



Applied Vision Association/Colour Group of Great Britain

ANIMAL VISION

Dept. Optometry & Visual Science, City University, Northampton Sq,
London EC1V 0HB,

(lectures in room CM507 (C304), registration/coffee in CM450 (C244))

Thursday 20th September 2007, 09.30-18.00

- 09.30 Registration & Coffee**
- 10.25** Welcome
- 10.30** John Saunders (City), John Jarvis & Chris Wathes (Royal Vet College) Calculating luminous flux and lighting levels for domesticated mammals and birds
- 10.50** Phillip Cassey (Birmingham) Avian discrimination of eggshell colour
- 11.10** Graham Martin & Craig White (Birmingham) Through birds' Eyes: What does vision tell us about the aquatic foraging of cormorants?
- 11.30 coffee & posters**
- 11.50** Mathew Berg, Raoul Ribot, Ben Knott (Bristol), Leo Joseph (CSIRO), Katherine Buchanan (Cardiff), Jim Bowmaker, David Hunt (UCL), Andrew Bennett (Bristol) Coloration and colour vision in a parrot ring species
- 12.10** Innes Cuthill & Aron Székely (Bristol) Coincident disruptive coloration
- 12.30** Richard Clarke (UCL) Bees preferentially encode higher-order image statistics that have ecological relevance.
- 12.50** Adrian Dyer (Monash/Mainz), Sabina Prack & Johannes Spaethe (Vienna) Honeybees and bumblebees trade-off colour discrimination for acuity.
- 13.10 lunch & POSTERS**

- 14.10** Paul Graham, Virginie Durier & Thomas Collett (Sussex) The co-activation of snapshot memories in wood ants
- 14.30** Graham Taylor (Oxford) Vision-based flight control in birds and insects
- 14.50** Almut Kelber (Lund) Colour perception in dichromatic animals
- 15.10** Andrew Parker (Oxford) The introduction of vision on Earth
- 15.30** Eric Warrant (Lund), Kerstin Fritsches (Queensland), Eva Landgren (Lund) & Richard Brill (VIMS) A tale of two fishes: The visual ecology of two deep-sea predatory fishes
- 15.50** **coffee & posters**
- 16.10** Stephanie Halford, Susana Piers & Russell Foster (Oxford) VA Opsin update: More than just a teleost photopigment?
- 16.30** Ronald Kröger (Lund) Multifocal optical systems in vertebrate eyes for acute colour vision.
- 16.50** Yakir Gagnon (Lund) Spherical fish lenses; optimization & adaptation
- 17.10** Christa Neumeier & Martin Gehres (Mainz) Seeing motion in fishes
- 17.30** **drinks & nibbles** (sponsored by the Dept. Optometry & Visual Science, City University)

Posters

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| Graham Martin (Birmingham), Raymond McNeil (Montreal) & Marina Rojas (Oriente) | Through birds' eyes: Vision and the foraging technique of skimmers (Rynchopidae) |
| Mathew Berg, Raoul Ribot, Leo Joseph, Katherine Buchanan, Andrew Bennett (Bristol/CSIRO/Cardiff) | Colour polymorphism and population divergence in a parrot ring species: a role for sexual selection? |
| Sarah Zylinski (Sussex) | Edge information alone elicits "white square" response in the common cuttlefish <i>Sepia officinalis</i> |
| Emma Kelman & Daniel Osorio (Sussex) | Cuttlefish perception of visual depth |
| Kit Longden & Holger Krapp (Imperial) | Activity modulation of optic flow processing neurons by an octopamine agonist in the blowfly |
| Wayne Davies, Livia Carvalho, Jill Cowing, Lyn Beazley, David Hunt, Catherine Arrese (UCL/Western Australia) | Bridging the gap: Ancestral trichromacy in mammals |
| Aman Saleem, Holger Krapp & Simon Schultz (Imperial) | Do fly & primate neurons code moving 2D patterns the same way? |
| Susan Theiss, Shaun Collin & Nathan Hart (Queensland) | Visual pigments and colour vision in elasmobranchs |
| Andrew Philippides, Natalie Hempel de Ibarra, Olena Riabinina & Thomas Collett (Sussex) | An analysis of the phases and dynamics of bumblebee learning flights |
| Y. Garcia, C. Torti, B. Povazay, B. Hermann, J. Erichsen, & W. Drexler (Cardiff) | Wavefront aberrations in peripheral vision |
| Jill Cowing, Catherine Arrese, Alison Oddy, Lynda Beazley, Wayne Davies, Livia Carvalho & David Hunt (UCL) | The genetic basis for colour vision in the fat-tailed dunnart, <i>Sminthopsis crassicaudata</i> |

Calculating luminous flux and lighting levels for domesticated mammals and birds

J. E. Saunders¹, J. R. Jarvis² and C. M. Wathes²

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This paper considers whether photometric calculations using standard human spectral sensitivity data are satisfactory for applications with other species or whether it would be worthwhile to use bespoke spectral sensitivity functions for each species or group of species. Applications include the lighting of interior areas and the design of photometers.

