Invertebrate vision

Ten distinct eye designs have been identified in the animal kingdom. Whereas vertebrates possess only one, invertebrates possess all ten, from simple assemblies of photoreceptors to advanced compound and camera eyes, which support a sophisticated range of visual behaviours. Many invertebrates have exquisite sensitivity to light, can distinguish a broad spectrum of colours, detect subtle polarised light cues, and negotiate obstacles at high speed. The basic principles used to acquire and process such visual information are remarkably similar across the animal kingdom. In invertebrates, these principles frequently involve neural tricks and short cuts, some of which have been successfully exploited to create artificial visual systems for robots. *Invertebrate Vision* is a complete synthesis of our current knowledge concerning how invertebrates see, the principles used to process visual information and how vision is used in the daily struggle for survival. It will appeal to anyone interested in the vision sciences.

ERIC WARRANT and DAN-ERIC NILSSON are Professors of Zoology at the University of Lund, Sweden. Warrant is interested in optical and neural adaptations for vision in dim light and studies species from nocturnal tropical insects to deep-sea fishes. Nilsson focusses on the evolution of eyes and visual processing and has studied much of the animal kingdom. His current research is centred around vision in the box jellyfish.

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Frontmatter
More information

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More information

Dedicated to our parents

Contents

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Frontmatter
More information

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More information

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Frontmatter
More information

Foreword: Reminiscences of the St Andrews and Canberra efforts on the compound eye

It gives me great pleasure that at least 30 of those at this first International Conference on Invertebrate Vision, and a third of the speakers, have worked in my lab at one time or another, and there did some of their best work. It has been a fascinating story at opposite ends of the world, expensive in time and funds, and an immense collaborative effort. The competence and camaraderie of these past associates is evident at this meeting. It is rewarding to see how many able students have gone on to successful careers after a basic training on the techniques for study of insect and crustacean vision. Many of the names mentioned below are now distinguished professors. Some are even still working on the same topic. The eye is the window of the brain; invertebrates offer some hope of understanding how vision works; there are many fascinating animals to study, and great practical applications have already emerged unexpectedly.

In 1960, I returned from California, from working on a book with Ted Bullock, to become Director of the Gatty Marine Laboratory of the University of St Andrews, Scotland. My predecessor, Jimmy Dodd, had taken his fish endocrinology group to another university, so I inherited about 2000 m^2 of empty lab space, with an aquarium, boats, and access to funds for extensions and equipment – a vast opportunity. My research fell by accident into the topic of the compound eye at a time when funding became abundant. In 1962, four students, David Sandeman, Reg Chapman, John Scholes, Jonathan Barnes, and I, were working on a variety of invertebrates, notably crab eye movements, crab axons and optic lobe, polychaete neurons and leg learning in cockroaches and locusts, when Burtt and Catton at Newcastle published a ludicrous account of the locust compound eye

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Frontmatter
More information

as a diffraction grating with summation of rays at different levels in the receptor cell layer. Two newly arrived students, John Tunstall and Steve Shaw, needed a topic and we decided to tackle the insect retina. Since 1952 I had been recording from neurons. We had built a workshop, appointed an electronics technician, and designed and built all the amplifiers and other apparatus. We built electrode pullers, cardan arms, shutters, and filter wheels as fast as we could, and described the photoreceptor fields by intracellular recording. Because he did not work by day, Scholes discovered photon arrivals for the first time in an insect eye and, with the electron microscope in the Zoology Department, Tudor Barnard described the palisade that appears in the dark-adapted eye and alters the light-guiding properties of the rhabdom. We ourselves had to devise the methods that we continued to use and improve later. They were years of rapid discovery; the students lived in the lab, day and night, fixed their cars in the workshop, cooked their meals in the lab kitchen, and never forgot the excitement of it. The lab freezer was always full of fish, lobsters, ducks, and pheasants they had somehow caught. A part of the joie de vivre sprang from the certainty that all would get a job without difficulty, and that real discoveries were being made. A summary of that early work on the locust is in the Stockholm Symposium of 1966 on the Compound Eye (ed. C. G. Bernhard). In 1966, I published 26 papers.

