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INTRODUCTION

Comparative, ecological, and developmental aspects of visual system design and function

To each vision must be brought and eye adapted to what is to be seen, and bearing some likeness to it (Plotinus, 3rd century C.E.).
The perfection of the eye gives me a cold shudder (Darwin, 1857).

Beliefs about our place in nature have long shaped our beliefs about the nature of vision. Theological accounts such as Plotinus's—which held that beauty of creation is manifest only to those who are close to God—placed the eye center stage in the 19th century debate on evolution. If the eye is perfect, natural selection is of little relevance, and Darwin (1874) was reassured by learning that the eye suffers chromatic aberration. Thus, physics and evolutionary theory gives Plotinus's aphorism a paradoxically different meaning from that intended. The adaption of the eye to what *needs* to be seen is the primary theme of this issue of *Visual Neuroscience*.

Compromises between spatial resolution, absolute sensitivity, spectral discrimination, and response speed—as well as energetic cost—reflect the needs of behavior. It is fortunate that the principles of physiological optics are quite straightforward—for example, bigger eyes collect more light and give higher quality images. Even so, the evolution of eye size remains incompletely understood. Here, **Fischer et al.** ask how small an eye can be. They describe compound eyes of a wasp with 6 μm facet lenses. The precise cellular anatomy of these tiny ommatidia is shared with the honeybee, indeed, the lobster, nicely illustrating the conservatism of development and anatomy, as well as its adaptability. One is tempted to ask how small a photoreceptor cell can be. In a review that raises the basic question of how one defines both eyes and vision, **Ramirez et al.** suggest a classification of simple light-sensing structures according to aggregation of light sensors and their directionality.

The question of how eyes are adapted to what is to be seen is the subject of classic accounts in visual ecology of how fish photoreceptor spectral sensitivities are matched to illumination in water (Lythgoe, 1979) and how receptor and ganglion cell densities are matched to habitat (Hughes, 1977). It is curious then that variation in photoreceptor spectral sensitivity across the visual field, which is widespread in animals, remains largely unexplained; here, **Temple** summaries this subject and discusses various explanations. Similarly, rods receive less attention than cones in studies of evolution and ecology, and it is pleasing that two papers here deal with rod vision. **Taylor et al.** examine changes in receptor distributions and spectral sensitivities over the life span in the rod-dominated retina of the tarpon, a raptorial fish, while **Morrow et al.'s** discovery of a new zebrafish rod opsin gene, *rh1-2*, that appears to be widespread in teleosts (but is not associated with their ancestral genome duplication) raises questions about the evolution of rod vision. Whereas the effects of water on the spectral composition of light are familiar, the consequences of its turbidity for spatial vision are less well known. **Lee and Bumsted O'Brien's** study of seahorse spatial acuity and retinal ganglion cell density addresses the problem of finding small objects in presence of scattered light. They find that a tropical species has a higher resolution than the temperate, which might be related to the fact that tropical waters are in general less turbid, favoring spatial resolution.

Beyond the optics and the retina, ecological principles of neural processing have developed since the 1950's, influenced by information theory and cybernetics. The use of motion flow fields for navigation (Gibson, 1979) has provided remarkable insights into neural processing, informed by an appreciation of behavioral requirements and the statistics of natural stimuli (e.g., Krapp & Hengstenberg, 1996). It is widely thought that motion-sensitive mechanisms are color blind, perhaps—following Gibson's principles—because chromatic information adds little to, or may even corrupt, the achromatic signal (Srinivasan, 1985). However, the notion that color and motion are processed by separate systems remains controversial. Here, **Stojcev et al.** examine chromatic sensitivity of movement detection in both bees and goldfish. They argue why chromatic information should be useful in motion detection and offer experimental evidence that it is indeed used for movement of objects against the background if not global motion flow fields.

To understand what the eye is adapted to see, one can ask what is overlooked. Thus, changes in illumination are commonly treated mainly as a problem to be "discounted" by mechanisms of object constancy. Nonetheless, **Wilson and Lindstrom** point out that shadows may be an important source of information, particularly about aerial predators to birds. In a fascinating proposal, they describe a feedback pathway from the avian isthmo-optic nucleus to the retina, which they argue has a key role in the detection of moving shadows. The devices that artists use to achieve verisimilitude with paint can reveal what information we use to interpret natural images. **Graham and Meng** examine the discrimination of images in very brief presentations and argue that paintings retain the spatial frequency composition characteristic of natural images, thereby tuning them to the mechanisms that transmit information from the eye to the brain.

The title of this special issue is "Comparative, ecological, and developmental aspects of visual system design and function," but the reader will find that only **Taylor, Loew, and Grace** address developmental issues in visual system evolution. This final paragraph is to acknowledge the relative absence of such submissions but also

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to point to where an evolutionary and developmental "evo-devo" approach to visual system design may find itself in a future issue. Unsurprisingly, comparative and ecological approaches to visual system design focus on the farthest ranges and special adaptations of eyes, as if any type of optical instrument could be realized by natural selection. Just as any visual system represents a variety of compromises between the physical features of spatial resolution, absolute sensitivity, and so forth, the mature visual system of any animal also represents a compromise between developmental programs filtered over evolutionary time to reliably produce both "basic" visual functionality and also specialized adaptations. For example, the same early genes organize species-typical eyes across vertebrates and invertebrates (Callaerts et al., 1997; Fernald, 2004); the relationship of the multiple types of spectral sensitivity shown in the explosive radiation of Lake Malawi cichlids can be traced to the multiple photopigments expressed in their stem ancestor's development (Kocher, 2004); the coordination of early features of retinal cell specification makes evolutionary movement between a primarily nocturnal or a diurnal eye a matter of far fewer genetic changes than the list of adult differentiating features would suggest (Dyer et al., 2009); the possibility of "knocking in" a third photopigment into a normally dichromatic primate and producing near immediate functional trichromacy suggests a central nervous system unexpectedly permissive of basic retinal changes (Mancuso et al., 2009). In time, understanding how development can be modified should give us a grammar to organize the multiple forms visual system design can take.

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