Proceedings

of the
AIC Interim Meeting 1987:

Stiles-Wyszecki Memorial Symposium on Color Vision Models

Florence, June 10 - 13, 1987

Sponsored by the
CIE Division 1: Vision and Color

On behalf of the AIC
edited by
Manfred Richter
1989

MUSTER-SCHMIDT VERLAG · GÖTTINGEN · ZÜRICH

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Editorial Comment

Contrary to former intentions it was decided by the AIC, in August 1988, to publish the Proceedings of the Florence Symposium by print, and the undersigned editor of the journal DIE FARBE was asked whether he would agree to do so. As this Symposium was extremely successful and its lectures were at a high scientific level, we were glad and felt honored, so we accepted with pleasure. As the papers of the meeting filled a whole volume of our journal, we decided to publish the papers as the volume 34 of our journal and to bring them out separately at the same time as reprints under the title "Proceedings". It is this edition you have before you.

Though we were anxious to make it appear as soon as possible, its special preparation inevitably took a lot of time, not least due to the long postal ways to and from the authors who live far spread over the whole globe. Therefore these Proceedings appear now with a great delay of more than two years after the meeting in Florence, and we regret this delay very much.

Nevertheless we hope that even now the papers of the beautiful symposium (which Prof. Dr. RONCHI of the *Istituto Nazionale di Ottica* at Florence had organized and prepared so successfully) will be appreciated. So we think that this edition will still now be accepted as an important contribution to the promotion of the science of color.

Manfred Richter

List of Participants

ADRIAN, WERNER, Prof. Dr.
University of Waterloo
301 Shakespeare Dr., Waterloo, N21 2T9 Ontario, Canada

AKITA, MUNEHIRA, Prof. Dr.
Kyoto Institute of Technology
Matsugasaki, Sakyo-ku, Kyoto, 606 Japan

ALPERN, MATHEW, Dr.
University of Michigan, Medical Center
1000 Wall Street, Ann Arbor, MI 48105, USA

BARTLESON, C. J., Dr. (†)
Research Laboratories, Eastman Kodak Company
59 Kodak Park, Rochester, NY 14650, USA

BOCK, DAVID R., Dr.
Box 53, Elmira
N3B 2Z5 Ontario

BODMANN, HANS-WALTER, Prof. Dr.
Lichttechnisches Institut, Universität Karlsruhe
Kaiserstr. 12, D-7500 Karlsruhe 1, Germany, Fed. Rep.

BUCHSBAUM, GERSHON, Dr.
Dept. of Bioeng., Univ. of Pennsylvania
Philadelphia, PA 19104–6392, USA

BUDDE, WOLFGANG
9 Kindle Court
Gloucester, Ont., K1J 6E1, Canada

CICERONE, CAROL, Prof. Dr.
University of Colorado
Campus Box 345, Boulder, CO 80309, USA

DA POS, OSWALDO
Department of General Psychology
Piazza Capitaniato 3, I-35100 Padova, Italy

DI PIETRO, GUILIA
Istituto Nazionale di Ottica
Largo Enrico Fermi 6, I-50125 Arcetri-Florence, Italy

DE VALOIS, KAREN, Dr.
Univ. of California Berkeley, School of Optom.
Berkeley, CA 94720, USA

DE VALOIS, RUSSEL, Prof. Dr.
Univ. of California Berkeley, School of Optom.
Berkeley, CA 94720, USA

DE WEERT, CHARLES M. M.
Psychological Laboratory
PO Box 9104, NL-6500 HE Nymegen, The Netherlands

EJIMA, YOSHIMICHI, Prof. Dr.
Kyoto University
Yoshidanihonmatsucho, Sakyo-ku, Kyoto, Japan

ESTÉVEZ, OSCAR, Dr.
Lab. Med. Physic., Univ. of Amsterdam
Meibergdreef 15, NL-1105 AZ Amsterdam, The Netherlands

GOURAS, PETER, Dr.
Dept. of Ophthalmology, Columbia University
630 W. 168 St., New York, NY 10032, USA

HOOD, DONALD, Prof.
Columbia University, Dept. of Psychology
116 Broadway, New York, NY 10027, USA

HUNT, ROBERT, Prof. Dr.
Kewferry House, 10 Kewferry Road
Northwood, HA6 2NY, England

HUTCHINGS, JOHN
The Pyghtle, Milton Ernest
Bedford MK44 IRF, England

IKEDA, MITSOU, Prof.
Tokyo Institute of Technology, Dept. Inf. Proc.
Nagatsuta, Midori-ku, Yokohama, 227 Japan

INDOW, TAROW, Prof.
Univ. of California Irvine, Dept. of Cogn. Sc.
Irvine, CA 92717, USA

JOHANSSON, OLOF
Yttersta Tvargrand 9, S-11726 Stockholm, Sweden

KAISER, PETER, Prof. Dr.
York University, Department of Psychology
4700 Keele Str., Downsview, Ontario M3J 1P3, Canada

KANEKO, AKIMICHI, Prof.
Nat. Inst. for Physiological Sciences
38 Nishigonaka, Myodaiji, Okazaki, 444 Japan

LEE, BARRY, Dr.
Max Planck-Institut f. Biophys. Chemie
Am Faßberg, D-3400 Göttingen, Germany, Fed. Rep.

LOZANO, ROBERTO, Dr.
Inst. Nac. de Tecnologia Industrial (INTI)
Cas. de Correo 157, 1650 San Martin, B.A., Argentine

MACLEOD, DONALD
University of California San Diego, Dept. Psych.
La Jolla, CA 92093, USA

MARTIN, PAUL
MPI f. Biophys. Chemie, Abt. Neurobiologie
Am Faßberg, D-3400 Göttingen, Germany, Fed. Rep.

MCCAMY, CALVIN
Macbeth Corp.
Box 230, Newburgh, NY 12550, USA

MCCANN, JOHN
Polaroid Corp.
750 Main Str., Cambridge, MA 02139, USA

MOLLON, JOHN, Dr.
University of Cambridge, Dept. of Exp. Psychol.
Cambridge CB2 3EB, England

MORI, LEO, Dr.
Research & Development Center, Toshiba Corp.
1, Komukai-Toshiba-cho, Saiwai-ku, Kawasaki, 210 Japan

NAYATANI, YOSHINOBU, Dr.
Osaka Electro-Communication University
Hatsu-cho, 18–8, Neyagawa, Osaka, 572 Japan

OBERASCHER, LEONHARD, Dr.
Universität Salzburg, Institut für Psychologie
Heinbrunner Str. 34, A-5020 Salzburg, Austria

PAULUS, WALTER, Dr.
Neurologische Universitätsklinik München
Marchioninistr. 15, D-8000 München 70, Germany, Fed. Rep.

POKORNY, JOEL, Prof.
University of Chicago, Eye Research Lab.
939 East 57th Street, Chicago, IL 60637, USA

POWELL, BRYAN,
Australian Broadcasting Corporation
GPO Box 9994, Sydney, NSW, 2001, Australia

REEVES, ADAM, Dr.
Northeastern University
360 Huntington Ave, Boston, MA 02115, USA

RICHTER, MANFRED, Prof. Dr.
U. d. Eichen 87, D-1000 Berlin 45, Germany, Fed. Rep.

ROBERTSON, ALAN R., Dr.
National Research Council
Montreal Road, Ottawa K1A 0R6, Canada

RONCHI, LUCIA ROSITANI, Prof. Dr.
Istituto Nazionale di Ottica
Largo Enrico Fermi 6, I-50125 Arcetri-Florence, Italy

ROTTER, FRIEDRICH, Dr.
Andergasse 65, A-1170 Wien, Austria

SCHEIBNER, HORST, Prof. Dr.
Physiologisches Institut, Universität Düsseldorf
Moorenstr. 5, D-4000 Düsseldorf, Germany, Fed. Rep.

SHEYELL, STEVEN
University of Chicago
5848 S. University Avenue, Chicago, IL 60637, USA

SMITH, VIVIANNE, Prof.
University of Chicago, Eye Research Lab.
939 East 57the Street, Chicago, IL 60637, USA

SPERLING, HARRY G., Dr.
University of Texas, Health Science Center
6420 Lamar Fleming Ave, Houston, TX 77030, USA

SPILLMANN, WERNER, Prof.
Winterthur Polytechnic, Dept. of Architecture
PO Box, 8401 Wintherthur, Switzerland

STROMEYER III, CHARLES, Dr.
Division Appl. Sciences, Harvard University
Cambridge, MA 02138, USA

STYNE, ALEXANDER, Prof.
University of Miami
POB 431468, South Miami, FL 33143, USA

TERSTIEGE, HEINZ, Prof. Dr.
Bundesanstalt f. Materialforschung
U. d. Eichen 87, D-1000 Berlin 45, Germany, Fed. Rep.

TONNQUIST, GUNNAR
Royal Institute of Technology
S-10044 Stockholm, Sweden

TREZONA, PAT, Dr.
National Physical Laboratory
33, Field View, Bar Hill, Cambridge, CB3-85X, England

VALBERG, ARNE, Dr.
Inst. of Physics, University of Oslo
Box 1038 Blindern, N-0315 Oslo 3, Norway

VAN TRIGT, C., Dr.
Lab. of Lighting Technique and Appl.
POB 218, NL-5600 MD, Eindhoven, The Netherlands

VIÉNOT, FRANÇOISE, Dr.
Museum d'Histoire Naturelle, Lab. de Phys. Appl.
43 Rue Cuvier, F-75005 Paris, France

VOS, JOHANNES, J., Dr.
Institute for Perception TNO
Kampweg 5, NL-3769 DE Soesterberg, The Netherlands

WALRAVEN, JAN, Dr.
Institute for Perception TNO
Kampweg 5, NL-3769 DE Soesterberg, The Netherlands

WALRAVEN, PIETER, Dr.
Institute for Perception TNO
Kampweg 5, NL-3769 DE Soesterberg, The Netherlands

YAGUCHI, HIROHISA
Dept. of Image Sc. and Eng., Chiba University
1-33 Yagoi-cho, 260 Chiba, Japan

YAMASHITA, YUKIO, Dr.
University of Chicago, Eye Research Lab.
939 East 57the Street, Chicago, IL 60637, USA

ZRENNER, EBERHART, Prof. Dr.
Max Plank-Labor Univers.-Augenklinik
Mathildenstr. 8, D-6000 München 2, Germany, Fed. Rep.

Mathew Alpern*, ANN ARBOR (Mich.):

Walter Stanley Stiles

(1901–1985)

Memorial Lecture**

DK 612.843.3
92 Stiles, W. S.

WALTER STANLEY STILES
* 15. 6. 1901
† 15. 12. 1985

W. S. STILES (or STANLEY, as friends called him) made fundamental and substantial contributions to understanding of vision and color continuously from about 1928 until his death, even in the quarter of a century of his life remaining after retirement. Both an outstanding experimenter and a superb theoretician, he was born the second of two children, the son of a London policeman. Without the advantage of education at one of the great English Public Schools which nurtured his country's scientific and intellectual elite, and largely unrecognized throughout most of his working life, he nonetheless changed the face of color science as only a very few of his predecessors managed.

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* *W. K. Kellog Eye Center, The University of Michigan,* Ann Arbor, Mich.

** This is an abstract and summary of a more extensive biography published elsewhere[1]. Constraints on space obligate the omission of citations of references, sources, discussion of evidence leading to the various inferences drawn, and even most of the acknowledgements for all the help I have had from others in my study of this singular life. I hope readers curiosities will be sufficiently aroused in places to stimulate them to read the original where all of these are given. It is necessary however to acknowledge with gratitude financial support from: *The Royal Society of London,* Vice President WILSON and Dean D'ARMS both of the *University of Michigan,* The *National Eye Institute* for a research grant, and *Research to Prevent Blindness* for a Senior Scientific Investigator Award and to thank Prof. J. W. S. CASSELS F. R. S. of *Trinity College Cambridge University* and Prof. Hugh L. MONTGOMERY of the *University of Michigan* for information about, and interpretation of the results of, the *Cambridge Mathematical Tripos* in 1923. They were elicited after the biography was submitted and are used here for the first time.

[1] ALPERN, M. (1988). Walter Stanley Stiles. In: *Biographical Memoirs of Fellows of the Royal Society*, Vol. 34 (1988), pp. 816–885

STILES was educated on the commercial side of a London secondary day school. The onset of the first World War coincided with the beginning of his third school year. With many of the better masters off fighting, the school fell into a nadir in its development. He left school after only five years and went to work in industry as a learner assay chemist having passed the *University of London* matriculation on his 16th birthday. He continued study (chemistry, physics and mathematics) in the evening. In October 1918, aiming to become an industrial chemist he obtained an entrance scholarship and enrolled at *University College, London.* After one year he switched to physics as his main subject. As an External Student of the University of London he was awarded the B.Sc. Physics degree with 2nd Class Honors in 1920. STILES then became a Junior Demonstrator under the famous physicist W. H. (later SIR WILLIAM) BRAGG who shared (with his son, later SIR LAWRENCE) the 1915 *Nobel Prize* in physics for pioneering work on the diffraction of X-rays.

After two years STILES' tenure at *University College* expired. In October 1922 he enrolled as an undergraduate in *St. John's College, Cambridge,* with the intention of taking Part II of the Mathematical Tripos in the spring of 1924. In the event he quit Cambridge after only three terms and in 1923 having completed no research became a lecturer at the *Portsmouth Municipal College.*

Sixty years later it is possible to reconstruct only by speculation the forces molding this decision, which more than almost any other changed the pattern of his life. He tells us only: *"Indifferent health and differences with my father causing me to throw up the course."* Indifferent health was part and parcel of his existence through most of the 62 years that remained in his life after this event but it did not obviate a lifetime of productive creativity and discovery. How much support for his education had come from his father until this moment I do not know. STILES must have contributed a substantial fraction himself at least since the age of 11 when he entered school in a free place. We know that when funds for a second Cambridge year were required his father was unwilling or unable to provide sufficient help. Is this all? Why did he not beg or borrow the necessary sum (it could not have been large) from other sources?

In the spring of 1923 STILES took Part I of the Mathematical Tripos and was among 17 placed in the 2nd class in a list including 51 firsts, 23 thirds and 11 taking an allowance for an ordinary degree. A second in Part I of a Cambridge Tripos is not an unknown event even for a life destined for distinguished scientific achievement. (For example, his future and long time friend and colleague, the physiologist W. A. H. RUSHTON, came up to *Emmanuel College, Cambridge,* the year before STILES and obtained a Part I second in 1924, i.e. the year after, and nonetheless managed a first in Part II after one more year.) But STILES was evidently depressed by

his mediocre performance and on the spur of that moment decided against a future as a professional mathematician.

Whatever the reason, the consequence was color science gained one of its great minds. After a solitary year as an academic, he joined the *Scientific Civil Service.* His research proper began when in March of 1925 he transferred to the *National Physical Laboratory (N. P. L.) Teddington* and was set to deal with problems of glare and visibility mainly those related to driving motor cars at night. Glare is a good distance from color science: the path between was illuminating engineering.

While introducing several fundamental advances in the understanding of glare and visibility, STILES became in fact an illuminating engineer with more than his share of field work outside on cold damp nights. He was the first to draw the distinction between discomfort and disability glare; this was significant because the operations defining the former are vague and difficult to quantify while those defining the latter are sharp, readily (and validly) measured by reliable and quite precise psychophysical techniques. He generalized the validity of the STILES-HOLLADAY equation of disability glare to a large variety of different test objects viewed in different field conditions and obtained in four different laboratories by different investigators in different parts of the world. This led to his invention of glare meters with enormous practical applications in the field; but it was also two giant steps on the path to color science. The first was a small patch of light whose threshold of visibility on a uniform background of variable intensity (including zero) became his major test probe. This had been done by many before but never with the versatility and depth of understanding STILES gleaned from it. The second was the equivalent background and the hypothetical construct which served as its foundation – the equivalence principle, which had important consequences not only for color but other visual phenomena: adaptation, visual acuity and space localization.

A continuing need in glare studies was a way to measure pupil area in the field. To this end STILES invented an ingenious subjective pupillometer. With his colleague B. H. CRAWFORD, he assembled the device but it could not be validated. Instead they proved that this pupillometer did not measure pupil area correctly because the fundamental principle upon which it was based was not applicable to the eye. This led of course to the discovery of the retinal directional sensitivity or the STILES-CRAWFORD Effects, a discovery which a contemporary who was to win a Nobel Prize for work on the vertebrate retina later called the major discovery of visual psychophysics in the previous three decades.

The final step on the road to color came when the question was raised whether advantages might accrue to illuminating highways with monochromatic, rather than white, light. This led STILES to measure increment thresholds of a test of one monochromatic wavelength on a background

of another. These "two color" experiments became a major thrust of STILES' experimental and theoretical work for the remainder of his life as an experimenter. They were important technically in adding a new dimension to the measurement of photoreceptor action spectra at a time when speculation was the only alternative to color matching. I have shown elsewhere[1] that they were also important substantively because the near certainty of modern theory that foveal color vision begins with the absorption of visible light in three species of univariantly signaling cones each with its visual pigment having an unique absorption spectrum is directly traceable to them. The objectivity of the new method was another innovation, one that ruffled the feathers of the contemporary color vision establishment, strongly biased by the prejudgment that the very subjective quality of color vision precluded any objective approach to its understanding.

On the theoretical side this work led to the development of the STILES Line Element perhaps the most complete and comprehensive rigorous statement of component color theory extant. Part of its elegance stems from the distance separating its empirical point of departure from the facts it explains. Although it was remarkably successful as such theories go, STILES always regarded it as incomplete. In his later days he sought ways to deal with some of the difficulties by transcending its componentness. In this he was not completely successful and a full zone line element theory incorporating all the attractive features of STILES original theory with opponent stage additions matching its rigor to deal with all the phenomena left unexplained by the original theory remains as a goal to be achieved by future color science with STILES' theoretical work on the problem as the paradigm.

STILES' legacy includes over one hundred scientific papers, essays and reviews. These papers are worth reading by today's students of color not only for their beauty and clarity of exposition, but for the numerous suggestions of experiments they bring to mind, experiments promising an extra ordinary payoff matrix if pursued with STILES's standards of rigor, detail and precision. The legacy also includes over 61 scientific notebooks which can be profitably studied in more detail than anyone has yet devoted to them. They do not always read so smoothly or polished as the published record, but they are rich in insights into his way of thinking:

> "15. 3. 44
>
> **Separation of brightness and chromaticity threshold**
>
> *What meaning can be attached to a statement that two lights which are only just distinguishable are (a) just perceptibly different in brightness but not in color (b) just perceptibly different in color but not in brightness?*

On my view the question has little interest because the answer to it does not lead to conclusions which could not be obtained directly from the line element. However, on my views a formal definition could be given as follows:

Two lights differ in brightness but not in color if they can be made indistinguishable by altering the energy of one light without altering its relative energy distributions.

Two lights differ in colour but not in brightness if they can be made indistinguishable by varying the relative energy distribution of one in such a way that its brightness was the same as it was originally.

Re the above, I think the real answer is that no precise meaning can be attached to the statements indicated.

At the Stockholm meeting of the C.I.E. in 1951 STILES was persuaded to remeasure the normal 2° foveal color matching functions obviating questionable assumptions about luminosity (used in establishing the color matching functions of the 1931 C.I.E. Standard Observer) by radiometric determinations of energies, on 10 normal subjects and a similar set of color matching functions for a large field on 49 normals. This latter set were duly incorporated in the C.I.E. 1964 Supplementary Standard Observer. These measurements required instrumentation more massive and complex than anything known in vision research before or since (excepting only its two clones the first built in Ottawa under STILES' watchful eye, the other, in Tokyo). 30 years ago GERALD WESTHEIMER called it the "cyclotron of vision research" when we visited the N.P.L. and I met STILES for the first time. My first impression of this elegant instrument was so memorable, that 25 years later I devoted a sabbatical year to experiments on its Canadian off-spring.

But it was the man himself who stands out in my recollection of the event. I knew something of his early papers on glare and on retinal directional sensitivity but I had yet to come to grips with the power of his *opus magnum* on two color thresholds. He had been elected to *Fellowship* in the *Royal Society* the year before and had, by this time, some of the aura of distinction I always associate with him. Quiet, modest, tranquil he was particularly diffident about the bit of work in which he was then involved and much more interested in what I had been doing than objective analysis of the relative merits of the two cases could justify. That realization struck home only many years later on reading and coming to understand the significance of the paper he published on the subject of his demonstration that day more than three years after this visit. There was not then or in all my conversations or correspondence with him (in which I sometimes spoke of, or wrote him ideas not carefully thought through) ever

even a hint (such as his friend WILLIAM RUSHTON could on occasion provide) that I was talking when I should have been listening. He was of course critical where criticism was justified, but criticisms were always modestly put, kindly suggested, invariably enormously rewarding.

One is inclined to put all this down to an especially kind and gentle nature in an extremely shy and modest English gentle man. But in preparing his biography I discovered a different side seen from the perspective of his more junior colleagues at N.P.L. which makes me suspicious that he may have also had a soft spot in his heart for Americans. For his N.P.L. juniors he was a remote and austere man whose friendship was difficult to cultivate. One dominant characteristic in their view is strength: strong personality, strong will and strong opinions. He was extremely able in discussions which made him aloof, formidable, even a little frightening to younger colleagues especially if differences in opinion were likely to arise between them. They saw him as a powerful intellect well aware of his capacities who left the impression of not gladly suffering fools.

Little of this comes through in the self doubts and uncertainties, the very human worries about the development of intellectual growth and career found in his notebook. He was a charming man fondly remembered by former assistants for his many personal kindnesses including encouraging them to take up further studies (in the case of now Dr. KENNETH SPRING, for example, first for a B. Sc. and later, as one of STILES' old colleges, an M. Sc.). But others besides colleagues at the N.P.L., could also meet the strong personality intolerant of fools: for example, the physicist DE VRIES who published results of "quick and dirty" two color-experiments done in isolated Holland during World War II with no references to STILES' prior (and more thorough) study of the phenomena. Moreover DE VRIES remained guilty of (the even greater sin of) not grasping the fundamental importance of the background in setting the adaptive state in these experiments long after reading of STILES' paper should have made it obvious.

STILES never developed a "school" as he might have done in a suitable academic chair. The subjects in which he achieved distinction were too small and unimportant to justify it when he took them up (they were, as he would write in his notebook, ". . . in a backwater state"). By the time, due in no small part to the elegance and fundamental quality of his own research, this was no longer so, he was ironically, too old. Still his years at N.P.L. brought him the collaboration of younger British scientists: Dr. B. H. CRAWFORD, Mr. C. DUNBAR, Mr., now Dr., K. H. SPRING and Dr. J. M. BURCH. After the war others made the pilgrimage to Teddington from all over the world as research fellows: Mlle, now Dr., F. FLAMANT from the *Institute d'Optique, Paris,* Senor J. CABELLO and Dr., now Prof. (of Physics at Valencia), M. AGUILAR from *El Institute de Optica 'daza de Valdes' Madrid,* Dr. S. R. DAS of the *National Physical Laboratory of India,*

Delhi, Dr., now Dean (of the School of Optometry, *University of California Berkeley)* J. M. ENOCH from the *Ohio State University, Columbus,* Dr., now Prof. (of Psychology, University of California San Diego) R. M BOYNTON and Mr., now Dr. and Prof. (of Information Processing, *Tokyo Technological Institute, Yokohama, Japan)* M. IKEDA from the *University of Rochester* and Dr. G. WYSZECKI from the *Division of Physics of the National Research Council, Ottawa, Canada.*

It is fair to state that he shaped for the better the work of all of these in various ways, some to a much greater extent than others. A wider circle includes those attracted by the elegance and fundamental nature of his science (carefully spelled out in rigorously reasoned papers) who strive to emulate his example. Through these, and through their students, STILES' influence will continue to enrich the understanding of human vision long after the issues his papers resolve are contemporary.

From the perspective of STILES' intellectual growth after retirement in June 1961, by far the most important of these "students" was GÜNTER WYSZECKI. Where in 1955 they first met I do not know, but early in 1958 WYSZECKI measured his color matching functions on STILES' Trichromator. In September STILES initiated the first of several extended (around nine-month) intervals as a visiting scientist in Ottawa which proved especially productive. From the first of these for example, emerged STILES' initial attempts to test the independence of his π mechanisms by test additivity and the beginning of the Canadian Trichromator. WYSZECKI was back in Teddington making more color matches in July of 1959 and from then on the collaboration flourished. There were several fundamental joint studies on the Ottawa Trichromator after it was completed in 1963, including the study of the break down of metameric matches at high radiance and a comparison of color matches of the same light by the maximum and minimum saturation techniques. This last is not itemized in STILES's bibliography appearing only in the 2nd edition of *Color Science,* along with more details on theory of the minimum-saturation technique than is customary in a journal article. *Color Science* is the book he and WYSZECKI began writing together in 1964. It quickly became the bible of the subject when the first edition appeared in 1967. This book is arguable the most enduring consequence of their collaboration.

STILES' and WYSZECKI's mathematical backgrounds were sufficiently compatible that STILES found in the younger man a suitable sounding board for the full depth and range of his ideas which may have been unique among his collaborators. WYSZECKI on the other hand was fully aware of the great opportunity it was to have such a gifted colleague and the two began a warm personal friendship lasting until WYSZECKI's untimely death.