In the same period, Malcolm Burrows (elected to the Royal Society in 1985) recorded the activity of all the muscles in the crab eyestalk and Pete Shepheard discovered that a crab remembers the position of contrasts in the surrounding world as a retinotopic projection. This discovery was taken up by Rudiger Wehner, who was just beginning his period of training bees to come to black bars on a vertical surface. The crab detects black/white edges quite separately from broad areas of black; this was our introduction to the two separate systems. The eye responds at angular velocities less than earth speed (15°/h), and the accuracy is much better than the interommatidial angle. The results were totally at odds with the Reichardt model of motion detection by the compound eye, as was the behaviour of the freely moving crab eyestalk in tremor and when recovering from an eye retraction.

At St Andrews we could catch drone bees, water beetles, and dragonflies in summer, and we found that we could record much more easily from insect eyes than from crabs or lobsters. I had a mysterious visit from the Professor of Genetics at ANU, David Catcheside, who looked over the Gatty. He was actually looking for staff, but said he

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Frontmatter
More information

had come to visit Professor Callan, who worked on giant chromosomes and occasionally removed lobsters from the tanks of specimens for classes.

In 1967, Steve Shaw and I had Grass and Lalor Fellowships to work at Wood's Hole, Massachusetts, where we took our recording gear and caught dragonflies at Prosser's pond, with a net made from one of Hazel Prosser's net curtains. There, I discovered fireflies winking at night in the bushes and collected them for electron microscopy of the light guides in the eyes. Steve got a job at Vancouver, and that first generation of students had left before we thought of going to Australia. 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!'

There was a new group around me by now, working seriously on optics and recording from compound eyes. I had a project with a physics student at Dundee University who built a wax model of a locust ommatidium and shone radar waves down the axis. We had great trouble with standing waves in it, caused by reflection at the end of the rhabdom, but we managed to get some measurements of angular sensitivity. We worked on superposition eyes of beetles for some years and Rick Butler, from Canada, started on the cockroach eye. While at Wood's Hole, I had another mysterious visit, this time from Dennis Carr, who was the third of the founding professors for the Research School of Biological Sciences in ANU, Canberra, Australia. Then a cable arrived inviting me to consider the fourth of those founding chairs. So I went straight from America to Australia, but, before accepting, I had a good look around several departments of Zoology in Australia, and travelled through Papua New Guinea and along the Solomon Islands and Fiji back to America to discuss the matter with my wife, Audrey.

I sent Ian Meinertzhagen out to Canberra to order equipment and get the labs ready. He was selected because he had run out of funds for his PhD and needed more time to produce complete maps of retina–lamina synaptic connections in various insects. We brought 18 pieces of luggage and four children, and flew out via Athens and Malawi, then by ship from Durban. In August 1969, we were met in Sydney by two drivers with RSBS cars. There was a house and a temporary lab ready. I also brought out a whole lab full of people from the UK; Ayis Ioannides was a scholar who couldn't go home to Cyprus, where there was a war on; David Sandeman, Peter Shelton, Ben

Walcott, and Rick Butler also came from the Gatty. Young post-docs Mark Tyrer with Jen Altman, David Young, and Eldon Ball, and an EM technician, Margaret Canny, from elsewhere. All of these were housed by ANU. Our very useful technician, Bob Jackson, was the son of the CSIRO workshop chief, and had grown up in Canberra, so he knew exactly where to find anything that was needed. Basically, we transferred the know-how from St Andrews to Canberra and started with a bang.

Allan Snyder turned up about a year later, not knowing one end of a rhabdom from the other. He worked closely with us for some years on the optics of ommatidia. That provided the inspiration for his analysis of polarising monomodal light guides and their application in long-distance transmission in light guides for communications. For this work he was elected to the Royal Society in 1990.

