



Michael F. Land

THE EYE

A Very Short Introduction

OXFORD

Michael F. Land



OXFORD
UNIVERSITY PRESS

OXFORD

UNIVERSITY PRESS

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

© Michael F. Land 2014

The moral rights of the author have been asserted

First edition published in 2014

Impression: 1

All rights reserved. No part of this publication may be reproduced, stored in
a retrieval system, or transmitted, in any form or by any means, without the
prior permission in writing of Oxford University Press, or as expressly permitted
by law, by licence or under terms agreed with the appropriate reprographics
rights organization. Enquiries concerning reproduction outside the scope of the
above should be sent to the Rights Department, Oxford University Press, at the
address above

You must not circulate this work in any other form
and you must impose this same condition on any acquirer

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

Links to third party websites are provided by Oxford in good faith and
for information only. Oxford disclaims any responsibility for the materials
contained in any third party website referenced in this work.

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.

Expand your collection of VERY SHORT INTRODUCTIONS

1. Classics
2. Music
3. Buddhism
4. Literary Theory
5. Hinduism
6. Psychology
7. Islam
8. Politics
9. Theology
10. Archaeology
11. Judaism
12. Sociology
13. The Koran
14. The Bible
15. Social and Cultural Anthropology
16. History
17. Roman Britain
18. The Anglo-Saxon Age
19. Medieval Britain
20. The Tudors
21. Stuart Britain
22. Eighteenth-Century Britain
23. Nineteenth-Century Britain
24. Twentieth-Century Britain
25. Heidegger
26. Ancient Philosophy
27. Socrates
28. Marx
29. Logic
30. Descartes
31. Machiavelli
32. Aristotle
33. Hume
34. Nietzsche
35. Darwin
36. The European Union
37. Gandhi
38. Augustine
39. Intelligence
40. Jung
41. Buddha
42. Paul
43. Continental Philosophy
44. Galileo
45. Freud
46. Wittgenstein
47. Indian Philosophy
48. Rousseau
49. Hegel
50. Kant
51. Cosmology
52. Drugs
53. Russian Literature
54. The French Revolution
55. Philosophy
56. Barthes
57. Animal Rights
58. Kierkegaard
59. Russell
60. Shakespeare
61. Clausewitz
62. Schopenhauer
63. The Russian Revolution
64. Hobbes
65. World Music
66. Mathematics
67. Philosophy of Science
68. Cryptography
69. Quantum Theory
70. Spinoza
71. Choice Theory

72. Architecture
73. Poststructuralism
74. Postmodernism
75. Democracy
76. Empire
77. Fascism
78. Terrorism
79. Plato
80. Ethics
81. Emotion
82. Northern Ireland
83. Art Theory
84. Locke
85. Modern Ireland
86. Globalization
87. The Cold War
88. The History of Astronomy
89. Schizophrenia
90. The Earth
91. Engels
92. British Politics
93. Linguistics
94. The Celts
95. Ideology
96. Prehistory
97. Political Philosophy
98. Postcolonialism
99. Atheism
100. Evolution
101. Molecules
102. Art History
103. Presocratic Philosophy
104. The Elements
105. Dada and Surrealism
106. Egyptian Myth
107. Christian Art
108. Capitalism
109. Particle Physics
110. Free Will
111. Myth
112. Ancient Egypt

113. Hieroglyphs
114. Medical Ethics
115. Kafka
116. Anarchism
117. Ancient Warfare
118. Global Warming
119. Christianity
120. Modern Art
121. Consciousness
122. Foucault
123. The Spanish Civil War
124. The Marquis de Sade
125. Habermas
126. Socialism
127. Dreaming
128. Dinosaurs
129. Renaissance Art
130. Buddhist Ethics
131. Tragedy
132. Sikhism
133. The History of Time
134. Nationalism
135. The World Trade
Organization
136. Design
137. The Vikings
138. Fossils
139. Journalism
140. The Crusades
141. Feminism
142. Human Evolution
143. The Dead Sea Scrolls
144. The Brain
145. Global Catastrophes
146. Contemporary Art
147. Philosophy of Law
148. The Renaissance
149. Anglicanism
150. The Roman Empire
151. Photography
152. Psychiatry

