Vision Research 172 (2020) 62–63

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Editorial

The astonishing diversity of vision: Introduction to an issue of *Vision Research* on animal vision

Trapped behind our own eyes we have a strong feeling of looking out at reality, perceiving the world with the detail and colours conveyed by the spatial and spectral sampling of our central visual field. Other animals see different worlds; most invertebrates would be classified as legally blind, but they are visually adept, and they often outperform us with ultraviolet sensitivity and polarization vision. Some animal eyes serve many purposes, whereas others are specialised.

The marvellous diversity of animal eyes reveals how natural selection shapes vision, and has led to general principles. Here one name comes to mind: Michael F. Land of the University of Sussex, known to friends and colleagues as Mike. Taking an evolutionary and ecological perspective for over half a century he has opened new fields, discovering unexpected eyes and visual functions, and finding general principles. Mike Land explains the physics and optics of vision with the clarity that comes from deep understanding. This issue of *Vision Research* celebrates Mike Land's lifetime in science.

1. Eye design

Mike Land's doctoral research in the early 1960s on the mirror-optics of scallop eyes showed how spatial resolution could be estimated from the structure and optics (Land 1965, 1968). Work on jumping spider eyes (Land, 1969a, 1969b), led to other spiders (Land & Barth, 1992; Land, 1985) and hence a wide range of invertebrates (e.g. Land 1982, 1984, 1989a, 1989b, 1997, 2000a, 2000b, 2003, Land & Eckert, 1985, Land, Burton, & Meyer-Rochow, 1979). For each eye he worked out the optics and calculated the spatial resolution. Mike introduced valuable optical techniques including ophthalmoscopic methods (Land & Barth, 1992; Land 1984, 1989b).

This work was underpinned by an influential formalisation of the physics of vision, including performance limits due to aberrations, diffraction and photon noise, and equations for calculating visual sensitivity, spatial resolution and contrast sensitivity (Land, 1981). For several decades Land (1981) chapter in the Handbook of Sensory Physiology and Land and Nilsson's textbook on Animal Eyes (Land & Nilsson, 2012) been valued accounts of physical and mathematical aspects of vision.

Here three papers continue the investigation of spatial resolution in animal eyes. Chaib, Ljungholm, Lind, and Kelber (2019) find that budgerigar spatial resolution is 6–8 times lower than human foveal resolution, and that their point resolution is no better than for sinusoidal gratings, which is consistent with evidence that birds have lower contrast sensitivity than mammals. A remarkable paper on the anterior lateral eyes of a jumping spider (Gote, Butler, Zurek, Buschbeck, & Morehouse, 2019) finds that the small eyes of juveniles achieve the same spatial resolution as the much larger adult eyes, but at the expense of absolute sensitivity, so that the juveniles need more light or higher contrasts for visual discrimination. It is tempting to focus on eyes that are in some way impressive, but they sometimes puzzle us by their apparent inadequacy. Here Kirwan and Nilsson (2019) behavioural tests of a millipede which has small compound eyes of about 35 ommatidia find spatial resolution of 0.018 cycles per degree, 3000 times worse than human foveal resolution, but sufficient to find dark shelters. Poor spatial resolution is a feature of insect ocelli, allowing them to complement the compound eyes by integrating intensity over a wide field, and hence to mediate flight stabilization. Here Wilby et al. (2019) use X-ray tomography to investigate the optics and visual fields of bumblebee ocelli in unprecedented detail, finding that ocellar fields of view are directed forward and dorsally, incorporating the horizon as well as the sky.

2. Retinal specialization and eye movements

Animal eyes rarely sample the visual field uniformly in space or time. At Berkeley in the late 1960s Land (1969a, 1969b) established how in jumping spiders the four pairs of eyes divide the visual field. The large, forward facing ”principal eyes” – which give these spiders an almost endearing appearance – image only a small spot in space, and the highest resolution of the principal eye retinas is restricted to a still smaller region, to form a retinal fovea within an optical fovea. These eyes therefore make scaning movements to see objects (Land, 1969a, 1969b). The principal eyes share their visual fields with much less acute lateral eyes. Thus, jumping spider vision operates at different levels of detail. A key task for jumping spiders is to distinguish prey from potential mates (Dolev & Nelson, 2014), which seems to depend mainly on the number of legs (Drees, 1952; Land, 1969a, 1969b). Similar simple rules might apply to object recognition by other species, and here Watanabe, Fujimoto, Hirai, and Ushitani (2019) show that pigeons learn object topology more easily than other spatial cues, which can allow view-point indpendence. They suggest that sensitivity to topology is a primitive component of the avian visual system.

