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Advances in Visual Ecology*

About 570 million years ago, the most spectacular event in the history of the animal kingdom occurred. In the space of just a few million years – the blink of an eye in geological terms – most of our familiar modern animals suddenly appeared on the Earth. They all had well-developed eyes. And they all used them as a matter of life and death. This explosion of new animal forms ushered in the Cambrian epoch, and with it a dangerous new world of fast-moving predators. Vision became the survival sense *par excellence*. Bigger and sharper eyes not only improved a predator's chances of spotting its prey, but also helped the prey to unmask the predator. This sensory arms race drove the rapid evolution of a sophisticated spectrum of visual systems, each designed to out-smart an adversary, possibly by detecting the tell-tale movements of a predator or by deciphering the subtleties of a near-perfectly camouflaged prey.

Vision also evolved in response to much gentler – albeit no less urgent – influences. The intertidal world of the beach crab, or the endless flat expanses which are home to the desert ant, consist of little more than the sharply delineated horizon between sand and sky. For these animals, nothing much of importance happens anywhere except here. Not surprisingly, the processes of evolution have concentrated most of their visual capacity precisely at the horizon. In the steaming jungles of New Guinea, the brilliantly coloured male bird-of-paradise performs a dance of such intricacy and beauty that few females are able to resist his charms. His stunning displays of plumage must be of the highest quality and precisely choreographed: the slightest mistake could make him appear immature, or, worse still, of another species, thus causing the female to beat a hasty retreat. In birds-of-paradise, as in many animals, vision is exquisitely matched to the intricate rituals of courtship.

These crucial influences – predation, habitat and courtship – have shaped the evolution of animal vision over the last 570 million years. Because eyes, like all sensory organs, are limited in their capacity to detect and process information, evolution has fashioned them to perform the most urgent tasks optimally, whilst neglecting – or even ignoring – less urgent tasks. This "matched filtering" of essential features in the visual world has been a major influence in the evolution of vision, and

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has led to the enormous variety of visual adaptations found in Nature today. With the generous support of the Wissenschaftskolleg and the Otto & Martha Fischbeck-Stiftung, Dan-Eric Nilsson and myself organised an intensive 3-day symposium exploring the role of matched filtering in the evolution of vision. This symposium, held at the Kolleg from March 30th to April 1st, was unique and brought together experts from fields as varied as image statistics, avian colour vision, and information processing. The blend of participants and the scope of the discussions turned out to be far better than any of us had anticipated. In the opinions of all who attended the symposium was an outstanding success, with two participants claiming it was the best meeting they had ever attended! This success was in no small part due to the hospitality of the Wissenschaftskolleg and the marvellous organisational skills of *Katharina Wiedemann* and *Joachim Nettelbeck* (to whom we are extremely grateful!)

The symposium participants were (in alphabetical order): *Tom Cronin* (University of Maryland), *Hans van Hateren* (University of Groningen), *Simon Laughlin* (University of Cambridge), *Dan-Eric Nilsson* (Wissenschaftskolleg zu Berlin & University of Lund), *David O'Carroll* (University of Cambridge), *Daniel Osorio* (University of Sussex), *Julian Partridge* (University of Bristol), *Dan Ruderman* (University of California, Los Angeles), *Mikhail Vorobyev* (Free University of Berlin), *Eric Warrant* (Wissenschaftskolleg zu Berlin & University of Lund) and *Jochen Zeil* (Australian National University). Several others attended as observers, including several Fellows (*Andreas Engel*, *Rainer Goebel*, *Eva Jablonka*, *Raphael Ritz* and *Ekkehart Schlicht*) and three biologists from the Humboldt University (*Peter Hammerstein*, *Andreas Herz* and *Bernd Ronacher*).

The purpose of the symposium was two-fold. First there was the pragmatic and slightly selfish purpose of obtaining feedback from our peers concerning the scope and content of our book-in-progress, *Visual Ecology*. Prior to arrival, each participant was given an outline of the entire book, as well as deep outlines of the various chapters we had assigned to them for peer review. We were particularly interested to find out whether we had omitted or over-emphasised concepts. The second purpose was intellectual, and quite unexpectedly this turned out to be the real joy of the symposium. I say unexpectedly because such a disparate crowd of people would normally never be found attending the same meeting, especially a meeting as open and deliberately unplanned as this one. Some in fact even wondered why they, of all people, had been invited at all. One even said to me, “Since when have I worked on visual ecology?” Comments like these made me sweat during the weeks prior to the meeting. Would such a group of people, many of whom had never met, actually work? Or would the whole thing be a spectacular flop?