153. Existentialism
154. The First World War
155. Fundamentalism
156. Economics
157. International Migration
158. Newton
159. Chaos
160. African History
161. Racism
162. Kabbalah
163. Human Rights
164. International Relations
165. The American Presidency
166. The Great Depression and
The New Deal
167. Classical Mythology
168. The New Testament as
Literature
169. American Political Parties
and Elections
170. Bestsellers
171. Geopolitics
172. Antisemitism
173. Game Theory
174. HIV/AIDS
175. Documentary Film
176. Modern China
177. The Quakers
178. German Literature
179. Nuclear Weapons
180. Law
181. The Old Testament
182. Galaxies
183. Mormonism
184. Religion in America
185. Geography
186. The Meaning of Life
187. Sexuality
188. Nelson Mandela
189. Science and Religion
190. Relativity
191. The History of Medicine
192. Citizenship
193. The History of Life
194. Memory
195. Autism
196. Statistics
197. Scotland
198. Catholicism
199. The United Nations
200. Free Speech
201. The Apocryphal Gospels
202. Modern Japan
203. Lincoln
204. Superconductivity
205. Nothing
206. Biography
207. The Soviet Union
208. Writing and Script
209. Communism
210. Fashion
211. Forensic Science
212. Puritanism
213. The Reformation
214. Thomas Aquinas
215. Deserts
216. The Norman Conquest
217. Biblical Archaeology
218. The Reagan Revolution
219. The Book of Mormon
220. Islamic History
221. Privacy
222. Neoliberalism
223. Progressivism
224. Epidemiology
225. Information
226. The Laws of
Thermodynamics
227. Innovation
228. Witchcraft
229. The New Testament
230. French Literature

231. Film Music
232. Druids
233. German Philosophy
234. Advertising
235. Forensic Psychology
236. Modernism
237. Leadership
238. Christian Ethics
239. Tocqueville
240. Landscapes and
Geomorphology
241. Spanish Literature
242. Diplomacy
243. North American Indians
244. The U.S. Congress
245. Romanticism
246. Utopianism
247. The Blues
248. Keynes
249. English Literature
250. Agnosticism
251. Aristocracy
252. Martin Luther
253. Michael Faraday
254. Planets
255. Pentecostalism
256. Humanism
257. Folk Music
258. Late Antiquity
259. Genius
260. Numbers
261. Muhammad
262. Beauty
263. Critical Theory
264. Organizations
265. Early Music
266. The Scientific Revolution
267. Cancer
268. Nuclear Power
269. Paganism
270. Risk
271. Science Fiction
272. Herodotus
273. Conscience
274. American Immigration
275. Jesus
276. Viruses
277. Protestantism
278. Derrida
279. Madness
280. Developmental Biology
281. Dictionaries
282. Global Economic History
283. Multiculturalism
284. Environmental Economics
285. The Cell
286. Ancient Greece
287. Angels
288. Children's Literature
289. The Periodic Table
290. Modern France
291. Reality
292. The Computer
293. The Animal Kingdom
294. Colonial Latin American
Literature
295. Sleep
296. The Aztecs
297. The Cultural Revolution
298. Modern Latin American
Literature
299. Magic
300. Film
301. The Conquistadors
302. Chinese Literature
303. Stem Cells
304. Italian Literature
305. The History of Mathematics
306. The U.S. Supreme Court
307. Plague
308. Russian History
309. Engineering

310. Probability
311. Rivers
312. Plants
313. Anaesthesia
314. The Mongols
315. The Devil
316. Objectivity
317. Magnetism
318. Anxiety
319. Australia
320. Languages
321. Magna Carta
322. Stars
323. The Antarctic
324. Radioactivity
325. Trust
326. Metaphysics
327. The Roman Republic
328. Borders
329. The Gothic
330. Robotics
331. Civil Engineering
332. The Orchestra
333. Governance
334. American History
335. Networks
336. Spirituality
337. Work
338. Martyrdom
339. Colonial America
340. Rastafari
341. Comedy
342. The Avant-Garde
343. Thought
344. The Napoleonic Wars
345. Medical Law
346. Rhetoric
347. Education
348. Mao
349. The British Colonial Empire
350. American Politics
351. The Silk Road
352. Bacteria
353. Symmetry
354. Marine Biology
355. The British Empire
356. The Trojan War
357. Malthus
358. Climate
359. The Palestinian-Israeli Conflict
360. Happiness
361. Diaspora
362. Contemporary Fiction
363. Modern War
364. The Beats
365. Sociolinguistics
366. Food
367. Fractals
368. Management
369. International Security
370. Astrobiology
371. Causation
372. Entrepreneurship
373. Tibetan Buddhism
374. The Ancient Near East
375. American Legal History
376. Ethnomusicology
377. African Religions
378. Humour
379. Family Law
380. The Holocaust
381. The Renaissance
382. The American West
383. The Industrial Revolution
384. The Enlightenment
385. The Middle Ages
386. The Victorian Era
387. The Cold War
388. The Space Age
389. The Information Age
390. The Digital Age
391. The Globalization
392. The Postmodernism
393. The Postcolonialism
394. The Poststructuralism
395. The Postmodernism
396. The Postcolonialism
397. The Poststructuralism
398. The Postmodernism
399. The Postcolonialism
400. The Poststructuralism