Continuing the theme of retnal specialisation Sibeaux, Keser, Cole, Kranz, and Endler (2019) find that the responses of guppies to moving dots depend on the colour and spatial location of a stimulus, and that there are sex differences. They suggest that responses are partly correlated with photoreceptor arrangement in the retina. Sajdak et al. (2019) report how ground-squirrel retinas vary during hibernation, finding that the cone mosaic is only transiently affected by structural remodeling during hibernation.

Specialisation of the visual field often necessitates eye movements, – which in smaller animals can be implemented by the head or entire body. An interest in animal eye movements led in the 1990s to Mike Land's ingenious and innovative studies of where people fixate when doing tasks like tea-making, in driving, or when playing sports (Land,

https://doi.org/10.1016/j.visres.2020.02.004

Available online 31 March 2020

2006). Here, Land (2019) provides a synoptic review, and other articles in this special Issue carry forward this legacy of segregating visual function in space and time.

3. Opsins of nocturnal eyes

Mike Land does not venture into molecular biology – referring to the "dark-art", mainly out of respect, – but keeps a sharp eye on this subject, especially its implications for visual ecology and colour vision. For example genetics is useful for studying sensitivity optimisations and visual ecology based task-driven solutions. Three papers here examine the spectral sensitivity using molecular techniques, revealing the visual pigment complement in owls and snakes.

Most birds have five types of visual pigment with spectral sensitivites that vary little with ecology and behaviour (Osorio, 2019), but owls offer exceptions. Here in four species of owl Höglund et al. (2019) find low RH2 (MWS) opsin levels and a lack of UV/violet (SWS1) opsin. This adds to a known trend for these nocturnal birds to loose UV cone sensitivity. However, from measurements of ocular media and oil droplets and sensitivity estimates for their rod-dominated retinae the authors suggest that owls retain UV sensitivity, perhaps allowing them to see UV reflecting feathers. At the other end of the spectrum de Vasconcelos et al. (2019) examined expression of long wave sensitive opsins (LWS) genes in five owl species spanning diurnal through to nocturnal lifestyles. Using immunohistochemistry they also looked at the retinal distribution of these photoreceptors. They find one species with a short wavelength shifted LWS pigment and another with reduced numbers of LWS cones. Further studies to identify environmental effects on variations of this kind would be attractive (Osorio, 2019).

Bittencourt, Hauzman, Bonci, and Ventura (2019) chose snakes to examine habitat- or habit-driven differences in the visual pigment genes and photoreceptor structure. Snakes are an interesting group because their visual systems are emerging from a period of nocturnality, and in common with lizards they lack the typical vertebrate duplex retina with distinct rods and cones (Osorio, 2019). Two species of mostly nocturnal vipers were chosen, one inhabiting savannah and one rainforest. Both have three opsin types (LWS, SWS1, RH1), and while showing assumed convergent adaptations to nocturnality including rod-like photoreceptors and UV sensitivity, no habitat driven diversity was found. The potential for a simple dichromatic colour sense is considered and likely limited to daytime activity.

References

Bittencourt, G. B., Hauzman, E., Bonci, D. M. O., & Ventura, D. F. (2019). Photoreceptors morphology and genetics of the visual pigments of *Bothrops jararaca* and *Crotalus durissus terrificus* (Serpentes, Viperidae). *Vision Research, 158*, 72–77.

Chaib, S., Ljungholm, M., Lind, O., & Kelber, A. (2019). Single target acuity is not higher than grating acuity in a bird, the budgerigar. *Vision Research, 160*, 37–42.

Dolev, Y., & Nelson, X. J. (2014). Innate pattern recognition and categorization in a jumping spider. *PLoS One, 9*(6).

Drees, O. (1952). Untersuchungen tiber die angeborenen Verhaltensweisen bei Spnngspinnen (Salticidae). *Zeitschrift für Tierpsychologie, 9*, 169–220.

Gote, J. T., Butler, P. M., Zurek, D. B., Buschbeck, E. K., & Morehouse, N. I. (2019). Growing tiny eyes: How juvenile jumping spiders retain high visual performance in the face of size limitations and developmental constraints. *Vision Research, 160*, 24–36.

Höglund, J., Mitkus, M., Olsson, P., Lind, O., Drews, A., Bloch, N. I., ... Strandh, M. (2019). Owls lack UV-sensitive cone opsin and red oil droplets, but see UV light at night: Retinal transcriptomes and ocular media transmittance. *Vision Research, 158*, 109–119.

Kirwan, J. D., & Nilsson, D. E. (2019). A millipede compound eye mediating low-resolution vision. *Vision Research, 165*, 36–44.

Land, M. F. (1965). Image formation by a concave reflector in the eye of the scallop, *Pecten maximus*. *Journal of Physiology, 179*, 138–153.