To our great relief the symposium was *not* a flop. Quite the contrary, the combination of participants – both socially and intellectually – was superb. Right from the first discussion, it was clear that the group dynamic was going to ensure progress. And progress we made in bounds. It rapidly became obvious that the concept of "matched filtering" – the unifying theme of our book – was a controversial one. *Hans van Hateren*, a physicist who applies information theory to understand early visual processing, challenged our definition of matched filtering. He claimed that the term, originally coined by signal processing engineers, was too liberally applied. Strictly, a matched filter is any filter whose response characteristics (defined by its impulse response) are matched to the signal to be detected. Strict matched filters do exist in Nature, the optical horizon foveation found in beach crab eyes providing an excellent example. It was our wish to widen the "spirit" of this strict definition. For instance, we wished to apply the term "matched filter" to any circuit of cells whose job it is to extract as much information as possible from an exclusive and vital aspect of the visual scene. Is the circuit of cells found in the monkey cortex, which responds only to another monkey's face, a matched filter for monkey faces? Strictly it isn't. Prior to the meeting, I thought that one of the nicest examples of matched filtering was the way that early visual processing is organised to perfectly "match" the statistical structure of natural scenes. But to make this match the circuitry must actually be organised with response characteristics precisely *opposite* to the structural characteristics of the scene. Paradoxically, this match comes about by an exact *mis*-match. According to engineering – and *Hans van Hateren* – this is absolutely the opposite of matched filtering. A lively discussion ensued, one that permeated every topic discussed during the remainder of the meeting. The conclusion was that the term "matched filtering" should be avoided, but that the concept of "matching" should be retained with caution. As a result of the discussion, we decided to devote much of the first chapter of the book to a discussion of matched filtering, in both its strict and liberal interpretations. In the end, there was no doubt in anyone's mind that "matching" had evolved in vision, and that vision thereby was essentially ecological.

The symposium was organised into three broad themes – the structure of the visual world, optimising the acquisition of visual information and the ecology of colour vision – the highlights of which I will briefly detail.

The structure of the visual world

The structure of the visual world is surprisingly orderly and predictable, a fact that has only been fully appreciated over the last two decades. The spatial, temporal and colour details of natural scenes are unexpectedly well-ordered and this has had an enormous impact on the way visual systems have evolved. In talks entitled “Light in terrestrial habitats” and “Light in marine and freshwater habitats” *Julian Partridge* and *Tom Cronin* respectively detailed the quality and distribution of natural light. As well as detailing the obvious sources of natural light in open environments (the sun, moon and stars) and how light varies throughout the day, *Julian Partridge* pointed out how the colour of objects, and of the light which illuminates them, is of paramount importance to visual ecology in closed environments. Most natural objects are green or brown, and upon this backdrop organisms can either advertise themselves (e.g. by being red or shiny), or camouflage themselves (e.g. by being dull or black). *Tom Cronin* went on to highlight the importance of light that is invisible to humans – ultraviolet and polarised light. Underwater scenes often have enhanced contrast when seen in this light, and many marine organisms take advantage of this. In a talk entitled “The statistics of natural images and matched visual coding in vertebrates”, *Dan Ruderman* went on to summarise our latest knowledge on the structural statistics of natural scenes. In particular he stressed that the statistics relevant to vision depend on whether one is considering the processes of early vision (where lower-order statistics are relevant) or those of higher vision (where higher-order statistics are relevant).

