

Active vision: Strategies and neuronal mechanisms of spatial orientation behaviour in insects

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It may appear plausible to assume that the control of complex behaviour requires a correspondingly complex brain. Our studies on several insect visually guided orientation behaviour show that this assumption is generally not justified. We investigate by behavioural, neuronal and modelling analysis which brain mechanisms enable insects (blowflies, hoverflies, honeybees) to move in their environments without colliding with obstacles and to find a goal by employing landmark information. With their miniature brains, flies or honeybees able to control highly aerobic flight manoeuvres and, in this regard, outperform any man-made autonomous system. To accomplish this extraordinary performance, flies and honeybees employ a clever trick: they shape actively by the specific properties of their own movements the dynamics of the image sequences on their eyes ('optic flow'). The complexity of the optic flow patterns and, thus, the computational effort of the brain to process this visual information are reduced by organising behaviour as a sequence of prototypical movements which are thought to be selected from a limited pool of possible movement prototypes according to a syntax that depends on the respective behavioral context. Because of the closed-loop nature of behavior, the different types of prototypical movements go along with retinal image displacements which are characterized by distinct spatiotemporal features. We have evidence that, the sensory input is shaped by the very nature of the prototypical movements in a way that greatly facilitates the neuronal analysis of complex sensory information.

Mirror optics in a vertebrate eye

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Many mesopelagic fish have evolved tubular eyes that have the potential for high spatial resolution and high sensitivity but suffer from restricted visual fields. Usually such eyes are upward-pointing to view the silhouettes of animals above them against the remnants of downwelling sunlight and have limited ability to detect bioluminescent or reflective objects in other directions. Several tubular-eyed mesopelagic fish extend their visual fields by eye movements or by having ocular diverticula. The latter generally have limited optical systems and low spatial resolution. However, one species, the brownsnout spookfish, *Dolichopteryx longipes* (Vaillant, 1888), has a well developed ocular diverticulum in which the retina receives light via a mirror. The mirror consists of a reflective multilayer stack derived from a retinal tapetum and measurements of stack organisation indicate that the mirror is a spectrally broadband reflector. Moreover, the reflective plates of the multilayer stacks are not orientated parallel to the surface of the mirror but, instead, plate angle changes progressively over the mirror's surface. Computer modelling indicates that this provides a well-focused image. This is the first report of an ocular image being formed in a vertebrate eye by a mirror.

Polarization Detection and Polarization Control in Photoreceptor Optics

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Polarization vision in aquatic animals has evolved for a variety of visual tasks, such as communication and contrast enhancement. Although the biophysical mechanism of polarization discrimination is well documented in invertebrates, the way individual photoreceptors in the retina of vertebrates detect polarized light has remained a mystery. By using a novel laser tweezer system to orientate individual goldfish photoreceptors into an axial "end on" orientation, double cone photoreceptors were found to display axial differential polarization sensitivity. This is the first direct experimental evidence in vertebrate photoreceptors of axial dichroism and a biophysical mechanism underlying polarization vision.

In addition to linear polarization vision, sensitivity to circular polarized light has also recently been discovered in a stomatopod crustacean. The mechanism of discrimination is centred on a unique photoreceptor cell type that converts circularly polarized light into linearly polarized. Computer modelling indicates that this photoreceptor creates a novel birefringent structure where an interplay between intrinsic and form birefringence results in an achromatic device. This is the first report of polarization control in typical invertebrate photoreceptor optics.

Orientation dependent acuity in the visual system of *Cupiennius salei*

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Cupiennius salei has, like most spiders, eight camera-type eyes - the anterior-median eyes are called principal eyes and have a moveable retina; all other eyes are referred to as secondary eyes and are equipped with a reflecting tapetum. Due to the tapetum the photoreceptors in these eyes are arranged in rows.

In this study the vertical and horizontal spatial resolution of one pair of secondary eyes (posterior-median eyes) was measured in behavioural experiments and compared to the theoretical retinal resolution as reported in histological studies (Land and Barth, 1992).

