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I was introduced to neurobiology, first by Don Kennedy, a great role model as a brilliant teacher-researcher, and later by Don Wilson, the genius behind the role of central rhythm generators in behavior. Kennedy and Wilson showed how much we have to learn about brains from studying the brain and behavior of invertebrate animals. Eric Kandel, Seymour Benzer, and Sydney Brenner inspired many of us by tackling the 'big problems' of neuroscience through the study of invertebrate animal models.

What books or articles influenced you most as a student? "*Nerve cells and insect behavior*" (1967) by Ken Roeder and "*What the frog's eye tells the frog's brain*" (1961) by Jerry Lettvin. They set the agendas for theory and practice in neuroethology.

What advice would you give to a new professor? I observed (via Kirschner, Kennedy, Wilson) that no matter how much you love research, take your classroom teaching seriously because your research will be better for it. It's worked for me.

If you hadn't made it as a biologist, what would you have liked to become? If only I had the talent, a musician or a mathematician, preferably both, but alas…

Your brand of behavioral neuroscience is called 'neuroethology' — why? It means I study behavioral acts and the neural systems that generate them through the lens of evolution — natural selection and adaptation. I love natural history and am fascinated by the way that evolutionary forces shape the behavioral acts by which an animal fits into its ecological niche.

What do you think are the big issues in neuroethology and what do you think are the biggest problems it is facing today? I fear that neuroethology is an endangered field, certainly in the United States, if not elsewhere, by governmental funding priorities. With the turn of the 21st century, the N.I.H. narrowed its funding portfolio primarily to emphasize four animal models: *Drosophila*, zebrafish, *Caenorhabditis* and mice; the 'Core-Four' model animals. They share one outstanding feature: genetic tractability. I have no problem with the Core Four receiving the lion's share of research funding. I just hope there can be some grant funds for non-genetic discovery science, like neuroethology, that will surely come from mining the biodiversity of neural systems and behaviour mechanisms. My worry is that the Core Four will become the *Final* Four.

In the age of translational biomedical science how do you justify neuroethology? The human genome project ushered in the age of the Core Four and the thriving, exciting, sister field of comparative genomics, which integrates evolutionary biology with biomedically-oriented genomics. Similarly, neuroethology has the same potential as a touchstone field. Neuroethology will help link human behavior, including neurological function and dysfunction (pathologies) to its evolutionary roots. Neuroethology is at base a comparative science; the comparative method rests on common evolutionary roots. From these roots grow diversity—function and even dysfunction — it's as true for physiological function as for anatomy and morphology.

Why do you emphasize evolutionary biology — is this personal? As a student I was always impressed with two great biologists, August Krogh and Theodosius Dobzhansky. Krogh's principle says "For many problems there is an animal on which it can be most conveniently studied" and Dobzhansky said, "Nothing in biology makes sense except in light of evolution." Big ideas and perhaps hard to implement at the bench, day-to-day, but they shine a bright light, even today.

What have been the most satisfying aspects of your career, so far? To have an academic career at a great research university, Cornell, where I've been privileged to have 'mentored' over 50 graduate students and postdocs, most of whom have their own successful academic careers. I'd like to think each person discovered how to make the most of their own talents in my lab because I don't teach how to do research. I've been very fortunate to have able younger colleagues come to my lab.

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Book review

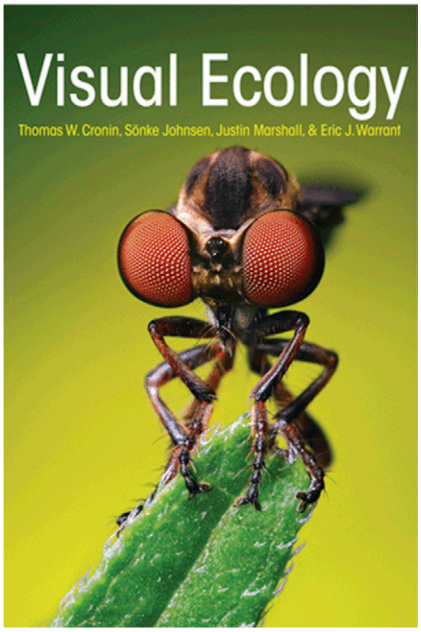
Ways of seeing

Michael F. Land

Visual Ecology
Tom Cronin, Sönke Johnsen, Justin Marshall and Eric Warrant
(Princeton University Press, Princeton, NJ; 2014)
ISBN: 978-1-400853-021

The scope of the subject of *Visual Ecology* was first defined by John Lythgoe in his 1979 book *The Ecology of Vision* [1], and was based on the physical nature of light in the world (which is the same for all creatures) and the physiology of the eye (which is much more diverse). The present authors have taken up Lythgoe's themes, but their definition of the subject is rather more comprehensive: "how visual systems function to meet the ecological needs of animals, how they have evolved for proper function, and how they are specialized for and involved in particular visual tasks." Most of the book remains mainly about physics and physiology, and the authors resist the temptation to stray too far into the potentially enormous field of vision in animal behaviour.

