural and behavioral phenomena...Any instinct theory that regards 'instinct' as immanent, preformed, inherited or based on specific neural structures is bound to divert the investigation—from fundamental analysis.

Mill would have loved that.

After World War II, ethology became a powerful force in Germany and spread with Tinbergen to Oxford, then moved to Madingley Hall, Cambridge, with Thorpe, Hinde, Bateson and many others. Even in my student days, however, Gray and Lissmann (1946) were taking pot shots at innate behavioural patterns. Throughout the 1960s and 1970s, the ethologists said they made an enormous effort to understand mechanisms by studying behaviour, but they in fact redescribed it in other words. The available theory could never be satisfactory because the amount of information in a behavioural pattern was dwarfed by the vastly greater information required for its explanation.

In his *Biographical Memoir of Niko Tinbergen*, Robert Hinde (1990) summarised the conflict between ethology and comparative psychology, with an effort to paper over the cracks: 'both sides were partially right.' This was whitewash and rubbish. Gradually, the battle died down, however, as it became obvious that ethology was descriptive natural history of whole animals, mainly vertebrates. Those with the techniques to study neural mechanisms of behaviour formed their own subject, neurobiology, with their own Congress of Neuroethology, but that alone did not help to identify the mechanisms of bees' visual discrimination, because most of the researchers on bees had been educated in the Continental system based on the philosophy of Kant and his successors. The whole subject was dominated by German biologists who somehow thought that empiricism was immoral.

Empirical laws

For the past 200 years, physical scientists have studied a system by changing the input progressively and recording quantitative data from the responses. Investigators looked for regular relationships between inputs and outputs, which were called empirical laws. The search for an empirical law was useful because a theory might be found to be consistent with it. When they were not able to see why such a law should exist, they hesitated to extend the law to cases varying much from those that were in fact observed. Mistakenly, the search for empirical laws was taught as a way to proceed scientifically. I still remember those never-to-be-forgotten practical physics classes at school in which we measured the volume of air at different pressures and the length of a copper bar while it was heated. We then described the empirical relationships as laws that were explained in terms of the motion of molecules, which became more and more real as we listened to our enthusiastic physics master. In fact, we had no evidence of molecules in our experiments—and they did not come into science by this route.

In the case of vision, the exact relation between input and output is even less useful. In the bee, these searches for exact relations between the features of the pattern and the percentage of correct responses hampered progress. Dozens of such papers by Crozier and his colleagues at Harvard and by Selig Hecht at Columbia were published in the *Journal of General Physiology* in the 1930s. This approach was futile when applied to a system such as vision, with many separate channels of transmission in parallel.

Starting on a new tack, Lindauer and Wehner in Frankfurt looked for empirical laws from 1965 until about 1973. Wehner (1967) trained bees to come to a square cross, or alternatively to a regular striped grating, and then plotted the choices between the training target and the same target rotated by various angles. A theory could be found for one set of results or the other, but not for both (Chapter 4).

In one favourable example, Wehner (1969) trained with a broad single bar and then plotted the scores of the discriminations between the original bar and the same bar at different angles. The scores fitted the increasing mismatch between the positions of the areas of black on the training and the test targets (Figures 2.1b and 4.5). To explain the results, Wehner proposed that the bees remembered a copy of the training pattern and compared it with each test pattern, but this guess led to the erroneous conclusion that the image was remembered in the brain of the bee.

Explanations consistent with the data

Most experimental data are explained by making an intuitive hypothesis that is compatible with them, such as postulating that a cat ate the missing cream. It is

not good enough, however, to accept a theory just because it is consistent with the data. This was, however, the commonly accepted way to proceed. The cat starts as a guess and, even if never seen, it can become an explanation of other events. Later authors refer to the cat as though it was seen eating the cream. If there really was a cat, however, it might have been innocent. Much of the discussion about theory in the scientific advances of the twentieth century was an effort to cover up the sad consequences of accepting erroneous explanations that were compatible with the data. In fact, like sex, everyone was doing it, and it was regarded as an ultimate necessity. Everyone hoped they had the true theory and that they would not be responsible for erroneous concepts.

Popper and the method of disproof

There is a way to make progress. If there is no cat, we can look elsewhere for the cream. This is the 'theory of disproof' attributed to Karl Popper (1935), whose ideas were popular with students about 1950. In Popper's view, progress requires a definitive experiment that excludes the cat. In the study of honeybee pattern vision from 1914 to 1989, the cat was the idea of parameters as parts of the image and memories within the bees, or alternatively the idea of a complete retinotopic memory of the image, but for some strange reason, the critical experiments to exclude either of these popular proposals were never done.

