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COLOR VISION CONFERENCE(U) CAMBRIDGE UNIV (ENGLAND)
DEPT OF EXPERIMENTAL PSYCHOLOGY J D MOLLON 15 MAR 83
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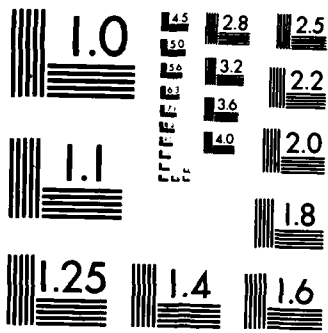
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REPORT DOCUMENTATION PAGE		READ INSTRUCTIONS BEFORE COMPLETING FORM
1. REPORT NUMBER	2. GOVT ACCESSION NO.	3. RECIPIENT'S CATALOG NUMBER
	AD-A125435	
4. TITLE (and Subtitle)		5. TYPE OF REPORT & PERIOD COVERED
Color Vision Conference		Final Report: 15 Jun 1982-15 Mar 1983
6. AUTHOR(s)		6. PERFORMING ORG. REPORT NUMBER
John D. Mollon		
7. PERFORMING ORGANIZATION NAME AND ADDRESS		8. CONTRACT OR GRANT NUMBER(s)
University of Cambridge Department of Experimental Psychology Cambridge, CB2 3EB ENGLAND		N00014-82-G-0111
9. CONTROLLING OFFICE NAME AND ADDRESS		10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS
Office of Naval Research (Code 442) 800 N. Quincy Street Arlington, VA 22217		61153N 42; WR04101001; 61153N 42; RR04209; RR0420902; NR 197-075
14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office)		12. REPORT DATE
Same as above		15 Mar 1983
		13. NUMBER OF PAGES
		11
		15. SECURITY CLASS. (of this report)
		Unclassified
		15a. DECLASSIFICATION/DOWNGRADING SCHEDULE
16. DISTRIBUTION STATEMENT (of this Report)		
Approved for public release; distribution unlimited.		
17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)		
Same as above		
18. SUPPLEMENTARY NOTES		
Conference papers to be published as: Mollon, J.D., & Sharpe, L.T. (Eds.) <u>Colour Vision: Physiology and Psychophysics</u> . London: Academic Press, 1983.		
19. KEY WORDS (Continue on reverse side if necessary and identify by block number)		
Photoreceptors, color matching, raster displays, electrophysiology, visual psychophysics, retinal mechanisms, color constancy, and visual perception.		
20. ABSTRACT (Continue on reverse side if necessary and identify by block number)		
A conference was organized that brought together 133 research scientists of diverse specialities to address a comprehensive review of the experimental and theoretical advances in color vision and to consider their application to the design of color-coding and color displays.		

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Final Report

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(a) The purpose of the conference was to bring together scientists and engineers from the diverse specialities in which color vision is studied (physiology, experimental psychology, human factors, optometry, physics) and to prepare a comprehensive handbook of current research. The meeting concentrated on human and primate color vision. Equal weight was given to physiological and psychophysical evidence. The topics for discussion ranged from microspectrophotometry of retinal photoreceptors to the phenomenological constancy of perceived hue in different illuminants. Tutorial material was included on the use of raster displays for color research.

A total of 133 delegates attended the meeting. The breakdown by nationality was as follows:

USA 41	Canada 6
UK 42	France 3
W. Germany 22	Denmark 2
The Netherlands 9	Norway 1
Switzerland 1	Italy 2
Japan 3	Spain 1

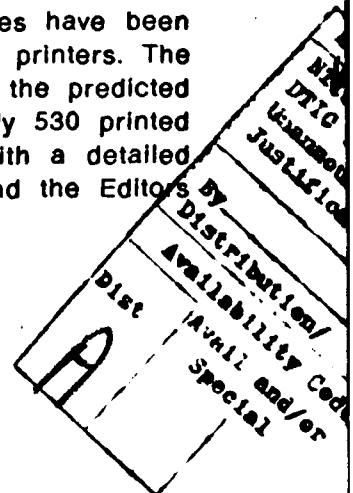
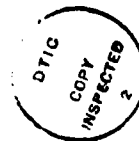
If delegates are classified into disciplines according to their institutional addresses, the following breakdown is obtained:

Engineering 21	Physiology 21
Genetics 1	Physics 13
Molecular biology 1	Psychology 38
Ophthalmology 12	Zoology 3
Optometry 12	Interdisciplinary 11

(b)

Fifty-seven papers were presented at the meeting and every author submitted a manuscript for publication. All manuscripts were refereed by the international committee. Two papers were rejected. The remaining papers have been accepted for publication in the book based on the meeting, but, in order that the book should be a genuinely useful handbook, all the manuscripts have been edited in detail to remove redundancies, obscurities and errors. All editorial changes have been agreed with the authors and the book is now (February 1983) at the printers. The book is being published by the London office of Academic Press and the predicted publication date is July, 1983. It will have a length of approximately 530 printed pages, will be illustrated with color plates, and will be provided with a detailed index. The title is 'Colour Vision: Physiology and Psychophysics' and the Editors are J. D. Mollon and L. T. Sharpe.

The detailed contents of the book are as follows:



'COLOUR VISION: PHYSIOLOGY AND PSYCHOPHYSICS'

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(c)The meeting was very successful in bringing together scientists from different specialities and different continents, and genuinely fruitful discussions were engendered between people who otherwise would have been unlikely to meet.

It is our hope, and that of the publisher, that the book resulting from the meeting will serve as a unique handbook to current research on color vision and will be more useful than a typical volume of conference proceedings. Among the topics of especial interest are: the first electrophysiological measurements from single primate photoreceptors; new and extensive microspectrophotometric measurements of human and primate cones; the first microspectrophotometric measurements from a human deuteranope; the presence of several dichromatic and trichromatic forms of color vision within a single primate species; electrophysiological recordings from single cells in the retina, lateral geniculate nucleus and visual cortex; effects of selective environments on the development of color vision; psychophysical measurements of thresholds for detection and discrimination; color constancy; and color coding.

Color vision was once a field of rather bitter controversy. This tradition was not in evidence at the Cambridge meeting, owing probably to the existence now of a common corpus of agreed knowledge. Thus there was no dispute about the number of types of retinal receptor and the gross spectral positions of their peak sensitivities (430, 530 and 560 nm) and it is equally agreed that there exist higher-order cells that receive signals of opposite sign from these receptors, thus allowing wavelength information to be extracted by the visual system. However, several areas of current dispute were identified at the meeting and are discussed in the book: Are there variations between normal observers in the wavelengths of peak sensitivity of their photoreceptors? Are there separate post-receptor channels for chromatic and spatial information, as has been held for the past decade, or do the same fibres in the visual pathway carry information about both hue and spatial detail, as several authors now suggest? Are there areas of visual cortex that are specialized for the analysis of color, as proposed by S. Zeki (in the present book Zeki's claim is supported by Guld, Anderson and Sjo from Copenhagen, and opposed by Kruger and Fischer from Freiburg). Why is our vision so odd when it depends on signals originating only in the short-wavelength receptors? (With respect to this question, the meeting revealed widespread agreement that part of the answer lies in the low numerosity of the short-wave receptors: several independent estimates suggest that they constitute less than 10% of all retinal cone cells.)

J. D. Mollon
February, 1983

PREFACE

We live in a world that is increasingly colour-coded. Not only are colours used for differentiation in technical fields such as electronics, transport signalling and military identification, but also the general public are daily exposed to colour coding in drugs, road signs, maps of transport systems and of large buildings, commercial packaging, advertising logos, teaching materials, and teletext systems. Colour visual-display-units are about to come into widespread use. Thus there are today strong practical reasons why we should improve our understanding of what limits our capacity to differentiate wavelengths, of how the neural analysis of colour is related to that of other attributes of the visual stimulus, and of why some 8% of the male population are deficient in colour discrimination.