Motion detection in the secondary eyes enhances the eye muscle activity in the principal eyes. We thus recorded the muscle potentials as a monitor for motion detection with a telemetric unit. Moving stimuli - sinusoidally modulated bright and dark stripes - were presented on a computer screen.

We found a significant increase of eye muscle activity for vertical gratings with a stripe width of only 1° visual angle, and with a width of 1.3° for horizontal gratings. Our results suggest that this night-active spider entirely exploits its theoretical retinal resolution and spatial summation in all subsequent neuronal processes seems thus improbable.

Lateral line photosensitivity in *Xenopus laevis*?

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Dermal behavioural photosensitivity has been known for over 100 years in a variety of vertebrates. Although the sensory receptor mediating this response remains uncertain, in some species there is evidence that the lateral line nerves convey the afferent signals.

In *Xenopus laevis*, superficial lateral line neuromasts are grouped into raised 'stitches'. Wholemounts of *Xenopus* skin immunostained with a polyclonal antibody raised against a *Xenopus* melanopsin peptide, show the presence of both heavily immuno-positive central components and several finer immuno-positive peripheral processes within each lateral line stitch. Both light and electron microscopic sections show dense intracellular staining in cells at the margins of the neuromast pore.

Given the known role of melanopsin as a photopigment within the retina and dermal melanophores, our localisation of it in neuromasts suggests that the lateral line organs may be photosensitive. This is supported by preliminary behavioural data showing relatively short latency behavioural responses to local illumination of ventral regions of *X. laevis* skin.

Although primarily sensitive to water displacement, lateral line organs have also been shown to be sensitive to chemical, thermal, magnetic and electrical stimuli in some animals. Our preliminary evidence of their photosensitivity suggests they are potentially sensitive to all sensory modalities.

Diet-related variation in the vision of two avian species

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Avian vision is highly developed and complex. Avian retinas contain rod and double cone photoreceptors, and four classes of single cones. Single cones are sensitive to red, green, blue, and violet/ultraviolet wavelengths, producing, it seems, tetrachromatic colour vision. All cones contain an oil droplet, rich in carotenoid pigments. These droplets act as selective filters, substantially modifying light detected by the photoreceptor. Using dietary carotenoid manipulations, we tested the effects of carotenoid availability on oil droplet absorbance properties in two species: the zebra finch and the crimson rosella parrot. We used microspectrophotometry to determine whether these manipulations affected oil droplet carotenoid concentration, a change that could alter the colour discrimination ability of birds, with consequences for individual behaviour and ecology. Oil droplet concentration was determined by measuring the cut-off wavelength at which no more light is transmitted. Significant increases in concentration were found in carotenoid supplemented birds, but only in one droplet type not affecting colour vision. Analysis also revealed the effect sizes resulting from the manipulation were dependent on retinal location. Our results reveal a response to dietary manipulation that potentially preserves spectral tuning of colour vision, and could also provide insights into the development of these droplets in the retina.

Seeing red: an arms race in the deepsea?

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The majority of deepsea bioluminescence is blue/green in colour because this portion of the electromagnetic spectrum transmits with least attenuation through seawater, therefore maximising the efficiency of visual communication in an otherwise dark environment. However, certain species of stomiid dragonfish, such as *Malacosteus niger*, go against this convention and produce a far-red light from their photophores. Although this form of bioluminescence cannot travel far through seawater, it does illuminate the area immediately around them and special adaptations in their retinas permit them to visualise this light source. Most deepsea animals are blind to this light, giving these stomiids the predatory advantage of covertly illuminating their prey. Recent work on lanternfish (myctophids), a common prey item of stomiids, has highlighted at least two species with potential longwave sensitivity. Mathematical modelling has shown that these two species could, theoretically, detect the far-red emissions of *Malacosteus niger* from as far away as *ca.* 7 m. The potential ability of these myctophid species to break through this covert illumination endows them with the selective advantage in predator avoidance and could be a recent adaptation in an ongoing arms race between predators and their prey.