Published spectral sensitivity data for a number of domesticated animals (human, turkey, duck, chicken, cat, rat and mouse) were used to calculate lighting levels for each species and compared with those derived from standard CIE human photopic and scotopic functions. Calculations were made for spectral power distributions of daylight, incandescent light and 12 fluorescent sources commonly used to light interiors. The calculated lighting levels showed clear differences between species and the standard human. Assuming that the resulting effects on the retinal illuminance determine the overall perception of the level of light, then there may be applications where these differences are important. However, evidence is also presented that the magnitude of these inter-species effects are similar to, or smaller than, those arising from other optical, physiological and psychological factors, which are also likely to influence the resulting perception.

Our results suggest that a judicious choice of three spectral sensitivity functions would satisfy most circumstances. Firstly, where the overall sensitivity is maximal in the medium to long wavelengths, then the standard CIE photopic function will suffice; secondly, in a small number of cases where the sensitivity centres on the short to medium wavelengths the CIE scotopic function should be used; and finally where an animal also has sensitivity in the UV region of the spectrum, an additional measure of the UV response should be included.

Avian discrimination of eggshell colour

Phillip Cassey

Centre for Ornithology, University of Birmingham

The broad range of eggshell colours in birds has long fascinated biologists. Yet there is no consensus about the relative contributions of various evolutionary causes and mechanisms that lead to variation in egg colouration and maculation within and across species. Here, I test a fundamental assumption of recently proposed signalling hypotheses of egg colour variation. Using a receptor-noise-limited colour opponent model of eggshell discrimination I assess whether individual birds in the superfamily Muscipoidea, an avian lineage renowned for their striking blue and otherwise coloured eggs, are capable of discriminating between the colours of eggs in different clutches. My results suggest that advanced, instrumental measures of eggshell coloration may obscure biologically realistic functions of phenotypic trait variation.

Through birds' eyes: What does vision tell us about the aquatic foraging of cormorants?

Graham Martin and Craig White

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Great Cormorants *Phalacrocorax carbo* show the highest known foraging yield for a marine avian predator and they are often perceived to be in conflict with human economic interests. They are generally regarded as visually-guided, pursuit-dive foragers, so it would be expected that cormorants have excellent vision much like aerial predators, such as hawks which detect and pursue prey from a distance. We have measured the aquatic visual acuity of five Great Cormorants (using a two-choice behavioural discrimination technique) under a range of viewing conditions (illuminance, target contrast, viewing distance) and found it to be surprisingly poor (comparable to unaided humans under water) and very inferior to that of aerial predatory birds. We have also measured visual fields and eye movements in Great Cormorants and found that these birds have a relatively narrow region of binocular vision which may be abolished upon immersion and spontaneously abolished by eye movements. However, unlike many birds, cormorants can see between their opened mandibles. A prey detectability model based upon the known acuity of cormorants at different illuminances, target contrasts and viewing distances, suggests that cormorants are able to detect typical individual prey items only at close range. We conclude that cormorants are not the aquatic equivalent of hawks. We suggest that their efficient hunting involves the use of specialised foraging techniques which employ short-distance pursuit and/or rapid neck extension to capture prey that is visually detected or flushed only at short range; much like the foraging techniques of herons. Like herons, the eye movements and visual fields of cormorants allow visual scanning for escaping prey in a wide arc about the head. The ability of cormorants to see prey held in the bill may function to aid its identification when it is brought to the surface, and aid its reorientation in the mouth before ingestion.

Coloration and colour vision in a parrot ring species

Mathew L. Berg¹, Raoul F. H. Ribot¹, Ben Knott¹, Leo Joseph², Katherine L. Buchanan³, Jim Bowmaker⁴, David Hunt⁴ and Andrew T. D Bennett¹

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Ring species, in which reproductively isolated forms are connected by a chain of intermediate populations, provide valuable insights into the maintenance of trait variability, divergence in sympatry, and the how small changes can lead to species level differences. The parrot *Platycercus elegans* of eastern Australia is highly variable in plumage coloration in the wild, ranging from pale yellow to deep crimson in the chest, rump and head. It has been suggested as the only known parrot ring species worldwide, and one of less than ~25 ring species amongst all organisms. We test hypotheses for the information signalled by the colour variation, and for the maintenance of the variability.

Coincident disruptive coloration

Innes C. Cuthill and Aron Székely

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Disruptive patterning is widely used in animal and military camouflage. High contrast colour patches create false bounding contours within the body as opposed to at its periphery. In his classic, and still definitive, account of animal camouflage, Cott (1940) noted that discontinuities at the body's edge are not the only clues to the presence of a cryptic animal; other salient features such as eyes and limbs must be concealed. He proposed that strategic placement of disruptive patterns, such that patterns are spatially coincident across adjacent body parts, would cause limb to blend with body, eye with face, and so otherwise conspicuous features would become unrecognisable. Given that there is no developmental necessity for colour patterns on disparate body parts to match, his arguments provided strong evidence for the adaptive nature of animal coloration at a time when Darwinism was far from dominant. However, perhaps because of this persuasive logic, coupled with fine illustrations of animals displaying such patterning, Cott's principle of Coincident Disruptive Coloration has never been experimentally tested. Using artificial moth-like stimuli with two-tone coloured 'wings' and edible two-tone coloured bodies, we show that coincidence of coloration across wing and body significantly reduces detection by wild birds in the field. We experimentally separate two contributions of the body-wing pattern coincidence to inconspicuousness: match of the body to its wing 'background', and the disruption of form central to Cott's hypothesis. We also present results from human visual search experiments that replicate these results under controlled viewing conditions.

