Preface

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The 21st Annual Karger Workshop was called ‘Vision with an Eye to Ecology’ and served as a platform to honour Prof. Barrie Frost of Queen’s University at Kingston, Ont., Canada. He has lived in Canada for over 40 years, but he still proudly carries the rich accent of a Kiwi. Growing up in New Zealand, he developed a fascination with animals in their environment. As a boy, when he heard a rustling or call from the bushes, his instinct was to pounce blindly and this continued in Canada. Ever the good father, Barrie once espied a garter snake and attempted to show his boys that snakes need not be feared. It was, however, a hot summer day, and the snake was uncooperative – Barrie was only able to show them several bite marks on his hands. Luckily he was much more successful in showing the world his fascination for brain and behaviour in the laboratory. Barrie has worked on a diverse array of animals including butterflies [Mouritsen and Frost, 2002], shorebirds [Pettigrew and Frost, 1985], owls [van der Willigen et al., 1998] and cats [von Grünau and Frost, 1983]. His love for the animal kingdom did not go unnoticed by others. Barrie is well known by undergraduate students and faculty as ‘the guy who pretends to be a jumping spider’ by placing his fingers upon his forehead as representative eyes (fig. 1). Many have used this example to convey Barrie’s contagious enthusiasm for science.

Fig. 1. Barrie Frost (left) is known among students and colleagues for his lively imitation of a jumping spider (right).

Although he has studied other sensory systems, Barrie is best known for his work on the neurophysiology of visual systems. He was very much influenced by J.J. Gibson and David Lee, both psychologists, and would emphasize the information afforded to the animal from motion in the optic array. Following David Lee, Barrie showed that neurons in the nucleus rotundus respond to looming stimuli and accurately signal time-to-collision to initiate avoidance responses [Wang and Frost, 1992]. Following

Gibson, in much of Barrie's work, including his contribution in this volume, he would distinguish local motion, which would be due to objects (prey, predators) moving in the environment, from global motion, which would be due to an animal's self-motion through the environment [Frost et al., 1990]. Stimulus composition and control was critical in Barrie's research. In his seminal studies on the responses of tectal neurons, rather than using black or white spots, he used kinematograms, where an object consisting of a collection of random dots moves across a background consisting of random dots. This is a more natural stimulus and the object in question is defined purely by motion, and not luminance differences. With this, Barrie was able to show that tectal neurons respond best when the object and background are moving in opposite directions and are likely critical for distinguishing figure from ground and camouflage breaking [Nakayama and Frost, 1983].

In keeping with Barrie's accomplishments in studying animals throughout the animal kingdom, for this Karger workshop we sought to include researchers who had explored vision in a disparate range of species, and in light of the animals in their environment. Craig Hawryshyn discusses the ability of salmonids to detect polarized light, which is important for their migratory habits. The ability to detect polarized light is critical to the behaviour and ecology of many species. In his review, Craig discusses the physics of light polarization, behavioural responses of fish to polarized light and the retinal mechanisms underlying the detection of polarized light. Pacific migratory salmonids exhibit developmental plasticity in the expression of ultraviolet sensitive cones and this plasticity is correlated with behavioural differences in the ability of salmonids to detect polarized light throughout their lifespan. Ultimately, this plasticity is likely an adaptation to their migratory habits and an excellent example of how incorporating an ecological approach can yield insight into visual system structure and function.

Toru Shimizu et al. highlight the similarities and differences between pigeon and primate visual systems with respect to behaviour and the brain. For example, behavioural tests have shown that pigeons can discriminate subtle differences in the faces of potential mates, but they do not attend to alterations in facial configuration (i.e. position of eyes relative to beak). Neuroanatomical studies reveal that different visual stimuli are processed in parallel along the collothamic pathway leading from the optic tectum via the nucleus rotundus to the entopallium. Thus, colour is processed in one stream and form in another within the same general pathway. This pattern

further extends to efferent targets of the entopallium, such as the lateral portion of the intermediate nidopallium, and thereby shares several similarities with the primate lemnothalamic pathway. Finally, they review evidence that the avian visual telencephalon is organized into columns, which are differentially expanded across avian taxa. The conclusion to be drawn from this review is that in order to understand these similarities and differences between avian and primate visual systems, we must adopt an integrative approach such that anatomy, physiology and behaviour are examined across a range of species.

Chris Heesy and Margaret Hall examine the constraints placed upon mammalian visual systems by their evolutionary history. Unlike other major vertebrate groups, all mammals are thought to have descended from nocturnal ancestors. There are several complementary lines of evidence to support this theory, including visual pigments, retinal structure and, in most species, a decreased reliance on vision. Heesy and Hall briefly review these features of the mammalian visual system as well as provide information on eye shape and binocularity to support the 'nocturnal bottleneck' hypothesis of mammalian evolution. In contrast to lizards and birds, non-primate mammals all share a nocturnal eye shape characterized by a larger corneal diameter relative to eye length regardless of whether they are nocturnal or diurnal. Mammals also differ from other vertebrates in that they appear to have much higher orbital convergence (i.e. the eyes face frontally) and broader overlap in their binocular field than birds or squamates. Both orbital convergence and binocular visual field overlap are higher in nocturnal than diurnal mammals and vary with ecology. Based on this additional evidence, it is clear that ecology not only plays a role in understanding the function of the visual system, but also its evolution among vertebrates.

Shaun Collin's submission emphasizes that for a complete understanding of the influences of ecology and phylogeny on the design of the visual system, it is essential to understand the basic *bauplan* of key representatives within each taxa. To this end, he reviews photoreception in hagfishes, lampreys, cartilaginous fishes and lungfishes noting that they have surprisingly sophisticated visual systems.

Eric Warrant and Marie Dacke provide a fascinating review of the visual cues that nocturnal arthropods use to navigate. Here, diversity is emphasized given the ecological constraint placed on the particular species. Whereas some species travel in the open and can take advantage of the celestial cues, others live in the understory

of a forest, and have a much more difficult task. Warrant and Dacke review the visual cues that are available to nocturnal arthropods, eye design, and the examples of the various forms of orientation and navigation that are accomplished.

Finally, Barrie Frost provides a 'taxonomy' of different forms of visual motion and suggests that there may be a hierarchy of visual motion processing in the brain. The neural mechanisms associated with the processing of dif-

ferent stages in the hierarchy are discussed and it is the intent that this taxonomy will help guide future neurophysiological research on visual motion processing.

We are indebted to Karger Publishers for their continued support for the workshop as well as to Walt Wilczynski, Blinda McClelland and Georg Striedter. We hope you enjoy reading these articles as much as we all enjoyed the workshop itself.

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