Adaptations of Indian carpenter and honey bees to diurnal and nocturnal lifestyles

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Most animals active in dim light either have well-adapted lens eyes or compound eyes of the superposition type. In the past years, the crepuscular bee *Magalopta genalis* has been shown to use its apposition compound eyes to orient visually in very dim light, and some of the mechanisms that underlie this ability have been revealed. Here I use a different approach and compare the ecology and visual organs of three species of carpenter bees (*Xylocopa*) and three species of honeybees (*Apis*). All three species in each genus co-exist in the Western Ghats of India but are active during different intensity windows. Adaptations and limits will be discussed in the context to the ecology of these species.

Colour flower detection by honeybees and bumblebees

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Finding rewarding colourful flowers is a primary task of foraging bees to enable colony survival. Whilst honeybees and bumblebees have very similar trichromatic vision (UV, Blue & Green photoreceptors), there are significant differences in how these two species sum visual signals which leads dramatic differences in both acuity and discrimination capabilities (*J Comp. Physiol. A* 2008 v194p617). Recent work also shows that both bumblebees (*Nature* 2003 v424p388) and honeybees (*Current Biology* 2008v18p953) demonstrate speed-accuracy tradeoffs when searching amongst similar colours. Here we show that the two species also have very different ways of deploying time resources when foraging amongst flowers; bumblebees employ a mechanism to slow down to solve more difficult tasks, whilst honeybees do not modulate response time depending upon the perceptual difficulty. Our findings are discussed in relation to the ecological relevance of bees deploying time resources to find flowers in different environments.

[supported by ARC DP0878968]

Foraging by bumblebees (*Bombus terrestris* L.) under patchy light conditions

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Insects foraging in a nature encounter diverse illumination colours and intensities and may have to move rapidly from one illuminant to the next. For pollinating insects, this could affect their ability to discriminate colours of flowers. Though bees possess colour constancy and thus can recognise colours correctly even when the illumination changes, this ability is not perfect and mistakes are possible. We sought to investigate the behavioural responses of bumblebees when faced with patchy, ecologically-relevant illumination.

We found that bees discriminated two similarly colours of stimuli more poorly under green light (resembling leaf-cover) compared with simulated daylight – i.e. the unusual illuminant is associated with a higher risk of mistakes. When a different group of bees was presented with patchy illumination simulating a woodland edge, some areas green, others resembling daylight, they exhibited a diversity of initial preferences for the two illuminants, with some visiting a majority of flowers under the daylight and others, more surprisingly, preferring flowers under the simulated leaf-cover. However, when there was no cost to mistakes, all bees gradually lost their preferences and became indifferent to the illumination. Thus we show the bees exhibit modifications of behavioural preferences according to the risk and cost of errors.

Dogs considered colour cues to be more informative than brightness

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Early behavioural studies on colour vision in the dog produced ambiguous results and gave way to suggestion that it is hardly used by the species in its normal life. In more recent works elimination of brightness cues in coloured stimuli permitted to show capability for discriminating certain colours in the dog, though the results turned out to be controversial. Nevertheless up to date the question if dogs use chromatic information for recognition of visual objects in natural scenes has not been answered yet.

In our studies we used an approach investigating the hierarchy of features in pattern recognition. According to this approach animals learn to discriminate stimuli differing in two features at the same time and then their spontaneous reaction to the combination reversal is tested.

Eight previously untrained dogs were presented with visual stimuli differing both in chromaticity and brightness (e.g. dark yellow vs. light blue) and test trials were then performed to establish which of the two was used by them during the discrimination. The dogs were trained and tested under natural ambient daylight conditions. It has been demonstrated that in the experimental situation colour proved to be a more informative cue than brightness.

The power of redundancy! What might the power spectra of cuttlefish body patterns tell us about signaling and camouflage?