Bees preferentially encode higher-order image statistics that have ecological relevance.

Richard Clarke

UCL

Because of the inherently ambiguous relationship between the real world and resulting visual stimuli, learning to use contextual image information in space and time is essential for survival. Determining which relationships are meaningful, however, is not trivial. Here we ask if some relationships of intensity and colour are more likely to be learned by the visual brain than others by training visually naïve bumblebees to recognise an artificial target flower according to both its intensity and colour under two spatial configurations of intensity: the first being consistent with natural variations of illumination intensity and the second less so. When trained to the first condition, bees learned a strategy that encoded the rewarding flower relative to its surrounding context. When trained in the second, they took twice as long to solve the same problem – despite the same amount of information (entropy) being present in the two scenes, and did so by ignoring the rewarding flower's spatial context. This discrepancy in the proficiency and in the nature of the image information used in the two conditions suggests that the visual brain is biased to more efficiently encode ecologically 'meaningful' image correlations, possibly as a means for resolving the behavioural uncertainty of images quickly and reliably. We use evolutionary computation to provide a simple, biologically plausible mechanism that explains these and related findings in terms of natural visual ecology.

Honeybees and bumblebees tradeoff colour discrimination for acuity

Adrian Dyer¹, Sabina Prack² and Johannes Spaethe²

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& Institut für Zoologie, Mainz, Germany

² *Department of Evolutionary Biology, University of Vienna, Althanstrasse 14, Vienna, Austria.*

AIM: Compare colour discrimination abilities of honeybees (*Apis mellifera*) and bumblebees (*Bombus terrestris*). Exp. 1. Differential conditioning was used to test 6 bumblebees on a simultaneous colour discrimination task using either ¹blue or yellow broadband stimuli (five-point star on a homogeneous background). A bee had to use both form and colour vision to solve the tasks, ensuring simultaneous colour discrimination. Data for bumblebees was compared to data for honeybee colour discrimination² using a 2-way between-group ANOVA. For blue [$F(1, 63) = 8.645$, $p = 0.005$, partial eta squared = 0.121] and yellow [$F(1, 56) = 11.798$, $p = 0.001$, partial eta squared = 0.174] stimuli bumblebee fine colour discrimination was significantly poorer than honeybees. Both bee species possess similar photoreceptors³, suggesting that differences in spatial or temporal signal integration might explain the observed differences. Exp. 2. A colour detection experiment was conducted in a Y-maze with bumblebees, and data compared to previously reported data for honeybee colour detection⁴. Bees flew into a decision chamber and detected in which arm of a Y-maze a coloured target was located. The minimum angle for which honeybees⁴ detect a colour stimulus (providing no green receptor contrast) is approximately 15°, but we found that bumblebees reliably detect these colour stimuli at angles smaller than 5°. CONCLUSION: Our findings suggest that differences in discrimination between these two bee species are likely to be due to a trade-off between visual acuity and colour discrimination, and that this trade-off is close to the limit imposed by noise in bee photoreceptors⁵.

1. Colour names refer to human visual system, see 2 for details.
2. Dyer AG, Neumeyer C. (2005) *J Comp Physiol A* 191: 547-557.
3. Peitsch D et al. (1992) *J Comp Physiol A* 170: 23-40
4. Giurfa M et al. (1996) *J Comp Physiol A* 178: 699-709
5. Vorobyev et al. (2001) *Vision Res* 41: 639-653.

The co-activation of snapshot memories in wood ants

Paul Graham, Virginie Durier and Thomas Collett

University of Sussex

Insects can guide themselves along a familiar route by retrieving and using visual snapshots that they have stored both along the route and at their destination and moving so that their current views match the target snapshots. To learn more about the matching process, we have investigated the interaction of snapshots by engineering a situation in which ants simultaneously retrieve two sets of memories. Ants were trained from a fixed start position to feed in one site, after which the feeder position was changed. It could take up to 30 trials before the ants headed directly to the new food site. We suppose that during this transition phase ants retrieve memories appropriate for both sites. We compared the ants' behaviour for two different sized separations between feeder sites. When the sites are relatively close together, the initial headings of the ants' paths rotated gradually from aiming directly at the first food site to aiming at the second food site, suggesting that ants' paths are controlled by the weighted average of two simultaneously activated snapshot attractors. By contrast, when the food sites were further apart, initial headings switched abruptly between the two sites – ants either headed for food site 1 or for food site 2. We show that these differences in transition behaviour can be simulated by the co-activation of snapshot attractors of restricted spatial extent, such that features encoded in a snapshot are only recognised if they occur within a limited retinal distance of the stored position of the feature.

