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RESEARCH TECHNIQUES AND IDEAS, 1950 ON¹

Several powerful new techniques became available as a result of wartime research. First, the electronic equipment developed for sonar and radar—particularly the availability of low-noise high-impedance amplifiers, the oscilloscope, tape recorder and automated cameras—encouraged a burst of effort to record everything of interest, particularly in the visual system. This was undertaken by Roeder at Tufts; Burt and Catton at Newcastle; Parry and Pringle in Cambridge, in the United Kingdom; McCann at Cal Tech; Bishop and Keehn at the University of Southern California; Kuiper at Gröningen; and Kuwabara, Naka and Eguchi at Fukuoka. It started with only a few devotees with electronics experience and access to a workshop; much of the equipment was modified surplus from the war. Because neuron activity was visible on a luminous screen, they were exciting experiments for students and the techniques quickly spread.

Second, in the 1950s, the wartime interest in operational research spilled out into biology (and economics and elsewhere). Systems analysis brought new ideas about control systems with feedback loops. The first sign was a rash of block diagrams, in which postulated causes in boxes—such as the motion of a target—were linked by arrows to effects, such as eye motion. Next arrived a thin sprinkling of quantitative data about these boxes and arrows, and some mathematical relations that fitted the data and were supposed to summarise the interactions.

Third, many universities purchased a transmission electron microscope, soon joined by a microtome for cutting thin sections of tissues embedded in araldite (another wartime production). About the same time, various techniques for staining individual nerve cells with silver salts, originally developed by Golgi and Cajal, were revived by William Holmes in Oxford and passed on to a number of English students—notably, J. Z. Young, Brian Boycott, David Blest and Nicky Strausfeld. Correlations between the anatomy and the physiological responses of neurons and synapses began to appear, culminating in the individual identification of the recorded neurons by injecting dyes through the microelectrodes. Theoretically, it became possible to identify every neuron,

record its activity and plot its various fields of sensitivity. Recording from the neurons, although hard ground to plough, was accepted as the only way to understand the control of behaviour.

Exciting new research

After World War II, Cambridge, England, like Cambridge in the United States, was a focal point for experimental analysis of the nervous system, neurobiology and animal behaviour.

There was indeed a revolution in all these fields, and of course many others too, combined with intensity of action, because those returning from war duty were catching up for lost time. They had ideas to unload, new techniques to carry them out and, for a time, they were building a better world.

In physiology in Cambridge, first-year lectures on the nervous system were given by Lord Adrian, who had been awarded the Nobel Prize in 1932 for his demonstration of nerve impulses and the discovery of the frequency code in single axons. In the practical class, activity in nerve fibres was made visible with an amplifier and cathode ray tube put together by Sir Bryan Matthews, who had perfected the string galvanometer that did the same job in the 1930s. Second-year lectures on the nervous system were given by Willie Rushton, who discovered the principle of univariance in vision, Andrew Huxley and Alan Hodgkin, who, with Jack Eccles, were awarded the Nobel Prize for medicine in 1963. At the time, they were working actively on the squid's giant axon membrane. In line with the time, the result was a set of empirical equations that fitted the data. Only later did Richard Keynes measure the ionic fluxes with radioisotopes.

The Zoology Department was stuffed with Fellows of the Royal Society and was committed to the experimental approach. Vincent Wigglesworth had a strong group working on insects. Professor James Gray was interested in the reflex control of movement. Eric Smith was an expert on the nervous system of annelid worms and echinoderms. Carl Pantin was the world expert on the nervous system of the sea anemone, such as it was.

On my arrival with a PhD studentship, I was given a key to a room on the second floor. It was quite empty and I had no particular topic. It was still vacation so few people were around. My nominal supervisor, Carl Pantin, had gone to Brazil for 15 months, so I went to the Marine Laboratory in Plymouth on my motorbike. I had been there on a course in marine biology in my second year at university. This time, I walked in and asked the director, Freddie Russell, if I could work there for a while on the Cambridge research table. There, quite by chance, I was instructed in the art of staining nerve fibres with methylene blue by a remarkable old professor. J. S. Alexandrowicz was a Polish refugee, once

Minister of Health and Director of the Medical Institute in Lwów. He had been a medical officer in the Polish and then the Russian armies, escaped through Persia (now Iran) and found sanctuary in England and the Plymouth laboratory after an adventurous war. Coming from the School of Zawarzin, Orlov and other Slavic neuron stainers, Alexandrowicz had, in 1932, published the classical account of the innervation of the crab heart. In the library, it was he who showed me where to find all the literature on the nervous systems of invertebrates and he thought nothing of translating verbatim from six or so European languages.

Back in Cambridge, as a research student, the situation was equally favourable. I happened to bring back to Cambridge some jellyfish, *Aurelia*, from the Norfolk coast and examined them with a newly invented phase-contrast microscope that Victor Rothschild had purchased to look at frozen bulls' sperm. Rothschild had been in charge of security of research during the war; it was he who had stolen a highly secret magnetron from Sir Mark Oliphant's lab and then returned it next day with a stern warning about security. Immediately, when I used his fancy new microscope, a network of large nerve fibres was made visible in the living state. This was something that no-one had previously observed, so I had a discovery in the bag that had to be exploited. That is why I became an electrophysiologist. I built all the electronics for recording from nerve fibres and inherited a massive old mahogany oscilloscope camera from Jerry Pumphrey, who had left for Liverpool in 1949. Pantin was still in Brazil, but he was so shy of students that he would run out of his bolthole if a student knocked on his door.

Before the war, Pumphrey and John Pringle had been visiting fellows with Bronk and Hartline at the Johnson Institute in Philadelphia, and had returned to Cambridge with the most advanced techniques of recording from nerve fibres. In 1938, Pumphrey had published the first recordings from chemoreceptors of the frog, while Pringle had a series of papers on recordings from mechanoreceptors in insects. In 1941, Pumphrey had been transferred to Admiralty Signals at Witley and was made responsible for calibrating radar for early warning of approaching aircraft. Pringle had been sent to the Teddington Radar Research Establishment (TRE) and for a time was in charge of all airborne radar work in Britain. He developed radar responder devices that led bombers to their targets. Alan Hodgkin had also been in radar research and had improved the device for detecting the small reflected signal. Many other brilliant biologists had been boffins in the war and it was no accident that when they all returned at the same time, Cambridge became a beacon of progress.

At the end of the war, when huge amounts of surplus equipment became available for next to nothing, they equipped their laboratories in a manner that would otherwise have cost a fortune. They also acquired large amounts of exactly the right kind of junk to make any other equipment that was needed. I remember finding in the basement of the Zoology Department dozens of American power

packs, transformers, oscilloscope tubes, boxes of assorted capacitors and resistors, automated gun cameras, pentodes and double triodes for push-pull amplifiers. Plenty more could be purchased cheaply in London in Tottenham Court Road and that was how I equipped the Gatty Marine Laboratory for electrophysiology in the 1950s.

Looking back, it is clear that the analysis of the nervous system was driven by the technological possibilities, as the electronic and optical instruments became available in the hands of those who understood them.

The Cambridge laboratories all had excellent workshops, with managers who provided tools, sheet metal and nuts and bolts, and willingly showed research students how to build whatever they needed. Superficially, Pringle was rather formidable, and did not supervise research students, but he answered my questions readily enough and allowed me to examine his equipment.