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Julesz (1981) raised the question of whether image segregation - or camouflage breaking - relies mainly on low-level image parameters such as mean luminance and spatial frequency. However most work on visual camouflage attempts to assess how well an animal matches local features in the visual environment in terms of texture, colour, luminance and so on. Similar parameters are used to make inferences about the efficacy of visual signals in terms of how they differ from a given background. The work presented here takes a more global approach to camouflage and signaling strategies through the comparison of the power spectrum of image collected in the field of camouflage and signalling patterns in the giant cuttlefish, *Sepia apama*, with those of the visual background. The power spectrum of natural scenes is known to fall roughly as the square of the spatial frequency, and evidence suggests the visual system exploits this scale-invariant property by reducing redundancies at an early stage to efficiently code salient data. We show that cuttlefish body patterns used by male animals in signalling mode show a different 'signature' power spectrum to the background, whereas the body patterns of camouflaging animals have power spectra the same as their backgrounds. We also provide evidence that the animals use backgrounds of different visual complexity to either signal or camouflage against. We discuss our findings in terms of what power spectra analysis might tell us about signal transmission/ camouflage, and how the spatial characteristics of signalling cuttlefish might aid high signal transmission at close range but provide camouflage over greater distances.

Computer Vision based Analysis of Moth Camouflage

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In this paper we present the use of computational learning algorithms to provide potential analogues of human and bird visual systems for the study of the cryptic and disruptive camouflage of moths. Images of a background tree bark are treated with triangular foreground targets textured using a fully automated computational synthesis system in a similar style to that described in previous work (Cuthill et al, Nature 2005, and Fraser et al, Proc. R. Soc. B. 2007). Two learning algorithms are used: a Support Vector Machine (SVM), a single 'strong' classifier and Adaptive Boosting (AdaBoost) a collection of many 'weak' classifiers. Classification of grey level treated images is based on learning discriminative features generated by image responses to banks of log Gabor filters for foreground and background texture. A significant advantage of AdaBoost is that it enables a convenient insight into the importance of particular features in the very high dimensional feature space for recognition. In this work we show that the proposed computational model gives recognition results similar to those of human studies and indicate which features contribute to successful recognition. The combined application of computational synthesis, learning and classification is novel and the experimental results and analysis are providing new insights into animal camouflage.

Disruptive coloration and background visual complexity

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Camouflage plays a crucial role in concealing animals from their predators, but even if an animal matches the background fully, any disparities between the phase of the pattern on the animal and the background, or its shadow, might give its location away. Even if the camouflage is detected, the predator must be able to recognize the animal as potential prey. Disruptive colouration works against shape recognition by using high-contrast markings to break up form (Cuthill et al. 2005, *Nature* 434, 72-74). We tested the hypothesis that disruptive colouration will be more effective when the colour patches on the animal appear to belong to different background objects compared to otherwise identical background colours on a single object. To do this we used computer-based experiments where human participants had to find cryptic targets on complex artificial backgrounds consisting of bi-coloured objects on a bicoloured ground. As predicted, error rates for targets matching multiple background objects were higher than for targets which had identical local contrast to single background objects. This provides evidence for disruptive coloration interfering with higher-level cognitive processing in addition to previously demonstrated effects involving low-level contour detection (Stevens & Cuthill 2006, *Proc R Soc B* 273, 2141–2147).

Eggshell patterns are evolutionarily conserved among birds
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The maculated appearance of avian eggshells has attracted considerable interest in evolutionary ecology and has been proposed to serve a variety of visual and structural functions. Hitherto, most of the investigations into differences in eggshell appearance have focused on anecdotal reviews and human perceived differences. Here we resolve the subjectivity of previous studies by combining calibrated digital photography with a parametric texture model to characterise eggshell appearance among a diverse range of avian species. Using hierarchical taxonomic models we demonstrate that different components of eggshell patterning are evolutionarily conserved in different ways. In particular, our results provide evidence that different aspects of eggshell appearance are responding to selection from multiple different evolutionary and ecological pressures.

Visual signals in the pollination of sexually deceptive orchids

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Sexually deceptive orchids of the genus *Ophrys* are pollinated by males of solitary bees and wasps. The flowers mimic the odour of a receptive female and thus attract males looking to mate. The imitated sex pheromone produced by the flower is highly specific and attracts only males of the target species. Optical floral traits such as size, perianth colour, and labellum shape vary significantly among species, but the functional significance of such traits in pollination is largely unknown.