When STILES took up the study of vision, rhodopsin was the only known candidate for the role of a visual pigment and the idea that the ini-

tial step in the process of visual excitation was photochemical was novel. A half century of futile search for cone visual pigments led to rather wild explanations for the receptor basis of color (e.g.: that brightness and color are coded separately at the very first stage of the visual process, or alternatively that all cone pigments are rhodopsin with their λ_{max} very nearly superimposed, all shifted 55 nm to a longer wavelength from its position in rods because of KUNDT's rule) which misled the mainstream of the subject. If we now know it to be otherwise, can be attributed to anyone man: it is W. S. STILES. He did this by the strength of his experimental results and the penetrating cogency and rigor of his theory. Several of his contemporaries managed to do almost his equal in one category or the other, but he stands alone when measured in achievements in both. He remained true to form even in his final paper. When in it he compared the flourishing state of our subject now to its state when he took it up, one searches in vain for the slightest hint as to how important his own seminal contributions were for the transformation from the one state to the other. *He was the greatest color scientist of the century.*

Author's address:
Prof. M. Alpern
W. K. Kellog Eye Center
University of Michigan
1000 Wall Street
Ann Arbor, Michigan, 48105, USA

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Bibliography of W. S. Stiles

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Wolfgang Budde, GLOUCESTER, Ont.:

Günter Wolfgang Wyszecki

(1925–1985)

Memorial Lecture

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GÜNTER WYSZECKI
* 8. 11. 1925
† 22. 6. 1985

Ladies and Gentlemen,

When PETER KAISER asked me to give this memorial lecture on GÜNTER WYSZECKI, I felt much honoured and gladly accepted this offer. PETER then said that this should preferably describe the person, the man and friend GÜNTER WYSZECKI, rather than the scientist and I agreed with him although this presented a much more difficult task. It was much easier for me to write the various obituaries for the *CIE Newsletter,* for the *NRC* house journal, for the official announcement and for the *Royal Society of Canada,* than to find the proper words to honour the person, the man and the friend. Consequently I decided to base this memorial not only on my own recollection but also on those of some of the colleagues and friends, which he had and I am indeed very grateful for the help, which I received. Quite a number of people have contributed to this memorial lecture but my special thanks go to JIM BARTLESON and PETER KAISER for their efforts. All these contributions are a testimony for the friendship and the admiration for the man, whom we honour in this symposium. My sincere hope is that I will succeed in doing him justice and I beg your – and his – forgiveness if I fail.

Most of you will probably know the relevant facts of Dr. WYSZECKI's career and the contents of his work. But let me briefly recapitulate some of the essentials and also some of the trivia which characterize him.

GÜNTER WYSZECKI was born in 1925 in – as he said – "a little town, where they make cheese", Tilsit in Germany, after which the Tilsiter cheese is named. In 1943, at the age of 18 he joined the destroyer and submarine school, because he had ideas of a career as officer, probably resu-

ming a tratition of the "VON WYSZECKI's" several generations earlier. But he found out – the hard way – that the was prone to motion sickness and this fact and the end of the war ended his career as an officer – for the benefit of color science. Instead of an officer of noble ancestry, he became, as several Japanese scientists wrote in their obituaries, a "Prince in the science of color".

At the end of the war his submarine was deliberately beached in the North of Germany and the compassionate captain ordered GÜNTER to form a work detail to "escort those horses in that field to Berlin". GÜNTER was thus saved the unpleasant terminal throes of battle and he could make his way back home, where he entered the *Technical University of Berlin,* to study mathematics and physics and to pile up rubble in the ruins of the destroyed city in the mandatory clean-up that was part of the tuition for all students.

When he was at the *Technical University* he acquired a motorcycle, which he used to commute between home and university. Occasionally he would offer a ride to some of his compatriots and managed to frighten them with his manoevering through the debris-strewn streets of Berlin. He also once invited Prof. RICHTER to such a ride but Prof. RICHTER never ever accepted such an offer again.

Later in his life – as JIM BARTLESON writes – it was one of GÜNTER's secret ambitions to own a "racy Corvette sports car". He also liked to hunt sharks in the ocean off the Florida coast. There must have been a suppressed adventurer lurking somewhere beneath the surface of calm dignity with which he confronted the world.

In 1953 he received his PhD-degree. For his thesis work he had chosen a subject in colour vision and one of his advisors was Prof. MANFRED RICHTER. Therefore GÜNTER often came to RICHTER's institute at the *Bundesanstalt für Materialprüfung,* and this was where I met him first.

Shortly after his graduation he was awarded a FULBRIGHT scholarship and he went for one year to DEANE B. JUDD at the *National Bureau of Standards* at Washington.

When GÜNTER has been in high school, his teacher told him that he had no facility for the English language and should not bother to learn it, because he never would. So, when he travelled to the United States in 1953 he went there with almost no knowledge of English. When he arrived at the Bureau, JUDD arranged a room for him in a boarding house and GÜNTER was on his own in a sea of foreign words. And I know this feeling, because when he had lured me to Canada in 1958 and I had arrived at Ottawa he had arranged a room for me in a boarding house and there I was in a sea of foreign words. During the first days GÜNTER went to a cafe to eat the only thing that he could order "Hamburger". That meal was repeated regularly for days and days until he felt that he had progressed well enough to order something else. He looked the waitress straight in

the eye and said: "Steak." She responded with a burst of for GÜNTER unintelligible words, probably asking him how he would have it done. But for him it was all confusing gibberish. So he looked at her sadly and said "Hamburger". So began the English career of the trilingual author of some of the best written textbooks in the English language. His first paper in the English language was published in 1954, just one year after he came to the USA.

In 1954 he had married Ingeborg RATHJENS. And – to jump a bit ahead in time – they had two children. But GÜNTER seemed to have a talent for avoiding the hassles of his wife giving birth: when his son was born in Berlin, GÜNTER attended a conference in the USA and when his daughter was born in Ottawa he was on a visiting tour in Europe. Nevertheless he was indeed a devoted father and I had often the opportunity to observe how he played with his children.

During his year at the NBS he met Dr. MIDDLETON of the *National Research Council of Canada,* who invited him to come to NRC. However, GÜNTER came back to Berlin and to Prof. RICHTER's institute. During these months we discussed a certain problem concerning integrating spheres and soon we had planned some experiments and a short while later we had a joint paper published. I also remember that we both were interested in the physical aspects of gloss and we had long discussions on this subject. But because Prof. RICHTER considered this a waste of time, we often sneaked out, armed with a pad of paper, to a Cafe across the street and there we spent hours of discussions over a cup of coffee.

GÜNTER tried to pay a three-months visit to the *Institute d'Optique* in France but an employment offer from the *NRC* cut this short. In justifying GÜNTER's employment at *NRC,* Dr. MIDDLETON had written: "I believe that we would be missing a great opportunity if we failed to obtain the services of Dr. WYSZECKI." GÜNTER joined *NRC* in 1955 and his impact became obvious when DAVID MACADAM wrote in 1959 that "Dr. WYSZECKI's Section is taking over world leadership in colour research".

At *NRC* GÜNTER quickly rose through the ranks, became Section head in 1965, Assistant Director of the *Physics Division* in 1982 and was nominated as Director of the planned *Institute for Optics* when his career was abruptly ended by his death. He was also an Adjunct Professor at the *School of Optometry of the University of Waterloo.*

His honours were many and his activities in scientific societies are too many to list them here. Let me just mention that the AIC honoured him with the *Judd Gold Medal,* that he was elected a *Fellow of the Royal Society of Canada* and that he was *President of the CIE* when, half way through his term, various diseases in quick succession wasted his body, which had been weakened by his seven year long struggle with leukemia.

As a scientist he was brilliant, clear thinking and and very efficient and his scientific work bears witness to that. You know his work and I will not prevail on this aspect.

As an administrator he was well organized and – a rare instance in modern bureaucracy – he was always able to reduce the administrative tasks to the unavoidable minimum, that is, he could home in on the essentials and dismiss unnecessary details. His preferred method was to bypass paperwork and solve the problems in personal discussions. In these discussions one could find out, that he was not only a good administrator but indeed a leader, who could keep a discussion well on the subject and would not permit detours to unrelated details. And if somebody strayed, GÜNTER was often able to cut him short with a joke. For example in one tedious session on a long and hefty document one committee member proudly announced that he had found a misprint on page 43. GÜNTER said: "Thank you. We put it there to see whether you had really read the document."

But besides being a scientist and an administrator he was also a teacher. And here he really was showing his human qualities. Dr. PRESTON-THOMAS, Associate Director of the *Division of Physics* expressed this adequately, when he said: *„He was what many years ago would have been described as a cultured gentleman, with the full and proper meaning given to each of the two words. As a result his contributions to discussions on almost any subject were always worth listening to. As were his lectures, which typically started out in a deceptively elementary fashion, almost inducing boredom in one with prior knowledge of the subject, and then rapidly and smoothly progressing to the heart of the matter he was dealing with. These lectures were laced with humour, as were his personal contacts."*

Yes, as a teacher he was indeed showing his best abilities: his patience, his devotion to the subject, his clear and orderly thinking and his ability always to come to the crux of the matter, to find the essential point and to paraphrase it clearly and describe it with the right and most adequate words. And also in his teaching he showed his great sense of humour, which he wisely used to smooth out difficulties and misunderstandings. This mixture of humour and patience is what I remember so clearly, particularly during my first years at *NRC*, when I started to write papers in English. He not only improved my English but also taught me how to write a paper in good order.

His abilities as teacher are well recognized in an issue of the Japanese JCIE Journal, where six scientists from Japan describe their experiences with Günter WYSZECKI. All had been postdoctorate fellows for one or two years at *NRC* and they finally considered themselves as "Dr. WYSZECKI's Japanese School". I think that Dr. WYSZECKI had somewhere in his heart a special affinity for the Japanese scientists. He admired their devotion to

work and their efficiency and eagerness to work hard and learn as much as possible. And I think they returned this feeling. Dr. Leo MORI wrote: *"The Japanese National Committee of the CIE and the Colour Science Association have lost the greatest advisor who taught us extensively from an international point of view"* and then he continues *"now we heartily miss the understanding advisor who has taught us with the warmest heart, and sometimes with a bit of a sharp joke. He seemed sometimes to be challenging me with his particular wit, but I could feel everytime his thoughtfullness and encouragement."* And similar words were written by the other students of Dr. WYSZECKI's Japanese School. Dr. OHTA wrote: *"I always remember his ingenious criticism and warm kidding during our discussions. He was a great kidder indeed"* and Dr. YAGUCHI, the most recent postdoctorate fellow at *NRC*, summarizes GÜNTER's efficiency as teacher nearly a generation after the first disciples had been taught in this Japanese school, writing: *"These graduates from the* "WYSZECKI *School" have now become leaders of colour science in Japan."* Small wonder that he was made an Honorary Member of the *Color Science Association of Japan*, an honor which is very rarely given to Japanese scientists and never to others.

GÜNTER was not a man who made friends easily and occasionally people would characterize him as either withdrawn or even snobbish. He kept his personal life to a large extent separate from his professional life and it is very significant that for the past seven years nobody but his family knew of his illness. Also not many people knew of his personal interests or hobbies and how he pursued them. It appears that he approached them with the same intensity as his professional work. For example in 1949 he took to table tennis and won a first price in a tournament. Then about at the same time he had taken courses in ballroom dancing and of course did so well that he won various prices in the annual closing events. He also at some time took up painting and I still remember one of his paintings, hanging on the wall of their apartement at Ottawa, a simple group of dark human figures on a red background, a picture having a surprising stark intensity. But it is interesting to note that would pick up such an acticity and, once he had mastered it to his satisfaction and to perfection, he would drop it and rarely speak about it again.

As JIM BARTLESON told me: *"The only thing in which he ever failed was his attempt to teach his beloved 'Argus', a Doberman pincher and Canadian Champion, to breed. The poor thing just never did catch on to what was expected of him."*

His last great hobby was the work at the rather run down farmhouse which he had bought. He and his wife renovated it with great skill, much love and with excellent taste and perfect feeling for style. We often discussed the best method for doing-it-yourself, because I had some prior experience in this.

It appear to me that GÜNTER made friends with people whom he either admired for their professional abilities and their attitude towards their work or with people who could match his sense of humour. He could not stand fools, or people who took themselves too seriously or people who preferred representation or form over contents or results. And here his humour could occasionlly turn quite abrasive.

But he always admired a person who was prepared to work hard and to give his best. Of course, he not only admired such people, he himself worked hard and set examples this way. Dr. R. BOYNTON wrote: *"He was fiercely dedicated to his work, a quality which, I imagine, may have sprung in equal proportions from aspects of his early background in Germany and his association with Deane Judd, a man of similar disposition where putting the nose to the grindstone was concerned."* And he continues: *"Perhaps most remarkable about Günter was that he exhibited such friendly, human and helpful qualities. Considering all that he had accomplished, together with the honors so justly heaped upon him, he might have become pompous, arrogant and rigidly opinionated. So far I could tell, he exhibited none of these qualities; instead he seemed to wear the badge of modesty, and was genuinely open to opinions from all sources, though not with any inappropriate diffidence. It was these qualities, I believe, along with his undoubtedly technical competence and burning intelligence, that enabled him to work so well with diverse groups and to accomplish so much in his regrettably truncated lifetime."* The modesty, which Dr. BOYNTON alluded to, expressed itself in the fact that GÜNTER rarely mentiond any of the honors or awards or promotions, which he had received and sometimes even his closest colleagues did not know about them.

PETER KAISER told me about GÜNTER's habit the following story: *"One day, during a visit to Günter's office, a secretary came in for some survey and her final question to Günter was: 'If you write a manuscript for a paper, how many drafts do you usually write, before you send it out?'. Günter thought and looked up and said: 'One'. She wrote it down on a piece of paper, said 'Thank you' and walked out. After she had left, I said: 'Günter, you must be pulling her leg'. He said: 'No. What I generally do, is that I sit back and think about what I want to say. When I have it very very clear in my mind, I write it down. And when I write it down I generally have it the way I want it, Peter'."* I think occasionally GÜNTER was also fibbing a little. Technically he was correct when he said that he wrote only one draft. But writing this involved the use of pencil and eraser in sometimes equal proportions. Although he undoubtedly had the general layout in his mind right from the beginning as the result of this sitting back, the details of the wording were sometines a long battle and at the end his desktop was covered with little black worms, coming from the use of the eraser. Many phrases would go through several drafts right at his

desk. But he would never let go out a draft, which he would not consider right and perfect.

GÜNTER's own sense of humour was quick and witty. Peter KAISER tells that during a visit he found GÜNTER working on the second edition of "Color Science". Peter said that the first edition often had been called the Bible of Colorimetry, what then would the second edition be called? And, as Peter tells: *"Without the bat of an eyelash he looked at me and said 'The New Testament'."*

There are many testimonies to good friendships with GÜNTER and I would like to be able to quote all of them. But instead let me just give an example in what Jim BARTLESON wrote:

"Among the fondest memories of many CIE and AIC meetings are the times when Günter and I 'played hooky'. After a week or more of strenuous meetings we would plan a little private excursion and slip away unbeknownst to anyone else. We saw many interesting places that way - churches in Bulgaria, the 1929 Exhibition grounds in Barcelona, museums and cheese factories in Holland, old familiar places in Berlin, back streets of London, the old town of Stockholm, a walk in the woods of Kyoto, rive gauche in Paris and so on - Günter loaded up with Aspirin for his pressure induced headaches and I with a load of film and a camera. A cardinal rule was not to refer to the work that we were doing. We dealt with only two subjects: trivia and philosophy. Oh, if only the world could benefit from the wonderful solutions to its problems, that were so meticulously constructed in those rambling discussions. We always ended up being refreshed and ready to surface again for more tedious work."

Let me close this memorial lecture with the slightly paraphrased words of Madame KARTACHEVSKAJA, who wrote: *"I had the pleasure to know Dr. Wyszecki for rather a long time in connection with the CCPR and the CIE activities. All the time I have been admiring very much his talent as a scientist, experimentalist and organizer and I shall always keep the warm memory of him as a man of great personal charm and of high human qualities" and, with an apology for her attempt to translate beautifull verse into prose, she concluded her letter:*

„One of our poets of the 19th Century said:

Do not say with anguish 'He is no more' about a companion, who was brightening all the world with his presence, but do say 'He has been with us' and say it with gratitude."

Author's address:
Wolfgang Budde
9 Kindle Court
Gloucester, Ont. K1J 6E1
Canada

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Peter K. Kaiser*, NORTH YORK, Ont.:

Opening Remarks

DK 061.3.053.5

The program organizer briefly reports on the genesis of the Symposium, and he gives some instructions for its performance.

Der Organisator berichtet kurz über das Zustandekommen des Symposiums und gibt Hinweise zu dessen Durchführung.

L'organisateur informe, en peu de mots, de la réalisation du symposium, et il donne quelques indications au sujet de son exécution.

Welcome to the Scientific part of the *Wyszecki and Stiles Memorial Symposium on Color Vision Models.* We gather on this occasion for two reasons. The first is to honor the memories of Dr. W. S. STILES and Dr. G. WYSZECKI.

The second reason is to infuse some vitality into the field of color vision modeling. Color vision modeling has not been very active during the last several years. For the CIE this is a rather unfortunate state of affairs. CIE Technical Committee 1-03 has the responsibility of finding a color vision model that could be used to transform luminance measures to brightness related measures. A transformation via a color vision model was desired because although the luminance of a source is reasonably independent of viewing conditions the brightness of a source varies critically on the viewing conditions and observer characteristics. Consequently, an empirical equation, as has recently been proposed as an interim measure is of limited usefulness due to the restricted conditions under which it is applicable. Converting from luminance to brightness via a color vision model should have the advantage of taking the observer and the observer's interaction with the viewing conditions into account.

In 1981 TC 1-03 was of the firm opinion that an acceptable color vision model would not be available in the foreseeable future. That opinion was reiterated in 1984. The CIE felt that before it temporarily gave up on the idea of producing such a conversion via a color vision model some action should be taken to stimulate movement towards advancing the state of the art of color vision models. Hence the idea of this symposium was born.

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* Chairman of the *CIE Technical Commitee 1-03: Models of Heterochromatic Brightness Matching,* Division 1: *Color and Vision.*

When I agreed to organize, with the help of TC 1-03 and together with the AIC, the technical program of this symposium both Dr. STILES and Dr. WYSZECKI were still alive. GÜNTER WYSZECKI was the president of the CIE and an active member of TC 1-03. He was very interested in the development of color vision models and a strong supporter of our committee. If you compare the 2nd edition of WYSZECKI and STILES' *Color Science,* to the first, you will note the addition of a chapter entitled *"Theories and Models of Color Vision"*. When GÜNTER died, we decided to call the symposium the *Wyszecki Memorial Symposium on Color Vision Models.* We approached Dr. STILES and he agreed to come to Florence to present a memoir in honor of GÜNTER WYSZECKI. Unfortunately in the interim, color science lost Dr. STILES as well. We decided that it would be fitting to change the name of the symposium its hence the current name of the symposium.

As you look through the program you will note that this meeting is organized in a way that is rather novel. First of all, there are no individual titles associated with the speakers' presentations. TC 1-03 decided to organize the program around a set of specific questions important to color vision models. The speakers were then asked to choose a question and prepare a presentation in response to it. We were absolutely amazed at the very high and enthusiastic initial responses we got from these speakers. Almost twice as many than we anticipated accepted our invitation. This presented a scheduling problem. We were not prepared to have a meeting where discussion time would be severely restricted, so some plan had to be devised.

This brings us to the second novel feature of this symposium, the minidebates. This idea comes from OSCAR ESTÉVEZ. In our minidebates each participant will have 10 minutes to make a position statement. Then the participants will discuss the issue among themselves after which the discussion is opened up to everyone. During the last several weeks, a number of people pulled out of this meeting, making it necessary to cancel some debates and ask people to present conventional type papers.

A third feature is that there are two extended formal presentations; the first and last papers. In a few moments JOHN MOLLON will tell us his view of the current state of the art of color vision models. The last paper by OSCAR ESTÉVEZ will be the state of the art of color vision models now that the symposium has neared the end. Hopefully, all participants told OSCAR in advance about the substance of their material so he could make a good start on his presentation. He has a very difficult job during these next two and a half days. He will be trying to assimilate all that transpires in an effort to properly relate what we have learned. Any assistance that formal and informal participants can give him, I am sure will be most appreciated.

The fourth feature is that at the end of almost every session there is general discussion. We hope that the limited discussion time at the end of each person's presentation will be used for clarification purposes. The general discussion can be used for any purpose relevant to the question under discussion. Tomorrow, afternoon, 30 minutes has been set aside for general discussion on any relevant topic. By this time it may be that some issues may start to crystallize and participants will want to have the time to raise their points of view. I have asked OSCAR to chair this session. It will give him the opportunity to steer the discussion in a way useful for preparing his state of the art presentation. And then there is a final concluding general discussion on Saturday after OSCAR has given his paper. The idea is that at the conclusion of OSCAR's presentation, he would be presented with questions of clarification. However, many of you may have ideas quite different than his. There may be specific points of disagreement or you may feel that some issues have not been adequately represented. The concluding general discussion provides the last formal opportunity for people to express their views. Some of you may know the OSCAR is presenting a work shop next week in Venice an the CIE meetings on the results of this symposium. So even this final general discussion period can be quite valuable to him when it comes to representing what has transpired here.

Now a word about timing. You have a program with the times specifically laid out. I would ask the chairpeople to keep an eye to the clock so that those who have not yet spoken will not have their time infringed upon. However, we have no parallel sessions. This is it. So if we get ahead of schedule in some parts that means the time can be used flexibly. I would ask that the chairpeople use their discretion as conditions dictate.

Finally, I would like to thank Dr. TERSTIEGE and the members of the *Istituto Nazionale di Ottica*, especially Dr. RONCHI, for providing the facilities and arrangement which we have already started to enjoy. A special thank you to the invited speakers all of whom have come with no travel or accommodation support from the organizing committee.

Author's address:
Dr. P. K. Kaiser
York University, Dept. of Psychology
4700 Keele Street
North York, Ontario M3J 1P3, Canada

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John D. Mollon*, CAMBRIDGE (U.K.):

On the Nature of Models of Colour Vision

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Current models of color vision are seldom analogues, but rather are schemata, whose components correspond to terms in a mathematical formula or algorithm. All models ought to be expressible as formulae or algorithms; but not all formulae are models. This paper summarizes some changes that may be required in existing models, and suggests a new way of interpreting the settings that a subject makes in flicker photometry and similar tasks.

Was ist ein Modell menschlichen Farbensehens? Gegenwärtig bestehende Modelle können nur sehr selten als Analogien betrachtet werden. Sie sind vielmehr vereinfachte Schemata, deren Bestandteile Begriffen mathematischer Formeln oder Algorithmen entsprechen. Alle Modelle sollten als Formeln oder Algorithmen darstellbar sein; allerdings kann nicht jede Formel als Modell angesehen werden. Dieser Aufsatz enthält eine Zusammenfassung von Modifikationen, die für bestehende Modelle von Bedeutung sein können; des weiteren wird eine neue Interpretation flimmerphotometrischer Versuchseinstellungen und ähnlicher Aufgaben vorgeschlagen.

Qu'est-ce qu' un modèle de la vision des couleurs? Actuellement les modèles typiques ne sont pas des analogues; elles sont des schèmes simplifiées dont les éléments correspondent aux termes d'une équation ou algorithme. Il faut que tout modèle soit exprimable comme formule mathématique; mais tout formule n'est pas un modèle. Dans cet article, on résume les modifications qu'il faut apporter aux modèles actuels; et on propose une nouvelle interprétation des mesures photométriques obtenues par la méthode de papillotement.

1. The nature of a satisfactory model

1.1: Models as analogues

The word "model" is one of the most promiscuously abused words in modern science, and often it is used as no more than a synonym for "theory". Properly, a model is an analogue, an analogical system, that allows us to understand an unfamiliar or little-understood system in terms of a familiar and well-understood system. The paradigmatic example is the wave model of light, where a known mechanical system provided a set of predictions about the behaviour of a less understood system, some of which were confirmed and some not.

* *Department of Experimental Psychology, University of Cambridge (UK)*

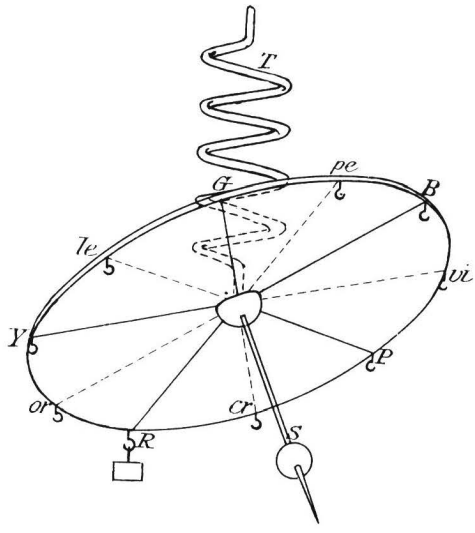

Fig. 1: E. HUNT's model of colour vision

E. HUNT's model of colour vision [15], shown in Fig. 1, represents one of the last truly mechanical models to be offered in our field. The model consists of a disk, which is mounted at its centre on a universal joint, is suspended from a spring balance, and represents a classical colour circle. Hooks are provided at various points on the under side of the disk and weights can be hung on the hooks to represent the quantities of lights of particular chromaticities. The resultant of any combination of colours can be obtained, HUNT explains, by hooking suitable weights at the appropriate points and noting the position of the spindle S on a fixed index below. The total luminosity of the light is represented by the stretching of the spring balance.

