

Evolution: Do the Eyes Have It?

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Abstract

Darwin pondered if the eye could not be explained by evolution by natural selection then his theory would be declared false. Since then much has been written on evolution of the eye, and the eye has come up again in debates on Intelligent Design. Two views have been held in regard to eye evolution: a single origin of eye-building genes with subsequent divergence to form camera-type and compound eyes or multiple origins from many genes providing a framework that allowed convergence on a few basic eye types. A wide spectrum of animals has opsin-coding genes and genes capable of forming eyes. The sea urchin has hundreds of genes homologous to those expressed in vertebrate eyes. Genes that do not ordinarily build eyes could be recruited for that purpose. To the Intelligent Design proponent, even conceding that anatomical eye evolution can be accounted for, and that the proteins in eyes could evolve from other sensory-related proteins, the origin of the first sensory pathway still needs to be explained. So do the “eyes” have it on the question of evolution? Surely on the anatomical level, Darwin has been vindicated, but on the cellular level many questions remain and proponents of Intelligent Design can still be expected to say nay.

Introduction

Charles Darwin expressed wonder at the eye and pondered if it could not be explained by evolution by natural selection, then his theory would be declared false. Since then much has been written on scenarios for evolution of the eye. In the mollusks there is represented a very plausible series of eyes that might correspond to stages in evolution from pin-hole camera in the nautilus to the camera eye of octopus that rivals in complexity the vertebrate eye. The eye has come up again in debates on Intelligent Design.

Darwin's Black Box takes up the challenge (Behe 1996). While conceding that anatomical eye evolution can be accounted for by gradual evolution, the author concludes that the sequence of reactions required to convert absorption of photons by rhodopsin into a nervous impulse and restore rhodopsin is an example of irreducible complexity. Perhaps Behe's book is misleading in suggesting that the reaction sequence in eyes had to evolve from scratch, because similar pathways exist for other sensory-neural pathways; however, Behe no doubt would contend that an antecedent pathway would still leave the origin of the first complex sensory pathway to be explained and that it would be irreducibly complex.

Critics of Intelligent Design claim that the vertebrate eye shows poor design, compared to the octopus eye, because light in the former must pass through ganglion cells before reaching the photoreceptor cells at the back of the retina, whereas the latter has photoreceptors at the front of the retina, directly in the light path. Skeptics might suggest that poor design means no God or one that leaves secondary causes to finish His work for Him. It seems overly speculative to

suggest that, therefore, man, the presumed crown of creation, was short-changed because he does not see as well as the octopus.

Eye Evolution and Genetics

In addition to the camera-like eyes seen in cephalopod mollusks, such as octopus, and in vertebrates, visual organs also include the familiar compound eyes of insects and other arthropods. Looking at the evolution of eyes in living organisms, some one-celled organisms have well developed light sensors, and eyes appeared soon after evolution of the animal kingdom. Curiously, even some box jellyfish (Phylum Cubozoa) of the primitive radially symmetrical group have eyes with well developed lenses (Nilsson et al. 2005). Eyes appear in the bilaterally symmetrical animals in the protostome invertebrate branch, including the Phylum Arthropoda (jointed leg animals), Annelida (segmented worms), and Mollusca (bivalves, snails, and cephalopods). Of course, eyes are characteristic of the vertebrates in the deuterostome group.

In a book devoted to the subject of eye evolution, Andrew Parker (2003) suggested that the sudden ability to see was the spark for the Cambrian Explosion, but he was taken to task by Simon Conway Morris (2003a). Conway Morris stated that eyes evolved many times over many steps. If Parker is correct then the eye evolved early in the Cambrian, and then it triggered an extremely rapid evolution in various phyla, the largest of which all exhibit eyes. According to Parker, the fossil record indicates that image-forming eyes probably evolved first in the arthropods, probably trilobites (Parker 2003). In most phyla, although simple photoreception is almost universally present, no eyes evolved, but eyes evolved later in Annelida, Mollusca, Onychophora, and Chordata. Conway Morris sees eyes as a factor, but not an especially important factor in the rapid evolution in the early Cambrian.

Two views have been held in regard to eye evolution. Gehring (2005) is a leading advocate of a single origin (monophyletic origin) of much of the eye-building genetic apparatus with subsequent divergent evolution. In support of a single origin of eyes is genetic data that shows that a mammalian gene can cause eyes to form in insects. According to this divergence model, one or a few ancestral “eye genes,” for example the regulatory gene *Pax6*, evolved in the ancestral bilateria, resulting in the first eyespot. The ancestral eye then evolved into the various

camera-type eyes (probably independently) and various compound eyes. Eyeless phyla are therefore degenerate or failed to develop eyespots further.