We studied the role of flower size, perianth colour and labellum pattern in pollinator attraction and guidance in the orchid *Ophrys heldreichii* and its specific pollinator, males of the long-horned bee *Tetralonia berlandi*.

Dual-choice experiments and video recordings of males approaching artificial flowers were carried out. We found that both green receptor-specific and colour contrast between the perianth and the background affects flower detection and discrimination. When males are given the choice between a labellum showing the typical whitish pattern or not, they do not discriminate between the two. We hypothesise that the labellum pattern does not play a role in attraction, but can allow the male to memorise an individual flower after experiencing the negative reward of a failed copulation attempt.

Information flow control by navigating animals: some unexpected similarities between vision and echolocation

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The echoes of natural habitats are highly complex and for an echolocator converting a stream of multiple overlapping echoes into a workable spatial representation of the environment requires elaborate information selection and processing both by internal and external mechanisms. Behaviourally, call design, calling behaviour and flight patterns can be adjusted to maintain workable information flow. We studied vespertilionid bats in a natural flight corridor along a forest road, which was experimentally narrowed in several steps by a camouflage net. We used laser scanning as well as acoustic tracking to relate the bats' flight and echolocation behaviour to the corridor dimensions. Echolocation and flight behaviour were then analysed using two perceptual concepts of information flow control similar to/derived from vision research. First, in flight, Doppler-shifts of echoes result in location errors. The magnitude of these errors is range dependent with a null at a certain distance from the bat. By changes in echolocation call design bats can shift this distance of zero error back and forth. As this has similarities with accommodation in vision, we termed this process 'acoustic focussing'. Bats adjusted their call design to corridor width in a distance dependent manner such that the mean ranging error was minimized. Second, optic flow is a well-studied concept in animal visual navigation. Its analogue in echolocating animals would be the flow rate of echoes. But echolocation is discontinuous and stroboscopic. We found that bats flew slower and called more frequently in narrower corridors, which resulted in an increased spatial calling density. Interestingly, that way bats kept the mean stroboscopic flow rate for the corridor walls constant.

What is binocular vision for? A birds' eye view

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Comparative analysis of visual fields leads to the conclusion that in the majority of birds the function of binocularity would seem to lie in what each eye does independently (diplopically) rather than in what the two eyes might be able to do together. Binocularity, which can be spontaneously abolished in many species, should be viewed as a consequence of the requirement of having a portion of the visual field that looks in the direction of travel. Such contralateral projection is necessary to gain a symmetrically expanding optic flow-field which specifies direction of travel and time to contact a target. It is particularly associated with the control of bill position and bill opening during feeding or in the provisioning of chicks. In birds which do not need such control of their bill, binocular field widths are very small suggesting that binocular vision plays only a minor role in the control of locomotion. In birds it may be more appropriate to discuss the function of contralateral rather than binocular vision since the latter term seems to bring with it assumptions concerning the percept of solidity and stereopsis with which binocular vision in the majority of birds does not appear to be associated.

Movement detectors projecting to the fish tectum

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Visually guided behavior in lower vertebrates is based on the detection of “key stimuli” by means of specialized neurons in the visual system. The detection begins at the retinal level, the output units of which, i.e. the retinal ganglion cells, send highly processed information to the primary visual centers of the brain, settled in the midbrain formation tectum opticum (TO). Axons of different “detectors” terminate at different tectal levels, forming three retino-recipient layers. In the superficial layer of TO, axons of direction-selective units (DSUs) are terminated. In the second, medial tectal layer projections of oriented selective units (OSUs), spot detectors and color-opponent units are terminated. Retinal output units, characterized by sustained responses to dark or light stimuli, project to the third, the deepest TO layer. DSUs projecting to the tectum were shown to comprise six physiological types according to their selectivity to sign of stimulus contrast (ON and OFF units) and their preferred directions: three directions separated by a 120°. Unlike DSUs the OSUs of fish retino-tectal system were shown to divide into two types – only by their preferred orientation (vertical or horizontal). Both DSUs and OSUs are characterized by small responsive receptive fields (4–5°) and the finest spatial resolution.