The contribution of Popper—the idea that theories could never be verified, only disproved—partially resolved the otherwise difficult acceptance of induction. Theories can never be proved because unforeseen observations can appear in the future. After Popper, theories that were consistent with the facts could be accepted as valid for the time being, but only if the effort to disprove them had been made. The disproof might have been useful if the discipline had in fact been applied when a theory presented itself, but none of those working on bee vision ever validated their theories. Also, until the 1990s, different theories were presented separately without reference to one another. So much for Mill, Popper, Kuhn and the rest of the philosophers of science.

The new paradigm

In the mid-twentieth century, explanations based on intuition or empirical laws gave way to a new attitude, based on fiddling with the mechanism; it was the era of Meccano, mending a bicycle or a radio, which led to understanding signals and machines. With the development of electrophysiology and cybernetics after 1945, the idea developed rapidly that sense organs acted as filters in parallel pathways. Recordings from neurons in the visual systems by Kuffler (1953 on the cat), Barlow (see below) and Burt and Catton (1952 onwards, on the locust) revealed examples that responded to complex stimuli such as a moving spot of the right size, but not to a simple flash of light. In 1952, at a supposedly

private meeting in Cambridge while I was a research student, Horace Barlow gave a seminar on the responses of frog retina ganglion cells, including one type sensitive to a small black spot, with an inhibitory surround. An American spy at the meeting distributed a report to all holders of US Office of Naval Research (ONR) grants in the United States (Mollon 1997) and Ted Bullock certainly knew of it. Much later, however, Lettvin et al. (1959) created widespread interest when they published similar work. That year, I visited Jerry Lettvin on the way to California to work on a book with Bullock and was less than impressed by their equipment, methods and flash in the pan.

In fact, the promise of this work was not fulfilled, partly because in invertebrates the neurons recorded were not representative and not identified; the real cues were not well defined and neuron specificity was not really demonstrated. The main reason, however, was that recording from only a single neuron at a time simplified the data, but blinkered our understanding about arrays in parallel and coincidences between neurons. In the years 1955–62, innate edge detectors were found in huge arrays in vertebrate retinas and mammalian cortex. Jander (1964) was stimulated by these studies of vertebrates. He combed the literature and proposed the general hypothesis that small feature detectors were the basis of vision in ants and bees; but, without the necessary equipment or techniques, it was only a guess. Later, McCann and Dill (1969) recorded from edge detectors in the optic lobe of a fly. Those working on insect visual behaviour flatly ignored these indications. There is some excuse for heading the wrong way when signposts are undeveloped, but no excuse when signposts from related disciplines emerge.

Forty years later, we are no further advanced in identifying the part played by any neuron for anything subtle in the visual repertoire of the honeybee (or other invertebrate). There has been a huge effort on the illusory unit motion detectors of the fly, but negligible electrophysiology of pattern vision of any invertebrate because no-one knows what features have been detected.

Kuhn and progress

Thomas Kuhn (1922–96) argued that scientific topics passed from an initial chaotic pre-paradigm stage into a productive period of growing understanding and satisfying results that fit the theories of the time. There is nothing there to object to. Ultimately, perhaps because new methods or technology are found, there is a crisis because anomalies accumulate and the accepted theory is no longer tenable. At this point, a new experiment or theory points the way to the next period of advances, and the cycle repeats.

At first, a new theory should be simple—that is, it should propose few new postulates or variables with acceptable relations between them. To survive, the theory must pass every test and there should not be a better theory. The new

theory must not account only for previous results and anomalies, it must predict further developments. Kuhn observed that from time to time a new technique—a new means such as the availability of electric power or a real discovery such as of x-rays—altered the way facts were collected and explained and there was then a shift away from the old towards the new. The new paradigm would not be acceptable to all, especially to those whose career was based on the old one. All ‘theories’ became transient and replaceable.

The route was familiar to Mill. Collection of data led to an inference or guess of causes. As a paradigm developed, a new theory would become more and more confirmed. At best, this was induction; at worst, mere intuition. Next, it was essential to design experiments that would probably establish or perhaps exclude the new theory. No philosopher, however, explained how to design the right experiments, which required intuition, lots of thought and extensive knowledge of the literature.