To be sure of plenty of jellyfish, I spent the next summer at the marine laboratory at Millport, on the Clyde estuary in Scotland. By chance, Gray and Rothschild were both there for the salmon fishing further north and I was able to show them the first recordings from a coelenterate nerve net. I spent the rest of my 10 years at Cambridge shuttling between marine laboratories, working on a range of fascinating animals, such as sea slugs, sea mice, sea pens, comb jellies, hydromedusae and corals on the reefs of the Red Sea. Later, while we were both at the Stazione Zoologica di Napoli in 1955, Pantin wrote to his friend Mick Callan, Professor of Zoology at the University of St Andrews, Scotland, who appointed me to the Gatty Marine Laboratory as a lecturer. I left Cambridge because there were no marine animals there and I needed a job.

In the three decades after the war, there was also enormous growth in support for universities and in particular for research. Cash for equipment and technical help was available for the asking. In 1958–59, I spent 15 months in California, working on a book with Ted Bullock, and visited most of the invertebrate electrophysiology labs in the United States, absorbing American methods of funding research, so that I was able to assemble a group quickly on my return to St Andrews.

The retina

Arriving back at the Gatty from the United States, my research fell by accident into the topic of the compound eye. In 1962, Burt and Catton at Newcastle published in the *Proceedings of the Royal Society* a ludicrous account of the optics of the compound eye of the locust as a diffraction grating with summation of rays at different levels in the receptor cell layer. This was impossible because the cells were full of black screening pigment. Three newly arrived students, John Scholes, John Tunstall and Steve Shaw, decided to tackle the insect retina

with intracellular microelectrodes. Adopting the best techniques that I had seen in Cambridge and the United States, we set up new heavy, steady benches, designed and built our own flat-bed electrode pullers, operated by a spring, and copied the Bak pre-amplifier with compensated input capacity and neutralised grid current. At the height of the Cold War, we imported large, heavy Russian copies of Leitz micromanipulators with a grease plate and extra-fine screw. We designed and built our own Cardan arms, using parts from tank gun sights, with a rapid-release screw, as on a sextant, with adjustment to one-tenth of a degree. We purchased narrow-band interference filters to arrange in a filter wheel for rapid changes of wavelength. At first, we used very small white pin lights close to the eye and only later moved to a xenon arc. Following the techniques published in 1961 by Ken Naka, we described the receptive fields of the locust photoreceptor cells by intracellular recording.

Because he worked through the night, when the locust eye became 1000 times more sensitive, Scholes discovered the 'bump' potentials caused by capture of single photons for the first time in an insect eye. Tunstall showed that the fields of the locust retinula cells were uncomplicated and Shaw explored the lamina monopolar cells. With Callan's electron microscope in the Zoology Department, Tudor Barnard described the palisade that appeared in the dark-adapted eye and altered the light-guiding properties of the rhabdom. After all, there were no peculiar optics. A summary of the results appeared in the *Stockholm Symposium on the Compound Eye* (Bernhard 1966).

As published in the same symposium, Pete Shephard discovered that a stationary crab eye remembered a retinotopic projection of the positions of surrounding contrasts, even with a brief exposure. Rudiger Wehner, who was just beginning his period of training bees to come to black bars on a vertical surface, noted this performance. The crab and the bee detect black/white edges quite separately from broad areas of black, with corresponding types of input channels, phasic for edges and tonic for areas. The crab eye responds at angular velocities less than earth speed (15° per hour) and the accuracy is much better than the interommatidial angle. The results were totally at odds with the Reichardt model (see below) of motion detection by the compound eye, as was the behaviour of the freely moving crab eyestalk in tremor and when recovering from a voluntary eye movement.

After the war, there was rapid growth at Baltimore and then Harvard, with Steve Kuffler, Furshpan and Potter. Bullock and Hagiwara set up an electrophysiological laboratory at the University of California at Los Angeles and found the crab heart ganglion to be the perfect preparation for synaptic interactions and spontaneous rhythms in single identified neurons. At the same time, Arvanitaki, in France, showed the way to record intra-cellularly from the giant nerve cells of *Aplysia* and set off another bandwagon that later took Eric Kandel on board.

The Germans took about five years to reach the level of expertise that I had seen in Cambridge. Hansjochem Autrum, who replaced von Frisch as professor at München, built an electrophysiological set-up and measured the spectral sensitivities of the three types of photoreceptors in the honeybee eye, as well as the angular sensitivity of receptors in the fly. He and his collaborators, Burkhardt, Wiedemann, Vera von Swehl and pupils, spread the techniques in Germany.

The 1960s was a rich new era for invertebrate physiological research. As recorded later in this chapter, a strong group developed rapidly in the Max Planck Institute in Tübingen. There, Scholes and later Kuno Kirschfeld studied the optics and recorded the noise in fly photoreceptors. In the Netherlands, Kuiper expanded a group at Gröningen, where Doekele Stavenga established his career on the insect retina. These, and a few others, went deeper into the optics and receptor physiology in the 1970s, which was the high noon of studies on the insect retina. Numerous new students graduated with advanced skills in recording, neuron identification, electron microscopy, the optics of light guides and online data analysis.

There was a new group around me by now, committed to a program on optics and electrophysiology of compound eyes. In 1967, I had a project with Gay Grimshaw, a physics student at Dundee University, who built a wax model of a locust ommatidium and shone radar waves down the axis. We had trouble with standing waves caused by reflection at the far end of the rhabdom, but managed to get some measurements of angular sensitivity. We also worked on superposition eyes of beetles for some years and Rick Butler, a student from Canada, found huge day/night changes in the receptor fields of the cockroach eye, but only two types of receptors, for ultraviolet and green.

The period between 1967 and 1969 saw the appearance of a number of official reports that foreshadowed hard times for disinterested research. The *Robbins Report* recommended putting the funds into teaching; the *Rothschild Report* recommended more contracts for more applied work, and direction from industry; the *Dainton Report* spelled out the inability of the State to support an ever-expanding university sector and suggested that too many PhDs were being produced in the pure sciences. The scientific fraternity noticed the clouds on the horizon. The new Principal of the University of St Andrews could not, or would not, be as generous as his predecessor, as shown by his letter to me dated 31 January 1967:

When you were with me there was one point I did not raise about your £6,000 for the Gatty. We both were talking on the assumption that it could be nothing but good to accept £30,000 from the Science Research Council. What will inevitably, and rightly, be asked is how far the £30,000 from the Research Council will commit the University to a take-

over [of the] operation, and hence mortgage our future funds and pre-judge academic developments. It would help me if you could give me more information about this.

Steven Watson.

That was the moment I decided to leave.

I had spent much of the 1965–66 academic year at Yale, teaching and writing, and so renewed my contacts in the United States. The money I earned was banked in the United States. In 1967, Steve Shaw and I had a Grass and a Rand Fellowship to work at Woods Hole, Massachusetts, where we took our recording gear and families. We studied the retina of dragonflies caught at the Prosser family's pond, with a net made from one of Hazel Prosser's curtains. There I discovered fireflies winking at night in the bushes and collected them for electron microscopy of the light guides in eyes by day. About that time, I met Ben Walcott in Eugene, Oregon, who said that he would come and join us at St Andrews. 'How can we find the funds?' I asked. 'No problem,' he replied, 'I will sell my aeroplane!'