Investigating the scale of view-based homing: how far can you roam with just one snapshot?

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It is known that insects can return to a location using only a remembered view or snapshot taken from that location. So called view-based homing has received much attention in recent years as people try to mimic insect performance with simple algorithms relying on simple visual processing. However, the extent of the area within which insects can navigate in natural environments using this simple strategy has yet to be determined. Information about the potential scale of view based homing is necessary before we can interpret the data coming from the radar tracking of homing bees which some authors have used to conclude that a map-like representation is required for navigation over the natural foraging range of bees.

Here we investigate this question by testing several insect-inspired view-based homing algorithms in a number of large-scale natural environments. Building on the work of Zeil and colleagues, we show that the information for homing exists in natural environments over large-scales (> 10s of metres). We further show how performance changes by considering information at different spatial scales and by using rudimentary feature extraction.

Estimation of the wavefront aberration for peripheral vision in the pigeon eye

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Animals with laterally oriented eyes have large, panoramic fields of view. The present quantitative study in the pigeon (*Columba livia*) eye has investigated the quality of the retinal image away from the central retina. The hypothesis is that peripheral vision in these lateral-eyed animals has high optical quality over a large visual angle.

The total amount of ocular aberrations was evaluated for 16 eyes using a Hartmann-Shack wavefront sensor. The orientation of the anesthetized animal's head was controlled by a stereotaxic system capable of rotation ($\pm 1^\circ$) about the eye's nodal point. The image was assessed for eccentricities up to 70° nasally and temporally.

For central vision, the values for defocus and astigmatism obtained by retinoscopy agree with the Hartman-Shack measurements. The measured astigmatism ($\leq 0.5D$) and defocus ($\leq 2D$) of the pigeon eye for increasing eccentricity (i.e. over a visual angle of 130°) are lower than expected theoretically. The total amount of aberrations also remains low, especially in the nasal visual field corresponding to the Red Field of the retina.

The results demonstrate that the pigeon eye has an important optical adaptation for panoramic vision. This wide-angle optical correction is most likely achieved by a peripheral modification in the shape of the cornea and/or the lens.

Distance estimation mechanisms in *Anura*

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For proper spatial orientation, animals utilize information about the physical parameters of the external objects. The aim of this work is to discuss what is known about constancy mechanisms of size and distance perception in frogs and toads. The stimuli were moving colored spheres with varying parameters which were color, size, velocity, and background texture. In the absence of structural background, prey-catching or escape responses of frogs and toads to the stimuli moving around on fixed distances were triggered depending on the perceived size of the object and perceived distance. Inappropriate reactions, i.e. escape of a prey-size object and trying to catch a very large one were evidently due to wrong estimation of the distance to the moving object. Functionally, such behavior corresponded to human visual illusions. In monocular vision conditions, pond frogs were provoked to demonstrate different approach behavior in response to an imitation of a moving off or oncoming prey when the distance to a "prey" was not changed. The key parameters that provoked the illusion were small changes of the object location on the monitor and the size of the object.

Spatial vision in birds and mammals

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Contrast sensitivity as determined from spatial sine-wave gratings has now become a common indicator of the ability of a vertebrate visual system to process spatial information. A detailed analysis of contrast sensitivity function data measured in a diverse range of birds and mammals, has shown that signal transfer theory can be employed to both define a model for these data and to quantify underlying optical and neural mechanisms. One important mechanism is lateral inhibition in the retina and modelled values of its associated point spread function were derived for each species examined. The values obtained were found to correlate well with retinal ganglion cell receptive field surround size measurements obtained directly from electrophysiology. A second important mechanism is optical attenuation, and optical modulation transfer function calculated from the model was found to closely match that determined from the double-pass optical probe technique. For most species examined, contrast sensitivity is considerably less than that for the human under similar stimulus conditions. Although this is due, in part, to a reduction in the performance of both optical and retinal mechanisms, the model indicates that poor cortical detection efficiency plays a significant role. Finally, an example is given of how an animal's contrast sensitivity function can be used to predict the perception of spatial information in a real scene or object.

