While the human eye can practically cope only with two aspects of light, brightness and colour, for many animals polarization is a further source of visual information. This fascinating phenomenon of polarization sensitivity is comprehensively treated by Horvath and Varju. Starting with a short introduction into imaging polarimetry – an efficient technique for measuring light polarization – various polarization patterns occurring in nature are presented. Among them are the polarizational characteristics of water surfaces, mirages and the underwater light field as well as the celestial polarization patterns affected by the illumination conditions of sunrise, sunset, clear or cloudy skies, moonshine and total solar eclipses.

The major part of the book is dedicated to the question: How can animals perceive and use the natural and artificial polarization patterns? Following a detailed compendium of the physiological basis of polarization sensitivity, several case studies of animal behaviour determined or influenced by polarization are presented. It is shown how arial, terrestrial and aquatic animals use the celestial and under-water polarization for orientation, e.g. how polarized light serves honeybees or ants as a compass. Further, it is explained how man-made objects affecting the natural optical environment may disorientate animals. For instances, as in the case where oil or glass surfaces, asphalt roads, or plastic sheets used in agriculture can be more attractive for water-seeking polarotactic insects than the water surface, and where mayflies lay their egg on dry asphalt roads or cars.

ISBN 3-540-40457-0

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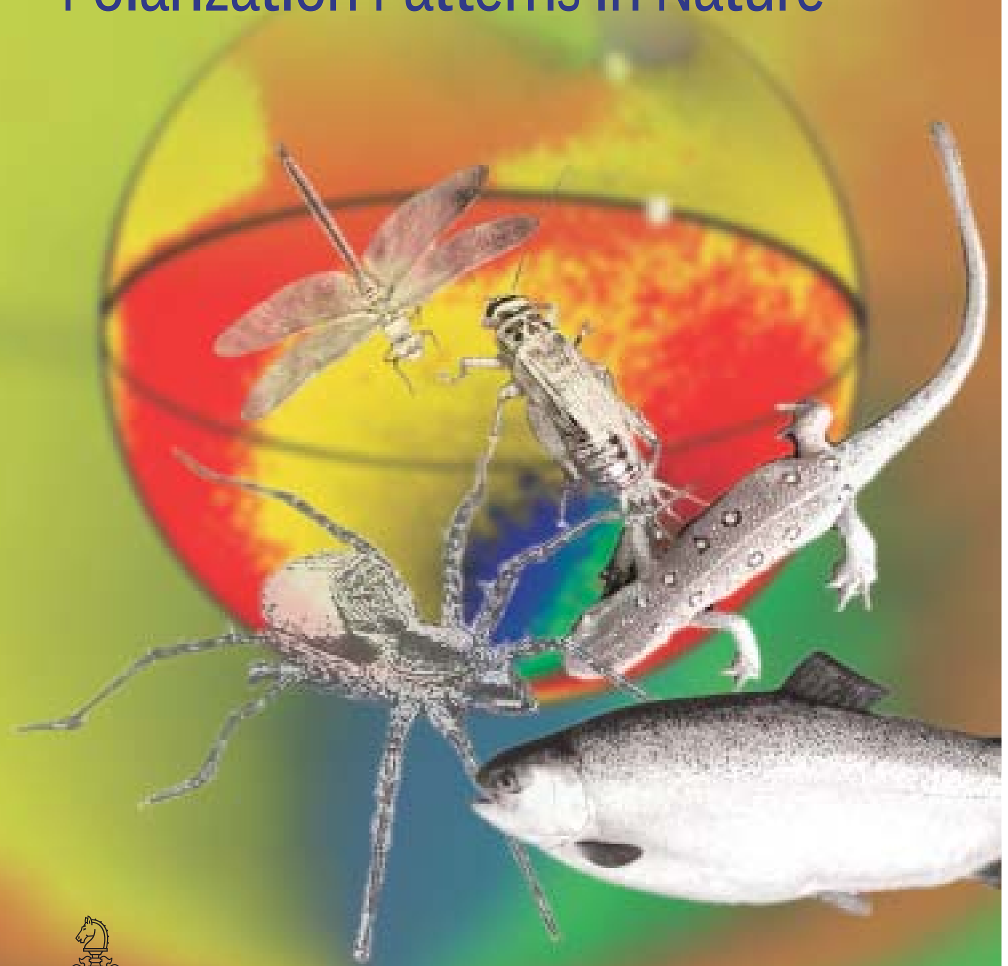
Horváth · Varjú