While working at the Marine Biological Laboratory in Woods Hole in 1967, I was invited to visit Australia to consider joining a new institute as a foundation professor. So, sadly, after 13 years building a research team at St Andrews, I resigned, on 5 February 1969. The attractions of selecting my own staff with adequate funding in a new environment in Australia were conclusive. St Andrews University also lost Professors John Burnett from botany and John Cadogan from chemistry—partly because at that time the university was not outward or forward looking and did not provide sufficient facilities for research. They could not even buy the essential journals for the university library. It is an important object lesson in the way that research groups rise and fall because individuals make use of opportunities when the time is ripe and go elsewhere when the funds dry up.

In 1969, I became a foundation professor of the Research School of Biological Sciences at The Australian National University in Canberra, bringing with me David Sandeman (on crab eyes), Rick Butler (on cockroach eyes), Peter Shelton (who later turned to the development of the insect eye), Agis Ioannides (on hemipteran eyes) and Ian Meinertzhagen (on retina-lamina connections), with Ben Walcott (on water beetle eyes) as a postdoctoral fellow—as well as their families and other staff from elsewhere. The numbers that became temporary emigrants tell plainly of the enthusiasm and commitment of that group.

As a vanguard, I sent Meinertzhagen ahead to Canberra to order equipment and get the labs ready. He needed more time to produce complete maps of the projections of axons from the retina to the lamina in various insects. Allan Snyder turned up about a year later, not knowing one end of a rhabdom from

the other. His work on the optics of ommatidia provided the inspiration for his analysis of polarising monomodal wave guides and their application for long-distance transmission in light guides for communications.

The new scholars from 1970 until about 1985 were given generous four-year PhD studentships, which seemed to be always available, and which included an allowance for a spouse and return fares. The students made recordings from small photoreceptor cells in various eyes, including mayflies and spiders, and eyes with mobile receptors. Laughlin, Doujak, Wilson, Lillywhite, Hardy, Dubs, Howard, Payne, Matic, Shi and others counted photon arrivals in a variety of insect eyes. They were exhorted to do an experiment every day to retain the skill.

There was a memorable period in the mid-1970s when Stavenga, Snyder and Laughlin, aided by Pinter, Srinivasan and Howard consolidated the data (mostly from our own lab) on photon captures, interommatidial angles, field sizes, lens apertures and rhabdom cross-sections, to produce a comprehensive theory of design of compound eyes for the known range of ambient light levels. During this period, Dubs, Guy, Laughlin and later Hardy, James and Howard analysed the function of the large lamina monopolar cells, which responded with a temporal derivative of the photon flux, minimised the noise and compressed the signal (Chapter 5). This became the best-understood example of optimisation of synaptic transmission in any nervous system.

We studied the movements of screening pigments in the day versus the night eye, as well as the light-adapted versus the dark-adapted eye. Some of the retinula cells themselves make large movements between day and night states in night-flying beetles and moths. By day, highly refractive guides carry light from the cone tip to the retinula cells in many of the nocturnal insects, but at night these eyes have a clear central zone where light from adjacent facets is summed. Some diurnal moths reach the theoretical limit of resolution in a superposition eye; some nocturnal beetles have very poor resolution and integrate light over huge fields as a strategy to collect as much light as possible for flight in starlight. In fact, in 1985, Doujak showed that a single crab ommatidium could detect a single bright star. We found that, in some beetles, the cone changed shape to adjust the optics between a light-guide eye by day and a superposition eye by night. Gert Stange showed that the dragonfly ocellus controlled pitch and roll in flight by summing the illumination from horizon to horizon, and Martin Wilson showed that the locust ocellus detected the position of the horizon mainly by UV contrast. This tradition is still alive in Sweden with Eric Warrant and Almut Kelber at Lund.

Interest turned to the recurrent problem of how to analyse the several parallel processing pathways in the insect visual system. For years, we had tried recording in the optic lobe, but the puzzling properties of the neurons in clamped insects could not be explained by the poorly known visual behaviour. Single neurons responded to moving edges, spots and changing intensity, but little else, with no indication of vision of shape or pattern. Enthusiastic electrophysiologists

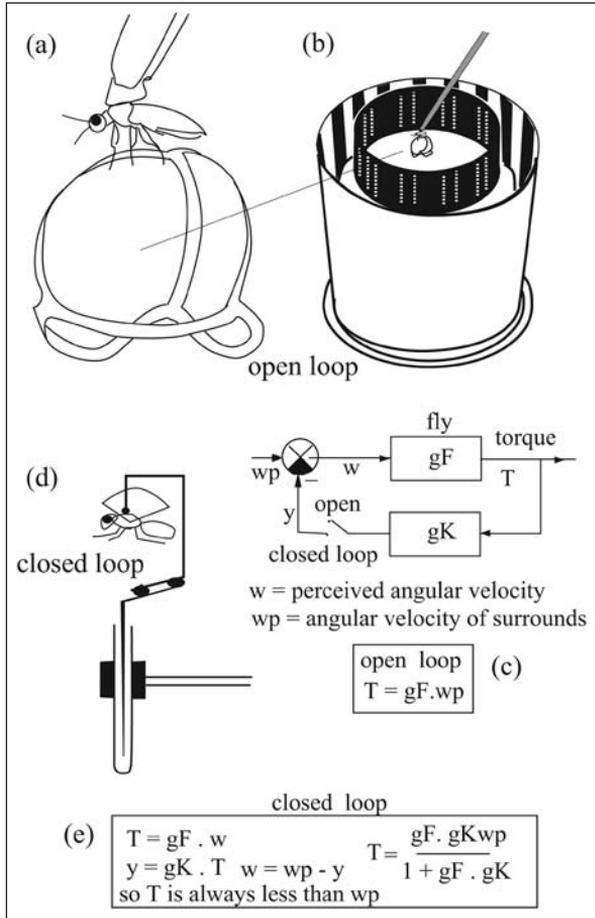
soon discover that an animal's behaviour is more likely to explain its neuron properties than vice versa. Willi Ribi described retina/lamina connections by Golgi-EM, which was just the edge of the neural jungle. A notable advance was Jenny Kien's discovery of neurons in the brain of the locust that could measure the angular velocity of the flow field. Similar neurons were found in the crab eyestalk by Sandeman and Erber, although more peripheral optic-lobe neurons were tuned to a low temporal frequency of passing edges.

In another significant advance, in 1984, Maddess discovered that optomotor neurons were most sensitive to a temporal frequency that increased as they adapted to high frequencies—that is, motion detection became more sensitive to faster motion. Danny Osorio identified neurons of the locust medulla and, with Andrew James, started the difficult task of characterising them by spatial and temporal resolution kernels. Later, with Ljerka Marčelja, I showed that several groups of insects had slow and fast motion-detector neurons (just as they had slow and fast neurons at all levels). Therefore they have the information to measure angular velocity from the ratio of the excitations of these two types of otherwise frequency-dependent neurons (see Figure 7.4). By that time, Srinivasan was interested in how the flying bee measured the perceived velocity and range of surrounding objects.