Land, M. F. (1968). Functional aspects of the optical and retinal organization of the mollusc eye. *Symposia of the Zoological Society of London, 23*, 75–96.

Land, M. F. (1969a). Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. *Journal of Experimental Biology, 51*, 471–493.

Land, M. F. (1969b). Structure of the retinae of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. *Journal of Experimental Biology, 51*, 443–470.

Land, M. F. (1981). Optics and vision in invertebrates. In H. Autrum (Ed.). *Handbook of sensory physiology, Vol. VII/6B* (pp. 471–592). Berlin: Springer.

Land, M. F. (1982). Scanning eye movements in a heteropod mollusc. *Journal of Experimental Biology, 96*, 427–430.

Land, M. F. (1984). The resolving power of diurnal superposition eyes measured with an ophthalmoscope. *Journal of Comparative Physiology A, 154*, 515–533.

Land, M. F. (1985). The morphology and optics of spider eyes. In F. G. Barth (Ed.). *Neurobiology of arachnids* (pp. 53–78). Berlin: Springer.

Land, M. F. (1989a). The eyes of hyperiid amphipods: Relations of optical structure to depth. *Journal of Comparative Physiology A, 164*, 751–762.

Land, M. F. (1989b). Variations in the structure and design of compound eyes. In D. G. Stavenga, & R. C. Hardie (Eds.). *Facets of vision* (pp. 90–111). Berlin: Springer.

Land, M. F. (1997). Visual acuity in insects. *Annual Review of Entomology, 42*, 147–177.

Land, M. F. (2000a). On the functions of double eyes in midwater animals. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences, 355*, 1147–1150.

Land, M. F. (2000b). On the functions of double eyes in midwater animals. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences, 355*, 1147–1150.

Land, M. F. (2003). The spatial resolution of the pinhole eyes of giant clams (*Tridacna maxima*). *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences, 270*, 185–188.

Land, M. F. (2006). Eye movements and the control of actions in everyday life. *Progress in Retinal and Eye Research, 25*, 296–324.

Land, M. F. (2019). Eye movements in man and other animals. *Vision Research, 162*, 1–7.

Land, M. F., & Nilsson, D. E. (2012). *Animal eyes.* Oxford University Press.

Land, M. F., & Barth, F. G. (1992). The quality of vision in the ctenid spider *Cupiennius salei*. *Journal of Experimental Biology, 164*, 227–242.

Land, M. F., Burton, F. A., & Meyer-Rochow, V. B. (1979). The optical geometry of euphausiid eyes. *Journal of Comparative Physiology, 130*, 49–62.

Land, M. F., & Eckert, H. (1985). Maps of acute zones of fly eyes. *Journal of Comparative Physiology, 156*, 525–538.

Osorio, D. (2019). The evolutionary ecology of bird and reptile photoreceptor spectral sensitivities. *Current Opinion in Behavioral Sciences, 30*, 223–227.

Sajdak, B. S., Salmon, A. E., Litts, K. M., Wells, C., Allen, K. P., Dubra, A., ... Carroll, J. (2019). Evaluating seasonal changes of cone photoreceptor structure in the 13-lined ground squirrel. *Vision Research, 158*, 90–99.

Sibeaux, A., Keser, M. L., Cole, G. L., Kranz, A. M., & Endler, J. A. (2019). How viewing objects with the dorsal or ventral retina affects colour-related behaviour in guppies (Poecilia reticulata). *Vision Research, 158*, 78–89.

de Vasconcelos, F. T. G. R., Naman, M. J. V., Hauzman, E., Baron, J., Ventura, D. F., & Bonci, D. M. O. (2019). LWS visual pigment in owls: Spectral tuning inferred by genetics. *Vision Research, 165*, 90–97.

Watanabe, A., Fujimoto, M., Hirai, K., & Ushitani, T. (2019). Pigeons discriminate shapes based on topological features. *Vision Research, 158*, 120–125.

Wilby, D., Aarts, T., Tichit, P., Bodey, A., Rau, C., Taylor, G., & Baird, E. (2019). Using micro-CT techniques to explore the role of sex and hair in the functional morphology of bumblebee (*Bombus terrestris*) ocelli. *Vision Research, 158*, 100–108.

Tom Cronin[a], Justin Marshall[b], Dan Nilsson[c], Daniel Osorio[d]

[a] *Department of Biological Sciences, University of Maryland Baltimore County, 1000 Hilltop Circle, Baltimore, Maryland 21250, USA*

[b] *The Queensland Brain Institute, The University of Queensland, St Lucia QLD 4072, Australia*

[c] *Lund Vision Group, Department of Biology, Sölvegatan 35, S223 62, Lund, Sweden*

[d] *School of Life Sciences, University of Sussex, Brighton BN1 9QG, United Kingdom*