Optimising the acquisition of visual information

It really comes as no surprise to discover that the orderly structure of the natural world has had a profound influence on the evolution of vision. In this section of the symposium we discussed how vision has evolved coding strategies which are “matched” to the type and quantity of information found in natural scenes. *Hans van Hateren,* in his thought-provoking talk entitled “Matched coding in early vision”, threw the entire concept of matched filtering into question, as mentioned above. The term “matched filter” – borrowed from engineering – should not be widened in meaning in the way we had intended. In his opinion, if a term must be used at all, it should be another, such as “tuned coding”, “ecological coding", "optimal coding", or "optimised coding". The lively debate that ensued didn't settle the issue, but all agreed that the concept of "matching" (and not exclusively "matched filtering") is important in understanding the evolution of visual adaptations. This was a notion well expressed by *Jochen Zeil* in his talk "Eye design and habitat", in which he emphasised the importance of the eye's optical structure as a first filter of visual information. He also brought to our attention the fact that a "natural scene" is very much animal-specific, its interpretation and perception being dependent not only on an animal's eye design, but also on the animal's behavioural interaction with the scene. *Simon Laughlin* then described how information acquisition is constrained and optimised by energetics and phototransduction. In his first talk – "The cost of seeing" – he convincingly argued that vision is extremely expensive in terms of energy, and that this provides an important ecological constraint on how large a visual system an animal of particular size and lifestyle can afford. Large visual systems are heavier, more complicated to produce, consume much more oxygen during transduction, and make animals more conspicuous to predators. His second talk – "The temporal properties of transduction and its relation to visual ecology" – dealt with how the speed of transduction in an animal is matched to the speed it moves, and to the brightness of its habitat, a matching which optimises information uptake. Slowly moving animals, or animals from dim habitats, tend to have photoreceptor membrane properties tuned to lower temporal frequencies. This principle also applies to the higher visual processing of motion, as well explained by *David O'Carroll* in his talk entitled "The visual ecology of motion". Because motion stimuli are most frequently generated by the motion of the animal itself, the processing of motion must be matched to the animal's lifestyle: fast-flying animals experience rapidly changing flow-fields, whereas hovering animals experience flow-fields which change much more slowly. Motion pathways in the brain provide wonderful matched filters for these flow-fields, and not surprisingly the temporal properties of an animal's motion pathway are tuned to the velocity of the flow-field it normally experiences, and thus to its ecology.

The ecology of colour vision

The colour of the world has been one of the most influential selection pressures in the evolution of vision. In terrestrial habitats the full spectrum of colours provided by solar radiation is accessible. In aquatic habitats this spectrum becomes more restricted with increasing depth because of the natural filtering properties of water. In two talks – "The meaning of colour and its ecology in primates" and "Form, colour, camouflage and advertisement" – *Daniel Osorio* expounded the ecological meaning of colour for terrestrial animals. Trichromacy in primates (including ourselves) seems to have evolved to optimise the detection of ripe fruit on a leafy background. For discriminating colours, we trichromats have a distinct advantage over dichromats, but compared to the many other animals which are tetrachromats, our sense of colour is probably rather crude. Such animals include birds, the topic of *Julian Partridge's* second talk, "The visual ecology of colour vision in birds". In this talk, he described how birds not only have (at least) four different visual pigments, but also possess coloured oil droplets in their retinas which filter the incoming light and massively increase the number of perceivable colours. While the world appears beautifully coloured to us, it is certainly stunningly coloured for birds. Such an elaborate colour vision system is important for birds because they rely heavily on colour signals during foraging (the colours of fruit and insects), mate selection (the colours of plumage) and orientation (the colours of sky regions). There are aquatic animals, especially from shallow tropical seas, which have an equally well-developed sense of colour, if not even better. In his second talk – "The ecology of vision in marine and freshwater habitats" – *Tom Cronin* explained how many aquatic organisms, including fish, are also tetrachromatic and rely on oil droplets in their retinas for heightened colour vision. Mantis shrimps, with up to 14 visual pigments and a battery of retinal colour filters, possibly have the most complex colour vision in the animal kingdom. These animals are very brightly coloured, and it is thought that they use their elaborate colour vision for recognising individuals of the same and other species. The final talk of the symposium – "Insects and flowers" by *Mikhail Vorobyev* – was a real eye-opener and shattered some comfortable beliefs about the nature of insect colour vision which most in attendance cherished. Not surprisingly, the discussion which followed was a heated one! It has long been maintained that the colours of flowers co-evolved with the colour vision systems of pollinating insects. However, recent work by Mikhail and his colleagues at the Free University in Berlin, have challenged this popular view and suggest that insect trichromacy evolved before flowers first appeared on Earth. At this very moment it seems that the ecology of colour vision in foraging insects is still an open book, but one that will prove to be a rewarding area of research in the future.

The ecology of vision is a fascinating and wonderful field of study because it encompasses such a wide variety of disciplines and approaches. Needless to say, it is precisely this diversity which makes a meeting on visual ecology such a rare and special event. That this rare meeting was such an unparalleled success is largely due to the even rarer vision of interdisciplinary scholarship and excellence which is the hallmark of the Wissenschaftskolleg.