This is a beautifully produced book. It is large (400 pages), and extremely well illustrated with appropriate colour and monochrome images throughout the text. The four authors from three continents are all excellent biologists who have worked with each other in the field — or more often the ocean — and are certainly the best people to have written a book like this. Sönke Johnsen is a rating physicist (and author of *The Optics of Life* [2]), but the other three are all well versed in physical, chemical and biological aspects of vision. Of the 12 chapters in the book, excluding the Introduction, five are mainly concerned with particular features of light that animals use or have to deal with (the optical environment, colour, polarization, vision in attenuating media and vision in dim light), four with eye structure and function (visual pigments, optical components, eye design, and spatial vision) and three are more related to behaviour (motion vision and eye movements,



orientation and navigation, and signals and camouflage). I would not hesitate to consult this book on any subject within its remit. In what follow I can only offer samples from a book of impressive scope.

Throughout the book we are reminded not to take for granted that other animals see the world as we do. "Resolution is arguably our best developed visual capability. Compared to many other animals, our eyes are not particularly sensitive to light; nor is our sense of color especially good. The undoubted splendors of nature's ultraviolet colors are totally invisible to us, as are the world's rich natural sources of polarized light" (pp.116–117). These themes are developed at length in different chapters: dim light in chapter 11, colour in chapter 7, and polarization in chapter 8. What is surprising is not that other animals have these capabilities but that we have lost or failed to develop them. Even among primates, tarsiers, bush babies and owl monkeys have excellent night vision (p. 270). Many birds have tetrachromatic vision, enhanced by oil droplets in the cones, and often have a channel in the ultraviolet (p. 154). Some fish can probably see polarized light, but amongst arthropods, with better suited receptors, this capacity is routine — mantis shrimps can even make use of circularly polarised light, a capacity involving some rather special optical engineering (p. 192).

Our ability to resolve well is the eventual outcome of experiments begun in the Cambrian period, half a billion years ago, when a wide variety of optical systems were tried out. Most are still with us: lens eyes evolved in molluscs and chordates, various types of compound eye in the early arthropods, and even eyes using concave mirrors in some invertebrates (p. 95). Perfecting the optics required the solution to several problems, not least of which was the evolution of lenses free from spherical aberration — the tendency of rays away from the optic axis to be over-focussed — which, in a spherical lens, produces an unusably blurred image. The solution is to vary the refractive index along a specific gradient that decreases from centre to periphery (p. 99), but how this is achieved and maintained in a growing lens remains a mystery. The evolution of vertebrates onto land involved the incorporation of the refractive cornea into the optical system, and a corresponding reduction in the power of the lens; amphibious vertebrates, such as the 'four-eyed fish' *Anableps*, have evolved some extraordinary optical solutions to the problem of seeing in two media (p. 101). I should come clean here. Much of this section of the book parallels *Animal Eyes* by myself and Dan-Eric Nilsson [3], which the present authors acknowledge, and apart from the superb illustrations there was not much new here, at least to me.

Another intriguing outcome of research over the past fifty years has been that the topography of the retina has adapted to fit the particular behavioural priorities of different animals. Ground-feeding birds, which spot food to the side, have an area of high ganglion cell density in the centre of the retina; those, such as raptors and owls, that look ahead to capture prey have their high density regions in the temporal retina, pointing forwards. More intriguing are sea birds, whose areas of interest are narrow strips corresponding to the region of sea surface along and below the horizon, and these have high density horizontal 'visual streaks' across the centre of the eye. Much the same applies to mammals — rabbits have visual streaks, primates and cats have forward-pointing high acuity regions (p. 139). Even in insects the same trends can be seen: male flies that apprehend females on the wing have higher resolution than females in the fronto-dorsal part of the eye, where females will be held during a chase (p. 134). Dragonflies, which capture prey from below, have their highest acuity region directed upwards. Crustaceans, such as fiddler crabs, that live on sand-flats have a streak around the eye corresponding to the horizon (p. 140). In 1977 Austin Hughes used the expression 'terrain hypothesis' to describe these fits between the retinal sampling pattern and an animal's way of life [4]. Extracting detail from the image is, it seems, expensive, and rationed according to an animal's visual needs.

On land, the air offers little impediment to vision, but in water, even clear water, this is not so. The first illustration in the book is a picture of a beautiful Chinese vase depicting sunfish, one very close, a second further away which has lost some of its brilliancy and clarity, and a third, further still, has almost faded into the background. Much later in the book, in chapter 9, the physical consequences of scattering are explored in detail. Scattering and attenuation reduce the contrast of an object relative to the background, so that at some distance it will become invisible, much as in a terrestrial fog. This sighting distance depends on the turbidity of the water, but also on depth, wavelength and viewing angle. Even in clear water large objects become invisible at distances of tens of metres, and there is not much that can be done about it. For fish, vision is compromised by the medium they inhabit.