The new territory, filters and neurons

In vision, the way forward was indicated by the arrays of single neurons in the primary visual cortex in mammals that each responded to an extremely simple feature—notably, the orientation of a moving edge (Hubel and Wiesel 1959). In this case, every neuron could be represented as a spatio-temporal filter with its own field, but the meaningful signal was carried by the coincidences of many neurons in parallel. The artificial-vision fraternity enthusiastically embraced the concept—as reviewed later by Hinton et al. (1986)—but robot vision needed much more.

Filter theory, like electrophysiology or neuron anatomy, is not sufficient to explain vision. First, it is essential to discover how many different kinds of parallel paths are active at any one time, exactly what is the meaningful part of the signals they carry, the excitation in each, how they are interconnected, the field sizes, the destinations, the time delays and finally the central reckoning. This leads slowly to an understanding of the way the parts work together. A systems analysis with interacting boxes (Figure 7.1) can be made only after the difficult behavioural analysis has been done—not before. Second, the visual system relies on the visual feedback from the movements that it controls. Vision is active, so the pinned-down preparation is only a beginning.

The new postwar paradigms in physics—notably, information theory, cybernetics, feedback, signal-to-noise ratios and modulation transfer functions—and the expectation that useful artificial vision would quickly follow, sustained the enthusiasm for recording from amphibian and arthropod visual systems. The studies of mammalian vision in medical schools led the way. In the period

from 1966 to 1974, it became established that at the front end of vertebrate vision there were arrays of simple filters in parallel that detected local intensity, directional movement of local contrasts and orientations of edges and contrasts.

A few pioneers enthusiastically proposed that behaviour would be understood in terms of nerve-cell interactions. As more and more results emerged from a greater variety of preparations, however, it slowly became obvious that this ideal would never be achieved, because the information content of behaviour was so low compared with that of neurons. Even in 1981, Rudiger Wehner, in his long review, could not reconcile the new work on the neurons of the optic pathways with the visual performance known at the time. It was also essential to direct research to the analysis of behavioural responses that might explain the activity of the neurons.

In the 1970s, new techniques became available for identifying single dye-marked neurons that were also recorded with a microelectrode, so theoretically, the physiological interactions could be reconciled with the anatomical pathways. There was some excitement at the prospect of working inwards from the retina towards the brain to discover what features of the image were detected. There was no final understanding, however, even of the directional motion detector neurons of the fly's lobula plate, which were exceptionally large. Even in this case, the results were at first misleading because an animal with a fixed head could not initiate the movements that were part of its vision.

In the insect optic lobe there are dense arrays of neurons in parallel and in series and it has proved impossible to track a sufficient fraction of the synaptic connections or decide which are inhibitory or excitatory. Many of the neurons—and perhaps all the small ones—function by graded potentials and have no action potential. Although it was possible, through the second half of the century, to record from many of the large ones in the insect optic lobe, behaviour was not explained by neuron responses. The reasons why are that the units of visual behaviour are not known; bees are freely moving and their vision is active, with continual learning from visual feedback from their own movements; they respond to only a small part of the image seen by the human eye; only a few parameters have been identified; and sensory integration depends on coincidences. Moreover, the behaviour of interest—visual recognition—was stored in an unknown language and appeared only briefly.

When we recorded neurons in the deep optic lobes of insects 45 years ago (Horridge et al. 1965), we found that very simple stimuli such as flashes and moving edges were adequate and the field sizes were very large. Some responded to sound, touch or body movements. How could a group of neurons with these properties carry the signals for vision? Certainly, the reassembly of an image would be impossible. Only much later, I gradually learned that the parameters that bees detected and the cues within their processing system were also very simple and were summed in local eye regions, and that they functioned as a

parallel array. In brief, large arrays of a few types of small feature detectors are summed together to form a few cues in each local region of the eye. The relation between behaviour and neuron activity lies in the coincidences of the responses of neurons with different inputs that lie in parallel in local regions. Again, the idea of multiple causes can be traced back to Mill.

Endnotes

1. Aristotle (384–322 BC) wrote the *Organon*. See Westaway (1937).
2. Francis Bacon (1561–1626), an English essayist, philosopher and politician, wrote the *Novum Organon*. See Westaway (1937).
3. Whewell also wrote *Novum Organon Renovatum*, as well as *History of the Inductive Sciences* (1837). See Westaway (1937).
4. Recounted in his autobiography (Mill 1873).