The new work in the 1980s on the perception of range from the angular velocity of the surroundings by flying insects led directly to practical applications. We formed collaboration with the research officer of the Guide Dogs for the Blind, Tony Heyes. We conceived the idea that a person with damaged vision might be assisted by an artificial insect eye stuck on the end of a finger, with an output in the form of a vibrator on the wrist. The eye-on-finger successfully measured the range and direction of the contrasting edges in view. Unfortunately, we could not find an industrial collaborator because there was little profit in making gadgets for the blind. Eventually, when the design of seeing robots became an urgent requirement after the nuclear accident at Chernobyl, our efforts attracted the attention of the Fujitsu Computer Company, which gave The Australian National University \$10 million for our know-how. Later, in the 1990s, the research was also supported by the US Air Force, the US Defense Advanced Research Projects Agency (DARPA) and NASA, which installed our artificial insect vision system into freely flying pilot-less helicopters and drone aeroplanes.

At the end of 1992, I found a topic for my retirement that required little equipment or expense: visual processing of patterns by trained bees. Since von Frisch had shown in 1914 that bees discriminate some pairs of flower-like patterns very well but fail to discriminate geometrical shapes of similar size, the subject made no sense, although plenty of good observations using vertical presentation were made before 1939. In the second half of the twentieth century, there had been a lot of published data on bee pattern discrimination but not much agreement about their interpretation (Chapters 9–12).

Figure 3.1 The optomotor response. a) and b) The beetle *Chlorophanus* was held by the thorax as it walked on a light maze of paper strip. A fixed black drum around it was pierced with holes that allowed stimulation of selected vertical rows of facets. Around this, the stimulating drum was rotated or oscillated. The situation was an 'open loop' because the beetle turned the paper, not itself. c) The open-loop situation. d) Land's experiment; the fly was fixed on a freely rotating pin and the head and body positions were recorded by an overhead video camera. The situation was a 'closed loop' because the fly could turn. e) Interactions in the closed-loop situation.



Sources: (a) and (b) after Hassenstein (1951); (d) after Land (1975).

Motion perception in the second half of the twentieth century

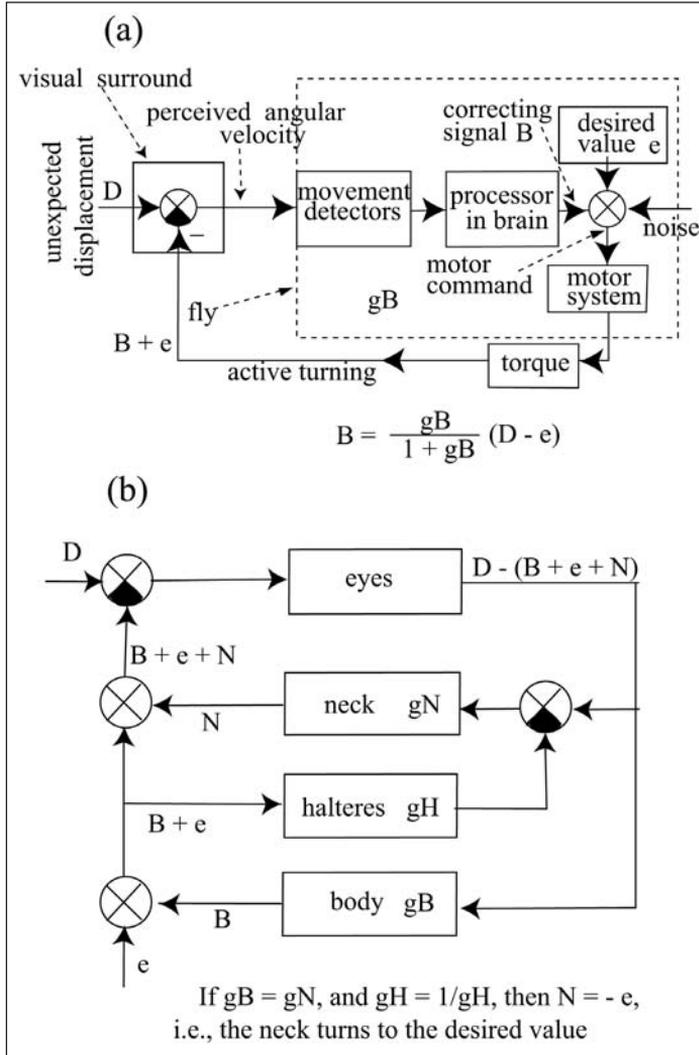
Up to the mid-twentieth century, there had been many descriptions of how particular insects responded to movement in the visual field, but little had been written about mechanisms. Long ago, Exner had pointed out that the detection of the movement of an edge necessarily involved the change in light intensity at one ommatidium followed by the same change at an adjacent ommatidium. The unit detector for motion would therefore have a preferred direction and a preferred angular velocity, with a peak response at the optimum coincidence rate and a fall-off of the response at either side of this peak. Such a detector, however, measures only the timing and therefore cannot distinguish between broad stripes passing rapidly and narrow stripes passing slowly. The motion detector gives a larger response to a more frequent passing of edges, up to a peak, declining at higher frequencies (Figure 3.3c). Also, any response implies either of two contrast frequencies on each side of the peak. With this mechanism alone, an insect would detect the directions of local motion in separate eye regions, but that is all—with nothing about pattern.

The optomotor response

We are all familiar with the way that our eyes follow the movement of the passing countryside seen through a train window. Many animals have a similar response when the whole visual field is moved around them unexpectedly. The eyes (if mobile), the head or the whole body follows the passive motion of the whole visual field on any of the three axes, roll, pitch or yaw. At its most dramatic, a hovering fly rotates in flight to track a patterned drum that is rotated around it. Typically, the eye lags behind the motion and there is a response over a range of low-oscillation frequencies.

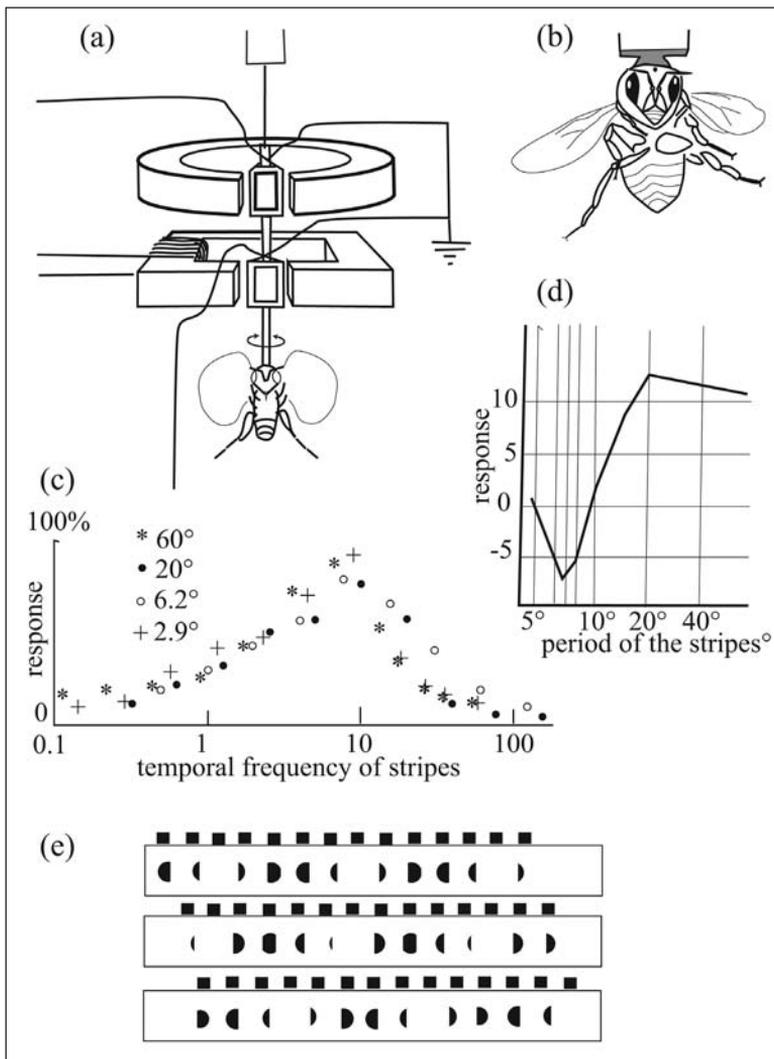
The optomotor response introduced several important ideas into the exact study of behaviour. The directional nature of the motion detection was established a century ago, and a function was inferred to be station keeping when hovering or on the surface of flowing water. The stabilisation of a straight path in locomotion was uncritically accepted. The machine-like performance strengthened the ideas of input–output relations and reflex control of posture by sensory processing that were characteristic of the first half of the twentieth century. In the bee, the response—like all motion detection—was green sensitive and colourblind, which gave rise to some controversy in the early twentieth century after von Frisch demonstrated colour vision in the bee.

