Michael F. Land

THE EYE

A Very Short Introduction

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UNIVERSITY PRESS

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Great Clarendon Street, Oxford, OX2 6DP,
United Kingdom

Oxford University Press is a department of the University of Oxford.
It furthers the University's objective of excellence in research, scholarship,
and education by publishing worldwide. Oxford is a registered trade mark of
Oxford University Press in the UK and in certain other countries

First edition published in 2014
Impression: 1

Published in the United States of America by Oxford University Press
198 Madison Avenue, New York, NY 10016, United States of America

British Library Cataloguing in Publication Data
Data available

Library of Congress Control Number: 2014930361

ISBN 978–0–19–968030–6

Printed in Great Britain by
Ashford Colour Press Ltd, Gosport, Hampshire

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Acknowledgements

I would like to thank the editorial team at Oxford University Press, particularly Latha Menon, for encouragement and advice on the text. Also my daughter Kate Land, who read all the text as an educated reader without specialist knowledge, and made numerous helpful suggestions; and to an optometrist friend, Colin Davidson, who helped with the final chapter on impaired vision.

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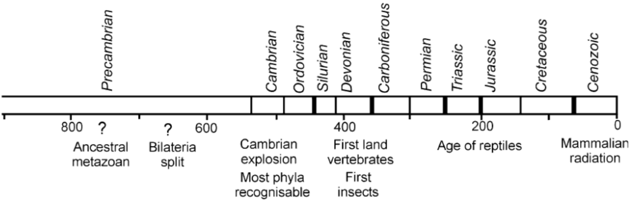
Chapter 1

The first eyes

Origins

Of all the senses, vision is the most versatile. It allows animals to navigate through the environment, seek out food, and detect and avoid predators. Good eyesight makes it possible to recognize other individuals and to communicate with them by gesture and expression. Hearing, smell, and touch can each fulfil some of these functions: sound is useful in communication, the chemical senses can identify food, and a rat in the dark can navigate by touch. But for many animals vision predominates, and its loss is more devastating than the loss of any other sense. Eyes come in many varieties, from the simple pit eyes of flatworms to the sophisticated compound eyes of arthropods and the single chambered eyes of vertebrates and cephalopod molluscs such as *Octopus*. These are discussed later in the chapter, and photographs of some of the more remarkable eyes are shown in Figure 7 towards the end of the chapter.

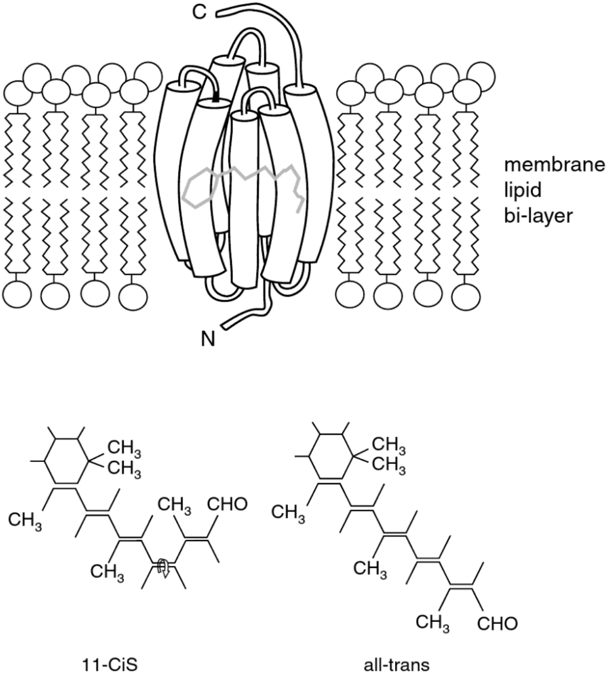
It seems that the evolution of eyes started very slowly in the Precambrian period and then took off during the Cambrian, between 541 and 485 million years ago. Since that time many refinements have occurred, but all the basic designs were in place by the end of the Cambrian (Figure 1). The earliest eyes for which we have a fossil record were not single-chambered eyes like ours,