Colour vision has never been the private preserve of any single one of the conventional disciplines of science. Its subtle but lawful complexities have attracted physicists, experimental psychologists, physiologists, ophthalmologists and optometrists. To this day, colour scientists are scattered among many different types of institution and their publications are similarly distributed among a variety of journals. In August 1982 an international meeting was held at Cambridge with the explicit purposes of bringing together colour specialists from different disciplines and of preparing the present handbook. It was the organisers' intention that the book should cover all aspects of colour vision, from the retinal photopigments to sensation; that equal weight should be given to physiological and psychophysical results; and that tutorial material should be included in order to introduce specific research problems and techniques to the non-specialist. We have concentrated on man - and on his primate relatives, who, it now seems, provide close models for both normal and deficient human colour vision.

Those who study colour vision are conscious that it is a field with a past. Much can be deduced about colour vision by purely sensory experiments in which an observer is asked to say whether two physically different lights appear alike or different; and the results have lent themselves to elegant geometrical analyses. Consequently, in the last three centuries, the problems of colour vision have engaged the attention of some of the most distinguished of natural scientists. It was fitting therefore that present meeting should be held at the University of Cambridge, the university of Newton, Thomas Young, Clerk Maxwell and Lord Rayleigh. Indeed, for many at the meeting, the beginnings of modern colour science were betokened by a holograph notebook (lent for display by the Fitzwilliam Museum) in which Newton recorded his purchase in 1667 of three prisms for three shillings. In an Appendix to the present book we have included the text of two talks given in conjunction with the meeting - an account by F. W. Campbell of Cambridge contributions to colour science; and a memoir by M. Alpern of the Cambridge physiologist W. A. H. Rushton.

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Cambridge last saw an international meeting on colour vision in 1947. The proceedings of that meeting (*Documenta Ophthalmologica*, vol 3, 1949) still repay careful reading; but we now enjoy an agreed corpus of physiological knowledge that was not available thirty-five years ago. In 1947 the spectral sensitivities of the photoreceptors, and indeed the number of types of photoreceptor, were matters for wide disagreement. No electrophysiological recordings were available from single cells in the primate visual system. Today, though they might make local qualifications, most colour scientists would agree on the following account of the early stages of colour analysis in the human visual system:

Our sensations of hue depend upon the relative rates of absorption of photons in three classes of retinal photoreceptor, which have peak sensitivities at wavelengths of approximately 560 nm, 530 nm and 420-430 nm. The short-wavelength receptors are rarer than the long- and middle-wavelength receptors. The spectral sensitivities (i.e. the curves that relate sensitivity to wavelength) of the different classes of receptor are broad and overlapping and the electrical signal of an individual receptor preserves no information about the wavelength of the light that is being absorbed. So, in order that the visual system should be able to separate changes in colour from changes in intensity, some post-receptor neurons receive inputs of opposite sign from different classes of photoreceptor. Among retinal ganglion cells and among the cells of the parvocellular layers of the lateral geniculate nucleus, there are two main classes of these 'colour-opponent' neurons. The most common type receives an input of one sign (excitatory or inhibitory) from the long-wavelength receptors and an input of the opposite sign from the middle-wavelength receptors; this type of neuron is also spatially opponent in that the two inputs are drawn from spatially distinct regions of the receptor array, a disc-shaped central region and a concentric surround. A somewhat rarer type of colour-opponent neuron receives an input of one sign from the short-wavelength receptors and an input of opposite sign from the long- and middle-wavelength receptors; in this case the excitatory and inhibitory inputs are drawn from the same disc-shaped area of the receptor array. The reader will be able to add flesh to this skeleton by referring to Sections I and IV of the present book.

On one central issue the present book probably marks a turning point. Thirty-five years ago colour scientists were concerned to develop psychophysical techniques for isolating the responses of individual classes of receptor - by removing other classes of receptor from play by means of monochromatic adapting fields, or by choosing spatial and temporal parameters that favoured one class, or by choosing observers who lacked one or more class. About eight years ago interest began to shift to psychophysical techniques for isolating different types of post-receptor channel. Thus it seemed that a liminal target was likely to be detected by 'chromatically opponent' channels if the target was of large area and long duration and if an achromatic adapting field was present. Under such conditions the spectral sensitivity of the eye has multiple peaks (one of which lies at a wavelength much longer than the wavelength of peak sensitivity of the long-wavelength receptors); and when targets, or adapting fields, of different