Polarized Light in Animal Vision

Gábor Horváth · Dezsö Varjú

Polarized Light in Animal Vision

Polarization Patterns in Nature



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With 127 Figures, 16 Plates in Colour

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Cover Photos: **Background:** Pattern of the angle of linear polarization α of skylight and earthlight displayed on the surface of a *sphere* and measured by 180° field-of-view imaging polarimetry in the blue part (450 nm) of the spectrum from a hot air balloon at an altitude of 3500 m. The colour code of α is given in → colour Fig. 4.5. More details can be found in Chap. 4.2. **Foreground:** Collection of some reprsentative polarization-sensitive animal species (dragonfly *Anax imperator*, house cricket *Acheta domesticus*, red-spotted newt *Notophthalmus viridescens*, spider *Pardosa lugubris* and rainbow trout *Oncorhynchus mykiss*), the polarization sensitivity of which is treated in Part III of this volume.

All figures in this volume were composed by Dr. Gábor Horváth

ISBN 3-540-40457-0 Springer-Verlag Berlin Heidelberg New York

Library of Congress Cataloging-in-Publication Data

Horváth, Gábor, 1963-
Polarized light in animal vision : polarization patterns in nature / Gábor Horváth, Dezsö Varjú.
p. cm.
Includes bibliographical references (p.).
ISBN 3-540-40457-0 (alk. paper)
1. Vision. 2. Polarization (Light)–Physiological aspects. 3. Animal orientation. 4. Physiology, Comparative. I. Varjú, Dezsö, 1932- II. Title

QP481.H65 2003
152.14--dc22 2003054309

Springer-Verlag Berlin Heidelberg New York
a company of BertelsmannSpringer Science+Business Media GmbH

http://www.springer.de

Printed in Germany

Production and typesetting: Friedmut Kröner, 69115 Heidelberg, Germany
Cover design: *design & production* GmbH, Heidelberg

31/3150 YK – 5 4 3 2 1 0 – Printed on acid free paper

Preface

The subject of this volume is two-fold. First, it gathers typical polarization patterns occurring in nature. Second, it surveys the polarization-sensitive animals, the physiological mechanisms and biological functions of polarization sensitivity as well as the polarization-guided behaviour in animals. The monograph is prepared for biologists, physicists and meteorologists, especially for experts of atmospheric optics and animal vision, who wish to understand and reveal the message hidden in polarization patterns of the optical environment not directly accessible to the human visual system, but measurable by polarimetry and perceived by many animals. Our volume is an attempt to build a bridge between these two physical and biological fields.

In Part I we introduce the reader to the elements of imaging polarimetry. This technique can be efficiently used, e.g. in atmospheric optics, remote sensing and biology.

In Part II we deal with typical polarization patterns of the natural optical environment. Sunrise/sunset, clear skies, cloudy skies, moonshine and total solar eclipses all mean quite different illumination conditions, which also affect the spatial distribution and strength of celestial polarization. We present the polarization patterns of the sky and its unpolarized (neutral) points under sunlit, moonlit, clear, cloudy and eclipsed conditions as a function of solar elevation. The polarization pattern of a rainbow is also shown. That part of the spectrum is derived in which perception of skylight polarization is optimal under partly cloudy skies. The reader becomes acquainted with the polarization of the solar corona and can follow how the polarization pattern of the sky changed during a total solar eclipse. We also treat the polarizational characteristics of water surfaces, mirages and the underwater light field. We explain why water insects are not attracted by mirages. Finally, the occurrence of circularly polarized light in nature is reviewed.

Part III is devoted to the description of the visual and behavioural mechanisms indicating how animals perceive and use natural polarization patterns. Surveying the literature, a detailed compendium of the sensory basis of polarization sensitivity in animals and humans is given. We also present several case studies of known behavioural patterns determined or influenced by polarization sensitivity. It is shown, for instance, how aerial, terrestrial and aquatic animals use celestial and underwater polarization for orientation. The role of the reflection-polarization pattern of water surfaces in water detection by insects is discussed. We illustrate how reflection-polarization patterns of anthropogeneous origin can deceive water-seeking polarotactic insects. The natural environment is more or less affected by human civilization and is overwhelmed by man-made objects, such as crude or waste oil surfaces, asphalt roads, glass surfaces, or plastic sheets used in agriculture, for instance. We explain why these surfaces are more attractive to water-seeking polarotactic insects than the water surface itself. We explain why mayflies or dragonflies lay their eggs *en masse* on dry asphalt roads or car-bodies. We show how dangerous open-air oil reservoirs can be for polarotactic insects and why oil surfaces function as insect traps. Some other possible biological functions of polarization sensitivity, such as contrast enhancement, intra- or interspecific visual communication and camouflage breaking are also discussed. Due to the interference of polarization and colour sensitivity, polarization-induced false colours could be perceived by polarization- and colour-sensitive visual systems. We calculate and visualize these false colours by means of a computer model of butterfly retinae, and investigate their chromatic diversity. Finally, a common methodological error is discussed, which is frequently committed in experiments studying animal polarization sensitivity.