The Crater Lake Cichlids of Cameroon – Visual Ecology, Opsin Molecular Evolution and Implications for Sympatric Speciation

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The tiny crater lakes Barombi-Mbo and Bermin in north-western Cameroon both house independently radiated species flocks of endemic Tilapiini-Cichlids. Morphological and ecological traits differentiate 12 and 9 species in each lake respectively. Using mitochondrial markers, Schliewen et al. (Nature, 1994) established that each of these species complexes evolved sympatrically in their respective lake. In cichlids, colour traits are known to promote sexual selection during mating and may serve as a reproductive isolation barrier (Seehausen et al., 1998). However, the underlying mechanisms of species recognition in these monomorphic, visually inconspicuous fish have yet to be elucidated.

We sequenced the rhodopsin and UV opsin genes of fifteen species and generated 3D models of the pigments. While the rhodopsin turned out to be highly conserved, we found the UV opsin in several species to show variation at amino acid sites influencing spectral sensitivity. Statistical tests (Dn/Ds) for selection support a scenario of purifying selection acting on the genes. Spectral reflectance measurements at five different areas of the body showed that some, especially the lower lip, strongly reflect UV light. The data shows significant variation between species. While this part of the light spectrum is invisible to humans, cichlids in shallow waters can detect it. We propose that UV signalling plays a role in sexual selection in these otherwise inconspicuous fish.

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Title: Visual fields in tool-using New Caledonian crows

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New Caledonian crows (*Corvus moneduloides*, NC crows hereafter) use and manufacture tools with a remarkable degree of behavioural sophistication. Tool-use involves transforming representations of properties of a target object (e.g. location & orientation) and of those of the tool (e.g. position & dimensions) into a motor plan for goal-directed actions. A recent study tracking the movement of tools used by wild NC crows probing for wood-boring larvae suggest they rely heavily upon visual and tactile cues throughout the task.

If tool-use in NC crows is visually guided then we might predict the visual field of NC crows to have adapted to accommodate for looking directly down the shaft of the tool as they hold it with their bill to afford a good view of the target. Binocularity might also be advantageous for gauging the depth of the target in the hole they are probing.

We are testing this hypothesis by mapping the visual fields of species in the *Corvus* genus, including Jackdaws (*Corvus monedula*), carrion crows (*Corvus corone*), Ravens (*Corvus corax*) and Rooks (*Corvus frugilegus*) in order to compare NC crow vision to that of its relatives.

Initial findings suggest NC crows have a larger field of binocular overlap just above the bill-tip than any other species tested; this is in part achieved through greater angles of eye movement. Therefore it appears tool-use in NC crows has coincided with morphological and sensory specialisations likely to aid the task and further work is necessary to determine how they utilise these specialisations during tool-use.

Spatial Organisation of the Cone Photoreceptor Mosaic of the Domestic Chicken (*Gallus gallus*)

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The domestic chicken, like most birds, has a keen sense of colour. This is due, in part to the presence of pigmented oil droplets found between the inner and outer segments of the cone cells. The oil droplets serve as a filter, sharpening the spectral response of the photoreceptor. The loci of these oil droplets form a uniformly distributed mosaic, with each type uniformly distributed within it, yet attempts at assigning a 'crystalline' structure have been unsuccessful. However, a measure of order (Cook J.E., *Visual Neuroscience*, 1996, 13(1), 15) indicates that the mosaic is in fact highly ordered. To investigate this further, a statistical analysis of connections found using a Voronoi based nearest neighbour analysis was undertaken. The results suggested that the high order may be explained by spatial constraints and a principle of exclusion – where the single cones exclude other single cones from the area surrounding them. A simple generative model constructed using this principle produced the same statistical distribution of neighbour pairings. Another analysis, using autocorrelograms (e.g. L.Galli-Resta et. al.1999, *European Journal of Neuroscience*, 11, 1461) was consistent with this mechanism. This analysis showed a long range order amongst the double and C-type cones (reflected also by the individual order parameters) contrary to the apparent absence of a crystalline structure. This anomaly is compounded by the lack of circular symmetry in the autocorrelograms and non-central exclusion zones in the crosscorrelograms. This aside, it would seem that the apparent complexity is due to the number of cone types, and thus a result of the need for a uniform sampling of a large number of spectral components.