Vision-based flight control in birds and insects

Graham Taylor

University of Oxford

Vision is a key sensory modality for flight control in birds and insects, but while optomotor responses have been widely studied from a physiological perspective, we know much less about how visual input is integrated with input from other sensory modalities in the feedback loops governing flight. Studying this is difficult because of the need to study either true free flight, or tethered flight that adequately simulates free-flight stimuli. In this talk, I will describe two new experimental techniques for studying vision-based flight control in birds and insects. The first uses wireless video camera technology to record onboard footage from freely flying birds. This enables us to monitor how saccadic head movements and nictitation influence the visual input that the bird receives during manoeuvres, and is combined with measurements from inertial sensors to study how visual input is phased with the body dynamics. The second technique uses modified computer data projectors to present realistic 3D scenes at up to 8000fps on a spherical projection surface surrounding a tethered insect. The insect is mounted in an airstream on a 6-component force-moment balance, and can be moved through a range of inertial motions independent of the visual stimuli presented to it. This virtual reality flight simulator enables us to study how input from different sensory modalities is combined to effect a dynamically meaningful flight control response. I will conclude by briefly summarising the preliminary data and findings from each technique.

Colour perception in dichromatic animals

Almut Kelber

Lund Vision Group, COB-Zoology, Lund University, Helgonavägen 3, S-22362 Lund.

The isoluminant colour space of trichromats (such as humans) can be depicted by a triangle, with the achromatic point in the centre and the spectral colours close to the edges. In the isoluminant colour space of dichromats, that has only one dimension, the achromatic point (in dichromats usually called neutral point) and a spectral colour have the same colour locus. Dichromats must therefore have the same perception of the wavelength at the neutral point (in horses, our model species here, around 480 nm) and an achromatic colour. It is often assumed that “for dichromats, there are no intermediate hues; when two colours are mixed, the result is either achromatic or a desaturated version of one of the basic hues” (e.g. Geisbauer et al. 2004, *Can J Zool* 82:660-670). This would let us assume that the neutral point divides the colour space into different colour categories. We have performed experiments on horses that indicate that horses do not treat the colour at their neutral point any different from other colour. Instead, they learn colours in a relative way, which may be comparable to perception of pitch in human hearing. Together with data on the tammar wallaby (Hemmi 1999, *J Comp Physiol A* 185:509-515) and in human dichromats (Wachtler et al 2004, *Vision Res* 44, 2843-2855), these data show that – although based on similar physiological mechanisms – colour perception in dichromats differs quite fundamentally from colour perception in trichromats.

The introduction of vision on Earth

Andrew Parker, *University of Oxford*

“In the country of the blind, the one-eyed man is king.” H.G. Wells’ famous dictum tells us something that may seem self-evident: *sight matters*. But imagine for a moment that the country of the blind is in fact the whole world, 550 million years ago. It’s a world where life is primitive and aimless, and evolution slow and painstaking.

Then something remarkable happens. Over the next five million years, the process of evolution kicks into over-drive. For the first time, animals evolve hard external parts. Both predators and prey develop armaments and defences. So in this relatively short space of geological time, animals from nearly all phyla leave their soft skins behind.

The “when” and the “what” of this “Cambrian explosion” have been known for some time. What has—until now—been speculation is the “why.” Why did this “Big Bang” of biology happen when it did? What caused it?

The best explanation we have is that it was the development of vision in primitive animals that caused the explosion. Precambrian creatures were unable to see, making it impossible to rapidly find friend or foe. With the evolution of the eye, the size, shape, colour, and behaviour of animals was suddenly revealed for the first time. Once the lights were “turned on,” there was enormous pressure to evolve hard external parts as defences and swimming oars, and claspable limbs to grab prey. The animal kingdom exploded into life, and the country of the blind became a teeming mass of hunters and hunted, all scrambling for their place on the evolutionary tree.

“[Parker’s] arguments seem very plausible to me.” —Francis Crick, 22 April 2003.

A tale of two fishes: The visual ecology of two deep-sea predatory fishes

Eric Warrant¹, Kerstin Fritsches², Eva Landgren¹ and Richard Brill³

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²*Vision, Touch & Hearing Research Centre, University of Queensland, Australia*

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Despite their great economic importance, almost nothing at all is known about the ecologies of deep-living swordfishes (*Xiphias gladius*) and escolar (*Lepidocybium flavobrunneum*). In my talk I will describe how the eyes of these two fishes can provide a window into their virtually unknown lives. The eyes of the swordfish are large and very sensitive, with acute frontally directed foveae. They are also heated by a specialised ocular muscle that produces fast vision (flicker fusion: 32 Hz) even in the very cold water of the deep. These results reveal that swordfishes are most likely to be fast visual predators at depths of up to 500 m during the day. The eyes of the escolar are also large and even more sensitive than those of the swordfish, but are more poorly resolved. Nevertheless, they possess foveae directed both dorsally and frontally. Since they lack ocular heating, escolar vision is slow, although it is fastest in warm surface waters (flicker fusion: 8 Hz). These results reveal that escolars are most likely to be slow nocturnal visual predators; cruising "smash and grab" hunters in warm surface waters at night when vision is fastest, spotting their prey from below.