The mid-water regions of the ocean, at a depth of about 500 m, provide a particularly interesting and challenging environment. Unlike the productive surface waters, very little food reaches the mid-water zone, and most of the fish and larger invertebrates survive by eating each other. This causes a kind of visual arms race — it pays to have large eyes to spot prey, and it pays to be as invisible as possible. The adaptations this produces are explored in chapter 11 on dim light, and 13 on camouflage. Eyes are usually large because of the low light levels (roughly moonlight in daytime) and are often directed upwards to spot the silhouettes of prey against the dim background light from the surface (p.276). Camouflage is achieved in various ways. Transparency is obviously effective, but some parts — the eyes and the gut — can't be made transparent, and a common alternative is to turn the sides of the fish into plane mirrors (p. 332). This works because the symmetrical distribution of light in the sea around the vertical means that light reflected from a vertical mirror has the same brightness as light that would have come through it. However, fish are not flat sided and, as Eric Denton showed in the 1960s [5], fish construct flat mirror surfaces by tilting the individual reflecting platelets in their scales into a vertical alignment. There is still the problem of the silhouette, and this is solved in many fish, squid and crustaceans by populating the underside with luminescent structures — photophores — whose output is adjusted so that the effect is to match the down-welling light, thus completing the illusion of invisibility (p.318). Bioluminescence has many other uses in the sea: illuminating prey, luring prey, distraction and mate attraction (p. 320). Indeed, below about 800 m it is the only effective source of light.

This book offers a wide-ranging review of much of what has been happening in the field of comparative vision since Lythgoe's book came out 35 years ago. Anyone interested in vision will enjoy reading it, and it is certainly suitable as a text book in biology courses. It is not expensive, given its content, and perhaps its only drawback is its physical bulk, which might make it hard to carry between classes.

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Quick guide

Thanatosis

Stephen M. Rogers and Stephen J. Simpson

What is thanatosis? 'Thanatosis' derives from the Greek word for death and describes an unusual behavioural state that has a number of different names: 'death feigning', 'playing possum' (after one of its exemplary practitioners), 'catatonia' and, more whimsically, 'animal hypnosis', but the term with the widest usage (among scientists at least) is the more neutral 'tonic immobility'. Thanatosis is characterised by a number of different features: catalepsy, immobility with a prone but stiff posture maintained by pronounced tonic muscular activity; 'waxy flexibility' of the limbs, which if moved by an external force maintain the newly imposed position for long periods; and unresponsiveness to external stimuli, while remaining fully aware of the environment. The onset of thanatosis is rapid and can persist from seconds to hours. Its termination is generally equally rapid, with the righting reflex reasserting itself and the animal then immediately able to perform at its full capacity.

Thanatosis is normally triggered in situations perceived to be of extreme danger, typically an imminent threat of predation, and elicited by strong and sustained tactile stimuli consistent with having been caught by a predator. As such, thanatosis is distinct from the freezing response that occurs when danger is first detected; rather, it is the terminal defensive response when all other options of evasion, fight or flight have failed. Thanatosis is of widespread occurrence in the arthropods and in all the classes of vertebrates, possibly including humans (hence 'scared stiff'). The movement of prey commonly releases killing behaviours by predators; thanatosis removes these stimuli and in doing so may prevent further short-term damage.

Are animals in thanatosis really feigning death? What survival advantage could such an extreme reaction provide, other than to assist predators in dispatching their prey? Some animals appear very conspicuous when in thanatosis; for example, the American Opossum (*Didelphis virginiana*) and hog nosed snake (*Heterodon* spp.) assume contorted postures with their eyes open and their tongues protruding from gaping mouths. They urinate, defecate and secrete a foul-smelling fluid from anal glands. The frog *Leptopelis rufus* releases an ammonia-like substance from its mouth. Do such 'death' displays act as an unusual form of camouflage, with the prey disguised as a long-dead version of itself? This interpretation is problematic. The strong stimuli typically needed to induce thanatosis mean that a predator will have encountered its prey in its 'live' form immediately beforehand. *Didelphis* opposums and *Heterodon* snakes enter thanatosis unusually easily; they may therefore be able to assume camouflage before a close encounter with their predator.

How can thanatosis increase survival chances? The more important aspect of their defence may be the substances that thanatotic animals secrete. Although reminiscent of putrescence, their smell is not identical to that of decomposition, but they are nevertheless highly repellent. 'Death' displays with chemical defences therefore segue into more obvious aposematic warning systems. Fire-bellied toads (*Bombina* spp.), for example, assume contorted postures akin to thanatosis when attacked (the unkenreflex) which reveal bright colours warning of their deterrent taste. The lack of movement of thanatotic prey may increase the chance that a predator will attend to warning signals and/or chemical defences and act accordingly, rather than focussing on overpowering its victim.

Thanatosis can sometimes deter by simply making prey too difficult to eat. The pygmy grasshopper *Criotettix japonicus* (Tetrigidae) always stretches out its body in three different directions when entering thanatosis, which orientates a number of spines into prominent positions. This posture specifically protects against predation by frogs, which are limited by the size of prey they can swallow whole; however, it offers little protection against birds.

Thanatosis may also facilitate the contrasting strategy of camouflaged inconspicuousness. Arthropods in thanatosis often assume characteristic postures, withdrawing their extremities