The second view exposes multiple origins for eyes (polyphyletic origin). A more basic set of genes allowed multiple origins converging on a few basic eye types. On the basis of molecular phylogeny, other researchers (Oakley and Cunningham 2002) have shown that the paired compound eyes of some seed shrimp evolved within an otherwise eyeless group of Ostracoda. The eyes of other Crustaceans, notably the Malacostraca (crabs, crayfish, lobsters) evolved independently. According to this convergence view, the ancestral animal had a number of genes, including regulatory genes and opsin genes, and that the key factor in eye development was not the presence or absence of genes, but a balance of many genes variously recruited to form the camera type eye independently in three or four distinct lineages and compound eyes in several lineages independently (Conway Morris 2003b).

Fernald (2006) gives an overview of eye evolution from a genetic standpoint, discussing the three protein families most associated with eyes: opsins, crystallins, and regulatory genes that code for transcription factors. The octopus and the vertebrate common ancestor occurred about 750 million years ago. About 70% of eye genes are commonly expressed in vertebrates and octopus, and 97% of these are estimated to have occurred in the ancestral bilaterian. He stated that 875 genes were conserved which might have a common regulatory network recruited at least twice. Vertebrates use ciliary opsin in photoreceptor cells, whereas invertebrates use rhabdomeric opsin. Fernald stated that certain transcription factors have been regularly recruited to build eyes. "The use of homologous genes to build nonhomologous structures may be at the heart of understanding eye evolution and evolutionary processes more generally." Eyes may have evolved independently 40 or more times (Fernald 2006, p. 1917).

The ciliary opsins of vertebrates can be introduced by the well studied function of rhodopsin found in the photoreceptors called rods. Light passes through the inner segment connected by modified cilia to the outer segment which has stacks of membranes. The membranes are studded with many copies of the protein opsin, each attached to a molecule of 11-cis retinal. Retinal absorbs light and changes shape, causing a shape change in opsin, leading to a nervous impulse being transmitted to the brain. Retinal must be converted back to its original shape before it can absorb more light. Cone opsins also have retinal but differ from rhodopsin and each other by a few amino acids in their sequence.

Human cone opsins maximally absorb red at 558 nm, green at 531 nm, and blue at 419 nm. Okano et al. (1992) found that the chicken retina contains four cone opsins and rhodopsin. Chicken red absorbs at 571 nm, green at 508 nm, blue at 455nm, and violet at 415 nm. Chicken green is similar to vertebrate rhodopsins absorbing a wavelength of 500 nm. They suggested that the ancestral opsin evolved from gene duplications into four opsins, as represented in chicken. Vertebrate rhodopsins diverged from green cone opsin later, after the divergence of the ancestral pigment into four groups. Animals had acquired ability to see color at least at the stage of the lowest vertebrates, but later most mammals lost color vision.

Yokoyama (1997) described site specific amino acid sequence changes that change wavelength specificity in opsins. The article also described the dichromatic cone vision of new world monkeys normally resulting from two different opsin genes. Old world monkeys are trichromatic. Human red opsin evolved from green opsin by three amino acid changes.

Arendt et al. (2004, p. 869) reported the discovery of a ciliary opsin in an invertebrate, the ragworm *Platynereis*. This worm has rhabdomeric opsin in its retina, as expected for an invertebrate, but ciliary opsin, similar to that of vertebrates, in its brain. The authors stated that “any feature specifically shared between them as a result of their common evolutionary heritage necessarily existed in . . . the last common ancestor of all animals with bilateral symmetry.” This opsin is expressed in ciliary structures in the brain. They believe that r-opsins in vertebrates persisted in retinal ganglion cells.

Bellingham et al. (2006) reported the discovery of a melanopsin in retinal ganglion cells of chickens that functions in the circadian rhythm and pupillary light reflex. Non-mammalian vertebrates have two melanopsins. Mammals have one melanopsin. Early mammals lost one melanopsin, two cone opsins, and extraretinal photoreceptors, coinciding with a nocturnal phase of mammalian evolution.

Another protein family associated with the eye is the crystallin family, especially found in the lens. Crystallins must exist for a long time in high concentration. These may have evolved from stressor proteins, then to beta crystallins, then to gamma crystallins, which were eye specific, perhaps originally in the retina and finally in the lens (Wistow et al. 2005). Mammals have gamma crystallins A-F. Fish have gamma crystallins M. Gamma N may have had ancestral function in the retina, and later was recruited for the lens. The highly accommodating lenses of birds required a softer structure and incorporated taxon specific

crystallins, often coming from enzymes, hence “enzyme crystallins.” Gamma N may not be functional in humans or chimps.

The most surprising of the eye related genes are the regulatory genes, including *Pax6* and related genes which can initiate eye development in diverse species. In *Drosophila* seven genes appear to control eye development: *eyeless* and *twin of eyeless* are *Pax6* homologs; *sine oculus*, *eyes absent*, *dachshund*, *eye gone*, and *optix* contribute to form a complex network.