HUNT's model serves us as an example of a true analogical model. But it also serves to show how a mechanical analogy can constrain the modeller's thoughts. HUNT has no imaginary hooks lying outside his disc on which he could hang imaginary weights that represented pure excitation of individual fundamentals. So his model constrained him, as its antecedent probably constrained Newton, from adopting a trichromatic theory of vision.

1.2: Models as schemata. Requirements for a model

But if, in colour science, the term "model" seldom now denotes a mechanical analogy, we nevertheless do have some shared understan-

ding of what we mean by the word. We seem commonly to mean a schema, a description of the neural substrate itself (rather than of an analogical system) but one stripped down to those essentials that are relevant to the behaviour being simulated.

Between the optical stimulus and the generation of the signals that control our behavioural responses, there intervene, we believe, a number of stages or sub-mechanisms or computational levels. By each sub-mechanism, or at each computational level, the input signals may be transformed. The relationship between particular sub-mechanisms may be a parallel or a serial one; and there may be recursive loops within the system. A model then is a schema of the sub-mechanisms and their relationships.

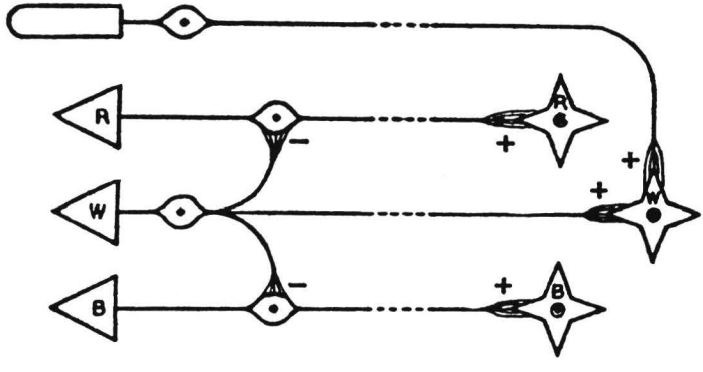

Fig. 2: ADAMS' model of colour vision

Fig. 2 shows the primordial ancestor of many modern models, that drawn so presciently by ADAMS in 1923 [1]. It looks strikingly familiar to us. There are three cone receptors plus rods, represented by the triangles and cylinder respectively. Two types of second-order cell gain chromatic specificity by drawing signals of opposite sign from different types of cone, while a third type of post-receptoral cell is non-opponent in its response. And we should not be too much troubled today by the 'w' where some might feel an impulse to put 'g'.

ADAMS' model provides some, but not all, of the features that we might expect in a complete neural model of colour vision. The following is a minimum list of the requirements that we might nowadays make explicit:

(i) *Specification of a set of receptors and other neural components.*

(iii) *Specification of the spectral sensitivities of the receptors and of the other transfer functions that relate the inputs of given components to their outputs.*
(iv) *Specification of how the transfer functions vary with adaptation.*
(v) *Specification of how particular human judgements or aspects of behaviour depend on particular output signals.*

Customarily, in colour science, the modeller gives us a graphical representation of the schema, but strictly this graphical representation should serve only to communicate the schema to others and to facilitate the mental manipulation of the model by those scientists who prefer a spatial mode of thought. It ought in principle to be fully replaceable by a set of definitions of the neural components and their connections, and a list of their transfer functions. It is nice to have the picture, but a picture could mislead us if it were implicitly to embody some feature that is not explicit in the formal statement or if it were to lead us to believe that there is an intrinsic connection between the computational algorithms and the neural substrate that carries them out. A picture is surely not one of the formal requirements for a model. Thus, we should probably describe as a model the formal account of π mechanisms that W. S. STILES gives in section 7.4 of the second edition of 'Color Science' [44]; but STILES always eschewed the vulgarity of a picture.

1.3: The relationships between models, formulae, and line-elements

What reason might we have for preferring a model to a formula that summarizes a given database? If we wish to predict the apparent brightness of a stimulus of known luminance, why in the long term should we prefer to have a model rather than the WARE-COWAN formula [19]? If we wish to predict whether two samples of cloth will be detectably different in colour, why might we prefer a model of colour vision to a colour-difference formula?

The advantage of the model is usually taken to lie in its greater universality. If we rely only on a summarizing formula, then sooner or later we shall want to extend its use beyond the domain in which it was constructed: either we shall want to deal with stimulus conditions that were not included in the original database or we shall want to predict a different aspect of human performance. In either case, we might suppose our predictions to be the more secure if they are based on a realistic model of the visual system rather than upon a formula that merely provides a succinct summary of the initial data set. This is not to say our model should incorporate implicit, unstated, knowledge of the visual system (the assumptions should all be laid out naked for us to see); but it may well be that the

model incorporates assumptions that are supported by evidence from a domain which the model is not itself intended to address.

However, the distinction between a model and a formula is not an absolute one. The implication of section 1.2 is that a properly formed model must itself be expressible, if not as single formula, at least as a complex algorithm. And indeed, line-elements, which are perhaps conventionally thought of as formulae, have most of the properties of models. A line-element [41] is intended to do the same job as a colour-difference formula, that is, predict whether two stimuli will be perceptibly different in colour or luminosity. But in the case of the line-element the terms of the equation are explicitly intended to correspond to sub-mechanisms within the visual system. In his interchange with MACADAM and WYSZECKI, recorded for us by the editors of the Soesterberg symposium, STILES described the line-element as 'an expression with structure whose terms can be associated with different mechanisms'. Fig. 3 reproduces an old hand-drawn lantern slide used by STILES to illustrate the 1961 line-element of FRIELE [10; 41]. This line-element was inspired by zone theories of colour vision; and the 'R–G' and 'Y–B' terms, which STILES shows separately, correspond to the two colour-differencing channels of such a model. Notice how the sensitivity of the 'R–G' channel is made to depend on β, which represents the state of chromatic adaptation. The FRIELE line-element goes a long way towards satisfying each of the five requirements listed above in 1.2; and thus it differs little from many current models. One could decline to call a line-element a model on the grounds that the line-element was too limited in its ambition, being intended only to predict chromatic thresholds; but in that case we ought not to speak, for example, of 'Models of heterochromatic brightness matching' (the title of the CIE Committee that organised the present symposium). One is led to a sneaking suspicion that it is the absence of a picture that commonly excludes line-elements from discussions of colour vision models.

Conversely, it must be said that there are 'models' in the colour literature that are little more than formulae that summarize a certain database. Models of this class may *appear* to make reference to sub-mechanisms or signals within the visual system; but in fact the postulated sub-mechanisms or signals are not closely tied to reality. It is models of this sort that WYSZECKI and STILES call "floating models" [44, pp. 284–286]. The modeller starts out with a mathematical formula that he or she thinks may summarize a certain data set. In order to improve the fit of the "model" to the data, or to accommodate new data, the modeller then arbitrarily introduces new, complicating, terms into the equation; and tries to persuade us that these terms represent processes within the real visual system – processes for which there is no independent evidence. 'Mathematical models' of this type should be recognized for what they are: summarizing formulae.

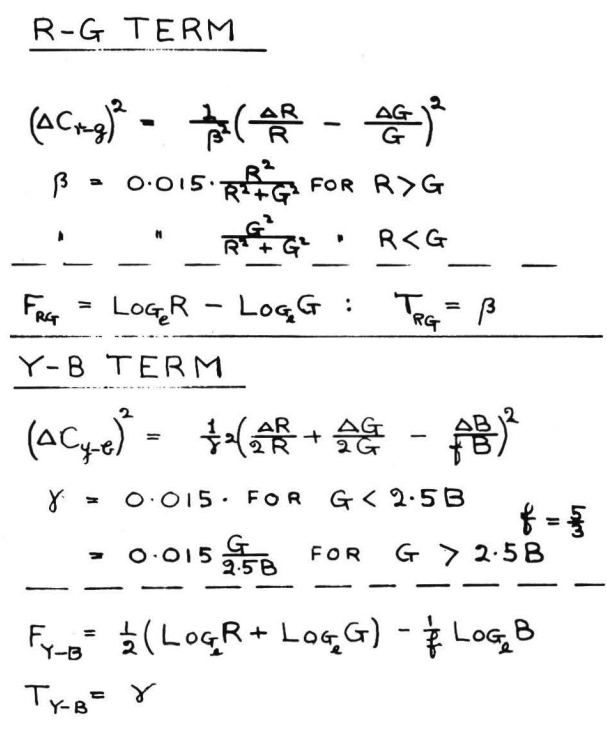

Fig. 3: FRIELE's line-element 1961, as summarized in a slide prepared by W. S. STILES

The present distinction between models and summarizing formulae, and the distinction that STILES [41] made between line-elements and colour-difference formulae, are closely related to a classical distinction in experimental psychology – the distinction made by MACCORQUODALE and MEEHL between *intervening variables* and *hypothetical constructs* [28; 7]. The terms of a summarizing formula are intervening variables: the truth of the original empirical observations is sufficient and necessary for the truth of any statement about the intervening variables, and the latter can be derived simply by suitable grouping of terms in the empirical laws. "Solubility" and "electrical resistance" are paradigmatic examples of intervening variables: they explain only in so far as they show a given instance to be an example of a general law. The terms of a true model or of a line-element are hypothetical constructs: we believe that the terms can be mapped on to some real entities (mechanisms, processes, or signals)

within the visual system and that the relationships between the terms are reflected by the structure of the model. The truth of the original observations is only necessary, not sufficient, for the truth of statements about the terms. The true model is thus a structure from which a particular result can be deduced. A floating model, in WYSZECKI's sense, is a formula in which intervening variables masquerade as hypothetical constructs.

1.4: An example: Land's model of colour constancy

For the purpose of distinguishing between a model and a mere formula or algorithm, a nice example is offered by LAND's original retinex model, which was designed to account for colour constancy [24; 25]. Recall that the model has two stages. First, a lightness image, or record, of the scene is obtained independently for each cone system. The lightness value at a given point in the record is obtained by relating the local signal of one cone type to the signal of that cone type at places remote in the field. Along each of these many paths one cumulates the log ratios of adjoining points (except only that ratios of less than a threshold value are discarded, in order to remove the effects of slow gradients of illumination). The second stage of the model is to obtain the ratios of the three records for any given point in the scene.

Now, it is often remarked that LAND's model contradicts what the electrophysiologists tell us. The accumulated physiology ostensibly suggests that there is a local extraction of the ratios of quantum catches in different cone types, and then some more global form of comparison of these ratios across the field [see, e.g. 4; 6] – whereas LAND's model places the spatially global comparison within a single cone system, preceding the comparison b e t w e e n cone systems.

For our present purpose, the relevant point is one that has been made by DAW [4], who attributes it to W. B. MARKS (it has been made independently to me by OSCAR ESTÉVEZ). Because LAND's calculation is cast in terms of ratios, it doesn't matter mathematically which ratio is calculated first, the spatial ratio of signals from receptors of the same type or the local ratio of signals from different cone types. For

$$\frac{\left(\frac{L_l}{L_s}\right)}{\left(\frac{M_l}{M_s}\right)} \equiv \frac{\left(\frac{L_l}{M_l}\right)}{\left(\frac{L_s}{M_s}\right)}$$

where L_l and M_l represent the local signals of the long- and middle-wave cones respectively and L_s and M_s represent the average surround signal for long- and middle-wave cones.

We should want to say that the two alternative formulae were equivalent (and their predictions must enjoy equal success), but we should not want to say that LAND's model was equivalent to the class of model in which the signals of different cone classes are first compared locally.

1.5: The fifth requirement

Of the requirements of a model listed above (1.2), the last is one that is prompted by the developments in visual science in the last two decades. We nowadays recognize that the array of retinal photoreceptors is examined in parallel by a variety of post-receptoral channels which extract different kinds of information from the image [5; 6; 37]. And the signals extracted by different types of second-order cells are transmitted to different sites in the brain [26; 27; 45]. Thus, separate pathways carry information from the retina to the superior colliculus and to the lateral geniculate nucleus; within the geniculo-striate system there is a striking separation of the magnocellular and parvocellular pathways [8; 33] and within the parvocellular system the on- and off-centre cells may carry two separate representations of the world [29; 39]. The three classes of cone receptors are known to be given different weightings in different channels.

This multiplication of parallel channels means that the action spectrum for visual performance will almost certainly vary according to the task that faces the operator. For different aspects of human performance – such as reading, avoidance of large objects, detection of faint targets at a distance, responding to sudden events in the visual field, control of the direction of gaze – almost certainly depend on different signals. So if a model of the visual system is to be developed for photometric purposes (as the CIE hopes), the model must include a specification of which human responses depend on which output signal of the model. (We may note in passing that there are no aspects of human performance, as opposed to verbal judgement, that have so far been shown to depend on the same signal as do heterochromatic brightness judgements.)

In determining which internal signal is relevant for photometric purposes, a crucial factor will be the dominant spatial frequency of the stimulus. Especially in the mesopic range of vision, where three cone signals and one rod signal are available, one might expect different action spectra and different degrees of additivity for different spatial frequencies, since it is very likely that the rod contribution to mesopic vision depends on the spatial-frequency content of the stimulus. The spatial resolution of the rod system is known to have an upper limit of only 7 cycles per degree, and in the range 1 to 100 scotopic trolands, this value is lower than the value for the long- and middle-wave cone systems [14, Fig. 6].

Several methods of mesopic photometry have been proposed [20], but what at present has not been specified is the range of spatial frequencies over which such methods are appropriate. Yet we can be certain that the weighting to be given to rod signals will change with the spatial frequency of the stimuli that are to be discriminated. Thus, the detection of a parked vehicle against a tarmacadam background at twilight requires only low-frequency information to be extracted from the spatial array and so will probably depend on a (magnocellular) channel that gives substantial weighting to rod inputs. But reading the number plate will depend on a channel that draws more of its input from cones.

2. The modal model of colour vision and the modifications it requires

2.1: The similarity of existing models

The purpose of this WYSZECKI-STILES symposium is not to set one person's model up against another. There is a great similarity among the informal models of colour vision that we all today carry in our heads. And there is a strong family resemblance among the many formal models in the published literature; their ancestry is clearly visible in the models of ADAMS, MÜLLER, JUDD and FRIELE. Each modeller (with honourable exceptions) has tended to offer a model that has fixed parameters and is directed towards one or two particular data sets. What we need to do now is to ask specific, technical questions about the details of the modal model, the shared model; and to ask how the behaviour of the model would vary as qualitative or quantitative changes were made to its elements. Examples of unanswered but tractable questions would be:

- What is the nature of the chromatic signal that opposes the short-wave signal? (Does it derive from the long-wave cones, from the middle-wave cones, or from some sum of their signals? Or does it itself depend on the interaction of the long- and middle-wave cones?)
- Is the adaptation at second-order sites subtractive or multiplicative or both (or neither)?
- Does the primate magnocellular system correspond to the luminance channel postulated by psychophysicists?

2.2.: The modal model summarized

A decade ago, in the late 1970's, a modal model was in common circulation in textbooks and was shared by many of us. There were three types of cone, each containing a distinct photopigment. The cones had fixed spectral sensitivities, with peak sensitivities in the yellow-green, the

green and the violet, at approximately 560, 530 and 430 nm. Any individual cone obeyed the *Principle of Univariance:* although the input to the cone can vary in wavelength and quantal irradiance, the output can only vary in one dimension [40; 34]. From the assumption of a fixed spectral sensitivity and that of Univariance it followed that the individual receptor exhibited additivity: if two wavelengths were each adjusted to give unit response when individually presented, then a mixture of the two would give the same response as would twice the radiance of either [40].

The cones obeyed WEBER's Law to high bleaching levels. The rods saturated. Transformations of the cone signals yielded one achromatic and two chromatic channels. The three channels corresponded to the three opponent processes of HERING. Flicker-photometric and minimum-border measurements tapped the achromatic channel, whereas heterochromatic brightness judgements depended additionally on the extra neural signal from the chromatic channels.

2.3.: Current developments

There is space here only to sketch some ways in which our shared model is being constrained and elaborated by recent findings.

Developments in molecular biology and protein chemistry have told us much more about the photopigments on which all our vision depends, and, it is argued below, are also influencing our view of the post-receptoral channels. We know that the protein parts (the opsins) of the photopigments are members of a much larger super-family of membrane receptor molecules that include the beta-adrenergic, the muscarinic acetylcholine and the serotinergic receptors [9; 13]. In each case the protein crosses the membrane seven times; and in the case of the photopigments the seven helices of the protein form a palisade that surrounds the chromophore. The most salient of the molecular biological findings of JEREMY NATHANS and his collaborators are (a) that the genes for the middle- and long-wave pigments lie very close together on the q-arm of the X-chromosome and (b) that the sequences are 96% identical for these two genes. On the other hand, the middle- and long-wave pigments are as different from the short-wave pigment as the latter is from human rhodopsin. The implications drawn by the molecular biologists are that the middle- and long-wave pigments diverged from each other very recently as a result of a gene duplication event, whereas their ancestor diverged from the short-wave pigment a very long time ago. This encourages the view – which has a long pedigree [23; 12; 33] – that human colour vision should really be envisaged as two relatively independent sub-systems, a modern system very recently overlaid on a much more ancient one. The ancient subsystem depends on a comparison of the signal of the short-wave cones, on the one hand, and some combination of the signals of the middle- and

long-wave cones on the other; this sub-system evolved purely to extract chromatic information and it is designed to recognize the overall sign and slope with which stimulus energy varies from one end of the spectrum to the other. (Subjectively, it divides colour space into warm and cool hues.) The modern sub-system depends on a comparison of the quantum catches in the long- and middle-wave cones and is parasitic upon an existing parvocellular pathway that remains sensitive to spatial detail. The evidence for this duplex view of colour vision is discussed in detail elsewhere [33]. The two sub-systems correspond to two axes of colour space that have been identified as fundamental in recent psychophysical analyses [3; 22].

However, the sub-systems suggested by recent physiology do not seem to correspond to the red-green and blue-yellow processes classically required by Opponent Colours Theory [16]. Thus, a channel that draws opposed inputs from the long- and middle-wave cones will be maximally polarised by red light and by blue, not green, light, since the minimum ratio of long-wave to middle-wave sensitivity occurs near 460 nm [32]. Psychophysical results are concordant with the view that the phylogenetically younger sub-system is not a "red-green" channel. For example, KRAUSKOPF, WILLIAMS and HEELEY [22] exposed observers to repeated modulation of chromaticity along a line running from pure yellow to pure blue, and found a loss of discrimination in all directions of colour space, even though the adaptation ought to have left undisturbed the putative red-green process of Opponent Colours Theory. On the other hand, adaptation along a tritan confusion line did leave almost undisturbed the chromatic thresholds along an axis that represented modulation only of the long- and middle-wave cones. Similarly, MOLLON and CAVONIUS [31] found that pre-adaptation to unique blue, which should leave the red-green process in equilibrium, nevertheless produced a large impairment of wavelength discrimination at long wavelengths where only the red-green process should be in play.

There is a second way in which the post-receptoral channels may not correspond to those postulated by HERING: the inhibitory input to a colour-opponent neuron may serve to restrict the spectral range of the cell's excitatory response rather than to lend it a bipolar mode of response [11]. LIVINGSTONE and HUBEL [26] have favoured such a view, writing: *"We assume that the point of opponency is to render ineffective things like diffuse light or white light, rather than to permit a cell to have two kinds of response."*

A third modification to the modal model comes from the increasing realization that chromatic and spatial signals are not separated at early levels of the visual system. The cells of the phylogenetically newer subsystem of colour vision (the midget ganglion cells and the parvocellular units in the LGN) have concentric receptive fields that are firmly divided

into excitatory and inhibitory regions, and thus such cells are sensitive to spatial contrast. At low spatial frequencies such a cell will exhibit wavelength specificity, but at higher spatial frequencies (when, say, one half period of a stimulus grating corresponds to the width of an excitatory field centre) it will respond to all wavelengths [17; 18]. The one system that does resemble a pure chromatic channel is the ancient mammalian sub-system that draws opposed inputs from the short-wave cones and the long-/middle-wave cones [33]. The component cells of this sub-system draw their opposed inputs from nearly congruent regions of the receptoral array and thus exhibit little sensitivity to spatial contrast. For this reason, and more basically because the short-wave cones are sparse, our spatial resolution and localization are very poor when they depend only on signals originating in the short-wave cones. Many of what used to be called "the anomalies of the blue cones" may now be seen as differences between the ancient and modern sub-systems of colour vision [33]. Fig. 4 shows a list of these anomalies, as recorded by STILES in his private journal at the astonishingly early date of 1949. Any model of colour vision must accommodate the differences between the two chromatic subsystems of the peripheral visual pathway.

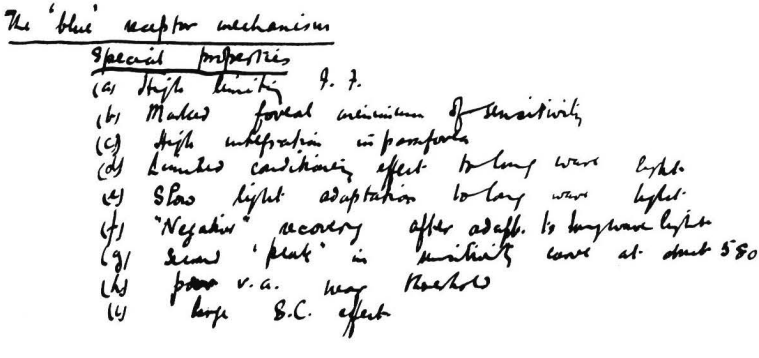

Fig. 4: STILES' list (1949) of the special properties of the short-wave system. The list reads: (a) High limiting F.f. [FECHNER fraction]; (b) Marked foveal minimum of sensitivity; (c) High integration in parafovea; (d) Limited conditioning effect to long wave light; (e) Slow light adaptation to long wave light; (f) "Negative" recovery after adapt. to longwave light [transient tritanopia]; (g) Second "peak" in sensitivity curve at about 580; (h) poor v. a. [visual acuity] near threshold; (i) large S. C. [STILES-CRAWFORD] effect. (From STILES' private notebooks, deposited in the Archive Room of the *Cambridge Psychological Laboratory*).

2.4: A third zone?

Many colour scientists, acknowledging that the second stage is not a HERING zone, suppose that the chromatic signals must necessarily be rearranged to give a central zone that does in fact correspond to the opponent processes of HERING. Such a zone, containing signals or cells that represent pure hues, is particularly common in models of colour appearance. Such models seem to rest on two psychophysical hypotheses that are left decently unspoken:

a) the hypothesis that particular neurons secrete particular sensations, and
b) the hypothesis that such neurons can secrete only the unmixed sensations, of red, green, yellow and blue.

At present, although there is evidence for central neurons that draw signals of the same sign from long- and short-wave cones and of opposite sign from the middle-wave cones, there is neither empirical evidence nor theoretical necessity for cells whose activity represents just one of the four pure hues[1]. All we know is that – under given conditions of adaptation and in the presence of a specified surround – certain chromaticities map on to certain sensations; and models of colour appearance are simply algorithms that summarize this mapping.

3. The nature of luminance

3.1: The signals used in flicker photometry and in minimum border settings

It was argued above (1.5) that a photometrically useful model must specify which output signal is used to control a given aspect of behaviour; and so it may be appropriate to end with a reconsideration of what signal, or signals, the observer uses when he is asked to set a minimum in heterochromatic flicker photometry or is asked to set a minimally distinct border [43]. It is commonly assumed that such settings depend on a channel that adds signals from the long- and middle-wave cones. A null is found

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[1] The issue is a more general one in brain science. We still do not know whether, at a central stage corresponding to conscious perception, there exist single neurons whose activity represents particular objects or words or concepts – the gnostic units of KONORSKI [21] or the cardinal cells of BARLOW [2]. There is more than one other possibility. On the one hand, central representations may depend on the pattern of activity in a local group of neurons, with a given unit contributing to more than one of the possible patterns. On the other hand, the unit of activity may be smaller than the individual neuron, so that different representations correspond to different spatial or different temporal patterns of activity within a single neuron.

when the alternating lights (or the juxtaposed fields in the case of the minimum border technique) give the same sum in this "luminance channel". The channel in question may be different in the temporal and spatial versions of the experiment; but in both cases the setting depends on the sum of long- and middle-wave cone signals.

Yet the retina is built to detect transients in time and space. In heterochromatic photometry, when a minimum flicker or minimum border setting is found, the long-wave cones will be seeing a transient of one sign while the middle-wave cones will be seeing a transient of the opposite sign [30]. It is implausible that post-receptoral channels are designed to allow these transients to cancel; and indeed, the observer will report residual flicker or a residual border at his final setting, provided that the two lights do not lie on a tritan line and provided that the temporal or spatial frequency is not so high that the residual transients simply lie below the contrast threshold.