VA Opsin update: More than just a teleost photopigment?

Stephanie Halford, Susana Piers and Russell Foster

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Vertebrate Ancient (VA)-opsin was first isolated from Atlantic salmon ocular cDNA ten years ago in 1997. Salmon VA-opsin shares 37-41% amino acid identity with the classical retinal opsins and 42% identity with chicken P-opsin. Furthermore, Salmon VA-opsin forms a functional photopigment when expressed *in vitro* and reconstituted with 11-cis-retinal. Significantly, VA-opsin is expressed in a subset of horizontal and ganglion cells in the retina and along with electrophysiological recordings provided the first demonstration that inner retina neurones could act as photoreceptors.

Subsequent *in situ* hybridisation studies demonstrated that salmon VA-opsin is also expressed in the pineal organ and habenular region of the brain, both structures either known to be or implicated in photoreception. Similar findings have been reported in many fish species including the common carp and zebrafish. Our original assumption was that the VA-opsin family would not be confined to teleosts but would also be represented in the other vertebrate classes. Despite the isolation of a VA-opsin homologue from the marine lamprey, all attempts to isolate VA-opsin from other vertebrates failed. This failure led to the suggestion that during evolution the VA-opsins were the ancestors to the tetrapod P-opsins and that direct homologues of VA-opsins would not be found in terrestrial vertebrates. This assumption was incorrect. The presentation will describe the isolation, characterisation and distribution of VA-opsins from both chicken and *Xenopus*. The possible photosensory tasks of the VA-opsins will also be considered.

Multifocal optical systems in vertebrate eyes for acute colour vision

Ronald H.H. Kröger

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Helgonavägen 3, 22362 Lund, SWEDEN; ronald.kroger@cob.lu.se*

Color vision provides a wealth of potentially relevant information. It is, however, far from trivial to create well-focused color images. The refractive index of any transparent material is a function of the wavelength of light, such that different wavelengths are separated by a lens and in focus in different planes (longitudinal *chromatic* aberration).

Multifocal optical systems are the biological solution to this problem. For monochromatic light, such systems have several distinct focal lengths. Each of these is used to focus a different spectral band on the retina. Multifocal optical systems are present in all vertebrate taxa we have studied so far, including agnathans. Vertebrates seem to have evolved tetrachromatic color vision and multifocal lenses very early and this may have been a crucial factor for the evolutionary success of the clade.

Vertebrate lenses have an internal gradient of refractive index that reduces longitudinal *spherical* aberration and leads to multifocality. We investigate the exact shape of the gradient in fish lenses (see Yakir Gagnon's contribution) and study how lens fiber cells that are devoid of all organelles quickly and exactly adjust the refractive index of the cytoplasm. A re-investigation of the suspension of the lens in teleost eyes revealed a complex system of ligaments that have not been described earlier.

We have understood that the apparently simple optical systems of vertebrate eyes are much more complex and sophisticated than previously realized. We continue to learn more about optics, image processing, intra-ocular signaling, phylogeny, and other topics.

Spherical fish lenses; optimization & adaptation

Yakir Gagnon

*Lund University, Department of Cell and Organism Biology, Zoology Building,
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Considerable efforts have been spent on finding the refractive index gradient of radially symmetric spherical lenses. Analyzing the paths of laser beams, deflected by the lens in a saline solution, has been one of the main methods used in determining the gradient.

The jump in refractive index between the surrounding medium (aqueous and vitreous humors) and the lens surface has posed a major problem for this procedure. This discontinuity leads to a singularity that makes it impossible to determine the RIG. The aims of this study were to (i) measure the thickness and RI of the lens capsule, (ii) determine the shape of the RIG in the peripheral cell layers of the lens, (iii) develop an optical model of a monofocal fish lens, (iv) use this model to understand how natural evolution has solved the problems arising from the singularity at the surface of the lens, and (v), if possible, understand why this is the optimal solution. We used lenses from the African cichlid fish *Astatotilapia* (formerly *Haplochromis*) *burtoni*. Lens capsule thickness was measured with a confocal microscope while the capsule's refractive index was measured with an interference microscope. Transmission electron microscopy was used to qualitatively determine differences in protein concentrations in the peripheral cell layers of the lens. Mean capsule thickness was $11.61 \pm 1.69 \mu\text{m}$ (standard deviation, $n = 5$) and the RI of the capsule was 1.393 ± 0.012 (standard deviation, $n = 4$). Densitometry showed that the protein concentration did not rise rapidly directly after the epithelium, but first at some distance from the lens surface (at about 92% of the lens radius). Using a non discrete model, we show that this flat refractive index gradient helps solve the lens' singularity. We argue that the special lens' gradient shape simplifies the regulation and optimization of the lens' optical properties.