Contents

Acknowledgements xiii

List of illustrations xv

- 1 The first eyes 1
- 2 Making better eyes 16
- 3 The human eye 28
- 4 The moving eye 40
- 5 The third dimension 52
- 6 Colour 63
- 7 Seeing and the brain 75
- 8 When vision fails 88

Further reading 99

Index 101

List of illustrations

- 1 Geological time-line **2**
- 2 Rhodopsin molecule embedded in the cell membrane of a photoreceptor **3**
- 3 Evolutionary tree of the animal kingdom **4**
- 4 Rhabdomeric and ciliary photoreceptors **6**
- 5 Diagrams of the four main types of single-chambered eye **9**
- 6 The main types of compound eye **9**
- 7 A selection of animal eyes **11**
© (a) Hans Hillewaert/
CC-BY-SA-3.0; (b) Thomas Shahan;
(e) Thomas Shahan.
- 8 (a) Lens with a homogeneous refractive index (b) Lens with a graded refractive index **17**
- 9 Lens with two foci **19**
- 10 Distribution of intensity across the Airy diffraction pattern **21**
- 11 The effect of low photon numbers **24**
From Figure 12.1, p. 142 in M. H. Pirenne (1967) *Vision and the Eye*. Science Paperbacks/Chapman and Hall
- 12 Diagram of a section through the human eye **29**
- 13 Mechanism of accommodation **30**
- 14 (a) Myopia; and (b) hyperopia **31**
- 15 Diagram of the cells in a typical vertebrate retina **35**
- 16 Responses of an ON-centre ganglion cell **36**

- 17 The blind spot **37**
- 18 Recording of movements of the left eye, head, and gaze while the author looked round his kitchen **42**
- 19 Pursuit and vergence eye movements **43**
- 20 The arrangement of eye muscles in the orbit **44**
- 21 Outline of the brain structures involved in the control of eye movements **45**
- 22 Eye movement recordings by Alfred Yarbus of a subject viewing a picture **47**
Springer and Plenum Press, New York, *Eye Movements and Vision*, 1967, pp. 171–77. *Eye Movements during Perception of Complex Objects*, A. Yarbus, with kind permission from Springer Science + Business Media B.V.
- 23 Left: a batsman about to strike a ball in cricket. Right: record of the gaze movements of a batsman before, during, and after the bounce of the ball **49**
- 24 Disparity **53**
- 25 Simple stereogram showing how images from different viewpoints can give rise to depth **55**
- 26 Random dot stereogram of the type devised by Bela Julesz **56**
After K. Brodmann (1914) *Physiologie der Gehirne*. In *Die Allgemeine Chirurgie der irnkrankheiten, Neue Deutsche Chirurgie*, Vol.11: *Enke*. From J. P. Frisby (1979) *Seeing*, p. 79. Oxford University Press
- 27 *The Grand Canal*, Venice, by Canaletto, about 1740 **58**
Superstock/Glowimages.com
- 28 The velocity flow field seen by a driver on a straight road **60**
- 29 Proportion of light reflected by various flowers and a leaf **65**
- 30 Spectral absorption of the three cone types and rods (dotted) **66**
- 31 Cone contributions to colour opponent ganglion cell responses **70**
- 32 Perceptual colour space **73**
- 33 The early visual pathway **76**
- 34 View of the *medial* face of the right cerebral hemisphere **77**
- 35 Organization of the visual cortex **79**