Fig. 5 offers an alternative interpretation of what the observer is doing – of what signals he is using – when he makes a minimum flicker or minimum border setting. Suppose that two monochromatic lights λ_1 and λ_2

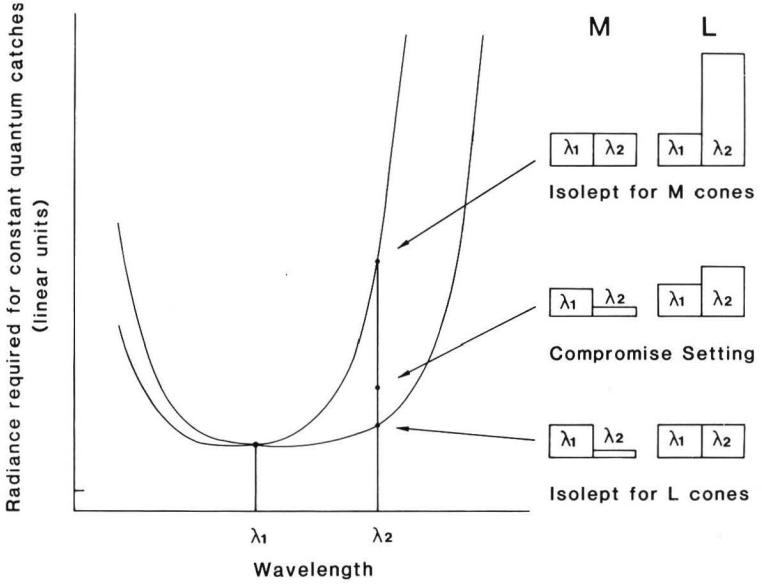

Fig. 5: An alternative interpretation of what the observer does when he or she is asked to make a minimum flicker or minimum-border setting in heterochromatic photometry. Two wavelengths, λ_1 and λ_2, are alternated in time or space. The observer adjusts the radiance of λ_2. To the right is shown schematically the resulting modulation of the middle-wave (M) and long-wave (L) signals at different radiances of the variable light.

are alternated, and that the second of these is the variable. If the observer is a protanope, there is no ambiguity about how he should make a setting: he should set the radiance of λ_2 so that it lies at what RUSHTON, POWELL and WHITE [38] called the isolept, i.e. the radiance at which it gives the same quantum catch in the middle-wave cones as does the first light; he achieves a 'silent substitution' for the middle-wave cones. Similarly, if he is a deuteranope he must go for the isolept for the long-wave cones. But what is the normal to do? Let us suppose (this is the crucial assumption in this alternative interpretation of luminance) that he has both access to the a.c. components of the long- and of the middle-wave signals. He would like to achieve a silent substitution for both the long-wave and the middle-wave cones, but if he sets the variable radiance to the isolept for one of the two classes, there will be a marked modulation of the other class (Fig. 5, right-hand side). So, we may suppose that he compromises. He sets the variable at a position between the two isolepts, a position where both the residual signals are small. The exact position of his setting will depend on the relative weighting that his visual system gives to the a.c. signals from the two types of cone, and this may depend, say, on the relative numerosities of different cone types. He will, however, never venture outside the window between the two isolepts; for outside this window, both the residual signals can only increase. Since his settings are constrained in this way, they will come close to exhibiting additivity, even though there is no reified signal within his nervous system that represents luminance.

3.2: Equal luminance

In the last decade there has been much interest in perception under conditions of equal luminance. Much of this interest has been based on the (unsupported) belief that an equiluminant stimulus will securely isolate the chromatic channels of the visual system [see ref. 30 for discussion and references]. Fig. 5 offers an alternative view of why some perceptual functions (such as stereopsis, spatial organisation, and motion perception) deteriorate under conditions of equal luminance. The window between the isolepts is a very special region, only occasionally entered in our ordinary visual life: it is the region in which the transients detected by the long- and middle-wave cones are of opposite sign. In the normal visual world, chromatic edges are more commonly accompanied by luminance edges; and under these circumstances the transients seen by the two classes of cone are of the same sign. So usually, L+ and M+ on-centre ganglion cells tell the same story about edges, as do the equivalent off-centre cells. But at equal luminance, in the window between the isolepts, the cortex will receive contradictory reports from on- and off-centre contrast-detecting cells of different types. And this may be the reason why some perceptual functions are impaired.

Acknowledgements

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Author's address:
Dr. J. D. Mollon
Dept. of Experim. Psychology
University of Cambridge (UK)
Downing Street
Cambridge CB2 3EB

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Johannes J. Vos and **Pieter L. Walraven,** SOESTERBERG:

Towards a Standard Fundamental Observer

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Merits and drawbacks are discussed of the Vos/Walraven, Smith/Pokorny and Estévez foveal primaries. A new set is proposed combining merits and avoiding drawbacks. As a by-product the input of a S-function to luminance was found to be inhibitory, rather than excitatory.

Vorzüge und Nachteile der fovealen Grundvalenzen nach Vos/Walraven, Smith/Pokorny und Estévez werden diskutiert. Ein neuer Satz wird vorgeschlagen, der die Vorzüge behält und die Nachteile vermeidet. Als Nebenprodukt wurde gefunden, daß eine S-Funktion zur Leuchtdichte hemmend und nicht erregend ist.

Ici on discute les avantages et les désavantages des primaires fovéales fondamentales de Vos/Walraven, Smith/Pokorny et Estévez. On propose une nouvelle série de ces fonctions qui maintient les avantages en évitant les désavantages. Comme un sous-produit, on a trouvé que la fonction S indique un procès inhibitoire au lieu d'excitant à la luminance.

1. Introduction

The absorption spectra of the cone photoreceptors determine, in first instance, the properties of color vision. We seem to have converged by now to only slightly different sets of proposed curves. The most relevant candidates, together with their main characteristics, are listed below.

Our set [1] and that proposed by SMITH and POKORNY [2] differ only by the assumption on the contribution of the short wavelength sensitive system to luminance. Ours does, and theirs does not. But otherwise the two proposals derive from the same basic data: CIE 1931 + dichromatic color vision reduction. The resulting action spectra do not differ by much. However, our system went further, by laying links to the BEZOLD-BRÜCKE effect and STILES' WEBER fractions, with a result that we could also produce relative receptor population densities.

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* *Institute for Perception TNO,* Soesterberg, The Netherlands

Table 1: The three colorimetric models compared

Vos/Walraven '71	Smith/Pokorny '75	Estévez '79
CIE 1931	CIE 1931	Stiles/Burch 1959
Luminance = L+M+S	Luminance = L+M	–
Dichromatic Photo- and Colorimetry	Dichromatic Photo- and Colorimetry	Dichromatic Colorimetry
Bezold-Brücke-Effekt	–	–
↓	↓	↓
System primaries receptor primaries Weber fractions receptor populations	Relative system primaries	Relative system primaries

Estévez' proposal [3] is typically different. Shortly, it says: Do not take CIE 1931, but the Stiles and Burch data [4]; and do not talk about luminance since we are concerned with color vision. He therefore came up with a different set of action spectra.

In this presentation we will accept Estévez' criticism to our assumptions, adopt his approach, but apply some corrections and additions:
- we will show that his transformation was not optimal;
- we will weave our extensions into the thus corrected Estévez system;
- we will propose an addition that re-introduces photometry, not as an input assumption but as an output result.

2. The optimal conversion

First we have recalculated the Estévez (*rgb*) to (*LMS*) conversion (Fig. 1). It shows three shortcomings:
- it has an S_λ curve that is negative in the red;
- it has L_λ and M_λ curves that do not fit well with deutan and protan spectral sensitivities.

By trial and error we made small variations around the Estévez dichromatic confusion loci and found that this could easily eliminate these drawbacks (Fig. 2). The method of looking for slight variations in the dichromatic confusion loci seems acceptable as, in 1971, we have shown that the dichromatic sensitivity is a more sensitive cue. The new set is even a small improvement compared to the Vos/Walraven and the Smith/Pokorny sets, which both were tuned to these dichromatic fits.

Conclusion:

We have obtained a better (rgb) to (LMS) conversion.

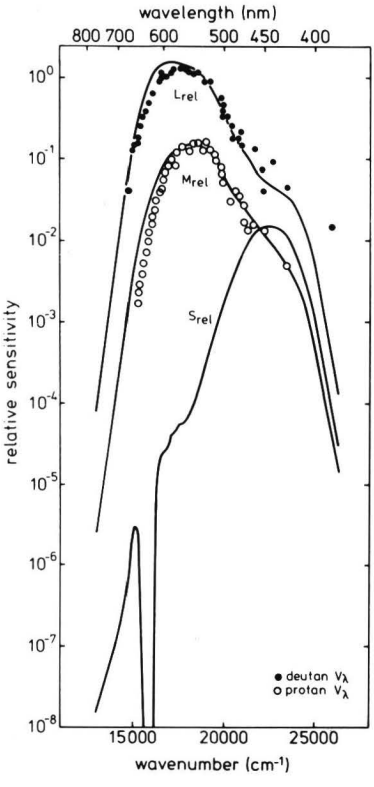

Fig. 1: The ESTÉVEZ foveal receptor system sensitivities, compared with literature data on dichromatic sensitivity

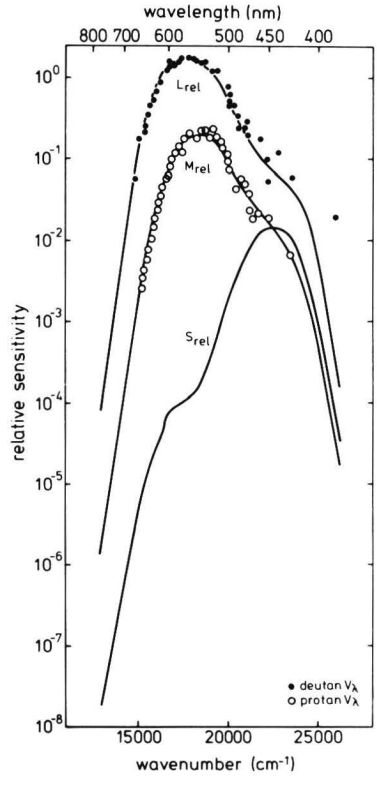

Fig. 2: Optimized data fit, also based on the STILES/BURCH two-degree colorimetric data

3. Relative mutual heights

To determine relative mutual heights per receptor we can use the BEZOLD-BRÜCKE effect. To put it simple (for a more sophisticated treatment, see [5]): the receptor sensitivities equal at the wavelengths of hue convergence (Fig. 3). We will call these receptor sensitivity curves l_λ, m_λ, and s_λ.

To determine relative heights per system we cannot anymore use the requirement that their envelope should equal V_λ, (for which we will take

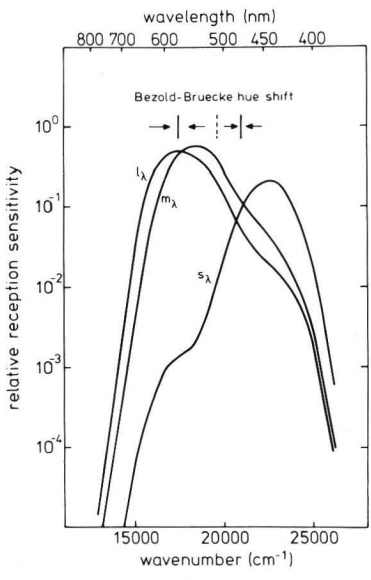

Fig. 3: The newly derived set of receptor primaries in their mutual sensitivity position. For comparison qualitative BEZOLD-BRÜCKE hue shifts with luminance are indicated

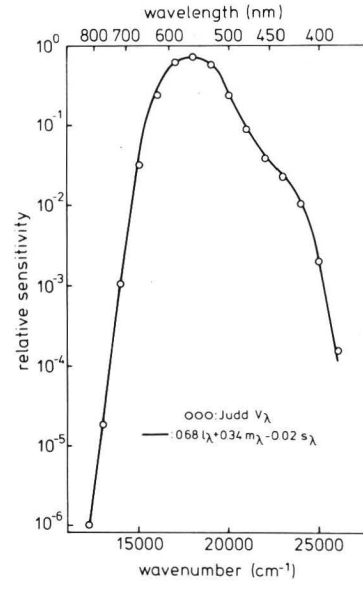

Fig. 4: Synthesis of V_λ by optimizing weighting factors for the three receptor inputs

the JUDD [6] version). But we may rephrase that statement as a question:

Which acceptable combination formula will produce V_λ from l_λ, m_λ, and s_λ?

Fig. 4 illustrates the surprising answer:

$$V_\lambda = 0.68\ l_\lambda + 0.34\ m_\lambda - 0.02\ s_\lambda.$$

We conclude:

1. that luminance contributions from L, M, and S receptors have weighting factors 0.68 : 0.34 : 0.02, which we will interpret, like before, as relative receptor population densities.
2. that the small S-input to luminance is inhibitory, rather than excitatory.

Conclusions

- The ESTÉVEZ conversion to fundamental primaries can be improved. The result is much closer to the VOS/WALRAVEN and the SMITH/POKORNY fundamentals.
- The S-system feeds negatively into luminance.
- Receptor populations relate as 0.68 : 0.34 : 0.02.

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Authors' address::
Dr. Johannes J. Vos
Dr. Pieter L. Walraven
TNO Institute for Perception
Kampweg 5
NL-3769 DE Soesterberg

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Joel Pokorny* and **Vivianne C. Smith***, CHICAGO:

L/M Cone Ratios and the Null Point of the Perceptual Red/Green Opponent System**

DK 612.843.317.2

The hypothesis that the ratio of long- to middle-wavelength sensitive cones can be estimated from heterochromatic flicker photometric sensitivity to red and green lights is reviewed. Evidence is presented that there is no link between the L/M ratio and the spectral locus of unique yellow.

Die Hypothese, das Verhältnis von im langwelligen zu im mittleren Wellenlängenbereich empfindlichen Zapfen könne aus der heterochromen flimmerphotometrischen Empfindlichkeit für rote und grüne Lichter bestimmt werden, wird überprüft. Es wird nachgewiesen, daß zwischen dem L/M-Verhältnis und der bunttongleichen Wellenlänge der Urfarbe Gelb kein Zusammenhang besteht.

On a examiné l'hypothèse que la proportion des cônes sensitifs dans la région des ondes longues, à ceux sensitifs dans la région des ondes moyennes puisse être déterminée par la méthode du papillotement des lumières rouge et verte. On présente l'évidence qu'il n'y a pas de connection entre la proportion L/M et l'onde dominante du jaune unique.

1. Introduction

Many theories of color vision postulate a reorganization of the signals from three cone types into parallel processing channels. These have frequently been modelled by sums and differences of the three cone types (e.g. [2; 5; 8; 14]). One channel, the luminance channel, signals a weighted sum of LWS and MWS cone signals. Two chromatic channels signal weighted sums and differences of cone signals. In this paper we are concerned with the relation of the weights of the LWS and MWS cone inputs to the luminance channel and to the red/green chromatic channel.

The luminance channel is characterized by its spectral sensitivity as measured by techniques such as heterochromatic flicker photometry and minimally distinct border [2]. If the relative cone spectral sensitivities are those of the SMITH-POKORNY fundamentals, we find that the sensitivity of the LWS cone is 1.6 that of the MWS cone in the summed response which fits the psychometric spectral sensitivity function [15].

The chromatic channels are characterized by their unique hues. Unique hues are colors which appear unitary or as psychologically unique percepts. For spectral colors, four unique hues may be identified; red, yel-

* *Eye Research Laboratories, University of Chicago*
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low, green and blue. The four unique hues are used as parameters in color vision models based on the perceptual aspects of color appearance (e.g. [5; 7]). For example, unique yellow is neither reddish nor greenish and is considered a null (or balance) point for a red/green color opponent mechanism. To achieve the correct spectral position for unique yellow, the weighting of the LWS and MWS cone contributions must be approximately equal. Thus there is a difference in average weighting of the LWS and MWS cones when the luminance and chromatic channels are computed. The question we wish to address in this brief communication is: Do the same constraints affect the weighting of the LWS and MWS cones for the luminance signal as for the chromatic red/green signal? To examine this question we wish to compare individual differences in the cone weightings for the luminance system with individual differences in the weightings for the red/green chromatic system. The question we pose is: Can the locus of unique yellow be predicted by the estimated L/M cone ratio derived from flicker photometry?

2. L/M cone ratios estimated from heterochromatic flicker photometric spectral sensitivities

Heterochromatic flicker photometry shows considerable variation in the color-normal population. A convenient estimate of the overall variability is the individual variation in the flicker sensitivity of a long wavelength relative to the peak of the function, the so-called red/green flicker ratio. The logarithms of the flicker ratios have a standard deviation of 0.07–0.10 log unit. This standard deviation does not seem much affected by age. It is however two to three times larger than the standard deviation of log red/green ratios for RAYLEIGH matches. Variables which affect both the red/green ratio for heterochromatic flicker photometry (HFP) and the red/green ratio for RAYLEIGH matches, such as pre-receptoral filtering and photopigment spectral variation, lead to a modest positive correlation between the two measures, about 0.4 [9, 13, 18] for 2° or larger field sizes.

DEVRIES [17] first suggested that individual differences in the red/green flicker ratios based on heterochromatic flicker sensitivity might reflect the proportion of cones containing the LWS and MWS photopigments. Qualitative support came from RUSHTON and BAKER's [13] comparison of red/green flicker ratios and retinal densitometry. Further, red/green ratios from females heterozygotic for protan and deutan color vision defects also point to an association between HFP and L/M ratios. CRONE [3] and ADAM [1] report that protan heterozygotes tend to be "green" sensitive (this decreased sensitivity to long-wavelength light is known as SCHMIDT's sign) and deutan heterozygotes tend to be "red" sensitive. If we assume that the defective alleles are associated with low pro-

duction of photopigment [11], then we may interpret flicker photometric spectral sensitivities as reflecting L/M cone ratios.

RAM VIMAL, a post-doctoral student in our laboratory collaborated with us and STEVE SHEVELL in a study that seems to confirm that the red/green flicker ratio does reflect the LWS to MWS cone ratio [16]. The experiment was designed to examine some aspects of the retinal cone mosaic. We used a two-point detection procedure aimed at establishing the number of quanta/cone and number of cones involved in foveal detection. Two aspects of the analysis are relevant here. First, the analysis gives an estimate of the LWS/MWS cone ratio in each observer's eye which can be compared with HFP. HFP spectral sensitivities were measured for the spectral range 510 nm to 700 nm. The LWS/MWS cone ratio was estimated by finding the linear combination of LWS and MWS which best fit the HFP data. The results showed reasonably good agreement between the foveal cone ratio derived from two-point detection and the foveal cone ratio derived from HFP. The LWS/MWS ratio for the first observer was 1.6 from the threshold experiment and 1.1 from the HFP experiment. For the second observer it was 4.0 and 3.4 respectively. Thus though our two observers appear to have disparate L/M cone ratios, the ratio estimated from the threshold experiment is in good agreement with that estimated from the HFP experiment for each observer. More recently, MICHAEL WESNER has data on three additional observers which also show agreement between the foveal cone ratio derived from two-point detection and the foveal cone ratio derived from HFP [19].

Given the hypothesis that the foveal cone ratio can be derived from HFP measurements, we can compute the possible range of cone ratios consistent with the variation of the data. This will be an upper bound. The result of the calculation [9] suggests that color-normal male individuals may have L/M cone ratios ranging from 0.5 : 1 : 1 (2 MWS cones for each LWS cone) to 10 : 1 or greater (10 LWS cones for each MWS cone).

3. Null point for the red/green chromatic mechanism as estimated by the spectral position of unique yellow

Is the large range of L/M cone ratios obtained from flicker photometry consistent with the variation of unique yellow? Two lines of evidence suggest not. The first is taken from a literature survey of population data concerning HFP spectral sensitivity and the spectral locus of unique yellow, and the second from data for both measures on a more limited number of observers.

A number of investigators report data on the spectral locus for unique yellow [4; 6; 12; 18]. The spectral location of unique yellow ranged from 577 nm to 584 nm and the standard deviation ranged from 2.0–4.8. If we

assume a mean of 580 nm and a standard deviation of 4.0, then the expected values of unique yellow in the population (± 3 SD) might range from 568 nm to 592 nm. If such variation were produced by variation in relative populations of the LWS and MWS photopigments, then (assuming the MWS cone weight is twice as great for the red/green opponent channel than for the luminance channel) flicker photometric ratios would have a range of only 0.084 log unit. Literature data [1; 9; 13; 18] show a far greater range of flicker photometric matches in the population, with standard deviations of 0.07–0.10 log unit. The range predicted from 3 standard deviations of the unique yellow population data represents only about 1 standard deviation of the population flicker photometric data.

A second line of evidence that L/M ratios and unique yellow are not linked can be found in WALLSTEIN's [18] data. He compared unique yellow with red/green ratios from heterochromatic flicker photometry in 16 observers. Data were gathered at four field sizes from 0.5° to 4.0°. Here we report only the 2° data. WALLSTEIN's first step was to obtain values for unique yellow in the same metric as the heterochromatic flicker photometric ratios. He obtained estimates of the spectral position of unique yellow from a device with contrinuous variation of wavelength and expressed the results in terms of a transformation to the CIE JUDD observer. The same observers also set a mixture equilibrium yellow using primaries of 545 nm and 670 nm. The correlation between the wavelength equilibrium yellow (transformed to an R/G mixture) and the mixture equilibrium yellow was 0.83, indicating that the observers were making the same perceptual judgement in both cases. Further, the high correlation indicates that prereceptoral filtering, which would alter mixture unique yellow settings but not wavelength unique yellow settings, was not a significant factor in this study. Finally the observers made an HFP match using the 545 nm and 670 nm primaries. The correlation between the log R/G mixture equilibrium yellow and the log R/G for heterochromatic flicker photometry was –0.4. Thus WALLSTEIN's data show a low association between unique yellow and HFP in the incorrect direction. In a further step, we can convert the R/G ratios to L/M cone ratios using the SMITH/POKORNY fundamentals. The L/M ratios for heterochromatic flicker photometry have a range greater than 20 : 1, while the L/M ratios for unique yellow have a range of only 2 : 1. This correlation of these L/M ratios is –0.29. This calculation emphasizes that the variation in L/M ratio from flicker photometry is large compared with that predicted by the variation in unique yellow. We suggest that, while HFP spectral sensitivities reflect receptor populations, the normalization for the red/green chromatic mechanism depends on other factors, perhaps on a normalization to the "average white" of the individual's environment [10].

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Author's address:
Prof. Dr. J. Pokorny
Prof. Dr. V. C. Smith
Eye Research Laboratories
The University of Chicago
939 East 57th Street
Chicago, IL, 60637, USA

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August 11, 1988

Carol M. Cicerone*, BOULDER COL.:

Constraints Placed on Color Vision Models by the Relative Numbers of Different Cone Classes in Human Fovea Centralis

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612.843.363.2

Measurements of the numerosity of L as compared to M cones in the fovea centralis of six color normal human observers are presented. The range in the relative numbers of L to M cones among individuals is shown to predict individual differences in the luminosity function as well as differences in characteristics of the red/green color opponent process.

Es werden Meßergebnisse über die Zahl der L-Zapfen im Vergleich zu der der M- Zapfen in der Fovea centralis bei farbennormalsichtigen Personen mitgeteilt. Es zeigt sich, daß der relative Schwankungsbereich des Verhältnisses L/M bei den einzelnen Versuchspersonen die individuellen Unterschiede in der V_λ-Funktion wie auch die Unterschiede in den Kennwerten für den Rot/Grün-Gegenfarbenprozeß voraussagen läßt.

On présente des mesures du nombre des cônes L en comparaison aux cônes M dans la fovéa centrale chez des hommes de vision colorée normale. On a trouvé que les fluctuations individuelles de la valeur L/M permettent de prédire les différences entre les valeurs de la fonction V_λ aussi bien que des caractéristiques du procès rouge/vert des couleurs opposées.

1. Introduction

The determination of the relative numbers of the different cone types in the retina is fundamental to our understanding of human visual sensitivity and color vision, and this information would be required for any quantitative models of human vision. Yet direct measurement which provide this basic information have not been previously made for all cone types.

For the most part there has been and continues to be a gratifying convergence of psychophysically derived evidence from humans [21] and anatomically derived evidence from baboon [9], macaque [11] and from the human retina [1] on the numerosity and distribution of the short-wavelength-sensitive (*S*) cones in the primate retina.

In the cases of the long-wavelength-sensitive (L) and middle-wavelength-sensitive (M) cones, there are no previous direct psychophysical measurements from which the relative numbers of L and M cones can be

* *Department of Psychology, CB 345, University of Colorado*

derived, and estimates based on various indirect means vary widely. To my knowledge, DEVRIES [3; 4] was the first to suggest that the individual variability in luminosity functions could be related to individual variability in the relative numbers of different cone types. RUSHTON and BAKER [15] subsequently reported that retinal densitometric measurements for individuals could be correlated to measurements of heterochromatic flicker photometry. RUSHTON and BAKER's estimate of the relative numbers of L to M cones in normal trichromatic observers spanned a wide range of 1 to 3 to 3 to 1. Another approach was based on estimates deriving from curve fits required to make various sets of psychophysical data consistent one to another. Examples of this kind of analysis include WALRAVEN's [19] and SMITH and POKORNY's [16] independent estimates based on fits of the cone primaries to the luminosity function; VOS and WALRAVEN's [18] estimate based on comparisons of WEBER fractions for the different STILES π-mechanisms; and WALRAVEN's [19] estimate based on the relative heights of the spectral sensitivity functions of the cone primaries. These estimates of the relative numbers of L and M cones vary between 1.6 and 2.0. There are as yet no morphological criteria whereby L and M cones can be distinguished. The only anatomical study known to us is MARC and SPERLING's [9] histochemical assay of baboon retina which produced an estimate of fewer L cones than M cones, in the ratio of 1 to 2. Although this estimate falls on one end of RUSHTON and BAKER's [15] range, it is quite the reverse of the indirect estimates based on other human psychophysical data as reviewed above.