Our monograph is in close connection with the treatise about planets, stars and nebulae studied with photopolarimetry edited by T. Gehrels (1974), the volume on polarized light in nature by Günther P. Können (1985), and the monograph of Kinsell L. Coulson (1988) on polarization and intensity of light in the atmosphere. When these volumes were published, the technique of imaging polarimetry was not yet available, thus the polarizational characteristics of natural optical environments were presented in the form of graphs or pairs of photographs taken through linear polarizers with two orthogonal directions of their transmission axes.

Due to imaging polarimetry developed in the last decade, the polarization patterns are visualized in our volume as high resolution colour/grey-coded maps of the degree and angle of linear polarization. All colour figures are placed at the end of the book. They are cited in the text as e.g. → colour Fig. 1.1.

Considering various kinds of point-source non-imaging polarimeters, including radar polarimetry, the reader is referred to the monographs of Egan (1985), Kong (1990), Azzam and Bashara (1992), Boerner *et al.* (1992) and Collett (1994), for instance. All relevant details of the physics of light polarization can be found in the text-books of Shurcliff (1962), Clarke and Grainger (1971), Kliger *et al.* (1990), Born and Wolf (1999), for example. The early knowledge about the sensory basis of animal polarization sensitivity and its biological functions was reviewed by Karl von Frisch (1967) and Talbot H. Waterman (1981). Rüdiger Wehner (1976, 1982, 1983, 1984, 1989, 1994, 2001) also wrote several important reviews and essays about this topic, especially on honeybees and desert ants. In addition to relying on our own contributions to the field, we have liberally quoted from the numerous publications of many other investigators with appropriate references given in each case. While the bibliography at the end of our book is not complete, it is fairly representative of the field.

June 2003, Budapest
Tübingen

Gábor Horváth
Dezsö Varjú

Acknowledgements

Financial support for the authors to write the book was given by the German Alexander von Humboldt Fundation, providing Gábor Horváth with a Humboldt research fellowship for 14 months at the Department of Cognitive Neuroscience of the Eberhard Karls University in Tübingen, thus making close cooperation with Dezs? Varjú possible. Many thanks are due to Professor Hanspeter Mallot, head of the department, who provided us with all the necessary equipment and materials. We appreciate the secretarial and technical assistance of Mrs. Annemarie Kehrer, Ursula Henigne and Dr. Heinz Bendele. The three-year István Széchenyi scholarship from the Hungarian Ministry of Education to G. Horváth is also acknowledged. G. Horváth received further financial support from the Hungarian Science Foundation (OTKA F-014923, T-020931, F-025826).

We are very grateful to the following scientists for reviewing different chapters (numbers in brackets) of the monograph: Kenneth Able (31), Marie Dacke (24), Michael Freake (29, 30), Uwe Homberg (17.6, 17.7), Almut Kelber (17.5), Kuno Kirschfeld (17.2), Thomas Labhart (17.4), Inigo Novales Flamarique and Ferenc Hárosi (28), Samuel Rossel (17.1), Rudolf Schwind (18), Nadav Shashar (26), Rüdiger Wehner (17.3) and Hansruedi Wildermuth (18.6). Apart from these scientists, S. Akesson, E.J.H. Bechara, H.I. Browman, M.A.J.M. Coemans, T. Cronin, R.B. Forward, W. Haupt, C.W. Hawryshyn, G.W. Kattawar, G.P. Können, M.F. Land, R.L. Lee, D.K. Lynch, E.P. Meyer, V.B. Meyer-Rochow, F.R. Moore, U. Munro, D.E. Nilsson, J.F.W. Nuboer, A. Ugolini, K.J. Voss, J.A. Waldvogel, T.H. Waterman, W. Wiltschko and J. Zeil provided us with important literature and information, which is acknowledged.