Figure 3.2 The interactions during visual control of locomotion with voluntary turning and 100 per cent visual feedback; 'g' is a measure of the gain in the internal loop. a) As usually portrayed for the fly. b) With the halteres included.



Source: From Land (1975).

Figure 3.3 The optomotor response of the bee, 1960s style. a) The bee was held by the thorax on a stiff rod attached to two small coils, the whole being hung on a thread within a large drum (not shown) and free to rotate. When the flying bee exerted a torque in response to the motion of the drum, the electrical signal flowed through both coils and controlled the electric magnet that held the bee in a constant position. The response was a measure of the torque. b) The usual posture of the bee, indicating slow flight. c) The normalised response to the rate of passing of bars on the drum, at four different grating periods, from 3° to 60° . d) The response at the optimum temporal frequency as a function of the period of the stripes. The points where zero is crossed indicate a spacing of 5° in the motion detector. e) The interaction between the bars of a grid and the array of ommatidia can result in perceived motion in the opposite direction to the stimulus, as in (d), caused by the Moiré effect between the spacing of the ommatidia and the bars.



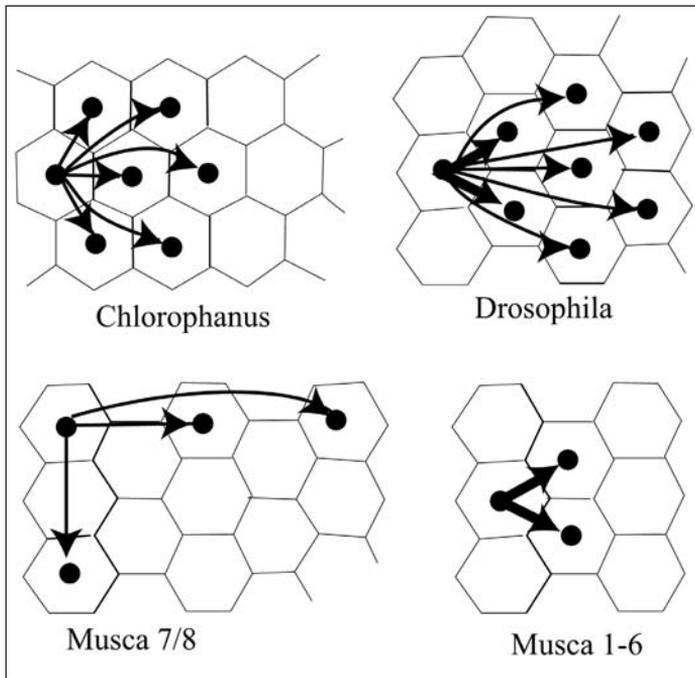
Source: (d) after Kunze (1961).

Various measures of the optomotor response have been made with a variety of insects—notably, the amplitude, the turning force generated by muscles of the neck or by the whole body in flight or the rotation of a ball or a maze of paper strip on which the insect walks (Figure 3.1a). When the body is fixed, the movements of the head as it follows the rotation of a surrounding drum are easily observed in many insects—for example, butterflies and locusts. At the same time, some neurons, particularly in the medulla, lobula and the neck muscles, are easily recorded and respond in a similar way to a moving striped pattern, so that several steps between the input and output can be recorded (Figure 3.5).

In a pioneering study in Königsberg, Lotte von Gavel (1939) plotted the optomotor responses of *Drosophila* to the movements of gratings at different periods at different light intensities. The central region of the eye had the highest resolution. The interesting point was that, as the period of the grating was reduced, the response reversed at a period near 9° . The reversal was correctly explained as a Moiré effect between the interommatidial angle and the grating (Figure 3.3e). The response beyond the reversal point showed that the resolution of the bars at the limit was better than that predicted by the interommatidial angle. The reversal also showed that the fly perceived the best correlation between the adjacent facets with the shortest delay, not the real direction of movement of the drum. At low light levels, the reversal occurred at a larger period of the bars, showing that the spatial tuning of the motion detectors had increased. In an earlier study, to explain why the period at the reversal point increased so much at low light levels, Hecht and Wald (1934) championed the improbable idea of a wide variety of receptor field sizes and sensitivities, and indeed interactions between sub-adjacent visual axes were later found (Figure 3.4). Even at this early date, there were sufficient data to show that insects detected the output of the motion detector as a vector without pattern, not the real image of the bars.

Most mobile animals make a predictable optomotor response when the visual scene is moved, yet this apparently strong reflex disappears when the animal moves itself. There had been many discussions about how the optomotor reflex was switched off during a voluntary movement. Using the popular new systems theory, Horst Mittelstaedt and Erich von Holst (1908–62) outlined the theoretical interactions that might combine visual stabilisation via the optomotor response with self-steering. About 1960, they defined the re-afferent signal, which was the sensory stimulus to the eyes as a result of head movement (Figure 3.2a). Their interactions between boxes joined by arrows influenced many subjects, from robotics to social science. Further, it was proposed that every central neural command to make a movement was accompanied by another command, called the ‘efferent copy’, which would exactly cancel the effect of the expected feedback, so that no optomotor response would follow.

Figure 3.4 The observed spacing of the interactions between ommatidia in the detection of motion in the optomotor pathway, with arrow thickness indicating the relative strength. There could have been other interactions in other channels that were not tested.



Source: After Buchner (1976).

With 100 per cent feedback at the speed of light as the animal moves, the optomotor response is an ideal illustration of the visual feedback loop (Figure 3.1). When the eye turns freely in the response it is said to be a 'closed loop'. The loop is broken when the eye is fixed and the output is measured as the turning force (mechanical torque) in flight or as the rotation of a ball held by the insect's feet. The preparation is then an 'open loop' (Figure 3.1a).