wavelengths are combined, the effect of the combination may be less than predicted by simple additivity. On the other hand, if a target is small and brief and if a monochromatic adapting field is present, then it may seem that detection is mediated by a 'non-opponent' pathway: the spectral sensitivity of the eye has a single peak and additivity is often found to hold. The dichotomy between 'opponent' and 'non-opponent' channels has proved a very fruitful concept in recent research and the reader will find that it is discussed, in various forms, in several papers in the present volume. Equally, however, the reader will find an increasing realisation that the psychophysicist's dichotomy has never agreed with the physiological knowledge outlined in the preceding paragraph: the same retinal ganglion cell may apparently signal either local achromatic contrast or the presence of homogeneous colour. The psychophysicist's 'channels' may represent the same cells operating in different modes; and central mechanisms may have to consider the output of a population of cells in order to separate spatial and chromatic information. On this issue, see especially papers 17, 35 and 39.

Some other recurrent issues can be identified in the pages that follow. Are there variations between 'normal' observers in the spectral positions of their photopigments (see papers 2, 4, 5 and 7)? Are the colour-specific neurons of the visual cortex grouped into 'columns' (papers 25 and 26)? Are there areas of prestriate cortex that are specialised for the analysis of colour (papers 26 and 27)? Why is our vision so odd when discrimination depends only on signals originating in the short-wave receptors (papers 40, 44-48)? What is the relation between, on the one hand, the opponent processes revealed by measurements of thresholds and, on the other, the phenomenological antagonism of particular pairs of hues (papers 33, 34, 35, 36 and 54)? How do we recognise the spectral reflectances of objects despite large changes in the spectral composition of the illuminant (papers 49 and 50)?

Very recently, colour vision research has found a new tool in the form of the computer-controlled colour television monitor. Raster displays of this type allow the generation of colour stimuli that vary elaborately in space, in time, and in chromaticity; but such displays have to be selected and used with care and we have therefore included two tutorial papers (11 and 12) that describe not only the versatility but also the limitations and pitfalls of computer-controlled displays. Specific uses of raster displays are illustrated in a number of other papers (13, 14, 21, 38, 40, 42, 49 and 51).

The papers included in this volume have been refereed. The editors and referees have deliberately not sought to impose a common theoretical approach on the papers selected for inclusion, but, in the brief time available, have tried merely to eliminate obvious non-sequiturs, internal inconsistencies, and obscurities of expression. We have not attempted to impose British spelling on our American colleagues. Since we hope that the book may provide bibliographic access to the scattered literature on colour vision, we have taken particular trouble to check references. We thank all the contributors for their helpfulness during the editing

process.

ACKNOWLEDGEMENTS

The meeting from which this book derives was primarily sponsored by the Human Factors Committee of the Scientific Affairs Division of NATO (Grant No: SA.9.3.03C(82/1)191-BAB). Additional support was given by the Royal Society; by the Wellcome Trust; and by the US Army Research Institute for the Behavioral and Social Sciences through its European Liaison Office at the European Research Office of the US Army, London. Preparation of this book has been supported by the US Naval Air Systems Command through a grant monitored by the Office of Naval Research, Arlington, Virginia (Grant No: N00014-82-G-0111) and by the aforementioned office of the US Army Research Institute. We, and our contributors, are grateful to the above bodies for making possible the meeting and the book. Statements of opinion in the text should not be construed as the opinions of the above bodies.

Throughout the planning of the meeting and the editing of this book we have been guided by an international committee consisting of Professor C.R. Cavonius (Dortmund), Dr. O. Estevez (Amsterdam) and Dr. J. Krauskopf (Murray Hill, NJ). We most sincerely thank these colleagues for their help. We have been indebted to Betty Clifton for secretarial assistance during the organisation of the meeting and the preparation of the book. We also wish to thank Professor N. J. Mackintosh and Professor R. D. Keynes for providing facilities for the meeting; Trinity College, Cambridge, for its hospitality to our delegates; and Mr. C. Hood for several kindnesses at the time of the meeting.

J. D. Mollon, L. T. Sharpe

Cambridge, January, 1983

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