2. Estimation of the relative numbers of L to M cones

In our study we attempted a more direct approach. When a tiny light on the order of a minute of arc is viewed by the fovea, its color appearance cannot always be predicted from the color appearance of a large patch of the same wavelength [6]. Our observers viewed wavelengths between 520 and 660 nm which were presented as stimuli of 1 min in visual angle and for 50 msec duration. Except for wavelengths near the ends of this range, the color appearance of each fixed wavelength sometimes appeared green and at other times red, yellow, or white. Since the lights were tiny, each flash stimulated only a few cones, and presumably slightly different cones from flash to flash are illuminated, leading to the differences in color appearance from flash to flash.

In order to exploit these observations so as to estimate the relative numbers of L to M cones, we developed a model to describe how the relative numerosity of a particular cone type affects the function measuring the probability of detection based on that cone type. In addition, to obtain two conditions, one in which detection is based upon quanta caught by L cones and a second in which detection is based upon M cones, we used the two-color procedure so elegantly employed by STILES [17]. For M

cone isolation we used a 520 nm test on a 640 nm background. For L cones isolation we used a 640 nm test on a 520 nm background. Using these conditions to isolate detection by L or M cones, we estimated the relative numbers of these cone types in fovea centralis of six color normal observers. We used three estimation procedures, each requiring additional elaborations of our basic model.

One way of estimating the relative numbers of L to M cones was based on a cone mosaic derived from the measurements of MILLER [10] who obtained 0.6 min center to center spacing of cones in the central fovea. Assuming a greater density of L cones, if the size of our test spot is progressively increased under M cone isolation conditions, the spot will illuminate an increasing number of M cones and the probability of detection function should become steeper. Indeed, when a match to the L cone psychometric function is attained, the ratio of the numbers of cones illuminated is an estimate of the relative numbers of L to M cones. This method yielded an estimate of the ratio of numbers of L to M cones between 2.0 and 2.3 for two subjects, while two others gave results indicating a ratio less than two, and for two more subjects, a ratio greater than two was obtained.

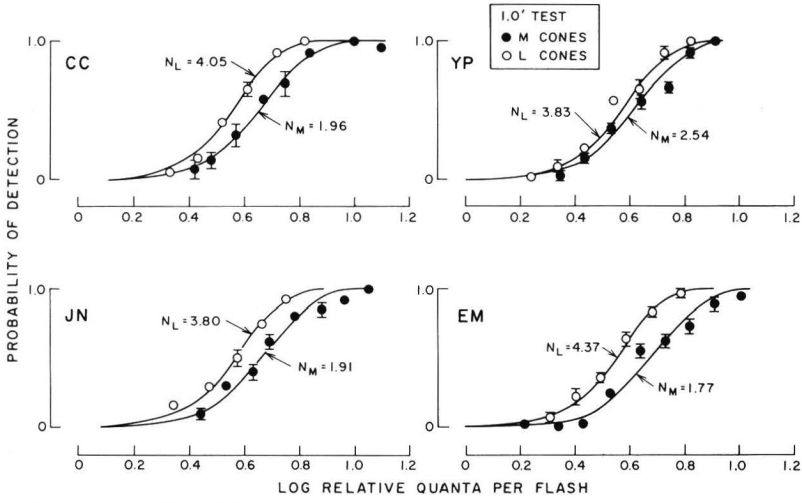

Fig. 1: Probability of detection functions for four of our six observers. The test of 1′ in visual angle appeared as a 50 ms flash upon a steady background of 3° in visual angle. M cones were isolated with a test of 520 nm and background of 640 nm (closed symbols). L cones were isolated with a test of 640 nm and a background of 520 nm (open symbols). The smooth curves are the best-fitting functions dictated by our model, from which we can estimate the number of L cones (N_L) and the number of M cones (N_M) contributing to the detection of a 1 min test light.

In order to refine our estimates, we extended our model to allow that if any one of the illuminated cones catches a specified number of quanta from any given flash, then the flash will be detected. As a consequence of this model we derived a relationship linking the relative numbers of L to M cones to the slopes of the probability of detection functions under L and M one isolation conditions for equal test sizes. This second method produced estimates of 1.41, 2.01, 2.06, 2.08, 2.16, and 2.24 for the relative numbers of L to M cones in our six observers.

Table 1: Relative numbers of L to M cones in fovea centralis

Estimates based on:	Subjects: CC	JN	YP	EM	VV	HA
Test sizes giving matching detection functions	2.0–2.3	2.0–2.3	<2.0	>2.0	>2.0	<2.0
Ratio of slopes of detection functions	2.06	2.01	1.41	2.24	2.16	2.08
Ratio implied by best-fitting theoretical functions	2.07	1.99	1.51	2.47	2.39	1.90

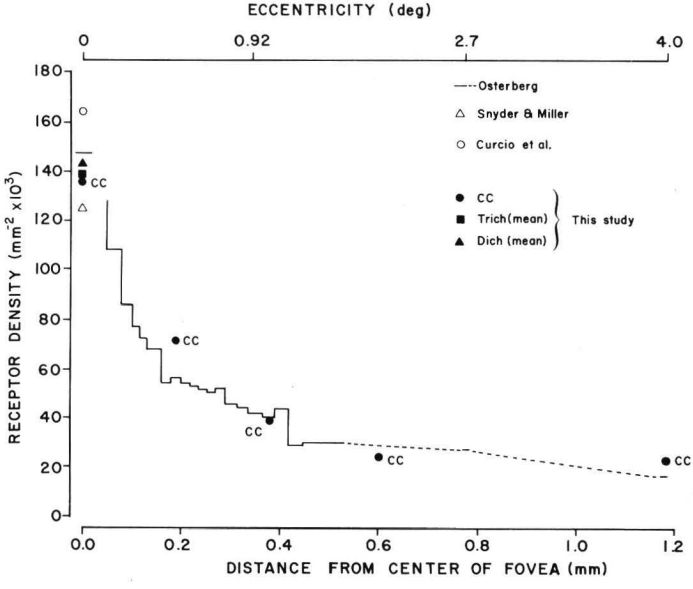

Fig. 2: Estimates of total cone density from our study for observer CC (closed circles), the mean value of six color normal observers (closed square), and the mean value of eight dichromats (closed triangle). These estimates lie close to the estimates of cone density from anatomical studies [2; 10; 13].

In our third elaboration of the model, we assumed that absorption of quanta by the cones follows a POISSON process. This allowed us to estimate the number of cones under each isolation condition which yielded the best fit of model to data. Figure 1 shows examples of such fits.

Table 1 summarizes the results from the three estimation procedures. The three estimates for each subject are closely comparable. The range over individuals is between 1.46 to 2.36. Over all subjects we obtain a mean value near two L cones for every M cone in human fovea centralis.

As a means of validating our methods, we compared our estimates of cone density based on the total numbers of cones illuminated by our test of visual angle one min to the densities estimated by anatomical results [2; 10; 13]. Figure 2 shows that when our estimates are cast against the estimates of these three anatomical studies on the total numbers of cones in the human retina near the fovea, there is good agreement. Details of our procedures for estimating the relative numbers of L to M ones are provided elsewhere [1 a].

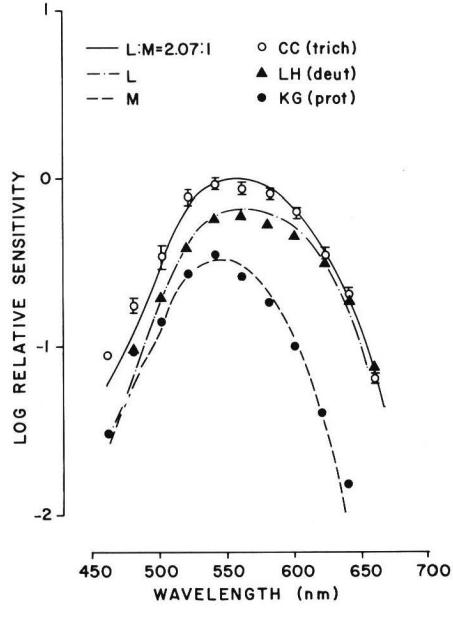

Fig. 3: Comparisons of the luminosity functions measured by heterochromatic flicker photometry for three observers as compared to theoretical functions. Deuteranope LH's results are compared to the SMITH and POKORNY [16] fundamental L function, protanope KG's results to the SMITH and POKORNY fundamental M function, and trichromat CC's results to the sum of the L and M functions, in the proportion 2.07 to 1, as dictated by our estimates for this subject.

3. The relative numbers of L and M cones determine the shape of the luminosity function

Shown in Figure 3 are comparisons of the luminosity functions measured by heterochromatic flicker photometry for three observers. Deuteranope LH's results are compared to the SMITH and POKORNY [16] fundamental L function, protanope KG's results to the M function, and trichro-

mat CC's results to the sum of the L and M functions, in the proportion 2.07 to 1, as dictated by our estimates for this subject. The fit is reasonably good.

4. Unique yellow is predicted by the relative numbers of L and M cones

We can use our estimates to predict the locus of unique yellow, one of the equilibirium wavelengths of the red/green mechanism of the opponent process color model. The wavelength seen by an observer as uniquely yellow, that is neither reddish nor greenish, is of theoretical significance, in that, for the unique yellow wavelength, the red/green code attains a value of zero. This may be written as follows: $N_L \cdot k_L \cdot L(\lambda) - N_M \cdot k_M \cdot M(\lambda) = 0$. Neural factors are embodied by the coefficients k_L and k_M. The relative numbers of different cone types are represented as proportionality factors, N_L and N_M. Here, we can neglect the S cones, which are unlikely to catch significant numbers of quanta for these yellow wavelengths, and the combined effect of quanta caught in L cones should equal that in M cones. Relying only on the relative numbers of L and M cones as the source of individual variability, we predicted that a range between 569 nm to 592 nm would span the wavelengths seen as unique yellow by color normal observers. A survey of some seven studies [5; 7; 8; 12; 14; 20; this study] yielded an observed range of 568 nm to 588 nm. These results are shown graphically in Figure 4. For four of our observers, we obtained both L to M ratios and unique yellow judgements. The results of these observers were used to estimate the form of the function shown here, which yielded for each L to M ratio a predicted unique yellow wavelength. The predicted range matches the observed range reasonably well. Also, the mean L to M ratio predicted a unique yellow which falls in the 95% confidence interval of the mean wavelength seen as unique yellow. What is shown with this analysis is that the individual variability in the range of wavelengths seen as unique yellow can be adequately modeled by individual variability in the relative numbers of L and M cones, without appealing to individual variability in the absorption characteristics of the cone pigments or in neural factors.

5. Summary

In summary, we have obtained estimates of the numerosity of L as compared to M cones in six color normal human observers. These estimates ranged between 1.46 to 1 to 2.36 to 1 as the ratio of the numbers of L to M cones in human fovea centralis, with a mean value near 2 to 1. The ratio has been applied to modeling the luminosity function and the unique yellow wavelength with satisfactory results, especially in reflecting the individual variability in the wavelength seen as unique yellow.

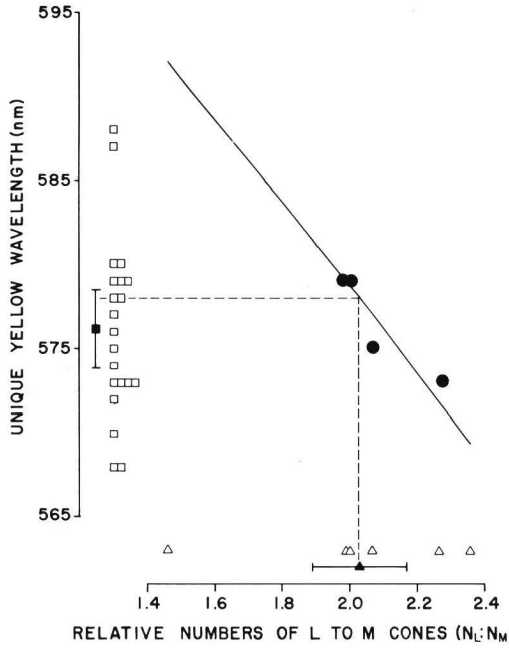

Fig. 4: Shown here is a comparison of our model predictions of the range of wavelengths which should be seen as unique yellow and the observed range [5; 7; 8; 12; 14; 20; this study]. For four of our observers (closed symbols), we obtained both L to M ratios and unique yellow judgements. The results of these observers were used to estimate the form of the function shown here, which yielded for each L to M ratio (plotted along the abscissa) a predicted unique yellow wavelength (plotted along the ordinate). The predicted range matches the observed range reasonably well. Also, the mean L to M ratio (closed triangle) predicts a unique yellow which falls in the 95% confidence interval of the mean wavelength seen as unique yellow (closed square).

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Author's address:
Dr. Carol M. Cicerone
University of Colorado
Dept. of Psychology
Kuenzinger Psychology Building
Campus Box 345
Boulder, Col. 80309-0345, USA

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Hirohisa Yaguchi*, CHIBA (Japan):

Signal Transformations from the Cone Stage to the Neural Coding Stage

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From the analysis of the relation among various visual functions obtained from one observer, it is suggested that (1) the L-cone and the M-cone signals are linearly transformed to the achromatic channel, (2) the r/g opponent color channel is linearly processed by the transformation of cone signals, and (3) the y/b opponent color channel is non-linearly processed by the cone signals of the L-cones and S-cones.

Das Ergebnis der Analyse der Beziehungen zwischen verschiedenen, von einer einzelnen Versuchsperson erhaltenen Sehfunktionen legt es nahe anzunehmen, daß (1) die Signale der L- und M-Zapfen linear transformiert in den Unbunt-Kanal eingehen, (2) der r/g-Gegenfarbenkanal nach Umwandlung der Zapfensignale linear und (3) der y/b-Gegenfarbenkanal von den Signalen der L- und S-Zapfen nicht-linear beaufschlagt werden.

Le résultat de l'analyse des relations entre les diverses fonctions visuelles que l'on a obtenues par un seul observateur, recommande l'hypothèse (1) que les signaux des cônes L et M entrent linéairement dans le canal achromatique, (2) que le canal des couleurs opposées r/g soit linéairement influencé par une transformation des signaux des cônes, (3) le canal des couleurs opposées y/b soit influencé non-linéairement par des signaux des cônes L et S.

1. Introduction

When we make a color vision model, we investigate the relation between the visual function at different stages. The visual functions are, however, different from observer to observer because of the individual differences of the ocular medium absorption, macular pigment, and so on. Such an individual difference sometimes becomes a problem to make a quantitative model. Therefore, a set of visual functions from a single observer is useful to make a color vision model.

I had an opportunity to work with the late Dr. WYSZECKI at *National Research Council of Canada.* There was the NRC Trichromator which was originally designed by the late Dr. STILES. A schematic view and details of the Trichromator are described elsewhere [1]. During my stay at NRC, I measured many kinds of visual functions using my own eye.

In this paper, I present some of these visual functions: the color matching functions, the luminous efficiency function by flicker photometry, and the opponent-color response functions. The relation among these visual functions has been discussed.

* *Dept. of Image Science, Faculty of Engineering, Chiba University*

2. Color matching functions

Color matching functions were measured by two methods; the maximum saturation method, and the MAXWELL method. A 2° bipartite field in a dark surround was used for both methods. The wavelengths of the three primary stimuli were 444.4 nm, 526.3 nm, and 645.2 nm. In the maximum saturation method, a test monochromatic stimulus presented in one half of the bipartite field is desaturated by the minimum amount required of one of the three primaries. The mixture of the test stimulus and the desaturation primary is color-matched by an appropriate mixture of the

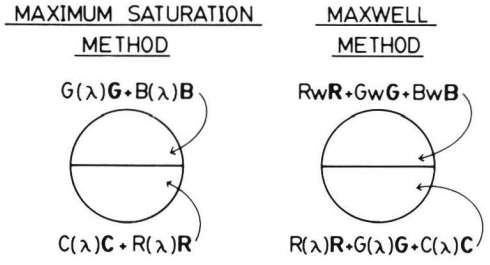

Fig. 1: Color matching in a bipartite field using the maximum saturation method and the MAXWELL method

remaining two primary stimuli appearing in the upper half of the bipartite field. The retinal illuminance of the test stimuli were 100 Td. In the case shown in Fig. 1, the test stimulus **C** desaturated by the red primary **R** is color-matched by an appropriate mixture of two primaries, **G** and **B**. The color matching functions are defined by

$$\bar{r}(\lambda) = -R(\lambda)/C(\lambda) \quad (1)$$

$$\bar{g}(\lambda) = G(\lambda)/C(\lambda) \quad (2)$$

$$\bar{b}(\lambda) = B(\lambda)/C(\lambda) \quad (3)$$

where $C(\lambda)$, $R(\lambda)$, $G(\lambda)$, and $B(\lambda)$ are measured in radiant powers of **C**, **R**, **G**, and **B** stimuli required to obtain a color match. In other words, the amounts $R(\lambda)$, $G(\lambda)$, and $B(\lambda)$ are the tristimulus values of the test stimulus **C**.

In the MAXWELL method, a fixed reference stimulus **W**, usually white, is presented in the upper half of the bipartite field. In the present experiment, a reference white stimulus was provided by mixing three primary stimuli of the Trichromator to give to chromaticity coordinates of D65 white ($x = 0.313$, $y = 0.329$) and a retinal illuminance of 1000 td. In the lower half, a mixture of the test stimulus **C** and two of the three primary stimuli is presented. The wavelength of the test stimulus determines

which two of the three primaries must be added to the test stimulus. If the test stimulus in a short wavelength region is employed as shown in Fig. 1, the red and green primaries are added to the test stimulus. In this case, the color matching functions are determined by

$$\bar{r}'(\lambda) = [R_w - R(\lambda)]/C(\lambda) \quad (4)$$

$$\bar{g}'(\lambda) = [G_w - G(\lambda)]/C(\lambda) \quad (5)$$

$$\bar{b}'(\lambda) = B_w/C(\lambda). \quad (6)$$

In this equation, R_w, G_w, and B_w are the tristimulus values of the white reference stimulus. In the MAXWELL method, a color match is always achieved at the reference white. On the other hand, a color match by the maximum saturation method is achieved at the chromaticity near test monochromatic color.

Fig. 2 shows the color matching functions measured by both methods. Open symbols are obtained by the maximum saturation method, and solid symbols are obtained by the MAXWELL method. If the proportionality and additivity laws hold strictly, the color matching functions derived from the MAXWELL method must be identical to those derived by means of the maximum saturation method. The red and green color matching

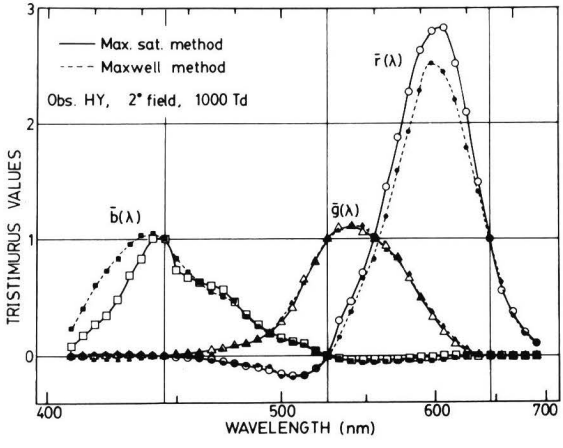

Fig. 2: Color matching functions obtained by the maximum saturation method (open symbols) and by the MAXWELL method (solid symbols)

functions are not much different from the maximum saturation method to the MAXWELL method. On the other hand, the blue color matching functions are different between two methods in the short wavelength region. A similar difference was also shown in WYSZECKI's data [2].

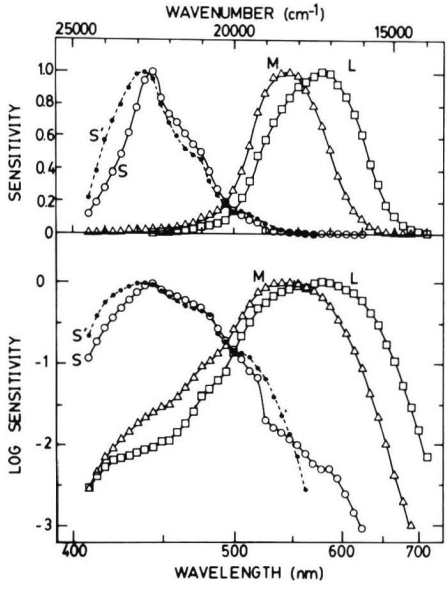

Fig. 3: Cone-sensitivity functions $S(\lambda)$, $M(\lambda)$ and $L(\lambda)$ derived from the linear combination of color matching functions obtained by the maximum saturation method. Cone sensitivity function $S'(\lambda)$ is derived from the linear combination of the MAXWELL color matching functions

3. Cone-sensitivity functions

In order to make a color vision model, the spectral sensitivity of each type of cones must be determined. Cone-sensitivity curves were determined under four conditions:

1. The cone-sensitivity functions should be linear combinations of color matching functions.
2. The cone-sensitivities should be positive values over the whole wavelength region.
3. The cone-sensitivity curve should have a single peak.
4. A shape of the cone-sensitivity curve is similar to that of the π mechanism. The short-wave sensitive cone is similar to the π_1, the middle-wave sensitive cone is similar to π_4, and the long-wave sensitive cone is similar to π_5.

The resultant cone-sensitivity functions are presented in the following equations.

$$L(\lambda) = 0.303\ \bar{r}(\lambda) + 0.579\ \bar{g}(\lambda) + 0.0091\ \bar{b}(\lambda) \tag{7}$$

$$M(\lambda) = 0.0223\ \bar{r}(\lambda) + 0.807\ \bar{g}(\lambda) + 0.0249\ \bar{b}(\lambda) \tag{8}$$

$$S(\lambda) = 0.0005\ \bar{r}(\lambda) + 0.0203\ \bar{g}(\lambda) + 1.000\ \bar{b}(\lambda). \tag{9}$$

These cone-sensitivity functions are normalized at the peak wavelengths. The color matching functions $\bar{r}(\lambda)$, $\bar{g}(\lambda)$ and $\bar{b}(\lambda)$ are obtained by the maxi-

mum saturation method. Since the blue color matching function by the MAXWELL method is deviated from that by the maximum saturation method, another blue cone sensitivity function $S'(\lambda)$ was determined by the following equation with the MAXWELL color matching functions.

$$S'(\lambda) = 0.0016\,\bar{r}'(\lambda) + 0.0663\,\bar{g}'(\lambda) + 0.955\,\bar{b}'(\lambda). \quad (10)$$

Fig. 3 shows the cone-sensitivity curves obtained by the linear combination of the color matching function.

4. Luminous efficiency function by flicker photometry

The luminous efficiency function was measured by means of flicker photometry. The flicker frequency was set at 20 Hz throughout the test wavelength region. A 2° full field was presented in a dark surround. The D65 white of 100 Td was used for the reference stimulus.

The experimental data was curve-fitted by the least squares method on the assumption that the luminous efficiency function by flicker photometry is a linear combination of luminous efficiency functions of the components. The function predicted by this linear model is

$$a(\lambda) = 0.515\,L(\lambda) + 0.512\,M(\lambda). \quad (11)$$

There is no contribution of the short-wave sensitive cone. An actual coefficient for $S(\lambda)$ by the least squares fitting was – 0.002. This value is negligible. Fig. 4 shows the comparison between experimental data and the predicted function. Correlation between experimental value and predicted

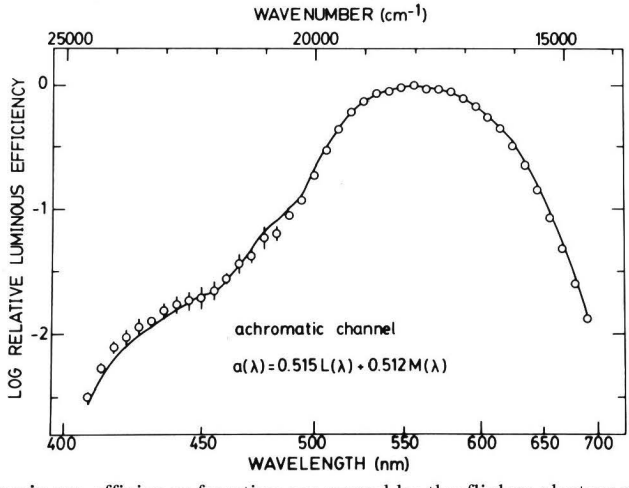

Fig. 4: Luminous efficiency function measured by the flicker photometry. Open circles show the experimental data, solid line shows a linear combination of color matching functions

value was 0.9992, which means an excellent fit. So, we can say that the signals from the long-wave sensitive cones and the middle-wave sensitive cones are linearly transformed to the achromatic channel. On the other hand, the short-wave sensitive cones do not contribute to the achromatic channel.

5. Opponent-color response functions

Opponent-color response functions were measured by hue cancellation method developed by JAMESON and HURVICH [3]. Monochromatic stimuli of unique hue were used for the cancellation stimuli except for red. A 690nm stimulus was used for the red cancellation stimuli. The r/g opponent color response functions are defined by $r/g(\lambda) = k_r E_g/E(\lambda)$ for red chromatic valence, and $r/g(\lambda) = -k_g E_r/E(\lambda)$ for green chromatic valence, where $E(\lambda)$, is the radiant power of the test stimulus, E_r and E_g are those of the cancellation stimuli. Coefficients k_r and k_g are determined by $k_g/k_r = E(513)/E(690)$. Similarly, the y/b opponent color functions are determined by $y/b(\lambda) = k_y E_b/E(\lambda)$ for yellow response function, and $y/b(\lambda) = -k_b E_y/E(\lambda)$ for blue response function, where $k_b/k_y = E(476)/E(571)$.