1. Geological time-line. Age scale in millions of years before present. Five major extinctions, in each of which more than 70% of the world's fauna disappeared, are shown as thicker bars

but were the compound eyes of trilobites. These animals had an external skeleton and scavenged the sea floor about 520 million years ago, until the great extinction at the end of the Permian, 270 million years later. The reason we know more about these eyes than any others is that their lenses were made of the mineral calcite, so they effectively came pre-fossilized. Animals with our kind of eye—the first fish-like creatures and the cephalopod molluscs—also evolved in the Cambrian, but whatever eyes they had have not fossilized. Although the Cambrian was a period when animals became more mobile and vision became a major sense, there are good reasons for believing that animals had some visual capabilities earlier than this. Trilobite eyes are already quite sophisticated, and must have had simpler antecedents. Stronger evidence comes from the photoreceptors themselves—the cells that respond to light and make vision possible. These are present in jellyfish, whose origins go further back into the Precambrian. Sadly, providing dates for evolutionary events before about 555 million years ago is fraught with problems, and estimates for the timing of the beginnings of multicellular animal life vary by at least a hundred million years.

What we can say, however, is that all animals, from jellyfish to man, share a particular molecule—rhodopsin—which is responsible for starting the process of converting light into the electrical signals that the nervous system can make use of. Plants, fungi, and even bacteria also have light receptive molecules, but none resemble animal rhodopsin, and we can assume from this rhodopsin evolved at much the same time as multicellular animal life. Rhodopsin is a two-part molecule. It consists of a protein (opsin) and, held within it, a smaller molecule—the 'chromophore'—related to vitamin A (Figure 2). This chromophore has a long chain of double bonds that



11-CiS

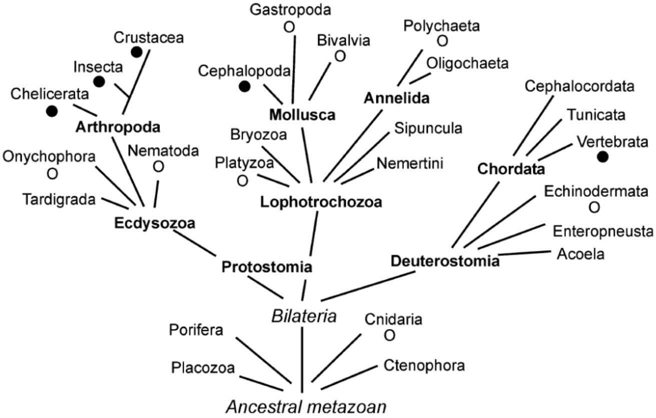
all-trans

2. Rhodopsin molecule embedded in the cell membrane of a photoreceptor. The membrane is a double layer of lipid molecules. Rhodopsin consists of an opsin protein, with 7 helices of amino acids that cross the membrane, and inside it (in grey) sits the chromophore molecule—usually a relative of vitamin A. This is shown below in its two forms: the 11-cis form before it is stimulated, and the all-trans form it converts to when a photon of light is absorbed. This conversion starts the visual process

are tuned to respond to light energy. When it absorbs the energy of a photon of light its structure changes, and this change initiates a series of biochemical reactions (known as the transduction cascade) that ultimately results in an electrical change in the photoreceptor cell, which is then transmitted to the nervous system. In all animals, this is the first step in vision.