Seeing motion in fishes

Christa Neumeyer and Martin Gehres

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Motion vision in animals can be investigated rather easily using the optomotor response. Measurements of spectral sensitivity in honeybees, goldfish, zebrafish and turtles revealed that one photoreceptor only (the "green" receptor or the L-cone, respectively) is involved, and that motion vision is "color blind". To see whether this is the case not only for "large field" motion detection, but also for "small field" object motion we performed training experiments in which goldfish had to discriminate between two test fields. Training stimulus was a moving red dot in green surround (speed: 7 cm/s), whereas a green test field without dot was unrewarded. Reducing the intensity of the green surround we found a small intensity range in which the fish were unable to see the red dot. Thus, object motion is color blind too! Even more surprising was the fact that the M-cone type is involved, and not the L-cone type as in the optomotor response.

Abstracts of posters

Through birds' eyes: Vision and the foraging technique of skimmers (Rynchopidae)

Graham Martin¹, Raymond McNeil² and Luz Marina Rojas³

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In birds, the position and extent of the region of binocular vision appears to be determined primarily by feeding ecology. Of prime importance is the degree to which vision is used for the precise control of bill position when foraging. Skimmers (*Rynchops*, Rynchopidae, Charadriiformes) exhibit a unique foraging behaviour and associated structural adaptations. When foraging they fly low and straight over water with the mouth open and the mandible partially submerged. Items that are hit by the lower mandible are grasped by a rapid reflex bill closure. It is believed that this unique “skimming” foraging technique is guided by tactile rather than visual cues. It is predicted therefore that the visual fields of skimmers will have similar topography to those of other tactile feeding birds. We determined retinal visual fields in Black Skimmers *Rynchops niger* using an ophthalmoscopic reflex technique. Contrary to expectation the visual fields of skimmers are not like those of other tactile feeders. They show high similarity with those of birds that feed by precision-pecking. The projection of the bill tip when the mouth is closed and when open (as in skimming) falls within the frontal binocular field and there is an extensive blind area above and behind the head. We argue that this visual field topography functions to achieve accurate bill positioning with respect to the water surface when skimming and, because foraging skimmers cannot determine the identity of what they are seizing as they skim, to permit the visual identification of prey items held between the mandibles after they have been taken from the water surface. When skimming, only a small portion of the binocular field, approximately 5° wide and extending 5° above the horizontal, looks in the direction of travel. The small size of this forward facing region of binocularity in skimmers suggests that control of locomotion in birds does not necessarily require extensive binocularity in the direction of travel.

Colour polymorphism and population divergence in a parrot ring species: a role for sexual selection?

Mathew L. Berg¹, Raoul F. H. Ribot¹, Leo Joseph², Katherine L. Buchanan³ and Andrew T. D Bennett¹

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Non-random mating is considered one way of promoting (or counteracting) polymorphism. For example, assortative mating is expected to reduce gene flow between morphs, leading to phenotypic divergence. Conversely, disassortative mating may help to maintain rare or intermediate phenotypes. Ring species, where a chain of intermediate forms separates two relatively divergent forms, provide an excellent opportunity to study the processes leading to polymorphism and population divergence. We studied a parrot ring species, the crimson rosella (*Platycercus elegans*). Genetic analyses indicate a relatively close relationship between the members of this species complex, but this study is the most detailed so far of their phenotypic variation. We used spectrometry and visual observations to assess coloration in all of the main forms. In the area studied, the complex consisted of several forms defined primarily by their red-yellow coloration, including a chain of clinally varying intermediate populations. As expected, we found a high degree of overall colour differences between populations, and greater polymorphism in intermediate populations. To study the influence of sexual selection on this system, we report (1) the frequencies of colour morphs across populations, (2) sexual dimorphism and condition dependence of coloration, and (3) the occurrence of (non-)random mating with respect to coloration in intermediate populations, including a zone of presumed intergradation between the most divergent forms. We discuss whether sexual selection may contribute to colour polymorphism in this system, and whether colour polymorphism promotes reproductive isolation despite possibly considerable gene flow.

Edge information alone elicits "white square" response in the common cuttlefish *Sepia officinalis*

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Cuttlefish are excellent animals for studying camouflage and invertebrate visual mechanisms as they exhibit rapidly changing body patterns which are under direct visual control. The "white square" component may be important in disruptive camouflage. Previous studies have shown it is displayed when white objects of an area similar to the white square are present in an animal's visual field. Here, by analysing body pattern responses of *S. officinalis* to high-pass filtered sections of white objects of a size known to elicit a white square response, I show that edge information alone provides a sufficient visual cue for this component to be displayed.

Cuttlefish perception of visual depth

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Cuttlefish adapt their body pattern to camouflage themselves in a wide range of conditions. We have been investigating the control of this behaviour by testing the relationship between the visual environment and the pattern displayed by the cuttlefish. Here we show that cuttlefish are sensitive to visual depth, and that they use 'real' 3-D information and (probably) pictorial depth cues to identify the substrate. The way in which the cuttlefish integrate multiple cues to background 'identity' suggests that camouflage selection may be better understood as a task resembling human object recognition than as simple pattern matching.