Immediately after World War II, one of von Holst's students, Bernhard Hassenstein, was a great enthusiast but so poor that he had to sleep in a laboratory cupboard. When I was in California, I remember that he had entered the state illegally through quarantine carrying a mud nest of a South American bird disguised as a pudding and a chocolate box containing luminous beetles. The connection between von Gavel and von Holst's student was probably the influential experimentalist Otto Koehler, who literally walked out of Königsberg when the Russian Army arrived in 1945 and escaped to the West.

In his classical experiments, Hassenstein fixed a beetle (*Chlorophanus*) by the head but allowed it to hold a paper ball that rotated beneath it as it walked at the centre of a horizontal drum (Figure 3.1a). Instead of the head moving, the

rotations of the ball were observed, so avoiding the visual feedback in the open-loop situation. The fields of view of the receptors could be restricted by fixed vertical slits. He found that:

1. The turning tendency is zero at very low and also at very high temporal frequencies of passing of stripes (contrast frequencies), but rises as a bell-shaped curve at medium frequencies, peaking in the range 1–20 hertz (Hz) for most insects.
2. The shape of this contrast frequency response curve is independent of the stripe period (spatial frequency) and is not altered by rearrangement of the component spatial frequencies in the pattern on the drum. The insect does not give the same response to the same angular velocity of different patterns.
3. When the contrast is reversed between two successive positions of a regular grating, the insect responds in the opposite direction, apparently making the best correlation it can between the successive distributions of intensity.
4. Adjacent receptors in pairs provide sufficient input to infer motion.

In 1950, Hassenstein showed his results to Werner Reichardt, a former air force officer who had been involved in a plot to kill Adolf Hitler, but who was then working as an electronics expert. Together they introduced the idea that the motion and its direction were computed by cross-correlation of the outputs of each pair of adjacent receptors. This was the minimum mathematical relation that was consistent with the data. Based on the newly emerging signal transmission theory, the pathways of the visual input were considered as filters and the outputs as variable pattern generators.

The success eventually led to the formation of the Kybernetic Forschungsgruppe at the Max Planck Institute in Tübingen, led by Hassenstein and Reichardt, who switched to work on the visual system of the flying fly. After 1965, Karl Götz and Kuno Kirschfeld joined the group. With a period of intense study of the optomotor response by Götz, Buchner, Reichardt, Varju, Wagner and others, work also covered many aspects of the fly's visual system. Later, Kirschfeld and Franceschini showed that just two adjacent visual axes were sufficient to give a response, and Buchner found that sub-adjacent axes also contributed (Figure 3.4). Götz initiated the isolation of the behavioural mutants of *Drosophila* that were later essential to the analysis of straight flight.

A student of Hassenstein, Peter Kunze (1961), gave an account of the optomotor responses of the bee, using the torque produced as the bee tried to turn in flight. The bee was clamped in the standard Tübingen apparatus of the time, which generated an opposite torque that compensated for the bee's efforts (Figure 3.3a). The responses rose to a peak with an increasing rate of passing of the bars on the drum and declined at higher temporal frequencies. The position of the peak near 10Hz was independent of the period of the grating (Figure 3.3c). At the optimum temporal frequency, the response fell to zero at a grating period

of about 10° and was in the opposite direction between 10° and 5° . Adjacent and sub-adjacent ommatidia are involved. The mechanism therefore detects the direction of the modulation sequence, not the direction of the motion, and is certainly not concerned with seeing the bars or the grating.

In this work on the fly and the bee, the insect was clamped and could not make a real turn or a saccade of the head, so there was no visual feedback. The stimulus was controlled by the experimenter and was unexpected by the insect. This had the effect of isolating the optomotor response. The insect soon learns that its efforts are frustrated, so these efforts decline in strength and have to be measured as smoothed averages over many repetitions. Even the posture of the bee changes from that in fast flight to that in slow flight or hovering (Figure 3.1b), as though it is aware that it is going nowhere. Also, the measure of resolution is an average, because it is the value at which the opposite turning tendencies from different parts of the eye exactly balance.

The next step, taken with *Drosophila* and *Musca*, was to introduce into the drum a vertical bar that could be moved independently of the background pattern in the fly's visual field. Later, this became a random-pixel bar on a random-pixel background, called the figure/ground stimulus. The insect would attempt to steer towards the moving bar despite the simultaneous movement of the drum. The researchers thought they were studying the fly's control of steering towards an object moving over a moving background. In a purely mathematical formulation of the interactions in motion perception, the responses were modelled with the same inputs and single output as in the optomotor response, but with an extra layer of non-linear interaction between the same elementary motion detectors to represent the moving bar. Poggio and Reichardt (1976) wrote an account with 125 pages of mathematics and Poggio produced 25 mathematical papers about the Reichardt model. There were many international presentations and a great deal of confidence in this methodology, but also a lot of criticism from elsewhere.

In his remarkably apposite poem of 1958, Frederick Winsor expressed it so:

This is the Cybernetics and Stuff
 That covered Chaotic Confusion and Bluff
 That hung on the Turn of a Plausible Phrase
 And thickened the Erudite Verbal Haze
 Cloaking constant K
 That saved the Summary
 Based on the Mummery
 Hiding the Flaw
 That lay in the Theory that Jack built.

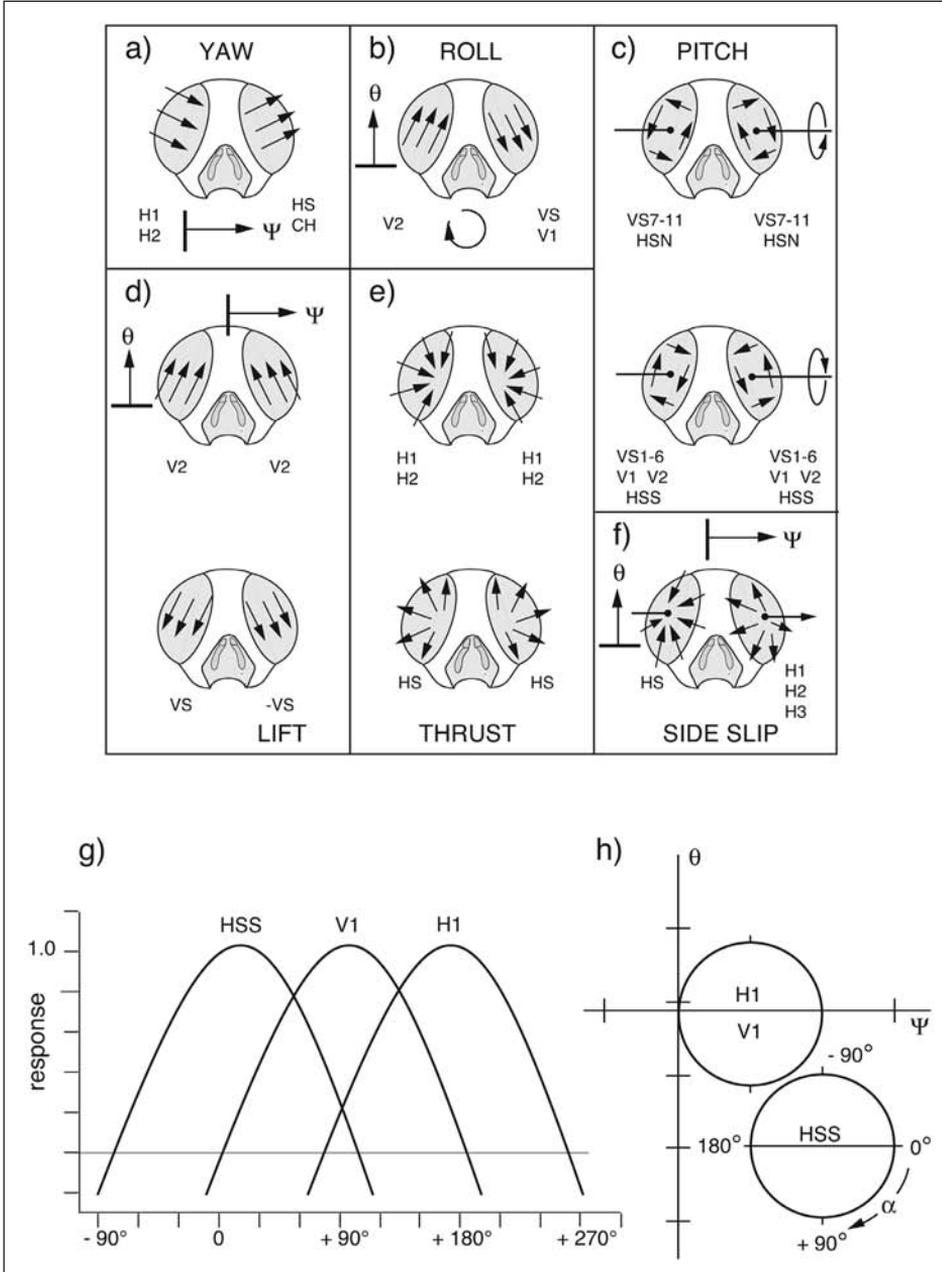
More usefully, and ignoring the maths, Hausen (1982) and Hengstenberg (1982) described in detail the fields and arborisations of the directional motion detector