A quick summary of early animal evolution

Before discussing the different kinds of photoreceptors and eyes it will be useful to have an outline of where eyes fit into the basic narrative of animal evolution (Figure 3). Of the earliest animal groups (phyla) the sponges (Porifera) do not have photoreceptors or anything remotely eye-like, so photoreception was not universal among the first animals. However, many animals of another early

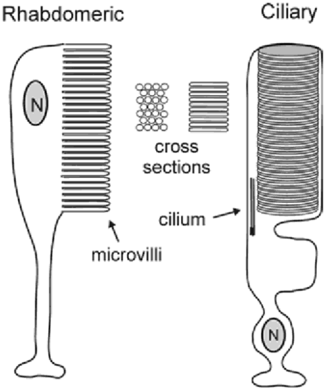


3. Evolutionary tree of the animal kingdom, showing the division of the Bilateria into three main superphyla, the Ecdysozoa, Lophotrochozoa, and Deuterostomia. Groups with eyes of some kind are shown with circles (○). Groups with eyes that resolve well have filled circles (●): these evolved only in the arthropods, the cephalopod molluscs, and the vertebrates. Latin names are used here, but convert easily to English equivalents by replacing the last 'a' with an English plural

phylum, the Cnidaria, which contains the sea anemones, corals, and jellyfish, do indeed have photoreceptors. In one class of cnidarians, the cubozoans that include the notorious Australian 'stingers', there are even eyes that really look like eyes, so the capacity to produce eyes was present from a very early stage of metazoan evolution. The Cnidaria, which are radially symmetrical animals, split off from the early metazoan line before the formation of the main animal phyla, collectively known as the Bilateria from their left–right symmetry. Most of these bilaterian animals moved forwards, and so had a head end where most receptors, such as eyes, were located. At some time in the late Precambrian the bilaterians split into three major groups, the Ecdysozoa, the Lophotrochozoa, and the Deuterostomia (Figure 3). Excellent eyes evolved in at least one branch of each group. Before the advent of molecular ways of tracing animal relationships only two major bilaterian groupings were recognized: the protostomes and the deuterostomes. The division was based on their different development: the names mean first mouth and second mouth, from the way the mouth and anus develop in the early embryo. The second of these groups—the Deuterostomia—is the group to which we humans belong, and contains the starfish, the sea squirts, and the chordates, from which the vertebrates arose. In 1997, the Protostomia were divided into their two present groups, the Ecdysozoa and the Lophotrochozoa, on the basis of new molecular evidence. Basically the Ecdysozoa are animals that moult repeatedly as they grow. They include the jointed-limbed animals (arthropods), and these comprise the Chelicerata (horseshoe crabs, scorpions, and spiders), the Crustacea (shrimps, lobsters, crabs, and many smaller classes) and the Insecta (beetles, flies, etc.). Most of the members of these groups have compound eyes and good—sometimes excellent—vision. The Ecdysozoa also include millipedes and centipedes, and perhaps surprisingly the nematode worms, which also moult but are mostly eyeless. The Lophotrochozoa (an unconvincing hybrid word meaning 'crest/wheel animals') include most of the rest: the flatworms, the molluscs, the annelid worms, and several smaller phyla. Of these, the cephalopod molluscs (octopus, squid, and cuttlefish) stand out as having eyes that are large, resolve well, and are similar in their capabilities to those of fish.

The first photoreceptors

Not surprisingly, photoreceptors evolved before eyes. There are basically two types of specialized photoreceptor cell in animals, known as 'rhabdomeric' and 'ciliary', and for many years it was thought that this distinction mapped nicely onto the protostome/deuterostome divisions of the Bilateria. To catch a reasonable proportion of the light that falls on them, photoreceptors need a high density of rhodopsin. Rhodopsin molecules are embedded in the membranes of the receptor cells (Figure 2) so increasing the rhodopsin density means having a greatly expanded membrane. Ciliary receptors are organized around cilia, hair-like structures found in a wide variety of cells. Typically the membrane is organized into stacks of lamellae or discs, as in the rods and cones of the human retina (Figure 4). A human rod has a total of



4. Rhabdomeric and ciliary photoreceptors, based on a receptor from the fruit-fly *Drosophila*, and a human rod. N is the nucleus. At the base of each receptor is the synaptic junction that connects with the nervous system