- 36 'Cartoon' reconstruction of a face **80**
 From D. Pearson, E. Hanna, and K. Martinez (1990) Computer Generated Cartoons. In Horace Barlow, Colin Blakemore, and Miranda Weston-Smith (eds), *Images and Understanding*. © Cambridge University Press 1990, reproduced with permission
- 37 The four lobes of the human cortex **82**
- 38 Appearance of the image in glaucoma and age-related macular degeneration **90**
 Shutterstock.com
- 39 Sub-retinal implant **93**
 modified from (left) *Science* 8 February 2002: Vol. 295 no. 5557 pp. 1022–1025 DOI: 10.1126/science.1067996. Reprinted with permission from AAAS and A. Stett, NMI; (right) Eberhart Zrenner, Karl Ulrich Bartz-Schmidt, Heval Benav, Dorothea Besch, Anna Bruckmann, Veit-Peter Gabel, Florian Gekeler, Udo Greppmaier, Alex Harscher, Steffen Kibbel, Johannes Koch, Akos Kusnyerik, Tobias Peters, Katarina Stingl, Helmut Sachs, Alfred Stett, Peter Szurman, Barbara Wilhelm and Robert Wilke. 2010 Subretinal electronic chips allow blind patients to read letters and combine them to words. *Proc. R. Soc. B* published online 3 November 2010. doi:10.1098/rspb.2010.1747
- 40 Sensory substitution **96**
 from medgadgets.com

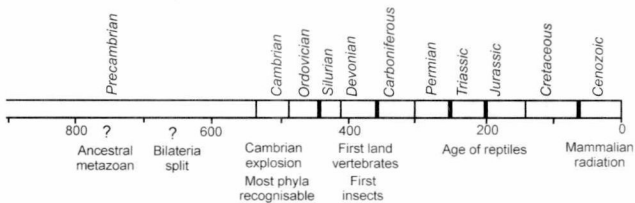
Chapter 1

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,

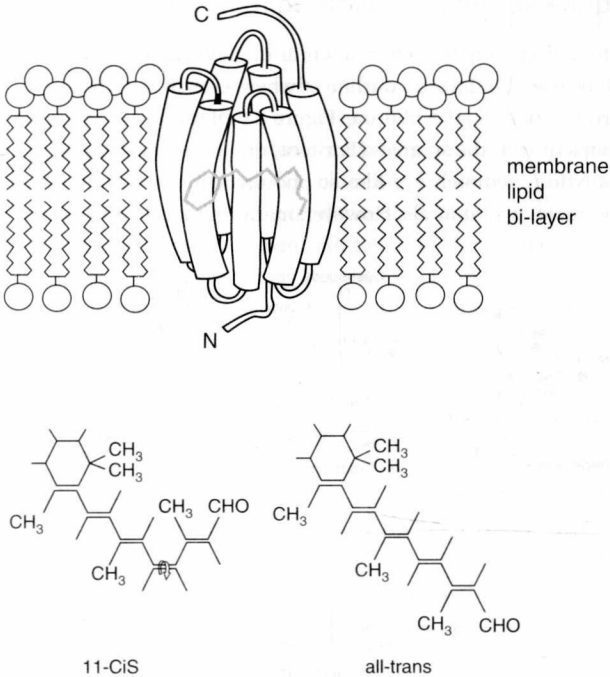


1. Geological time-line. Age scale in millions of years before present. Five major extinctions, in each of which more than 70% of the world's fauna disappeared, are shown as thicker bars

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

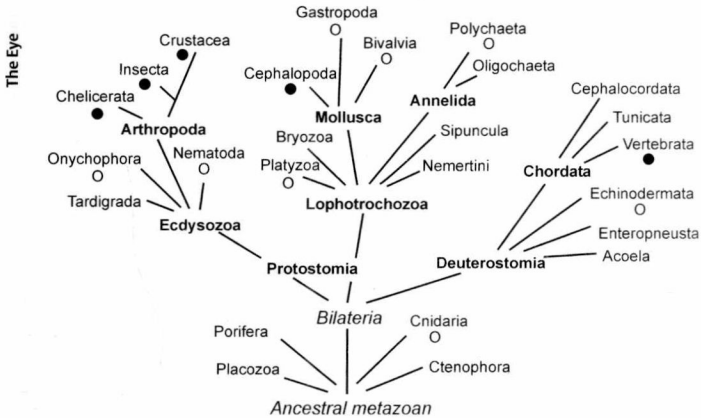


2. Rhodopsin molecule embedded in the cell membrane of a photoreceptor. The membrane is a double layer of lipid molecules. Rhodopsin consists of an opsin protein, with 7 helices of amino acids that cross the membrane, and inside it (in grey) sits the chromophore molecule—usually a relative of vitamin 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