We are also grateful to the following students and colleagues for their continuous help during the polarimetric investigations in the field and the evaluation and visualization of the polarization patterns: András Barta, Balázs Bernáth, Ferenc Mizera, Gergely Molnár, Bence Suhai, Gábor Szedenics, Drs. Sándor Andrikovics, József Gál, Ottó Haiman, György Kriska and István Pomozi.

The polarimetric measurements in Finland, in the Tunisian desert and in Switzerland were possible due to fruitful cooperation with Professors Viktor

Benno Meyer-Rochow, Rüdiger Wehner and Hansruedi Wildermuth. Many thanks for their financial support, valuable help and encouragement.

Mária Horváth-Fischer and János Horváth rendered indispensable help and support during the field experiments in the Hungarian Great Plain (Kiskunhalas, Kecel and Kunfehértó).

All figures adopted from the cited sources are taken over in this volume with the permission of the publishers.

Many thanks to our wives, Heide Varjú and Zsuzsanna Horváth-Tatár who ensured the ideal and quiet familiar atmosphere, which was one of the most important prerequisites of our work. We dedicate this monograph to them.

Gábor Horváth is very grateful to Professor Rudolf Schwind, who introduced him into the wonderful world of polarized light and its role in animal vision during his one-year postdoctoral fellowship at the Institute of Zoology of the University of Regensburg in 1991–1992.

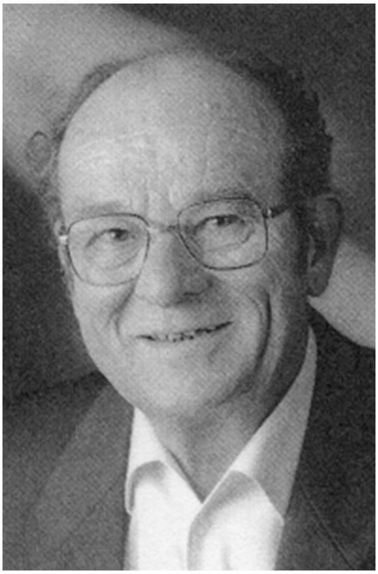
Last, but not least, we are also very much indebted to Springer-Verlag, especially to Drs. Dieter Czeschlik and Jutta Lindenborn. Dr. Czeschlik agreed without hesitation to publish the book, and from Dr. Lindenborn we received valuable advice while preparing the manuscript.

About the Authors

Gábor Horváth was born in 1963 in Kiskunhalas, Hungary. In 1987 he received his diploma in physics from the Loránd Eötvös University in Budapest. Then he was a research assistant at the Department of Low Temperature Physics of the same university, where he investigated electrical percolation processes in granular superconductors. In 1989 he received a doctoral fellowship in the Biophysics Group of the Central Research Institute for Physics of the Hungarian Academy of Sciences (Budapest), where he developed a mathematical description and computer modelling of retinal comet-like afterimages. He obtained his Ph.D. at the Eötvös University in 1991. His thesis in physiological optics is a computational study of the visual system

and optical environment of certain animals. In 1991 he was offered a one-year postdoctoral position in the Institute for Zoology of the University of Regensburg (Germany), where together with Professor Rudolf Schwind he started to study the polarization patterns of skylight reflected from water surfaces. Then he was a postdoctoral fellow at the Department for Biological Cybernetics of the University of Tübingen (Germany) for 1 year. Here, he investigated experimentally the polarization-sensitive optomotor reaction in water insects and natural polarization patterns together with Professor Dezs? Varjú. In 1993 he finished his postdoctoral dissertation in computational visual optics to obtain the degree "Candidate for Biophysical Science" awarded by the Hungarian Academy of Sciences. For this treatise he won the first International Dennis Gabor Award. In 1993 together with Dezs? Varjú, he won also the biomathematical Richard Bellman Prize from the journal of Mathematical Biosciences. He also received several best paper awards of different Hungarian popular-scientific journals. He won the first prize of the Hungarian Biophysical Society three times. In 1994 he received the *Pro Schola* award from the Áron Szilády secondary school, where he studied earlier. Presently he is an associate professor at the Department of Biological Physics of the Eötvös University and leader of the Biooptics Laboratory. He received the Hungarian István Széchenyi (4 years), Loránd Eötvös (9 months), János Bolyai (3 years), Zoltán Magyary (1 year) scholarships and the German Alexander von Humboldt fellowship (14 months). His main research interest is studying experimentally as well as theoretically the optics of animal eyes, polarization sensitivity of animals and the polarization characteristics of the optical environment. He developed different kinds of imaging polarimetry, by which he records and visualizes the polarization patterns in nature. He conducted several expeditions and polarimetric measuring campaigns in Hungary, in the Tunisian desert as well as in the Finnish Lapland. His wife, Zsuzsanna Tatár-Horváth teaches mathematics and physics in a secondary school in Budapest. His sons, Loránd and Lénárd were born in 1991 and 1999, respectively.