The r/g opponent-color response curve is curve-fitted on the assumption of the linear transformation by the cone signal. In this case, $S'(\lambda)$ instead of $S(\lambda)$ was used for the sensitivity of short-wave sensitive cone

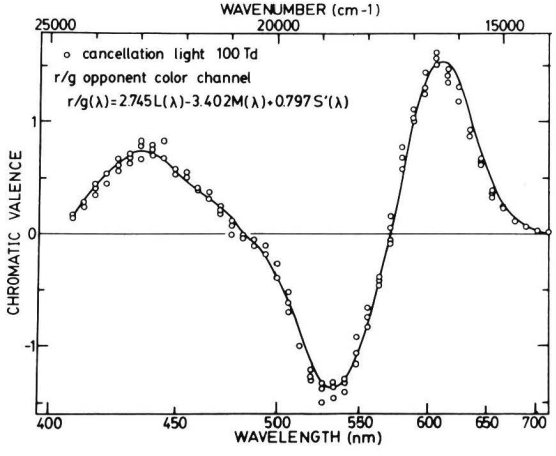

Fig. 5: The red-green opponent-color response function measured by the hue cancellation method. Open circles show the experimental data, solid curve shows the opponent response function predicted by the linear transformation model

because of its good fitness. The predicted r/g opponent function is presented as

$$r/g(\lambda) = 2.745\,L(\lambda) - 3.402\,M(\lambda) + 0.797\,S'(\lambda). \quad (12)$$

Fig. 5 shows an excellent fit over the whole wavelength region. The r/b opponent response curve is, however, not well fitted by the linear transformation hypothesis as shown in the broken line in Fig. 6. Therefore, we must introduce a non linear tranformation hypothesis for the y/b opponent color process. The non linear transformation suggested by WERNER and WOOTEN [4] was applied here. The predicted y/b opponent-color function is

$$y/b(\lambda) = [0.991\,L(\lambda) - 0.021\,M(\lambda)]\,5.4 - 2.217\,S'(\lambda). \quad (13)$$

The fitness becomes well. Furthermore, you can notice that the coefficient for $M(\lambda)$ is negligibly small. It suggests that the middle wavelength cone could not be transformed to the y/b opponent color process.

6. Conclusions

1. The long- and middle-wave sensitive cone signals are linearly transformed to the achromatic channel. The short-wave sensitive cone, however, does not contribute to the achromatic channel.

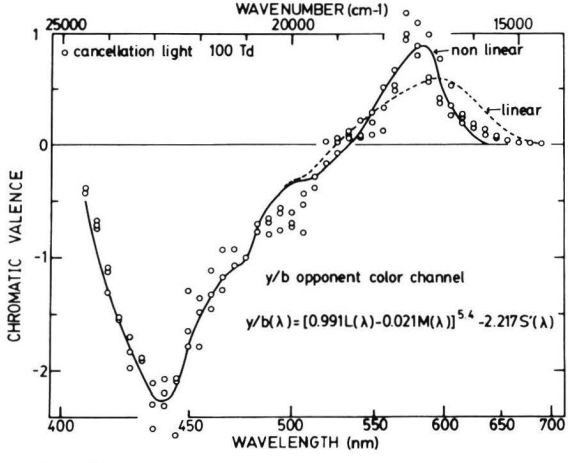

Fig. 6: The yellow-blue opponent-color response function measured by the hue cancellation method. Open circles show the experimental data, a dashed curve is predicted by the linear transformation model, and a solid curve is predicted by the non-linear transformation model

2. The *r/g* opponent color channel is linearly processed by the transformation of cone signals.
3. The *y/b* opponent color channel is non-linearly processed by the cone signals of long- and short-wavelength cones. The middle-wave sensitive cones signals are not transferred to the *y/b* opponent color channel.

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Author's address:
Dr. Hirohisa Yaguchi
Dept. of Image Science and Engineering
Chiba University
1–33 Yayoi-cho
Chiba, Japan 260

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Russell L. De Valois*, BERKELEY, Cal.:

Color-Opponent and Non-Color-Opponent Information in the Visual System

DK 612.843.3

Some 30 years ago we reported that most macaque geniculate cells are color-opponent: RG cells (differencing the outputs of L and M cones); and YB cells (differencing S and [L+M] cones). Neither quite corresponds to perceptual RG and YB axes, suggesting a later (cortical) stage of color processing. In dispute is the luminance path(s). We suggest three luminance paths, which may well have somewhat different properties: magno cells; some non-opponent parvo cells; and multiplexed with color in RG opponent cells.

Vor 30 Jahren haben wir berichtet, daß fast alle Zellen im Genikulatum des Affen farben-opponent sind: RG Zellen (die die Differenz des Antwort von L und M Zapfen ergeben) und YB Zellen (Differenz S und [L+M] Zapfen). Keine von diesen entsprechen den perzeptuellen RG und YB Achsen, was eine spätere (kortikale) Stufe der Farbenbehandlung andeutet. Wir schlagen drei Helligkeitswege vor (die vielleicht auch andere Eigenschaften haben): Magnoeinheiten, nicht-opponente Parvoeinheiten und mannigfaltige, mit Farbe in RG opponente Einheiten.

Il y a une trentaine d'années nous avons trouvé que la plupart des neurones dans le corps genouillé du macaque montrent une opposition de couleurs: les cellules RG (indiquant la différence des activités entre cônes L et M); les cellules YB (la différence entre cônes S et [L+M]). Ni les unes ni les autres ne correspondent exactement aux deux axes perceptuels, rouge-verte ou jaune-bleu, ce qui suggère qu'il y a une autre étape (corticale) de traitement des couleurs. La voie (ou les voies) de la luminosité reste encore un sujet de controverse. Nous proposons pour la luminance l'existence de trois voies (qui pourraient avoir certaines différences entre elles): des neurones magnocellulaires, certains neurones parvocellulaires, et ceux qui transmettent la luminance en multiplex avec la couleur dans les neurones RG.

For my contribution to this symposium I have been asked to comment on the existence and role of color-opponent cells in the visual system. It is not clear how appropriate a consideration of color-opponent cells is for a symposium honoring STILES and WYSZECKI, because neither of them gave much if any thought to color-opponent organization – no doubt because their primary concerns were with processes almost totally determined by receptor characteristics alone. Nonetheless, I would like to take this occasion to express my great admiration for the superb work they did on elucidating many aspects of vision function.

* *University of Californiay, Dept. of Psychology and Physiological Optics, Berkeley, CA.*

However awkwardly this contribution may fit into a celebration of STILES' work, it may be appropriate at this time since it is now approximately the 30th anniversary of our discovery of color-opponent cells in the primate visual system [1], and the concurrent discovery by SVAETICHIN and MACNICHOL [2] of somewhat similar cells in the fish retina. Our findings of color-opponent cells in recordings from single cells in the macaque lateral geniculate nucleus were later confirmed by WIESEL and HUBEL [3], and since then by literally dozens of other investigators. There in fact have never been any contrary claims from physiological studies with respect to the presence of such cells in the early visual path of higher primates. However, there was initially considerable resistance from psychophysicists to accepting the HERING-like idea of an opponent-color organization, due no doubt to the overwhelmingly popular HELMHOLTZian viewpoint then present in the psychophysical community. (A very prominent psychophysicist wrote me a fatherly letter at the time, strongly advising me that if I published the obviously falacious evidence that there were color-opponent cells in the primate visual pathway I would destroy my career!) Only gradually was the position accepted that there need be no conflict between the presence of three independent cone types and of an opponent organization to the neural processing of the output of these receptors.

Ironically, the major point of continuing debate on the physiological side is not whether opponent cells exist, but whether there are any *but* opponent cells in the parvocellular pathway; that is, whether any of the cells in the four parvocellular geniculate layers are spectrally non-opponent, presumably carrying only luminance information. Note that no one has ever found a retinal ganglion cell or a geniculate cell which receives its input from only a single cone type, as the simple HELMHOLTZian view would predict. Rather the issue is whether, in addition to the opponent cells which are differencing the receptor outputs, there exist non-opponent cells which sum the outputs of at least the L and the M cones to give something like the V_λ function.

On the basis of recordings from a considerable population of (almost exclusively) parvocellular geniculate cells in macaques, DE VALOIS, ABRAMOV and JACOBS [4] postulated that the cells fell into three pairs of response types, two spectrally opponent and one non-opponent. These we termed RG cells (+R–G and +G–R), on the basis of the approximate color appearance of the spectral regions to which such cells gave their maximum excitation and inhibition; YB cells (+Y–B and +B–Y); and non-opponent cells. We presented evidence [4; 5] that the RG cells were differencing the outputs of the L and M cones; that the YB cells were differencing the outputs of the S and L (or the S and [L+M]) cones; and that the non-opponent cells were summing the outputs of the L and M cones. WIESEL and HUBEL [3] suggested in effect the same six types of cells (three

pairs), although they distinguished them on the basis of their spatial receptive fields. This evidence for just two pairs of opponent cell types was disputed by DE MONASTERIO and GOURAS [6] and others, who postulated as many as 26 different cell types. Recent evidence by DERRINGTON, KRAUSKOPF and LENNIE [7], using more elegant stimulus presentation techniques than earlier investigators, quantitatively confirmed our initial categorization of the spectrally opponent cells.

One of the questions raised by the organizers of this symposium is "Is it useful to employ the concept of opponent channels?" A literal interpretation of this question leads to a very clear and obvious answer, namely that it is not only useful but obligatory to employ the concept of opponent channels if one wants one's model of visual function to bear any relation to the actual organization present in the primate visual nervous system. One would hope that it would not take any more than 30 years for this point to get through to even the most impermeable of minds. A more interesting, if strained, interpretation of this question is "Why did we evolve opponent-color channels? What do thery do for the organism?" It seems to me that there are at least two answers to this question. One is that color information resides not in the output of individual cone types (a point that many people obscure for themselves and others by referring to cones by color-names), but in the differences between the outputs of the different cone types. Opponent-color cells, then, are extracting precisely the relevant data for color vision. Another answer to this question, put forth most clearly by BUCHSBAUM and GOTTSCHALK [8], is that the different cone types (especially the L and the M cones) overlap in spectral sensitivity so much that sending the cone outputs separately up the visual path would be very redundant. Spectrally-opponent cells, responding as they do to receptor differences, minimize this redundancy.

As we pointed out in 1966 [4], the responses of RG and YB cells to a first approximation correspond to the perceptual RG and YB axes (hence our so terming them), but to a second approximation do not. Specifically, RG cells respond uniformly to all short wavelengths (with excitation in the case of +G–R cells and inhibition in the case of +R–G cells), rather than showing the triphasic response one would expect from the reddish appearance of very short wavelengths. The response shape seen in geniculate cells is what one would expect from a differencing of L and M cones; the triphasic perceptual function necessitates an input from S cones in the same direction as the L cone input. Also, the short-wavelength end of the YB cell response function is maximal at very short wavelengths, in the violet, rather than in the blue as one would expect from the perceptual YB axis. In short, we modeled the cell responses as resulting from differencing pairs of cone types; the perceptual color axes cannot be derived from such simple subtractions. This same point has recently been made very clearly by DERRINGTON et al. [7], in their study of

the responses of geniculate cells to stimuli modulated along different color axes. They showed that RG cells modulate their responses along a constant S-cone axis, and YB cells along a tritan axis, neither of which corresponds precisely to the perceptual color axes.

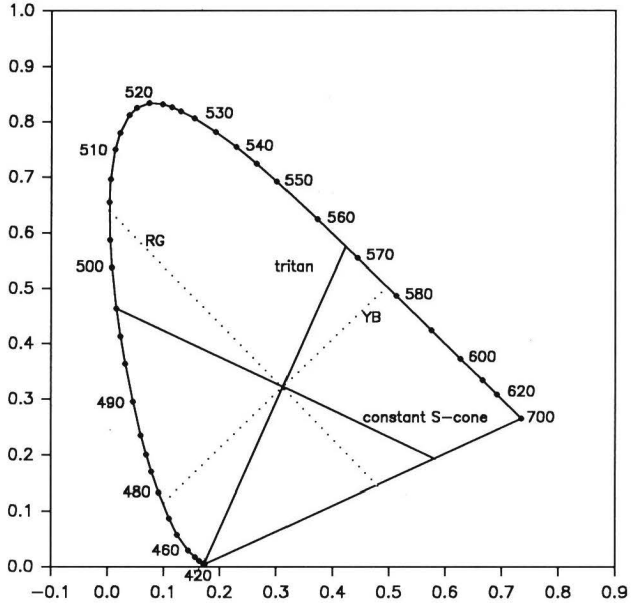

Fig. 1: CIE chromaticity diagram with geniculate-cell and perceptual axes. In solid lines: modulation axes of RG opponent cells (constant S-cone axis) and YB opponent cells (tritan axis). Dotted lines: approximate perceptual RG and YB axes.

This discrepancy between the characteristics of geniculate cells and perception (see Fig. 1) suggests the possibility of a later stage of interaction, at some cortical level, in which the information is transformed with a rotation of both color axes. In fact, one often finds cells in the striate cortex whose responses correspond closely to the perceptual RG axis, with excitation to both spectral extremes and inhibition in the green, or vice versa. However, there is not as yet sufficient evidence to indicate whether striate cells fall into restrictive classes, as we and now others find geniculate cells to do.

As mentioned above, a major dispute with respect to the organization of information in the path from eye to brain is with respect to non-opponent cells, which presumably carry luminance information. There is gen-

eral agreement that the cells in the magnocellular geniculate layers are largely if not entirely spectrally non-opponent. However, our evidence [4; 5] and that of WIESEL and HUBEL (their type III cells [3]) that there are spectrally non-opponent cells in the parvocellular layers has been disputed by several more recent investigators. For instance, PADMOS and VAN NORREN [9] showed that many and perhaps all cells which would be classified as non-opponent by our tests, since they show excitation to a flash of any monochromatic light across the spectrum (or uniform inhibition in the case of mirror-image cells), can in fact be shown to give the opposite response in the presence of a strong chromatic adapting field. Likewise, DERRINGTON et al. [7] find no parvocellular cells which modulate only in the pure luminance plane. However, in the case of both of these types of experiments, the deviations from pure luminance responses on the part of a significant fraction of parvocellular cells is quite small: many of the cells DERRINGTON et al. [7] classify as RG opponent in fact give very large responses in the luminance plane and very feeble responses to red-green variations. It would seem more reasonable to categorize such cells as carring luminance rather than red-green color information.

Another complication in the question of how luminance and color information is transmitted up the visual path is that we have shown that most if not all RG opponent cells multiplex color and luminance information, shifting from opponent to non-opponent response characteristics as a function of the spatial frequency of the stimulus [10]. With full-field stimuli or those of low spatial frequencies, the cells give opponent responses to red-green modulations and almost no response to white-black or monochromatic luminance variations; with patterns of high spatial frequencies, the same cells respond to luminance but not color variations. DE VALOIS and DE VALOIS [11] have shown that this is predictable from a consideration of the cone inputs to these cells, the nature of which was first described by WIESEL and HUBEL [3].

I would therefore propose that there are at least two and perhaps three different luminance pathways from retina to cortex: (a) magnocellular path, (b) multiplexed with color in the RG opponent parvocellular cells, and (c) perhaps a class of non-opponent parvocellular cells in addition. Each of these luminance paths is presumably involved with a different aspect of visual information, and each may have somewhat different spatial and temporal properties. For instance, magno-cells respond to higher temporal frequencies, and optimally to somewhat lower spatial frequencies than parvo-cells. Furthermore, the magno-cell path is largely discrete through the cortex as well (with strong input to area MT), and there is considerable evidence that this system may be mainly devoted to dealing with movement information. Thus "luminance information" coming up this path may well have very different characteristics than the "lumin-

ance information" coming up the parvo-cell paths. It is conceivable, of course, that not only might the spatial and temporal properties of these various luminance paths differ, but their precise spectral sensitivity as well – S cones, for instance, might be summed with L and M cones in one path but not in another.

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Author's address:
Prof. Dr. R. L. De Valois
University of California
Dept. of Psychology and Physiol. Optics
9210 Tolman Hall
Berkeley, CA., 94720, USA

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Akimichi Kaneko*, OKAZAKI:

Conversion of Trichromatic Cone Responses to Color-Opponent Responses in the Second-Order Neurons in the Turtle Retina**

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Chromatic information received by three sets of cones is converted into opponent responses in the second-order neurons, horizontal cells. The mechanism involves subtype-specific feedforward and negative feedback connection between cones and horizontal cells. The negative feedback is mediated by an inhibitory neurotransmitter, γ-aminobutyric acid.

Die von den drei Zapfenarten empfangene Farbinformation wird in den Neuronen zweiter Ordnung, den horizontalen Zellen, in Gegenfarbensignale umgewandelt. Der Mechanismus schließt subtyp-spezifische Mit- und Gegenkopplungsverbindungen zwischen den Zapfen und den horizontalen Zellen ein. Die Gegenkopplung wird durch einen inhibitorischen Neurotransmitter, die γ-aminobutyrische Säure, vermittelt.

L'information chromatique que les trois sortes des cônes ont reçue, est transformée, dans les neurones secondaires (ce sont les cellules horizontales), aux signaux à couleurs opposées. Ce mécanisme comprend des co- et contre-couplages entre les cônes et les cellules horizontales. Le contre-couplage est effectué par l'acide γ-aminobutirique comme transmetteur neural.

1. Introduction

The vertebrate retina receives chromatic information by three sets of cones having different spectral sensitivity and processes it into opponent responses at an early stage of the neural network. The underlying mechanism responsible for the color opponent responses of biphasic and triphasic horizontal cells has been studied extensively in the past decades. The model proposed by FUORTES and SIMON [1] on the turtle retina has been widely accepted as the most plausible interpretation. Their model involves subtype-specific feedforward and negative feedback connections between cones and horizontal cells (Fig. 1). Similar model has been suggested also in the fish retina based on the subtype-specific synaptic morphology of cone terminals [2]. The feedback effect from horizontal cells to cones was first demonstrated by BAYLOR et al. [3], who showed

* *National Institute for Physiological Sciences, Okazaki (Japan)*
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that polarization of a horizontal cell by injection of an extrinsic current caused polarization of opposite polarity in nearby cones. In spite of popularity of the feedback synapse, direct supporting evidence was not abundant.

γ-Aminobutyric acid (*GABA*) has been suggested as a candidate of the neurotransmitter of a subtype of horizontal cells, the monophasic horizontal cell. This type of horizontal cell is characterized by its hyperpolarizing responses to monochromatic light flashes of all visible wavelengths [4; 5]. However, inhibitory role of *GABA* in the cone horizontal cell network was not well elucidated.

Difficulty in analyzing the retinal circuitry arises partly from the complicated network of closely packed retinal neurons. Even if one could observe an expected effect in target cells, it may well be an indirect effect

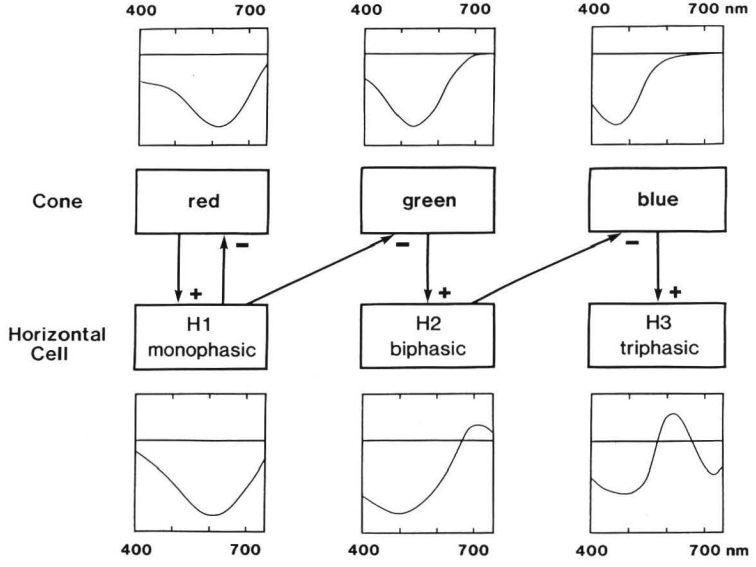

Fig. 1: A model of the outer plexiform layer of the turtle retina. Modified from FUORTES and SIMON [1]. Arrows indicate synapses and the direction of signal transmission. Positive sign represents the sign-conserving synapse at which the response polarities of presynaptic and postsynaptic cells are identical. Negative sign represents the sign-inverting synapse at which the response polarity of presynaptic cells is reversed in the postsynaptic cell. Curves in boxes illustrated above each type of cones or below each type of horizontal cells represent the envelop of response amplitudes of each cell to monochromatic light flashes of various wavelengths (in the spectral range of appraximately between 400 nm and 750 nm). Horizontal straight lines in the boxes indicate the dark membrance potential level: deflections above this level indicate depolarizing responses, while deflections below this level indicate hyperpolarizing responses.

caused on other cells which have connections with the target cell. Solitary retinal cells dissociated from the network provide an ideal preparation to get out of such complexity. They are particularly suitable for examining the chemosensitivity, not only because they are independent of interaction with other cells, but also because they are free from the diffusion barrier, or from a population of surrounding cells which sequester the applied chemical compounds such as amino acids from the extracellular space by an active uptake [6].

This paper summarizes our recent studies [7–10] of the effect of *GABA* on various types of solitary photoreceptors dissociated from the freshwater turtle (*Geoclemys reevesii*) retina. Our results provide a new piece of supporting evidence for the *GABA*-operated negative feedback connection from monophasic horizontal cells to red-sensitive and green-sensitive cones.

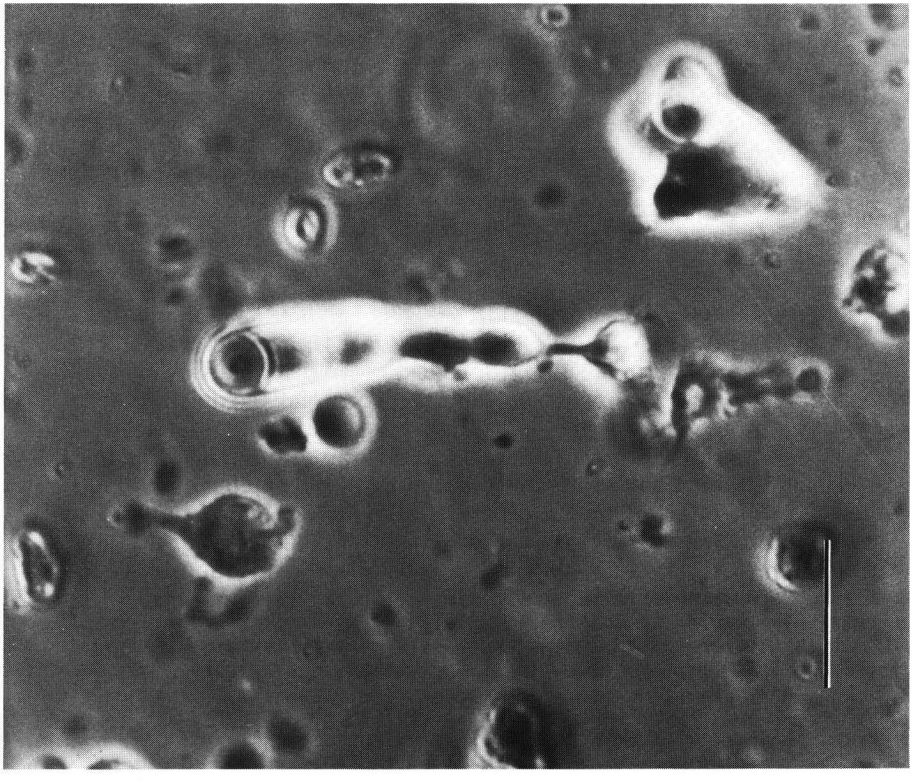

Fig. 2: Photomicrograph of a single cone containing red oil droplet dissociated from *Geoclemys reevesii*. Calibration, 20 μm.

2. GABA-induced responses in solitary cones

2.1: Morphological identification of turtle photoreceptors

Turtle photoreceptors are classified morphologically into seven types [9; 10] by their unique cell shape and by various colors of the oil droplets located at the distal end of the inner segments; four types of single cones, one type of double cone consisting of the principal and accessory members, and one type of rod. These morphological features are unequivocal markers for identification of spectral subtypes [9; 10].

2.2: Difference in GABA sensitivity among cell types

Solitary photoreceptors (an example in Fig. 2) were recorded by the whole-cell mode of patch clamp technique [11] under direct visual control. The resting membrane potential of all types of solitary photoreceptors was usually between -30 mV and -40 mV. When *GABA* was applied ionophoretically to a cone containing red oil droplet (holding potential, -60 mV), an inward current was evoked (Fig. 3). There was a large regional difference in *GABA* sensitivity; highest at the axon terminal and lower at the distal part of the cell. The single cone containing red oil droplet (red-sensitive cone) and the single cone contraining orange oil droplet (green-sensitive cone) had a high *GABA* sensitivity. The least effective dose determined by a pressure application of known concentration of *GABA* was approximately 100 nM. On the contrary, *GABA* sensitivity in single cones containing non-fluorescent colorless oil droplet (blue-sensitive cone) or rods was extermely low.