neurons in the deep optic lobe of the fly (the lobula plate), which gave responses to motion like those of the whole animal. These large neurons sum the motion stimulus in three axes around the head within quite wide fields (Figure 3.5). They illustrate regional specialisation, overlapping fields and coding of yaw, pitch and roll by different overlapping groups of neurons, but none responds to small objects. This result elaborated the earlier conclusions of Götz, based on systems analysis, that the outputs of the motion detectors ran towards the flight-control mechanism. Later, Egelhaaf (1987) described in the fly some neurons that responded to motion of a small object but were inhibited by large-field motion, as known in moths, locusts and dragonflies. He combined them with the large-field motion detectors to explain the responses to the figure/ground stimulus with one homogeneous type of elementary motion detector.

Technical problems appeared in the late 1970s. The frequency range of the optomotor response was too low to apply to free flight. The response strength of the clamped insect was an arbitrary measure, a feeble shadow of that of the freely flying fly, and measurable only when summed over numerous repetitions of the stimulus. Smoothing the output prevented observation of the small jumps made by the eye (called saccades) that later proved crucial for flight control. Mittelstaedt's control theory (Figure 3.2a) omitted the saccades and was wrong for other reasons (see below). Even worse, the clamped insect quickly learned that its efforts to turn were in vain, so the response changed and waned. Work on locusts by Rowell (1971) and later with Reichert (Rowell and Reichert 1991) at Basel indicated several separate neuronal systems. The method of systems analysis, inferring interactions from observations, was suitable for a single channel, but could not separate or characterise several unknown pathways that functioned in parallel. The main weakness, however, was in the data, which recorded a weakened optomotor response but obscured the main agent, the saccades.

There was a persistent difficulty in finding the way forward, because the response plotted as a function of the angular velocity depended strongly on the pattern, being weak for a sparse pattern and strong for a crowded texture, and therefore was no use as a measure of the angular velocity. Such a mechanism was useless for an insect flying in a wind. The response in *Drosophila* was too slow, rising to a peak at about 1Hz and falling to zero at about 10Hz, irrespective of the pattern or angular velocity. In short, the motion-detecting system was unsuitable for a freely flying insect that had to avoid obstacles.

Figure 3.5 a-f) The peak directional sensitivities and approximate fields of the principal motion detector neurons on the optomotor pathway in the fly; V = vertical directions; H = horizontal directions; Greek letters show the coordinates. g) Responses as a function of the direction across the eye. h) Representative fields and their spatial relations.



Source: After Hausen (1982).

Since the work of Kennedy (1940) on the free flight of locusts and mosquitoes, it had been clear that those insects detected their angular velocity and direction relative to the ground and controlled the direction and speed of their migrations according to wind and weather. The difficulty was highlighted by the discovery of neurons in the brain and ventral cord of locusts, and later in dragonflies and bees, which responded in such a way that they could measure angular velocity irrespective of pattern. The way that insects find the source of an odour is to turn upwind when they detect it and then follow the plume upwind, which requires detection of speed over the ground.

The rot really set in at the International Congress of Entomology in August 1972, when Mike Land presented new observations on the behaviour of a fly that was fixed by the thorax but was free to move its head and rotate on a pin (Figure 3.1c):

While flying, but free to rotate, flies [*Calliphora*] show two kinds of head movements. (1) Rapid saccadic movements with amplitudes of up to 20° relative to the direction of the body axis and durations of c. 20 ms. These head movements...are accompanied by body turns which slowly bring the body axis back into line with the head. (2) Stabilization movements which tend to keep the axis of the head still with respect to the surroundings. (Land 1975)

In other words, the head makes a saccade that is so fast that it leaves the body behind and the optomotor system does not notice. The head is then held in the new position by the optomotor response while the body catches up. Human vision is rather similar, but more predictive.

Continuing Fred Winsor's (1958) version of the scientific method:

This is the Space child with Brow Serene
Who pushed the Button to Start the Machine
That made (Hay of) the Cybernetics and Stuff
Without Confusion, exposing the Bluff
That hung on the Turn of a Plausible Phrase,
And shredding the Erudite Verbal Haze
Cloaking Constant K

For a decade, there had been doubt about whether the equations describing optomotor behaviour were related to the mechanism, but errors of thought and misuse of the mathematical muse were no longer the point when serious flaws were disclosed. The first flaw in the house that Jack built was that the fly's head had been clamped, so it could not see the effects of its own turns. The second flaw was the insensitivity of the equipment and the misleading averaged data that had omitted the saccades.

In studies of photographs of male flies chasing females in free flight, Land and Collett (1974) characterised the mechanisms by which the flying fly fixated on a small moving object, measured its angular velocity and turned to pursue it. Others separated the components. Srinivasan and Bernard (1977) found that the response of the fly to small moving objects, such as a bar, and to broad-field stimuli, such as the background, had different time constants, and Olberg (1981, 1986) distinguished the object-detector neurons of the dragonfly from the optomotor neurons.

Meanwhile, Strausfeld and his collaborators were anatomically separating the neurons specific for the chasing behaviour from those for the optomotor response. The connections were not to the flight muscles, as predicted from the Reichardt theory, but to the neck to turn the head. Later, we found that the directional motion detector neurons in several groups of insects were of two types—the slow optomotor ones and faster ones going up to 200Hz. As more electrophysiology and anatomy appeared, motion detection became more complex, there was not a single unit motion detector and the details required by the Reichardt theory were not found (see Figure 6.6). It was realised that mathematics could not be connected directly to behaviour and the whole idea of computational neurobiology was a house of cards. Of course, not everybody agreed, but books full of rubbish were published on the subject for years after.