Dezsö Varjú was born in 1932 in Hungary. In 1956 he received his diploma in physics from the Loránd Eötvös University in Budapest. In the same year he left Hungary and joined as graduate student a group of biophysicists headed by the late Werner Reichardt at a Research Institute of the Max Planck Society in Göttingen, Germany. There he was involved in the investigation of movement perception in insects and of phototropic and light growth responses of the slime mold *Phycomyces*, on both experimental and theoretical levels. In 1958 he received his Ph.D. from the Georg August University in Göttingen. In the same year the group moved to the Research Institute for Biology of the Max Planck Society in Tübingen. In 1959 he obtained a one-year postdoctoral position at the California Institute of Technology in Pasadena with Max Delbrück, where he continued his investigations into the light and gravity responses of *Phycomyces*. Returning to Tübingen, he started to study nonlinear signal transformation and binocular interactions in the human pupillomotor pathway at the above-mentioned institution. Afterwards he examined frog retinal ganglion cells. Later, he frequently changed the objects of his investigations, because he was looking for biological problems, the mathematical modelling of which promised to be fruitful, and each new object gave him the opportunity to become acquainted with a new chapter in biology. In 1968 the Eberhard Karls University in Tübingen offered him a Chair for Zoology, which was soon renamed the Department for Biological Cybernetics. The general field of his research during the last 30 years was invertebrate behavioural neurobiology with a special interest for localization and orientation. In



1983 he organized the triannual conference of the German Association for Cybernetics on these topics. His activities included both experimental investigations and mathematical modelling. His experimental animals were the beetle *Tenebrio*, the stick insect *Carassius*, the crabs *Carcinus*, *Leptograpsus*, *Pachygrapsus*, the crayfish *Cherax*, the bugs *Triatoma*, *Gerris*, *Notonecta* and the hawk moth *Macroglossum*. From 1969 until 2001 he was member of the Editorial Board of Biological Cybernetics and since 1993 of the Advisory Board of the Journal of Comparative Physiology A. He spent his sabbaticals in the laboratories of friends in Canberra and Sydney (1980/81, 1986/87, 1991/92). In Tübingen he conducted research with guest scientists from Argentina, Canada, USA, and most frequently with Gábor Horváth from Hungary. Since October 1997 he is Professor Emeritus of the University of Tübingen.

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Part II: Polarization Patterns in Nature

Part III: Polarized Light in Animal Vision

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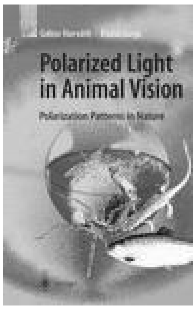

Polarized Light in Animal Vision
Polarization Patterns in Nature
Horváth, Gábor, **Varjú**, Dezsö
2004, XXIV, 447 p. 111 illus. and 16 color plates, Hardcover
ISBN: 3-540-40457-0

Due: November 13, 2003

179,95 €

About this book

While the human eye can practically cope only with two aspects of light, brightness and colour, many animals use polarization as a further source of visual information. The text starts with an introduction into imaging polarimetry, an efficient technique for measuring light polarization, and moves onto a description of the various polarization patterns occurring in nature, such as celestial polarization.The major part of the book is dedicated to the fascinating question: How do animals use polarization patterns? Following a compendium of the physiology of polarization sensitivity, several case studies are presented, such as honeybees or ants using polarized light as a compass or aquatic animals orientating by the underwater polarization. Further, it is explained how man-made objects affecting the natural optical environment may disorientate animals. For instance, as in the case where oil or glass surfaces can be more attractive for water-seeking polarotactic insects than the water surface.

Written for:

Scientists, graduate and undergraduate students

Keywords:

- polarization
- vision
- animals orientation
- optical environment
- visual information
- imaging polarimetry