Gehring (2005) perhaps gives the strongest case for all eyes evolving from a common ancestral eye. He identified *Pax6* as a master control gene for eye development and proposed a new theory about the monophyletic origin of the eyes in evolution. *Pax6* can induce ectopic eyes (some place other than the head) in both insects and vertebrates. Not only can Pax genes induce eye formation ectopically on antennae, legs, and wings, but mouse *Pax6* causes ectopic eyes in *Drosophila*. “Because the evolution of a prototypic eye is a highly improbable stochastic event that is not driven by selection, the hypothesis of a polyphyletic origin of the eyes, arising 40 to 65 times independently, is extremely unlikely and incompatible with Darwin’s ideas” (Gehring 2005, p. 175). *Pax6* related genes have been found in all bilateria analyzed so far, ranging from planarians to humans.

Since echinoderms share deuterostome ancestry with the Phylum Chordata, it is of particular interest to examine the recently decoded genome of the sea urchin (Sea Urchin Genome Sequencing Consortium 2006). The sea urchin has hundreds of genes homologous to mammalian sensory genes, including eye genes. Photoreceptor genes apparently are expressed in the tube feet. Does a sea urchin really need hundreds of sensory genes with no eyes, ears, or nose? Perhaps the deuterostome ancestor evolved eye genes without eyes, or possibly it had eyes and lost them, and these genes were retained for a different use in the sea urchin. Or perhaps the developmental genes evolved even before the protostome-deuterostome split at least 750 million years ago, such that the sea urchin shared a common pool of genes common to animals. These genes, sometimes, in a certain balance, developed eyes while, at other times, were used in developing unrelated structures. Kozmik et al. (2007) reported nine Pax genes in amphioxus, also lacking eyes, including four newly described homologues of *six* and *eyes absent*.

Brodbeck and Englert (2004) reported that the mouse has nine Pax genes. Many of these same genes are used in development of mammalian kidney. Thus these regulatory genes exhibit pleiotropy, being expressed in many different tissues. Compared to Gehring (2005), they have

suggested a different view of master control genes and hierarchies, and prefer the concepts of circuits and networks instead. “Evolution is conservative, since components of networks . . . are redeployed in different species and in the development of different organs. At the same time evolution is exploratory and will not use the identical module again but try different combinations of factors, build in additional feedback loops, involve additional components, and abandon others” (Brodbeck and Englert 2004, p. 253).

Conclusion

Could it be that the ancestor of the deuterostomes was a bottom-feeding dweller in the dark? Perhaps many genes accumulated for other sensory functions, as noted in the sea urchin, and then when the first shallow water chordate evolved, these genes were re-wired as photoreceptors and, using the ancient eye-organizing gene, evolved into a camera-type eye. It might have been similar to the hagfish to begin with, which feeds near the bottom and has rudimentary eyes. Eyes that evolved in the dark might also be expected to have a reflective layer behind the retina, as nocturnal animals have today, and hence the photoreceptors being at the back of the retina to receive the reflected light was not such a poor design after all. The total light path would be less obstructed by ganglion cells if the light goes through the ganglion layer once, then to the photoreceptors, some passing on to the reflective layer, and then, without further interference, back to the photoreceptors. Mammals probably evolved in nocturnal niches while dinosaurs dominated the daytime. Could mammals have evolved without the retina rear-most design? Photoreceptors inside the ganglion layer would receive reflected light after it passed twice through the ganglion layer and hence be less effective.

Much research has gone into satisfying Darwin’s anxiety about the complexity of the eye. The evidence from both extant and extinct species gives a plausible series of steps for the evolution of camera-type and compound eyes. Do eyes demonstrate gradual evolution? One still has to wonder why even the earliest animals had genes capable of forming eyes and why the visually challenged sea urchin is loaded with hundreds of genes homologous to those expressed in vertebrate eyes. This paradox has emerged as an important theme in the field of evolutionary development (Yoon 2007), so that complex new forms do not require many new mutations or many new genes but instead small changes to existing genes and developmental plans, a sort of “tool kit.” Major events in evolution may not depend on new genes or the appearance of new

body parts, but the right ecological situation to allow a new expression of genes already present. Conway Morris (2003b, p. 166) calls this inherency, whereby the same basic building blocks of complex structures are available before being recruited for new and more sophisticated tasks so that “emergence relies more on co-option and redeployment than invention.” So do the “eyes” have it on the question of evolution? Surely on the anatomical level, Darwin has been vindicated, but on the cellular level many questions remain and proponents of Intelligent Design can be expected to still say nay.

Perhaps the ancestral animal had thousands of genes, all existing in a delicate balance and carrying immense potential. In one daughter lineage, gene duplication and selection achieved a new balance to develop a complex organ like an eye out of that inherent potential. In another daughter lineage, some other set of circumstances at a different time or several times, also allowed that potential to be expressed as eyes. But perhaps that delicate balance in the ancestral animal that was so early achieved in life’s history, but so improbably due to gradual steps, and unlikely to have received its immense potential from chance, was a gift from the Creator of information that was present before the creation of the universe.

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