Evo Edu Outreach (2008) 1:352–354
DOI 10.1007/s12052-008-0073-4

EDITORIAL

Introduction

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Published online: 7 October 2008

Several things are happening as you read these words. Photons, massless packets of electromagnetic radiation, are traveling in straight lines from their source, bouncing off the page (or being projected from a screen), and streaming into your eyes. As the rays of light pass across your transparent, curved corneas, they make a transition from traveling in air to traveling in liquid, and the difference in refractive index between these two media causes their path of travel to change direction. As they pass through your lenses, which contain stacked crystallin proteins with refractive properties, they are bent further such that they become focused onto your retinas, sheets of light-sensitive cells (photoreceptors), at the back of your eyes. The efficiency of this process is enhanced by the adjustment of your pupils' diameters to admit the right quantity of light and the deformation of your lenses by specialized muscles inside your eyes to improve close-up focus. Meanwhile, muscles attached outside your eyes are working to keep both of them focused on the same point and are enabling your eyes to scan back and forth across the page in a coordinated manner. As the photons enter your photoreceptors, they strike a molecule of retinal (a modified form of vitamin A), which is joined with an opsin protein (a G-protein coupled receptor protein) that snakes in and out of the membrane of your photoreceptor cells. Contact with an incoming photon causes the retinal to change physical conformation, setting off a complex biochemical cascade within the cell that ultimately generates an electrical signal that is sent to your brain. There, the information from millions of photoreceptors is combined to provide details on contrast and color, the upside-down images formed on the two retinas are combined and inverted mentally, and the resulting images are interpreted—in this case, as words printed on a page.

Not long ago within the scope of human history, the complexity of intricate organs such as eyes seemed overwhelming—miraculous, even. The precise mechanisms by which such structures carry out their roles seemed inexplicable, and no alternative but divine creation could be seriously proposed to account for their origin (Paley 1802). Nevertheless, the determined efforts of countless scientists have revealed a great deal regarding the form, function, diversity, and origin of eyes. In particular, recent generations of researchers wielding an impressive array of genetic, molecular, and other tools have refined our understanding of eyes and other complex biological structures to a level that would have been unimaginable only decades ago. This special issue of *Evolution: Education and Outreach* is a celebration of these achievements.

The basic framework for a natural explanation for the origin of eyes was assembled 150 years ago by Charles Darwin (1859). Darwin suggested that eyes, like other biological features, are the product, not of miracles, but of history. According to Darwin, the gradual evolution of what he called "organs of extreme perfection and complication" could be accounted for by the non-random preservation and accumulation of slight, beneficial chance modifications—that is, by natural selection acting on the variation generated by mutations. Drawing on what was, for the time, an impressive knowledge of biological diversity, Darwin presented his case for the gradual evolution of complex organs like the eyes currently reading this introduction (and, one would hope, about to read the other articles in this special issue).

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Darwin did not succeed as well as he might have liked on this front. His friend, the prominent American botanist Asa Gray, wrote to Darwin in January 1860 that "what seems to me the weakest point in the book is the attempt to account for the formation of organs,—the making of eyes, &c by natural selection." Darwin concurred in his response written the following month: "About weak points I agree. The eye to this day gives me a cold shudder, but when I think of the fine known gradations, my reason tells me I ought to conquer the cold shudder."[1] In any case, 150 years of empirical and conceptual advances have made the nineteenth century information upon which Darwin built his case seem trivial by comparison. Indeed, as the papers in this special issue demonstrate, our current understanding of eye evolution has moved far beyond the simple beginnings laid down by Darwin.

The general processes now recognized to be involved in complex organ evolution are reviewed and illustrated using eyes as a case study by yours truly (Gregory 2008). The peer-reviewed papers presented in this issue by experts in their fields provide a further introduction to this information, most of which is, unfortunately, unknown to non-specialists. In this regard, Oakley and Pankey (2008) and Piatigorsky (2008) provide discussions of the genetic and molecular components of eye evolution: a former "black box" whose contents are now being well illuminated. Regarding vertebrate eyes, Lamb et al. (2008) review information based on comparisons of modern species, while Young (2008) discusses the eyes of early fossil fishes. Turning to some of the most diverse groups of animals on Earth in terms of both species numbers and types of eyes, Buschbeck and Friedrich (2008) cover insects, Cronin and Porter (2008) discuss crustaceans, and Serb and Eernisse (2008) provide an overview of mollusks.

Focusing on the sorts of modifications that can occur after complex eyes have evolved, Gerl and Morris (2008) discuss the basis and biological consequences of color vision, Zimmer (2008) highlights the extraordinary eyes found in flounders and stalk-eyed flies, and Espinasa and Espinasa (2008) discuss the loss of eyes in cave-dwelling fishes. Finally, Novella (2008) provides a discussion of the vision problems found in humans that represent "scars of evolutionary history," while Petto and Mead (2008) and Thanukos (2008) discuss some concepts and misconceptions about complex organ evolution that are important from a teaching perspective.

Although eyes have always been a focal point in disagreements regarding evolution, it is important to note that confidence in the effectiveness of scientific research and in the historical factuality of evolution, and not defensiveness in the face of unscientific criticisms, is the reason so much is now known about eyes. The primary purpose of this special issue, therefore, is not to counter the claims of anti-evolutionists (though this is a welcome side effect) but to focus on several interesting and important scientific themes. First and most simply, these papers provide a glimpse into the vast body of knowledge regarding eyes and their origins that is usually not accessible to non-specialists. Second, the papers make it clear that there is no such thing as "the" eye. Eyes come in a remarkable diversity of forms, some of which undoubtedly seem bizarre from a human perspective but which may nonetheless be quite effective for the organisms possessing them. Third, several of the authors make it clear that the evolution of complex organs is often indirect and non-linear and that the most fruitful approach is to consider the individual components of eyes rather than the organs as a whole. In particular, it is important to evaluate the histories of the genes, developmental pathways, and cellular features individually, as these may have followed different paths to their shared current endpoint. This raises a fourth important point, namely, that the study of complex organ evolution depends on insights from a variety of disciplines emphasizing different levels of analysis, including comparative anatomy and biochemistry, genetics and molecular biology, cell and developmental biology, and paleontology. Finally, these articles illustrate that, even knowing as much as we now do, there are many intriguing questions yet to be answered by future generations of scientists.

Acknowledgments I offer my sincere gratitude to the various authors who invested precious time in this project, to Niles Eldredge and the editorial management of the journal for their support, and to the numerous expert reviewers who provided valuable comments on the manuscripts.

[1] By April 1860, Darwin had apparently moved on to other worries. As he wrote to Gray: "It is curious that I remember well time when the thought of the eye made me cold all over, but I have got over this stage of the complaint, & now small trifling particulars of structure often make me very uncomfortable. The sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!" He dealt with the evolution of features obviously detrimental to survival, such as peacocks' tails, in 1871.

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