2.3: Ionic mechanisms of GABA-induced currents

The polarity of *GABA*-induced current may appear contradictory to what is expected from the inhibitory effect of *GABA*, because the inward current depolarizes the cell membrane. We soon realized that the current induced by *GABA* is carried by Cl^- almost exclusively. Diffusion of Cl^- from the suction pipette to the cell interior raised the intracellular Cl^- concentration ($[Cl^-]_i$) soon after the rupture of the patch membrane. To observer the effect of *GABA* on intact cells (before $[Cl^-]_i$ increase), we recorded voltage responses of solitary cones immediately after rupture of the patch membrane. Within a few second after the rupture, *GABA* caused a hyperpolarization in a cell whose resting potential was -37 mV. This observation strongly suggests that *GABA* induces a membrane hyperpolarization in intact cones.

3. Physiological role of GABA-operated feedback circuit

The present study has demonstrated that turtle cones are sensitive to *GABA* and that the senitivity varies among subtypes. It is inferred that

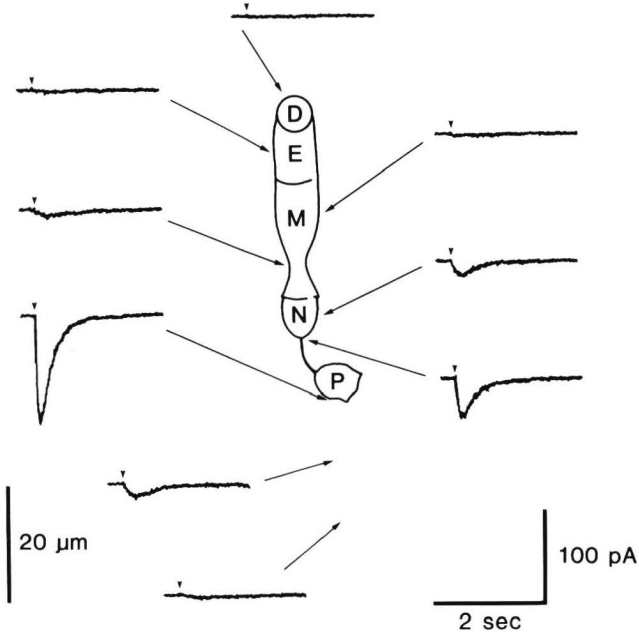

Fig. 3: Responses of a single cone containing red oil droplet to *GABA* applied ionophoretically at various positions on the cell surface. The recording suction pipette was positioned at the cell body. Holding potential was –60 mV. *GABA* was applied ionophoretically by passing brief current pulses (5 ms, 25 nA; timing indicated by arrow heads) through a fine-tip glass micropipette. At the pedicle the dose of *GABA* evoked a response whose amplitude was about 1/3 of the maximum. Braking current –5 nA. Responses to *GABA* applied 10 and 20 μm away from the pedicle are also illustrated to demonstrate a limited distance of *GABA* diffusion. D, oil droplet; E, ellipsoid; M, myoid; N, cell body containing the nucleus; P, cone pedicle.

both red-sensitive (except for the accessory member of double cones) and green-sensitive cones have high sensitivity to *GABA*, while blue-sensitive cones and rods have very low sensitivity. It is tempting to believe that *GABA* is the transmitter substance used in the interaction between the monophasic horizontal cell and red-sensitive and green-sensitive cones, since *GABA* was effective at a concentration as low as 100 nM, and the *GABA* sensitivity was clearly localized to the cone pedicle where they make contacts with horizontal cells.

Finally, we wish to speculate the functional aspects of the *GABA*ergic negative feedback synapse from monophasic horizontal cells to red-sensitive and green-sensitive cones. In the dark, cones release their transmit-

ter tonically. There are a number of reports that transmitter substance of cone photoreceptors depolarize horizontal cells [12–15]. Depolarization triggers release of *GABA* from monophasic horizental cells [16; 17], which, in turn, causes membrane hyperpolarization in both red-sensitive and green-sensitive cones. Illumination of light hyperpolarizes photoreceptors, and sequence of events of the opposite polarity is expected to occur during light flashes.

It seems possible that the negative feedback interaction (Fig. 1) plays three important roles in the function of the retina; color opponent responses of biphasic horizontal cells, center-surround antagonism, and the gain control of cone output. If the forementioned sequence of events in the neural chain starts from the red-sensitive cone, and is relayed by the monophasic horizontal cell to green-sensitive cones, biphasic horizontal cells respond with depolarization to red light. If and when the negative feedback operates between red-sensitive cones and monophasic horizontal cells bidirectionally, such interaction would result in surround antagonism in red-sensitive cones, since the spatial summation in monophasic horizontal cells is much larger than in red-sensitive cones. This circuit may also contribute in compressing the light-evoked voltage responses of both red-sensitive cones and horizental cells.

Morphological studies have shown that biphasic, and triphasic horizontal cells also have subtype-specific connections [18]; biphasic cells with green-sensitive and blue-sensitive cones, and triphasic cells with blue-sensitive cones. It is also shown that these types of horizontal cells neither accumulate *GABA* nor have machinery to synthesize *GABA* [19–22]. Low *GABA* sensitivity in blue-sensitive cones agree with those reports, but the question how these types of horizontal cells communicate with photoreceptors still remains open.

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Author's address:
Prof. A. Kaneko
National Institute for Physiological Sciences
Mijodaiji, Ozaka 444, Japan

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Adam Reeves*, BOSTON, Mass.

Transient Desensitization of Opponent Channels: A Review

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Darkening or turning off a yellow field can make one insensitive to blue (transient tritanopia). Turning off (or turning white) red or green fields can also make one less sensitive to red or green. Such transient desensitizations of the RG/YB opponent color pathway may in turn influence brightness.

Erlöschen oder Abbdunkeln eines gelben Feldes kann zu vorübergehendem Verlust der Blauempfindlichkeit führen (transiente Tritanopie). Erlöschen oder Aufhellen eines roten oder grünen Feldes kann sich ebenfalls in einem zeitlich beschränkten Verlust der Grün- bzw. Rotempfindlichkeit auswirken. Solche vorübergehenden Empfindlichkeitsverluste der RG/GB-Systeme können wiederum den Helligkeitseindruck beeinflussen.

Éteindre un champ jaune (ou l'assombrir) peut rendre insensible au bleu (transient tritanopia). Éteindre un champ rouge ou vert (ou le blanchir) abaisse la sensibilité au rouge ou au vert. De telles désensibilisations des canaux antagonistes (RV/JB) peuvent, à leur tour, influencer la luminance apparente.

1. Introduction

When the intensity or wavelength composition of an adapting field is suddenly altered, thresholds of stimuli detected by the opponent hue channels [1] may rise abnormally [2; 3]. The purpose of this brief review is to list the conditions responsible for this desensitization effect. With short-wave tests the effect reaches over 2 log units and well deserves MOLLON and POLDENS's term *transient tritanopia* [3; 4]; Y/B opponency is clearly indicated [5; 6; 7]. For middle or lang-wave tests, desensitization reaches only about 0.6 log units, but also requires an opponent (R/G) account [8]. It appears that only MW and LW cones are involved in R/G desensitization [8], although all three cone types are involved in Y/B [9]. The various desensitization effects may be grouped together under the rubic of opponency, as the conditions producing them are similar in Y/B and R/G (although whether analogous black/white opponent effects exist is unknown). The conditions include (see below) a non-neutral field (e.g., well above 500 nm in Y/B); a steady, rather than slowly flickering, adaptation; and a limited range of field intensities. The effect is retinal, as it does not occur with dichopitc stimulation [4]; indeed, transient tritanopia is measurable in the ERG [10].

* *Dept. of Psychology. Northeastern University, Boston*

The desensitization results show that the sensitivities of the putative luminance and opponent channels may vary independently. For example, after adaptation to steady red, green, or blue fields, an abrupt drop in field intensity increases the sensitivity of the luminance channel [8], but decreases that of R/G [8; 11]. In so far as brightness depends on contributions from both luminance and hue channels, models for brightness will need refining to take account of such opposite-going sensitivity changes.

2. Conditions for desensitization

2.1: Field changes: decrements in intensity

The following set of five conditions, met jointly, will generate opponent desensitizations following a decrement in field intensity:

a) Field intensity should be within an approximately 4 log unit photopic range, which is 6.4 to 10.4 log quanta/sec/deg^2 in R/G [11] and 8.3 to 12.3 log quanta/sec/deg^2 in Y/B [4].

b) Fields should be steady during adaptation, since transient desensitization virtually disappears if the field is flickered at 1 of 2 Hz throughout adaptation, in both Y/B [12; 13] and in R/G [8; 11]; note that very slow flicker rates, which permit the adaptations of the cones to change, can also produce opponent effects [14].

c) Fields should not be 'neutral' – that is, neither white [15], nor yellow in R/G [8], nor unique green in Y/B [5; 6] – but just how different from neutral the fields should be is not known.

d) Field intensity should drop as least 0.6 log units in Y/B [4]; the equivalent figure in R/G has not been obtained.

e) Tests should be isolated to the opponent channel under study: this is not easy to ensure in R/G, as the luminance pathway may take over detection [4, 8], but it may be done with appropiate long-wave tests [11; 15]. In Y/B, isolation of short-wave tests is possible when using long-wave fields, but not with short-wave fields, on which detection shifts to MW cone pathways at low intensities, and so the blue side of the Y/B opponency must be inferred [5].

That Y/B desensitization (transient tritanopia) can be so much greater than R/G desensitization might suggest that the Y/B pathway is organized differently than the R/G pathway, perhaps even involving a unique B anomaly [4]. However, this may simply reflect the relative separation of the SW from MW and LW cone action spectra. The spectral separations imply that on (non-bleaching) long-wave fields the ratio of Y to B will greatly exceed that of R to G. Hence, turning off such a field will change Y/B more than R/G. The Y/B change can however be reduced to an appropriate level by attenuating the field rather than turning it off [4].

The same small opponent desensitization will then occur as in R/G; the appropriate attenuation is predictable from spectral overlap and the adaptation states of the cones alone [8].

2.2.: Field changes: increments in intensity

Field intensity has been raised in just one study [17], in which large Y/B desensitizations occurred on very bright bleaching yellow fields. This contrasts with the abolition of transient tritanopia found at bleaching levels when the field is turned off [4; 16]. It is not known whether analogous phenomena exist in R/G.

2.3.: Field exchanges

Although the original studies mostly employed an abrupt decrement in field intensity, transient desensitizations may occur after on field is exchanged for another. Exchanges have been of wavelength, with either luminance held constant, in R/G [15], or with effectiveness for a detection pathway held constand (silent substitution), for π-1 [4], for π-5′ [18], for π-5 [19], and for π-4 and π-4′ [20]. In π-1, the effect on threshold is over 2 log units, but in π-4, π-4′ and π-5′, the effect is small (typically 0.4 log units), and in π-5, it is tincy (0.1 log units). Although the data suggest an explanation of the π-4 and π-5 results in terms of R/G opponency [20], the π-5 result shows that the opponency is not symmetrical.

3. Time course

Opponent desensitization has a relatively slow time course, typically lasting many tens of seconds [2; 12; 15; 19; 21], in all studies of field decrement or field exchange. A secondary oscillation occurs in Y/B within 10 sec of field onset (only at bleaching levels) in the sole study of field increments [17]. In the model of PUGH and MOLLON [5], the slow time course is captured by time-constants between 10 and 35 sec. Such sluggishness is in obvious contrast to the time-course of recovery of the luminance channel, in which desensitization (CHRAWFORD effect) lasts about one-fifth of a sec or less before recovery ensues. However, the degree to which both Y/B and R/G desensitization occurs is heavily influenced by adapting field flicker, for rater between 20 Hz and 1 Hz, which might suggest a much shorter time constant [8, 12, 13]. This point is not yet resulved.

4. Significance

Heterochromatic brightness differs from luminance: monochromatic red and blue lights appear brighter than predicted from their flicker-photometric luminances [22], and the brightness of lights tends to increase

with their saturation (the HELMHOLTZ-KOHLRAUSCH effect). Thus brightness that typically been modelled as a sum pf positive functions of luminance and opponent channel responses [23]. One might therefore expect that desensititation of either of the opponent channels should decrease brightness. This expectation awaits empirical confirmation.

It is unclear whether transient desensitization has any functional utility in itself, or even is a by-product of some other process. Perhaps it simply reflects a sluggish adaptation of the opponent hue pathways. The luminance pathway may have evolved under greater pressure, as the penalty for such sluggishness would be large if contour, form and movement are primarily determined by luminance.

It is also unclear whether opponent desensitization matters in practice. The intensity ranges for the Y/B and R/G effects do span the light levels encountered in daily life, but some of the other requirements are less clear-cut. Of interest here are non-neutral color fields in the environment; that is, areas in which the predominant wavelengths are to one side of a neutral point (e.g., areas of grass, leaves, and blue sky for R/G). With steady fixation, it is known that slow flicker (1 to 2 Hz) of a non-neutral adapting field essentially prevents desensitization [8; 12]. Eye movements may vary the retinal location of any environmental non-neutral field sufficiently frequently to mimic this effect of flicker, and prevent opponent desensitization even when field conditions are otherwise optimal. However, they may not; this must depend on both the visual scene and the task. Desensitization likely depends on both the extent of non-neutral fields and the constancy of their retinal locations.

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Author's address:
Prof. Dr. A. Reeves
Department of Psychology
Northeastern University
360 Huntington Avenue
Boston MA 02115, USA

Manuscript received:
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Karen K. De Valois*, BERKELEY:

To what Extent is Color Information Analyzed Independently of Spatial and Temporal Information?

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Both detection and appearance of isoluminant chromatic stimuli depend upon spatial and/or temporal variables, color being present predominantly at low spatiotemporal frequencies. In addition, the spatial and/or temporal variations in simultaneously present luminance patterns can profoundly affect the detectability and the appearance of chromatic stimuli. Color masks luminance, but near-threshold luminance patterns facilitate color detection.

Wahrnehmung und Erscheinung von gleichhelligen Farbenreizen hängen beide von räumlichen, bzw. zeitlichen Veränderungen ab, Farben hauptsächlich bei unteren raumzeitlichen Frequenzen. Die räumlichen bzw. zeitlichen Veränderungen in gleichzeitig anwesenden Helligkeitsmustern können zusätzlich auch das Erkennen und Erscheinen von Farbreizen tiefgreifend beeinflussen. Farbe verschleiert Helligkeit, aber Helligkeitsmuster in der Nähe ihrer Schwelle erleichtert Farbenentdeckung.

La détection et l'apparence des stimuli chromatiques isoluminants dépendent des variables spatiales et temporelles; la couleur se voit surtout aux basses fréquences spatiotemporelles. De plus, les variations spatiales et/ou temporelles dans les modèles lumineux qui sont présents simultanément peuvent fortement influencer la détectabilité et l'apparence des stimuli chromatiques. La couleur masque la luminance, mais les modèles de luminance qui sont près du seuil facilitent la détection de la couleur.

In the absence of either spatial or temporal variation (or a combination thereof), perception related to the spectral character of the incident light is lost. Color drains rapidly from a Ganzfeld [1]. Even in the presence of spatial or temporal variation, no chromatic variation can be detected if the spatial or temporal frequency is sufficiently high. There is thus no analysis of color information which is truly independent of spatial and/or temporal contrast. The question of interest, then, becomes the form of the dependence of color analysis on spatial and temporal variables. We shall briefly consider spatiotemporal variations both of chromaticity and of luminance, and their respective effect upon both the detection and the suprathrehsold appearance of chromatic stimuli.

Condider first the effect of spatial and temporal variations in chromaticity in the absence of luminance variation. The d e t e c t i o n of an isolu-

* *University of California* at Berkeley, CA., *Dept. of Psychology and Physiological Optics*

minant pattern depends strongly upon both spatial and temporal factors. KELLY [2] has measured the chromatic spatio-temporal contrast-threshold surface for isoluminant, drifting red/green gratings, using image stabilization techniques. He reports that at temporal frequencies below about 0.2 Hz, the visual system behaves as though it were a perfect temporal differentiator. For any given spatial frequency, a plot of threshold modulation against drift velocity (on log-log coordinates) yields a straight line with a slope of 1 in this low temporal frequency region. Further experiments suggest that the sensitivity to very low temporal frequency modulation is directly proportional to the local temporal frequency and independent of spatial frequency, velocity and orientation.

When the temporal frequency is greater than 0.2 Hz, simple temporal differentiation does not appear to occur. If spatial chromatic contrast sensitivity is measured without image stabilization, the resulting function typically shows a rapid fall-off with increasing spatial frequency and no significant low frequency attenuation [3; 4], in contrast to the clear spatial bandpass character of the luminance contrast sensitivity function. This behavior can be well modeled by a consideration of the spatial receptive field characteristics of chromatic opponent cells such as those seen in the retina or the lateral geniculate nucleus (LGN) [5]. When the spatial frequency is very low, however, some low frequency attenuation appears [6]. If the image is stabilized and temporal frequency is carefully controlled, the spatial contrast sensitivity function becomes bandpass, with the region of peak sensitivity varying with temporal frequency [2]. It is clear, then, that sensitivity to chromatic contrast in the absence of luminance contrast depends markedly upon the spatial and temporal parameters of the stimulus.

When the task is to detect an increment in chromatic contrast (still with no associated luminance contrast), spatial (and probably temporal) factors are still important. The presence of a high-contrast chromatically-varying isoluminant grating will reduce the detectability of a superimposed grating of identical spatiotemporal and chromatic character [7]. The spatial-frequency dependence of such masking is shown by the filled triangles in Fig. 1. If the contrast of the background ("mask") grating is varied, it is found that when the mask contrast is near threshold, detection of the test is facilitated, but as mask contrast rises, detection threshold also increases [8]. The form of the contrast-masking function is very similar to that seen for the masking of a luminance grating by a similar luminance grating. As long as contrast is scaled in terms of multiples of the mask detection threshold, the color and luminance functions are virtually superimposable. Contrast-masking functions for color and for luminance are illustrated in Fig. 2.

The suprathreshold appearance of color, as well as the detection of chromatic contrast, depends to some extent upon spatial and temporal

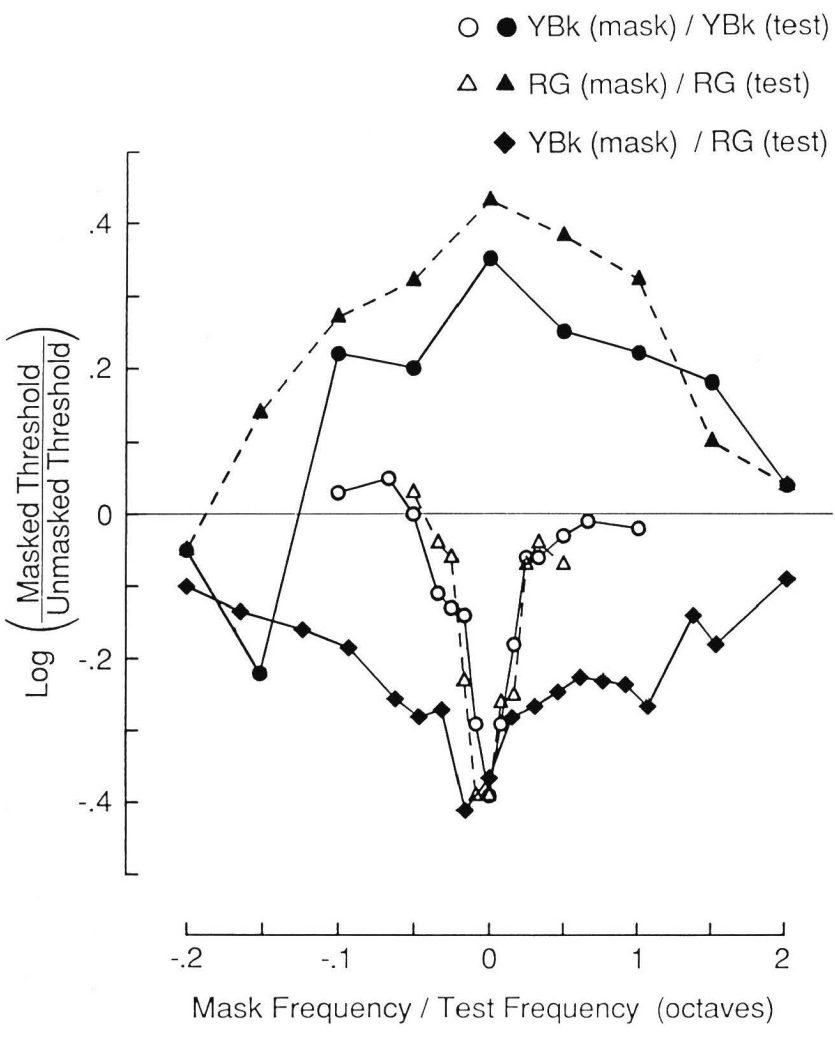

Fig. 1: Spatial frequency dependence of luminance and chromatic masking. Open circles show the facilitation of luminance detection by very low contrast luminance masks. Filled circles show masking of luminance by high contrast luminance masks. Open triangles show facilitation of color by low contrast color masks. Filled triangles represent masking of color by high contrast color masks. Diamonds illustrate facilitation of color detection by suprathreshold luminance masks. (From SWITKES et al. [8])

factors, although complete and thorough investigations are lacking. It is known that RAYLEIGH matches, for example, vary with temporal frequency [9].

Another demonstration of the influence of spatiotemporal factors upon the appearance of suprathreshold chromatic stimuli is the induction of color in a test field produced by an inducing field of different chromaticity. Depending upon the spatial characteristics of the pattern, the test field may appear shifted in color either away from the color of the

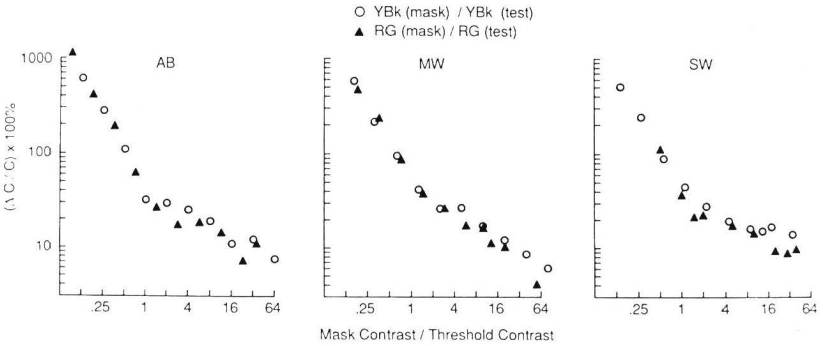

Fig. 2: Contrast dependence of the masking of luminance by luminance (open circles) and of the masking of color by color (filled triangles). (From SWITKES et al. [8])

inducing field (contrast) or towards the color of the inducing field (similitude, also known as assimilation or the spreading effect of von BEZOLD) [10]. When the inducing field is temporally modulated, the magnitude of the induction also depends strongly upon temporal frequency [11], being strongest for low temporal frequencies and falling off rapidly as temporal frequency increases. When the inducing and test fields are presented simultaneously in parallel stripes, both the direction and the magnitude of the color shift depend upon the respective chromaticities of the two fields [12].

Perhaps the more interesting question is how the analysis of chromatic information depends upon the spatiotemporal variation of associated luminance patterns, since it is rare in nature to find isoluminant chromatic variation. The detection of chromatic contrast can be either impeded or facilitated by the simultaneous presence of luminance contrast. The contrast of a luminance masking grating can be high without reducing the detectability of a superimposed isoluminant chromatic grating if the two patterns differ significantly in spatial frequency [7]. When

they are similar in frequency, the effect of a luminance mask is highly dependent upon the contrast of the mask relative to its own threshold [8]. Luminance gratings of contrasts up to roughly 30 times their own thresholds not only do not impede detection of a frequency-matched chromatic grating, they actually facilitate it. The increase in chromatic contrast sensitivity due to the presence of a luminance "mask" occurs over a broad range of relative mask test spatial frequencies, unlike the reduction in sensitivity produced by a high-contrast luminance mask. The spatial frequency dependence of the facilitation of the detection of chromatic patterns by a suprathreshold luminance mask is shown in the filled diamonds in Fig. 1.

Such interactions between chromatic and luminance patterns depend not only upon spatial frequency and contrast, but upon orientation, as well [13]. Both the relatively narrow tuning for spatial frequency (in the case of a high-contrast mask) and the orientation selectivity of chromatic-luminance interactions in simultaneous masking strongly suggest a cortical origin for these effects, as opposed to the different spatial contrast sensitivity functions for color and luminance. These, as noted earlier, can be understood on the basis of precortical receptive field characteristics of cells which respond both to luminance and to color [5].

Not only does the simultaneous masking between color and luminance appear to depend upon cortical processes, but it is most easily explained by assuming interactions at a stage at which color and luminance are coded separately, since the effects of a chromatic mask upon detection of a luminance test grating are not symmetric. (Chromatic masking gratings never facilitate luminance contrast detection in this paradigm. Once the mask has exceeded its own threshold it begins to reduce sensitivity to a simultaneously presented luminance pattern of similar spatial frequency and orientation.) The simplest model would incorporate one-way inhibition from a color channel onto a luminance channel, and an inefficient excitatory input from a luminance channel into a color mechanism. Such an interpretation is not, however, obligatory.

The spatial and temporal characteristics of luminance patterns which are simultaneously present can also have significant influence upon the suprathreshold appearance of chromatic stimuli. A monochromatic luminance grating will appear to change in chromaticity as its spatial frequency varies [14]. Changes in both hue and saturation may occur. In particular, as spatial frequency increases up to about 20 c/deg, saturation will appear to decrease markedly. Similarly, the hue of a flickering monochromatic light may change as the flicker frequency changes, even

[1] Personal communication by R. Nygaard

though mean luminance and chromaticity do not vary[1]. It may be possible to explain these effects by considering the relative activity in chromatic versus achromatic channels, which might be expected to vary with spatial and/or temporal frequency.