The new scholars from 1970 until about 1985, were given generous 4-year ANU scholarships, which seemed to be always available, and which included return fares. So there was a steady flow from Cambridge and Europe to Australia. (One, indeed, was arrested drunk in charge of a bicycle.) Training was in optics, electrophysiology, electron microscopy, online data processing by computer, and the relation of neuron activity to behaviour. Most worked on compound eyes or ocelli. Everyone who wanted a job in those days could find one with that training. The students made a daily effort to record from difficult eyes with small receptor cells, mayfly eyes, spider eyes, eyes with mobile receptors. On a bad day you might find one seeking comfort in the secretary's office. Laughlin, Doujak, Wilson, Lillywhite, Hardie, Dubs, Howard, Payne, Matic, Shi, and others counted photon arrivals in a variety of eyes. We were the only lab in the world doing that kind of work, and most recordings of day–night changes, absolute and contrast sensitivity, measurements of noise, and optics of unusual insect eyes were first done in Canberra. The policy that I introduced was to insist on extensive technical training, to provide apparatus and assistance, then let the students keep their data and publish their own work. This policy produced winners from the best of them. There was endless spin-off, stimulation to learn more, and little stress from outside.

There was a memorable period in the mid 1970s when Stavenga, Snyder, Laughlin, added to by Pinter, Srinivasan, and Howard, consolidated the data (mostly from our own lab) on photon capture, 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 Hardie, James, and Howard analysed the function of the large lamina ganglion cells, which produce a temporal derivative of the photon flux and compress the signal. Later Laughlin went on to show that the properties of these cells minimise the noise and maximise the signal. This became the best-known example of optimisation in a visual system, and Laughlin was elected to the Royal Society in 2000.

There were abundant funds for international visitors. We had quite a name; as a rest home in the sunshine for American professors escaping their winter and income tax, or as a culture shock for Japanese professors who found themselves doing the washing up. One Swedish Head of Department asked me to take his proposed successor and teach him a thing or two. A German professor cleverly persuaded me to provide a job for someone he could not stand any longer. A cash-strapped English university asked me to help out for a couple of years by funding one of their bright chaps (recently also elected to the Royal Society). From 1987 to 1996, we were a marriage bureau for the pretty Asian students. Maddess, Dubois, Aleksic, Osorio, James, Holmqvist, and Giger all found bliss there. Because he did not, Joe Howard was obliged to wear a sarong when he had no clean underwear.

Meanwhile, as a result of the move to Australia, we had analysed the retina in many insect groups by recording from retinula cells, by detailed anatomy and by optical methods. Gert Stange showed that the dragonfly ocellus controls pitch and roll in flight by summing the illumination from horizon to horizon, and Martin Wilson showed that the locust ocellus detects the position of the horizon mainly by ultraviolet light. We distinguished between the day and the night eye instead of the light- and dark-adapted eye. Some of the retinula cells in night-flying beetles and moths make large movements between day and night states. By day, highly refractive guides carry light from the cone tip to the retinula cells in many of the nocturnal insects that have a clear zone in the night eye. 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 star light. In fact, in 1985, Doujak had shown that a single crab ommatidium could detect a star. With Eric Warrant and Almut Kelber, this tradition is still alive at Lund.

A recurrent problem was, and still is, how to analyse the several parallel processing pathways in the insect visual system. For years

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Frontmatter
More information

we had tried recording in the optic lobe, but the puzzling properties of the neurons in fastened insects could not be explained by the poorly known visual behaviour. 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 success was Jenny Kien's discovery of neurons in the brain of the locust that were tuned to the angular velocity of the flowfield. Similar neurons were found in the crab eye-stalk by Sandeman and Erber, although most optic lobe neurons are tuned to a low temporal frequency of passing edges. In another significant advance, in 1984, Maddess discovered that optomotor neurons are most sensitive to a frequency that increases as they adapt to high frequencies, that is, the system becomes more sensitive to faster motion. Danny Osorio identified neurons of the locust medulla. Later, with Ljerka Marcelja I showed that several groups of insects have slow and fast motion detector neurons (just as they have 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.