Angular velocity

A flying vehicle must be sensitive to the perceived angular velocity of nearby objects and the surrounding panorama. Indeed, the early block diagrams used to summarise the optomotor response had in fact used angular velocity as the variable (Figures 3.1 and 3.2), but no-one had noticed. The importance of the whole gradient of angular velocity of the optic flow was taken by J. J. Gibson from classified wartime work on landing aeroplanes at Farnborough, England, and later published in an influential book on the subject.

One of my students, Jenny Kien, discovered two neuron types in the deep optic lobe of the locust, one (M1) sensitive to forward motion across the eye, the other (M2) to backward motion. The relation between response and velocity was independent of the period of the stimulating striped pattern. Neuron M1 received inputs from small fields 1–5° in diameter, with the maximum response to interactions between every fifth ommatidium along a horizontal row. The M2 neuron had maximum effect with every sixth ommatidium. The optimum excitatory interval corresponded with an angular velocity of 20° per second (Kien 1975). Although this mechanism solved the problem of velocity measurement by demonstrating different spacings of the inputs, the result was ignored for years.

In the 1980s, John Kennedy returned to the topic and, with David (1979a, 1979b, 1982), showed that freely flying *Drosophila* responded to the angular velocity of the flow field and to parallax, but not to the contrast frequency. In Canberra, we worked out the use of the angular velocity by the flying bee to measure range and avoid obstacles (Lehrer et al. 1988), and later Srinivasan et al. (1996) showed that bees measured angular velocity irrespective of direction and integrated it to measure the distance flown over the ground.

On mature consideration, it was obvious that after damage to their wings that spoiled the equal traction on the two sides, bees, dragonflies, butterflies and flies quickly adjusted and flew in a straight line. Also, insects can fly in a straight line inside a moving motorcar without turning towards or against the perceived motion outside the car. In the literature, there are many examples of how damaged insects rapidly learn to adjust their normal posture and movements—notably, when a leg is removed, and in the demonstration of learning of postural positions of the legs by headless locusts (Horridge 1962). A complex robot cannot survive in an unpredictable environment without rapid learning mechanisms to assist in the control of its posture and movement. Similarly, we rapidly learn to ride a bicycle or steer a boat with a tiller.

The control of straight flight in the fly

With little previous warning of its explosive contents, in 1984, Martin Heisenberg and Reinhard Wolf published a book about the way that the fly *Drosophila* controlled its flight path in the horizontal plane. As described further in Chapter 7, they showed that the fly responded quite differently to visual feedback from its own active motion and to passive rotation of the visual scene around it. They also showed that the saccades indeed controlled the straight flight of *Drosophila*, and later discovered that there was a dead reckoning of angular turns, so they kept a tally of all turns and could return to the starting direction. These discoveries meant that the averaged responses of a fly with fixed head were no longer relevant. For decades, the stabilisation of the flight of the fly on a straight track had looked like an inflexible optomotor reflex, but this revolutionary analysis done on *Drosophila* showed that if one wing was damaged or if the feedback loop was modified, the fly could quickly learn by operant conditioning how to reset the controls and steer once again on a straight course. The learning is called ‘operant’ because the fly makes voluntary movements and correlates its intentions with the resulting feedback.

Just as the fly can learn to fly on a straight course visually without an isolated beacon although its wings are not symmetrical, by making tentative test saccades in either direction, it can learn to direct its course towards a target that rewards it with scented or warm air. Flight speed (thrust and lift) and turning in the yaw plane can also be modified by learning. The fly finds its goal by checking the results of making saccades. More and more, it is apparent that the responses to

visual motion are rapidly changed by other actions of the insect. The concept of an optomotor reflex has been replaced by a goal-directed action with continual operant learning of all motor outputs, providing active stabilisation against unexpected movements. This surprising result probably applies to all insects. For years, Reichardt and his colleagues at Tübingen ignored the early work of Kennedy (1940), the saccades later recorded by Land and the efforts by Heisenberg at Würzburg.

A research group with Martin Egelhaaf at Bielefeld has now taken up the enormous challenge of recording from the visual system and at the same time displaying to the eye the visual input in three dimensions (in open loop) that would eventuate if the eye were not clamped. They started by recording the exact motion of a fly, and its head movements, as it flew about in a box with a pattern on the inside surface. The pattern seen by the two eyes was then computed for that flight trajectory. The real stimulus at the eye was presented as the input to a computer model of the proposed motion detectors, represented by one of the large field detectors of horizontal motion of the lobula plate. Because the neuron is working outside its linear range at the saccades, the responses are insensitive to the choice of pattern in the visual field. It is still true that the responses of the fly's motion detectors are tuned to temporal frequency, not spatial frequency, and do not measure angular velocity. The way they interact, however, with the distribution of different spatial frequencies in the natural background, and an active control of gain, is dominated largely by the saccades, as in the two-dimensional situation in the horizontal plane. In other words, the optomotor component no longer dominates.

If we stand back in a critical mode, we see that the optomotor response is now just a mechanism for recovery from unexpected displacements during locomotion. The figure/ground stimulus was discarded when the separate fast and slow parallel channels with small and large fields were discovered. In the fly, the control of direction is dominated by the saccades, and insects have a memory of the retinotopic positions of outstanding contrasts at each place and of the accumulated angle turned. The motion detection is still consistent with the Reichardt model, as indeed any directional motion detection should be, and some synaptic circuits have been proposed, but not yet securely identified. Also, in the fly, the analysis will have to be extended to the halteres and the motor neurons (Figure 3.2b).

The bee often flies very slowly and appears to be different in its flight control, but it could turn out to be similar to the fly. The bee scans from side to side in flight, with small saccades of the head. In the natural environment, and in tunnels with patterned walls, the bee integrates the measured angular velocity of the flow field and remembers the distance travelled over the ground, but also detects the flight speed mechanically with head hairs and the antennae. The bee equalises the angular velocity of the flow field on the two sides and

adjusts the flight speed to maintain a preferred angular velocity of the flow field irrespective of the pattern. Whether this is fundamentally different from the fly awaits further experiment, and it would be nice to have corresponding data from other insects to see how far the flight control is adapted to lifestyle.

It was a mixed blessing that most of the work was on the housefly and *Drosophila*. Being wandering scavengers, these flies have relatively simple visual behaviour compared with the bee.

The perception of motion by flying insects illustrates the fashions of the decades and how the Tübingen optomotor response was attacked in the work of Land and Collet, Goodman, Hausen, Hengstenberg, Möhl, Rowell, Strausfeld, Wehrhahn and many others, as the system became better understood, and then replaced by Heisenberg and Wolf. The mechanism of free flight of the fly is now being intensely studied by Martin Egelhaaf and colleagues. There is also a major effort in the United States to identify every synaptic connection between the neurons of the *Drosophila* optic lobe in an effort to separate all the arrays and systems with partially overlapping inputs and outputs. The story has not concluded.

Endnotes

1. A large number of personal names appear in this chapter. Further details can be found in the bibliography.