Activity modulation of optic flow processing neurons by an octopamine agonist in the blowfly

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How does visual processing depend on the locomotor state of the animal? The dynamic ranges of self-motion-induced visual motion vary with locomotor states such as flying and walking. As signalling is a significant energy cost, neural coding may be adapted to the requirements of the current state. In many invertebrates, the neurotransmitter and neurohormone octopamine is associated with "fight or flight" responses. We used an octopamine agonist chlorodimeform (CDM) to induce an elevated arousal state in the blowfly, *C. vicina*, while measuring the responses of the motion-sensitive spiking neurons V1 and V2. These neurons respond to motion in the ipsilateral visual field with motion preferences that match optic flow patterns generated by self-rotations. CDM increased the V2 spontaneous activity by 170% and significantly increased the cells' direction-selective response range. The response range was also significantly increased in the contralateral visual field, which would increase the specificity of the V2 response to a roll rotation. In V1 cells, CDM increased the spontaneous activity by 130%, but the directional-selective response range was unchanged. For both cells, the stimulus response latency was significantly reduced with CDM, by 15% for V2 and 10% for V1. Our findings suggest that during flight or stressful situations, octopamine may elevate the activity of visual interneurons, facilitating rapid responses to visual motion. Both the dynamic response range and roll rotation-specificity of V2 are increased, consistent with the higher probability of encountering faster roll-rotations during flight.

Bridging the Gap: Ancestral Trichromacy in Mammals

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Vertebrate photoreceptors express four cone pigments (*LWS*, *SWS1*, *SWS2*, *Rh2*), in addition to a rod opsin (*Rh1*), whose spectral sensitivities range from ultraviolet (360 nm) to red (560 nm) and are retained throughout the teleost, amphibian, reptilian and avian radiations. However, eutherian mammals have lost the short-wavelength sensitive 2 (*SWS2*) and medium-wavelength sensitive 2 (*Rh2*) genes and are mostly dichromats with the retention of short-wavelength sensitive 1 (*SWS1*) and long-wavelength sensitive (*LWS*) opsins. Despite a major reduction from tetrachromacy to dichromacy in the ancestor to all mammals, very little is known concerning the evolution of the early mammalian visual system. Thus, in this study we investigated the visual pigments of an iconic Australian mammal: the duck-billed platypus (*Ornithorhynchus anatinus*).

Using a set of degenerative primers, we successfully PCR-amplified partial sequences for *SWS2* and *LWS* opsins, as well as *Rh1* rod opsin from platypus genomic DNA. Subsequent *in silico* probing of the platypus genome using these partial sequences as bait allowed the full gene structures of *SWS2*, *LWS* and *Rh1* opsin genes to be determined. Phylogenetic analysis of these opsins indicates they are orthologues of visual pigment genes present in other vertebrates. Each coding sequence was expressed *in vitro* with 11-*cis* retinal to give peak spectral sensitivities of 451 nm (*SWS2*), 550 nm (*LWS*) and 498 nm (*Rh1*). Only exon 5 of the *SWS1* gene could be detected with no *Rh2* gene ever found. These results imply that the novel route to dichromacy in this monotreme is unique compared to other mammals. The presence of *SWS1* in phylogenetic groups that pre- and post-date the speciation event that gave rise to the monotremes, suggests that the mammalian ancestor also possessed *SWS1*. Along with the *SWS2* and *LWS* genes, this study supports our hypothesis that early mammalian colour vision was based on trichromacy.

This work was funded by grants from the Biotechnology and Biological Sciences Research Council, the Leverhulme Trust, and the Australian Research Council and Biotechnology.

Do fly & primate neurons code moving 2D patterns the same way?

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When we observe a moving pattern, we perceive the whole pattern to be moving, rather than its components moving in different directions. The neural correlates of this perception of pattern motion are found in area V5/MT of the primate visual system. The more tractable visual system of the fly may aid in understanding the mechanisms underlying 2D motion processing. How do fly neurons code moving 2D patterns? How does it compare with mammalian 2D motion processing? Activity in the fly H1 neuron is known to be involved in the visuo-motor control. We recorded activity from this neuron in blowflies and studied the tuning response for plaids with different inter-plaid angles. We find that the H1 neuron responds stronger to the overall pattern than to its individual components although it is not as sharply tuned. A model of fly neural coding that can explain this response is similar in many regards to models that describe V5/MT neurons of the mammalian visual system. This suggests a general principle of processing 2D pattern motion across species, and we can use the fly as a model system to probe its mechanisms.