Like Heisenberg and Wolf (I am sorry they are not here), I had never considered that the Reichardt theory could explain the visual control of free flight of insects. I visited John Kennedy and his student, David, at Imperial College, London, before they published in 1986. They had found that freely flying *Drosophila* measures the angular velocity of the flow-field and could detect parallax, as one object moved behind another nearby. This work encouraged me to look at range estimation by walking mantids as they reached the end of a twig, and to think about mechanisms of visual control of free flight. Fortunately, Srinivasan wanted to come back to Canberra from Zürich, and he soon brought Miriam Lehrer from there each summer to teach us how to train bees. We also brought Zhang from Academia Sinica, Beijing.

This new group started on the visual detection of objects by the flying bee. We found that bees measure the range to surrounding objects by measuring the relative angular velocity induced by their own motion. The mechanism could be applied to artificial vision. We joined forces with Tony Heyes of the Royal Guide Dogs for the Blind, and with a grant we progressed towards making an eye-on-finger that worked on the same principle, but we could not find a manufacturer for a gadget for the blind. Then, after Chernobyl blew up, the Japanese Fujitsu Co., anxious to make vision for mobile robots, gave ANU 10 million dollars for our know-how. The principles were later sold again to the

American military and to NASA, to install in helicopters and small autonomous flying vehicles. Srini went on to show that in their dance, bees report the distance flown as the integrated velocity over the duration of the outward flight, and that they learn rules about how to run mazes. For this work Srini was elected to the Royal Society in 2001.

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, for which the months of Australian sunshine are ideal. 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. After many experiments with the Y-choice box for flying bees that was first used by Srini and Lehrer in Canberra in 1987, I concluded that bees discriminate a few types of cues but patterns in the image are not re-assembled, and there is doubt that they see any pattern or objects as we do. There are a variety of coarsely tuned pre-adapted wide-field filters for a few very simple common parameters of the visual world, and that is all. So we finally get around to the question 'What do insects see?' and conclude that the bee brain detects the range and directions of a few simple cues, from which they construct a map at each place. It is not often that research destroys its own topic, but it is now clear that there is no vision of pattern, only a subtle way to make a sparse map of the surrounding panorama. Bees, and probably all invertebrates with eyes, suffer from perpetual blindsight, in that they can detect a variety of cues but they do not reconstruct patterns.

In retrospect, the enthusiasm for research was nurtured in a surprising number of young scientists by insisting on a broad basic understanding ranging across behaviour, optics, anatomy, electrophysiology, and online data-processing and difficult techniques to carry the work ahead. The aim was an experiment every day; the key was the choice of the right experiments, patience but persistence, and then encouraging students to publish so that those who did the work got the acclaim. We consciously avoided nasties, such as radioactivity, carcinogens, infections, toxins, vivisection of vertebrates, or mechanical danger. We had a mania for the experimental approach, adequate funds, no interference from management, good libraries, and relative isolation from distractions. Those were the days!

Adrian Horridge

Preface

The invertebrates – animals without backbones – constitute the vast majority of all known species of animal life on Earth. From a giant squid swimming in the dark cold depths of the sea to a tiny ant foraging in the leaf litter of a rainforest floor, the invertebrates have conquered almost every imaginable habitat. This extraordinary adaptability is in no small part due to their sense organs, and particularly their eyes, which help them find food, locate mates, escape predators, and migrate to new habitats. Even though most invertebrates do not see as sharply as we do, many see much better in dim light, can experience many more colours, can see polarised light, and can clearly distinguish extremely rapid movements. Moreover, they do all this with eyes and brains a fraction the size of our own. It is this small size – and comparative simplicity – that has allowed scientists to unravel many of vision's most fundamental principles, as equally applicable to a dragonfly as they are to us. Due to their small size, invertebrates often rely on comparatively simple circuits of cells to efficiently decipher complex visual information. Many of these circuits – and the computations they perform – seem ingenious to a human observer. Indeed, many have already been used with great success to create artificial visual systems for robots, aircraft, and autonomous vehicles.