Recognition of rotated symmetrical patterns and perception of 3-D objects by chicks.

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Young poultry chicks trained to discriminate bilaterally symmetrical from an asymmetrical 2-D pattern readily generalize about symmetry to novel patterns. We have found that this generalization extends to patterns that are consistent with a 60 degree rotation of the symmetrical pattern on a spherical surface. We discuss this preliminary finding in the light of the fact that animals normally view bilateral symmetry on 3-D objects (i.e. other animals).

Sexual dimorphism of the visual system in a long-horned bee and its implications on mating ecology

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Sexual dimorphism in the peripheral sensory organs is common in Hymenopteran insects, and usually attributed to differences in behavioural tasks between sexes. Males often possess elongated antennae and enlarged eyes, which are of particular use in mate detection and mating behaviour. One of the most extreme examples is found in the European honeybee, *Apis mellifera*. The drone's sensory organs are tuned to detect females as quickly as possible. The compound eyes cover almost the entire head. Facet number and diameter are increased and inter-ommatidial angle decreased in comparison to females. This results in higher visual acuity and contrast sensitivity. However, data on sexual dimorphism in solitary bees are relatively scarce.

Long-horned bees are particularly striking due to their apparent morphological dimorphism, mainly in the antennae. We present results of an investigation on the visual system of *Tetralonia berlandi* (Apidae:Eucerini). Similar to honeybee drones, males exhibit greatly enlarged eyes as well as large facets in the fronto-medial region of the eye, indicating higher acuity. Based on morphological and behavioural results we conclude that these specific adaptations enhance mate detecting capabilities in males.

Patterns of Plumage Brightness In An Island Bird Population

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The island of Bermuda, situated 1,030 km off the coast of North America, holds a resident population of Eastern Bluebirds. Previous observations have noted the 'bluer blue' of head and rump feathers of Bermuda bluebirds when compared to mainland populations. However, these plumage comparisons have all been qualitative and thus considered less than compelling evidence for significant evolutionary divergence. We measured plumage reflectance of museum specimens from Bermuda (n = 12) and North America (n = 28) and found no significant chromatic differences between the two geographic regions. However, we did find a significant difference in male rump brightness (achromatic contrast), with Bermuda birds exhibiting brighter plumage. We have collected body feathers from adult birds captured in Bermuda and the mainland U.S. and will test for differences in brightness among different populations to determine how plumage brightness varies across the species' range. Comparisons between oceanic islands and mainland populations can provide unique insight into the evolution of novel plumage characters.

Comparing image structure with local motion structure in real life optic flow

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We analyse video sequences generated by physically moving a camera through various visual scenes to examine the structure present in sequences of frames as well as the spatial structure of the calculated motion output. We show that the motion signal maps generated by a two-dimensional array of correlation-based motion detectors (2DMD) vary systematically across space with changes in the motion field containing important cues to self motion as well as scene structure. For each movie sequence we filtered the motion signals with first-order differential of Gaussian filters to extract a measure of the spatial continuity of the flow-field. We also extracted the power spectra of both the static image sequence and the dynamic motion outputs and examined to what extent the motion structure was dependent on the image structure. Despite the substantial levels of noise affecting the motion signal distributions - attributed to the sparse nature of optic flow and the presence of irregular camera jitter - we are able to observe characteristic patterns as well as differences between environments, such as indoor and outdoor scenes. Considering the information present in the spatial layout and variation of the motion signal distributions arising from real-life image sequences helps us to understand optic flow processing in the context of the constraints on possible motion patterns introduced by the structure of natural images. Different aspects of the structure of the motion may allow us to separate the different underlying causes of the motion signals.

Supported by EPSRC and The Leverhulme Trust