Visual pigments and colour vision in elasmobranchs

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The majority of elasmobranchs (sharks and rays) studied to date possess both rod and cone photoreceptors in their retinæ. Virtually nothing is known, however, about whether elasmobranchs possess multiple cone types, and therefore the potential for colour vision, or how the spectral tuning of their visual pigments is adapted to their different lifestyles. In this study we measured the spectral absorbance of rod and cone visual pigments in three species of ray and four species of wobbegong sharks using microspectrophotometry. All three ray species have a single rod visual pigment and three spectrally distinct cone types with varying wavelength of maximum absorbance (λ_{\max}) values. This shows for the first time that at least some species of elasmobranchs have the potential for trichromatic colour vision. In the wobbegong sharks, however, only a single cone type has been found using this technique so far in only one of the four species. Interestingly, the single rod visual pigment λ_{\max} value differs among the four species, with one species having a blue-shifted visual pigment similar to deep sea elasmobranchs. All four wobbegong species occur in relatively shallow depths and utilise different habitats. The blue-shifted rod visual pigment could be an advantage for crepuscular activity when the underwater spectrum is dominated by shorter wavelengths of light, while the rod visual pigment of the other three species is more adaptive to a diurnal lifestyle. The next step for this project is to identify and sequence the opsin protein genes for these species and others, in order to determine which genes are present and therefore what type of visual pigments should be expressed in the retina.

An analysis of the phases and dynamics of bumblebee learning flights

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When bees and wasps leave the nest to forage they perform learning flights [1]. Analysis of the learning flights of solitary and social wasps has identified several components of the flights which seem to be adapted for the active acquisition of visual information [2, 3, 4]. Here we present an analysis of the learning flights of bumblebees when they are close to their nest in the ground. A colony of bumblebees was located under a textured white carpet with an upright black cylinder 10-20 cm from the nest hole. Flights start with a phase in which the bee flies in tight circles close to the nest hole and low on the ground. This component seems to be less prominent in the learning flights of other insects that have been recorded. It leads into the more usual semi-circular arcs which resemble those of solitary wasps [2, 3]. These arcs appear to consist of a number of linked phases with behaviour consistent across arcs.

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Wavefront aberrations in peripheral vision

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This study investigates the hypothesis that the off-axis vision of avian eyes is adapted to their environment. The aim is to provide important information about the underlying mechanisms by which the quality of the pigeon's vision is maintained away from the eye's central axis (e.g. frontal vision). In humans, the importance of peripheral vision is often dismissed due to the lower density of photoreceptors in the eccentric parts of the retina, and also because of the reduced optical quality of images formed by off-axis rays.

Pigeons are highly visual and possess a very specialized retina with adaptations for peripheral viewing. The eyes of pigeons are laterally positioned, providing a panoramic view of the world. Most birds also have a secondary specialization of the temporal retina. Retinoscopy studies indicate that the pigeon eye is largely corrected for off-axis aberrations, but the extent of this correction and how it is achieved is unknown.

In the preliminary phase of this project, aberrations in human peripheral vision are measured to provide data for comparison with our subsequent findings in birds. A Hartmann-Shack wavefront sensor (HSWFS) has been developed to measure the ocular aberrations in the eye. The light returning from the eye is imaged onto the lenslet array of the HSWFS. Using a modal reconstruction, the Zernike coefficients are calculated up to fifth order. The wavefront measurements are performed at different eccentricities, as determined by different fixation points. The results indicate that astigmatism increases with increasing eccentricity. This trend is evident not only with the value corresponding to oblique astigmatism, but also in the amount of secondary astigmatism.

The genetic basis for colour vision in the fat-tailed dunnart, *Sminthopsis crassicaudata*

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Trichromacy in mammals has been widely reported in primates. More recently, microspectrophotometry (MSP) has identified three classes of cone photoreceptors in certain species of marsupial. One such species is the fat-tailed dunnart (*Sminthopsis crassicaudata*), with cone pigments at 535, 509 and around 360nm.

Using PCR on dunnart genomic DNA and retinal cDNA, we have amplified full-length sequences that are orthologues of the longwave-sensitive (LWS) and shortwave-sensitive (SWS1) cone opsin genes and the Rh1 rod opsin gene. The LWS and SWS1 sequences were expressed *in vitro* and the recombinant pigments regenerated with 11-*cis* retinal; the resulting absorbance spectra showed peak values at 533 and 363nm, thereby identifying the 535 and 360nm pigments identified *in situ* by MSP as LWS and SWS1 pigments.

Despite numerous attempts, we have been unable to amplify a distinct third cone opsin sequence that would account for the 509 nm pigment and we could find no evidence for a duplication of either the LWS or SWS1 gene.

In situ hybridisation was carried out on dunnart cryosections with riboprobes homologous to LWS, Rh2, SWS2 and Rh1 opsins. Both the LWS and Rh1 probes showed strong hybridisation to the outer nuclear layer, whereas all the other riboprobes failed to hybridise, consistent with the absence of an expressed SWS2 and Rh2 opsin.

The basis for the 509nm pigment remains therefore uncertain. A feature of this pigment is its similarity to the peak absorbance of the rod pigment at 512nm, and this is also seen in other marsupials with a middlewave-sensitive (MWS) pigment. One possibility therefore is that the MWS pigment is encoded by an Rh1 opsin gene expressed in cone photoreceptors and it may be significant that we have found evidence for the presence of two distinct Rh1 genes in the dunnart genome.