This book explores the most important functional modalities of visual sensation in invertebrates and how vision is used in daily life, from the capture of light and its neural processing, to the ways invertebrates use vision to orient, to navigate, to avoid predators, and to find food and mates. Two early chapters (Chapters 1 and 5) deal with the optical designs and spatial resolution of invertebrate eyes, and how they have evolved to match the ecological constraints imposed by habitat and lifestyle. Ten distinct eye types have been identified in the animal kingdom. Whereas vertebrates possess only one of them,

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Frontmatter
More information

invertebrates possess all ten, from simple assemblies of photoreceptors that underlie phototaxis to advanced compound and camera eyes that support a sophisticated range of visual behaviours. Once light reaches the retina, the photoreceptors must absorb and convert its energy into the electrical signals that are ultimately responsible for visual perception. The cellular and biochemical mechanisms that are responsible for this conversion in invertebrates are dealt with in Chapter 2. As Chapter 3 reveals, the eyes of invertebrates are also remarkably sensitive, with photoreceptors that function as highly efficient photon detectors, allowing many species to see extremely well in dim light. This sensitivity tends to increase at night, and decrease again during the day, a modulation that is caused by a biological circadian rhythm. The cellular and physiological mechanisms responsible for the circadian change in visual sensitivity are explained in Chapter 4. The transition from night to day is not the only environmental transition that has influenced the evolution of vision in invertebrates – many species make frequent transitions between air and water, two media with very different optical properties. These differences have had a significant influence on the evolution of vision, and are the subject of Chapter 6. Both above and below the water surface, invertebrates (like vertebrates) rely on many different kinds of visual information to execute the daily tasks of life. They need to distinguish the sizes, colours, and locations of features in their habitat, to respond to conspecifics, detect predators and prey, negotiate obstacles during locomotion and recognise familiar landmarks during homing. To successfully ‘see’, invertebrates rely on colour, polarisation and motion cues, the acquisition and neural processing of which are dealt with in Chapters 7–10. The book concludes with two chapters that explore the visual abilities of the honeybee, one of our best-studied invertebrates. These chapters ask how invertebrates actually use vision once all the various modalities of information have been processed. How, for instance, do bees use vision to negotiate obstacles during flight, or land gracefully on a flower, or calculate and remember the distances and routes flown to and from familiar landmarks? The answers to these questions – all of which involve a neural analysis of optic flow – are revealed in Chapter 11. Possibly the most poignant question of all is posed in Chapter 12: apart from the obvious differences in spatial and spectral resolution, do bees actually see the world as we do? Using elaborate pattern recognition experiments as support, the answer, it seems, is ‘no’.

This fascinating story, of how invertebrates see the world, is told by the leading experts in the field. A recurrent theme is that vision is intimately related to ecology. The eyes and visual system of the dragonfly, a fast-flying diurnal hunter, are very different from those of a bottom-dwelling deep-sea crab – lifestyle and habitat have both played a profound role in the evolution of vision within the invertebrates. The great variety of eye designs and processing strategies found among the invertebrates is not only testimony to this inescapable fact, but also provides an unending source of wonder and excitement for those of us privileged to work with them.

This book resulted from an enthusiastic gathering of 123 scientists at the first International Conference on Invertebrate Vision, held at Bäckaskog Castle in Sweden, from 7 to 12 August, 2001. We wish to thank all the participants for inspiring the creation of this book, and for the warmth and excitement we all shared during that remarkable and eventful week. We are particularly indebted to our authors, whose chapters reveal the beauty and intricacy of the invertebrate visual system and whose hard work has made this book possible. We also wish to thank our editor at Cambridge University Press, Martin Griffiths, who has, with very good humour and patience, put up with countless broken deadlines and steered this project to completion.

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Dan-Eric Nilsson