Other phenomena have been reported which demonstrate the profound influence of spatiotemporal luminance patterns upon the appearance of chromatic stimuli which are clearly suprathreshold. The apparent spatial position and extent of a color-varying stimulus may be partly determined by the presence of a luminance pattern. Under certain conditions, for example, a colored field will appear to fill a region whose borders are delineated by luminance contrast, even though the actual colored field is not coextensive [15]. The color may even spread to fill a region which is defined by illusory contours. Similarly, the movement of a high-contrast luminance pattern may appear to "drag" a nonmoving chromatic stimulus, when the chromatic pattern is of low contrast and is presented in the periphery[2]. Although these phenomena are very interesting and are of potentially great significance in our ultimate understanding of color vision, we do not yet even have a thorough knowledge of the conditions under which they occur. We certainly do not understand their origins.

In summary, it is clear that the analysis of color information is not independent of spatial and temporal variations in any rigorous way. The detection of chromatic contrast is possible only when the spatiotemporal parameters of that contrast lie within certain bounds. The color appearance of chromatic stimuli also is affected by both spatial and temporal characteristics of the chromatic pattern which is being viewed. Similarly, both the detection and the suprathreshold appearance of chromatic stimuli can be a function of the spatiotemporal parameters of luminance patterns which are simultaneously present in the field of view. In light of our broad (though clearly fragmentary) knowledge of such effects, it is most remarkable that colored objects do not appear to change their colors dramatically as we and they move through the world. Ultimately, the constancy of color analysis and appearance will be more impressive than its failure.

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Author's address:
Dr. K. K. De Valois
University of California
Dept. of Psychology and Physiol. Optics
3210 Tolman Hall
Berkeley, CA., 94720, USA

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September 30, 1987

Lucia R. Ronchi*, FLORENCE:

Achromatic Vision in Multichannel Modelling

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The paradigm "Achromatic vs. chromatic-opponent channels" is one of the keystones of the recent visual literature. However, a number of hypotheses upon which it is based, have not been confirmed. This does not infirm the solidity of the concept of "luminance channel" in itself, but the term "channel" still waits to be properly defined.

Die Frage „Unbunt-Kanal gegen bunte Gegenfarben-Kanäle" ist einer der Angelpunkte in der neueren Litertur zum Sehvorgang. Aber eine Anzahl der grundlegenden Hypothesen ist noch keineswegs gesichert. Dies bedeutet keine Beeinträchtigung des Begriffs „Helligkeits-Kanal" als solchen, wohl aber wartet der Ausdruck „Kanal" noch immer auf eine saubere Definition.

Malgré le fait que des hypothèses de base du paradigme de la coexistence des canaux achromatique et chromatiques n'ont pas été confirmées, la solidité du concept de "canal de luminance" n'est pas infirmée, mais le term "canal" n'est pas encore défini.

1. The traditional belief: achromatic vision is "basic"

In the textbooks, the visual function is first presented in achromatic terms. Thus, in a black box paradigm, the system itself represents a "luminance channel". In addition, the several experimental findings described in the specialized literature are often fitted into serio-parallel models, and hypotheses are made about the existence of subchannels, tunable on different stimulus features (for spatial frequency, orientation, etc). In this way, a basic, self-standing achromatic visual science is developed.

The students next passing to consider color vision, get the convinction that it is a luxury or a surplus. Even the congenital dichromatism is regarded as a scientific tool, rather than a real handicap. The subjective colors in the BENHAM top, and the perception of heterochromatic equiluminous patterns [1] seem to represent limiting cases, not infirming the basic flavor of the achromatic vision.

Inspired to the above principle is also the concept of brightness to luminance ratio [2; 3], as resulting from the combination of data on flicker fusion and direct heterochromatic match. Its dependence on wavelength is intended as a deviation from unity, that is from the basic, reference, achromatic response. In this context [4] the luminance (L) of

* *Istituto Nazionale di Ottica, Arcetri-Firenze*

(monochromatic) stimuli of unit radiance is identified with the $V(\lambda)$, and their brightness is considered as the addition of luminance and an "extra" signal, a surplus, a color glow, possessed by the stimulus in the pair whose bandwidth is narrower. Now, as reported by BRINDLEY [5], one may be able to learn, after careful training, to assess a quality, namely the "luminance", as defined by CIE. But subjects not so specially trained make settings that depart from ABNEY's law. After WYSZECKI [2] the criterion for making heterochromatic brightness matches may change with time, because of a decrease in the weighting factor applied by the observer to the color glow. In our opinion, this change with training is in the direction of supporting the "basic" nature of the achromatic vision but this proof is not generally considered as probative (KAISER's personal communication).

2. Opening the box

Trichromacy is one of the keystones of normal vision. The three cone types are considered by BRINDLEY [5] as "three channels".

This view is to be reconcilied with the basic achromatic aspect of visual function discussed in the previous section. "Opening the box" one fails finding the "lumunous cones" hypothesized by some authors. The same photoreceptors subserve both achromatic and chromatic vision [6]. An alternative view is that achromatic vision is due to the additive combination, in proper proportions, of the responses of the three kinds of cones. In principle, this might even occur in the retina itself, provided "linearity" allows [6]. But recently, ESTÉVEZ [7] has called the attention on the possibility that cone pathways never combine additively, so that the threshold response is a matter of prevailing sensitivity, at the cortex, in line with early views, from HELMHOLTZ to PIRENNE, and recently supported by BOYNTON [8]. In conclusion, even in the most "basic" traditional situation, opening the black box raises more questions than providing answers.

3. Multichannel modelling including opponent-color channels

As recalled above, multichannel models are often proposed to represent various aspects of achromatic vision. One sees in the literature that various authors extend multichannelling, to cover chromatic vision also. Thus, the achromatic channel is flanked by the opponent-color ones. But, in this way, the achromatic vision loses its "basic" flavour, color as a surplus. Various channels seem democratically alike. They may be independent, or interact with one another, or both the situations may even coexist, by creating contradictory percepts [9]. The concept of tuning to specific experimental situations is shared by achromatic and chromatic channels, in view of the experimental evidence that achromatic and

chromatic vision exhibit different spatio-temporal properties, respectively. However, opening the black box, to identify the underlying structures result in such complicacies [1], that the doubt that "a luminance channel exist" becomes legitimate.

Some authors [10] have been proposing an alternative single-channel model, by selecting those electrophysiological findings which allow straightforward tools for convoluting the spatio-temporal porfiles. In this frame, both chromatic and achromatic responses are simply different ways of using the same pathway, served by a small, sustained (X-type) receptive field, with R/G opponent characteristics. The center and the surround are antagonistic, and may have different spectral sensitivities, one determined by long-wave cones, and the other by middle-wave cones.

3. What is a channel?

It seems to us that to reply to the question "Is there a luminance channel" implies an unambiguous definition of the term channel itself. Now, by revising the available literature, we noted that various authors use this term with different meanings, sometimes in a passive sense, someother times in an active sense, or even with either sense in the course of the same paper. That is, a channel may be a photoreceptor type, with its photopigment [5], or a receptor field (group of photoreceptors) [10], or it may consist of both (active) receptor field and (passive) pathway to the brain, or a channel is the whole visual system (receptor field + pathway + central detector), or the detector itself, alone, is considered as a channel. Now, after the modern version of MÜLLER's doctrine of specific energies, the detectors are "labelled lines". This is compatible with both serial and serio-parallel preprocessing [11]. However, it implies that, after the detectors, the perception (and the discrimination) of suprathreshold stimluli require further processing, at higher levels [12]. This may be of relevance, for instance, when evaluating the brightness-to-luminance ratio. Flicker fusion, underlying the estimate of the achromatic luminance, probably implies a class-A experiment, in BRINDLEY's sense, implying less central visual facilities. On the other hand, the direct heterochromatic brightness match, where the observer is requested to judge brightness by making abstraction from one quality of the compared stimuli, the hue difference, is probably a class-B experiment, requiring more central structures.

In conclusion, the reply to the question "is there a luminance channel" is yes or not, according to what "channel" means.

4. The postulated existence of a luminance channel

Investigators gathering psychophysical responses, in addition to drawing practical conclusions, may be virtually requested to insert their

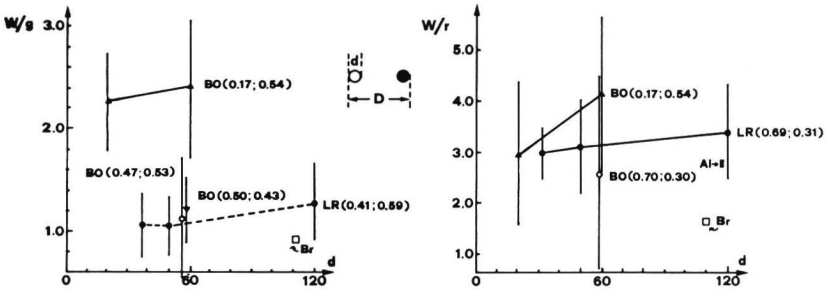

Fig. 1: Ratios of white-to-green (left) and white-to-red illuminances (right) at the brightness match vs. dot diameter [13]

findings in one of the existing models, to ascertain to what extent experimental data can be fitted in it. In this connection, let us consider how the postulated existence of a luminance channel is viewed through some data recently obtained by us [13; 14].

Let us consider two small dots of different colors. One is white, or yellow or greenish, so that its brightness is mainly determined by the achromatic luminance channel. The other is red. Throwing out-of-balance the red-green opponent system, an extra-brightness is expected. In fact, the brightness-luminance ratio, determined in direct heterochromatic brightness matches, exceeds unity. Let us wonder now what happens when the dots are increased in size. One might expect that the brightness match requires less red light, in the size range where the RICCO's area for the achromatic (suprathreshold) brightness response is exceeded, while the chromatic-opponent response is still integrating over space. Now, an evidence along these line is not striking when the size is increased in the usual manner, that is, by leaving constant the local "density" (Fig. 1). On the other hand, less red light is needed, at the heterochromatic brightness match, when the dots are thrown out-of-focus (Fig. 2). At this point it seems of help the multichannel modelling based on the distinction bet-

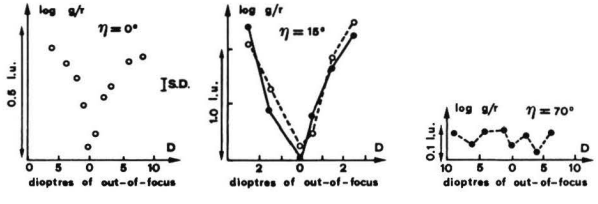

Fig. 2: (Log) ratio of green-to-red-illuminances, at the brightness match, for a point-like source vs. the degree of out-of-focus, at various retinal eccentricities [14]

ween X- and Y-cells, differentially related to the achromatic and chromatic-opponent channels, which are also differently sensitive to the spatial frequency content of the target [15]. Now, one of the effects of defocus is just of attenuating the higher spatial frequencies, in the image of the border. However, even if, a model based on the postulated existence of a luminance channel fits the data, there remains the fact that the heterochromatic instrumental assessment holds only in the plane where the eye is at focus, while the human behaviour is also controlled by the conspicuity of the defocussed target.

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Author's address:
Prof. Dr. Lucia Rositani Ronchi
Istituto Nazionale di Ottica
Largo Enrico Fermi, 6
I-50125 Arcetri-Firenze

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Barry B. Lee* and **Paul R. Martin,** GÖTTINGEN:

The Physiological Basis of the Luminosity Function

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Flickerphotometry is used as a technique for determining the spectral luminous sensitivity of the human observer. We have shown that it is the phasic, non-opponent, magnocellular system of the primate visual pathway which underlies this task, supporting the viewpoint that classical psychophysical channels have a physiological basis.

Die Flimmerphotometrie dient als Technik zur Bestimmung der spektralen Hellempfindlichkeit des menschlichen Beobachters. Wir haben zeigen können, daß das phasische, magnozelluläre System der Sehbahn beim Primaten diese visuelle Leistung unterstützt. Dies bekräftigt die Auffassung, daß klassische psychophysische Kanäle eine physiologische Grundlage haben.

La photométrie à la technique du papillotement est utilisée à la détermination de la sensibilité spectrale lumineuse des observateurs humains. Nous avons montré que c'est le système phasique, non-opposé et magnocellulaire de la voie visuelle des primates qui soutient cette puissance visuelle. Cela affirme la conception qu'il y a une base physiologique des canaux classiques de psychophysique.

1. Introduction

The human photopic luminous efficiency, or V_λ function, which was first defined by the CIE in 1924, relates the luminance of spectral lights with their radiance. It is based largely on results obtained with heterochromatic flicker photometry, a method which avoids the difficulties associated with heterochromatic brightness matching. In this technique, two lights of different wavelengths are alternated at, say, 10 Hz and their relative intensities adjusted until the sensation of flicker is minimised or abolished. The two lights are then defined as having equal luminance. This technique relies on the abolition or minimisation of some sensation as the relative intensities of two spectral mixtures is altered, and is thus effectively a threshold determination. This differs from heterochromatic brightness matching which can be viewed as a suprathreshold scaling procedure.

* *Max-Planck-Institut für biophysikalische Chemie, Abt. Neurobiologie,* Göttingen.

The similarity of the V_λ function when measured in different ways [13] suggests a common underlying mechanism is being tapped. Since the old-world monkey possesses trichromatic vision similar to that of man [1; 2; 4], it is appropriate to seek the physiological mechanisms underlying such tasks as flicker photometry in species such as the macaque. The two major functional systems of the macaque visual pathway are one made up of phasic, non-colour-opponent ganglion cells projecting to the magnocellular layers of the lateral geniculate nucleus, and another consisting of tonic, colour-opponent cells projecting to the parvocellular layers of the nucleus [9].

Since the psychophysical task used to derive the V_λ function involves the minimisation of luminance flicker, and the phasic system in very sensitive to luminance contrast [6; 7] it might be a suitable physiological substrate for the V_λ function. On the other hand, it has been suggested that the colour-opponent system, when presented with rapidly flickering stimuli, might do a kind of 'double duty' and also underlie the luminance function [5]. We have studied this question by measuring ganglion cell responses to heterochromatic flicker, and relating their performance to flicker photometry. The phasic, non-colour-opponent cell class can be identified as the one that is responsible for psychophysical performance.

2. Experimental methods

2.1: Preparation and recording

Activity of retinal ganglion cells was recorded from the eye of the anaesthetised, paralysed macaque monkey. Animals were anaesthetised with an intramuscular injection of ketamine (10–20 mg/kg) and thereafter with halothane (1–2% during surgery, 0.2–1.0% thereafter) in a 70%/30% N_2O/O_2 mixture. EEG and ECG were recorded as a control of anaesthetic depth. Cells were classified as phasic, non-opponent or tonic, colour-opponent on the basis of their responses to spots of different wavelengths; in doubtful cases, contrast thresholds were estimated with white stimuli. This is a reliable means of distinguishing between these two cell systems [6; 7]. Results were obtained from about 100 cells of different types.

2.2: Visual stimulation

Heterochromatic flicker was generated with crossed polaroid filters in two stimulus beams which were then combined and passed through a rotating polaroid filter. Interference and/or neutral density filters in the two beams allowed selection of the relative intensities of the colours in the flicker. Mean retinal illuminance was about 1400 trolands, with a

field size of 4°. Usually, a colour was alternated with white, which served as a reference, but flicker between two colours was also extensively tested. Since the V_λ function of the macaque is similar to that of man [4], we calibrated stimuli in terms of the CIE 1964 supplementary 10° V_λ function. Calibration was achieved using a scanning spectrophotometer (Photo Research, 702A/B). The 10° V_λ was considered suitable since cells had receptive fields several degrees eccentric to the fovea. We chose luminance itself as an intensity variable to best show up deviations in cell behaviour from this norm.

3. Results

We studied the responses of macaque ganglion cells to flickering stimuli under a large variety of conditions, both using heterochromatic flicker and using luminance flicker of different spectral compositions. Both phasic and tonic ganglion cells (including blue on-centre cells with S-cone input) were able to respond to flicker to well above 40 Hz.

Phasic cells responded strongly to heterochromatic flicker between lights of different luminance. However, their response was almost abolished when the two flickering lights were of equal luminance. This implies that phasic cell activity passes through a minimum corresponding to minimisation of subjective flicker, and there was a striking correlation between the minimisation of activity of the phasic cells and the minimisation of flicker for observers viewing the same stimulus. To quantify data, we subjected responses to FOURIER analysis. The amplitude of the first harmonic for a phasic cell is shown in Fig. 1A for four wavelengths flickered against white. Minima are seen close to a ratio of one, indicating that the cell's spectral selectivity is very similar to the V_λ function.

From such curves we could estimate the point of minimisation of phasic cell activity and compare these minima with that expected from the 10° V_λ function. Deviations were usually less than 0.1 log units over the whole spectrum. This is illustrated in Fig. 1B, where deviations of three phasic cells are plotted. For comparison, we asked two human observers to minimise flicker when viewing the same stimulus at 10° eccentricity, and the deviations of the values they set from the 10° V_λ are shown in Fig. 1C. Minimisation of subjective flicker by these observers agrees well with the minimisation of activity of phasic cells.

The results of Fig. 1 show that the psychophysical minimisation of flicker occurs when the output of phasic, non-opponent cells in minimised. Other properties of phasic cells were also those required of a channel responsible for the V_λ function. The location of minima were almost independent of flicker frequency between 1 and 40 Hz. Other requirements are that transitivity and additivity should apply. By transitivity is meant

that, given three spectral mixtures, A, B and C, if A and B and then A and C are matched for luminance with the technique, then B and C will also match. By additivity is meant that A should also match 1/2 B + 1/2 C. We have also been able to demonstrate these two properties in phasic cells.

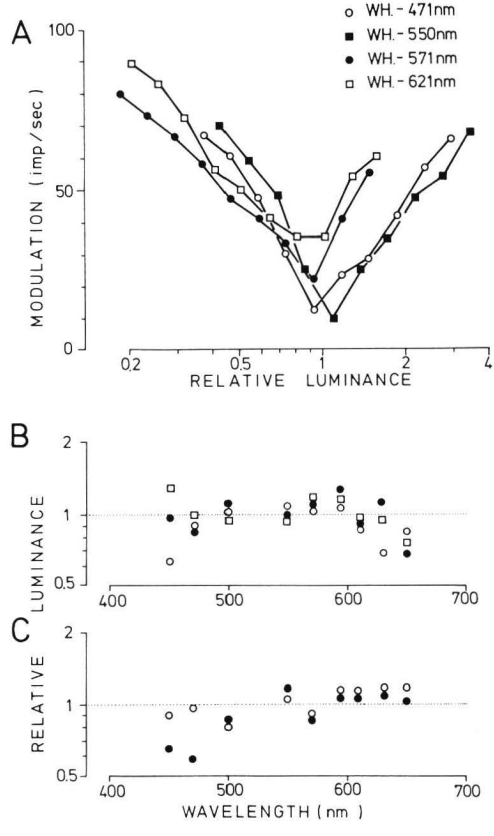

Fig. 1 A: Amplitude of response of a phasic off-centre cell (the first harmonic from a Fourier analysis of responses) is plotted against luminance ratio for four wavelengths flickered against white. The intensity of the chromatic component was increased stepwise, and in each condition cell activity averaged over 6 seconds. Frequency was 10 Hz, and time resolution 2 ms. All curves pass through a minimum close to a ratio of one. B. Deviations of minima calculated from curves such as those in Fig. 1 A from the 10° V_λ function at different wavelenghts. C. Deviations of minima in subjective flicker for two human observers viewing the same stimuli at 10° eccentricity.

Responses, of tonic, colour-opponent ganglion cells displayed qualitatively different properties, and an example is shown in Fig. 2 A. With this red on-centre cell, we flickered between white and red (621 nm). In contrast to the behaviour of phasic cells, a strong response is apparent throughout the whole range of ratios, but the phase of the response gradually undergoes a shift of almost 180°. Fig. 2 B displays a quantitative analysis of the changes that occur.

The results of Fig. 2 A were typical for colour opponent cells. Details of the changes in response and phase with luminance ratio were very dependent on wavelength and frequency, however. The explanation for this behaviour of opponent cells is likely to lie in a latency difference of the opponent cone mechanisms [4]. Such a latency difference will result in a phase shift between opponent mechanisms, so that with heterochromatic flicker a response at the fundamental frequency will always be present.

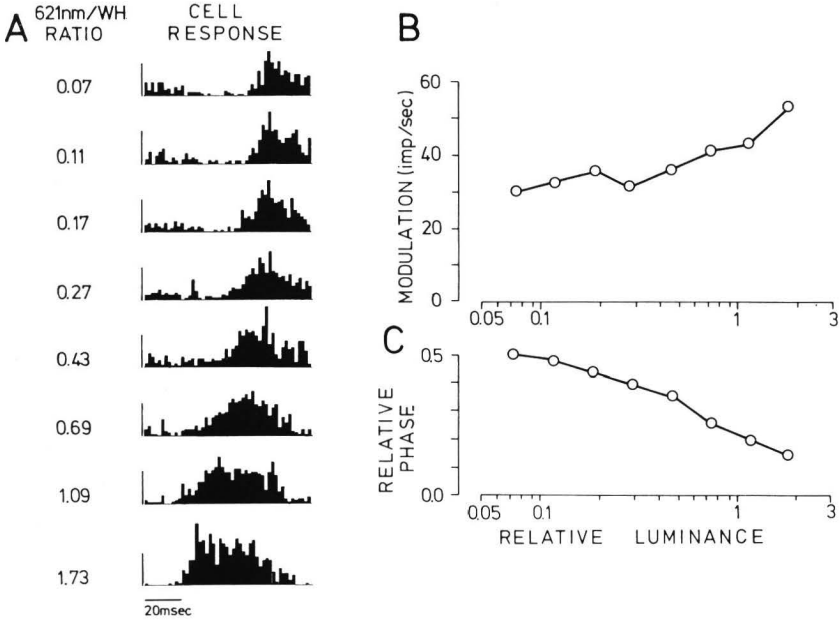

Fig. 2 A: Responses of a red on-centre retinal ganglion cell to heterochromatic flicker (10 Hz) between 646 nm and white. Histograms show the cell response over one cycle at different 646 nm/wh luminance ratios as indicated at left. Cell firing was averaged over 10 s for each histogram, binwidth was 2 ms; calibration bars represent 100 imp/s. In B, a quantitiative analysis of the cell's responses.

It thus seems unlikely that minimisation of subjective flicker could be based on the activity of tonic cells. However, it could be argued that tonic cells, as a population, might show minimal activity at isoluminance. We tried combining opponent cells in various ways, but it proved impossible to show any kind of minimum in such a population.

4. Discussion

A system responsible for heterochromatic flicker minimisation must possess a sensitivity similar to the V_λ function, independent of the flicker frequency used. It should also demonstrate transitivity and additivity. We have been able to show that the phasic cell system possesses all these properties. Tonic cells display none of them.

We conclude that the phasic, magnocellular system is responsible for the luminous efficiency function derived from heterochromatic flicker photometry. It seems likely that other techniques by which the same luminous efficiency function is obtained, for example the minimal distinct border technique [13], may also rely on the minimisation of activity of this cell system.

4.1: Is there are a luminance channel?

The luminosity function is defined by heterochromatic flicker photometry, and by other techniques, all of which involve some kind of threshold determination. We suggest that the phasic cell system is the substrate for the 'luminance channel' defined in this way.

A luminance variable has also been incorporated in psychophysical opponent colour theories and colour systems. It is unlikely, however, that the phasic cell system is involved in scaling of suprathreshold spectral mixtures, for its dynamic range is too small, and it is too transient in response. Tonic, colour-opponent cells are able to carry both chromatic and brightness information, for it is possible to reconstruct colour spaces on the basis of tonic, opponent cell activity alone [12; and these Proceedings]. Nevertheless, luminance is a useful variable for plotting responses of opponent cells [11]. When intensity-response curves for different wavelengths are plotted against stimulus radiance, they scatter widely along the abscissa; when luminance is used, they group together, all peaking near the same intensity value. Plotting in this way has thus a strong normalising influence.

It is likely, however, that activation of the phasic system is necessary in other tasks such as motion detection [3; 10] or stereopsis [8], which depend on luminance differences. Thus, phasic cells, although making up only 10–15% of retinal ganglion cells [9], play an important role in many psychophysical tasks.

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Authors' address:
Dr. B. B. Lee, Dr. P. R. Martin
Max-Planck-Institut f. Biophysik. Chemie
Abt. Neurobiologie
Postfach 2841
D-3400 Göttingen

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Charles F. Stromeyer III*, CAMDRIDGE, Mass.:

Luminance Channel in Humans**

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A luminance channel that summates signals from M and L cones was demonstrated in human vision by threshold measurements for green and red lights flickering at 25 Hz, in-phase and antiphase and having different amplitude ratios. The light was superposed on large red or green adapting fields (~ 4000 td). The properties of the luminance channel resemble properties of the responses of macaque magnocellular LGN cells found by Lee et al.

Durch Schwellenmessungen mit grünem und rotem Flimmerlicht von 25 Hz in Gleich- und Gegenphase und bei verschiedenen Amplituden-Verhältnissen konnte für das menschliche Sehen ein Helligkeits-Kanal aufgezeigt werden, der die Signale der M- und L-Zapfen summiert. Das Flimmerlicht wurde großen roten und grünen Adaptationsfeldern (~ 4000 Trol) überlagert. Die Eigenschaften des Helligkeits-Kanals ähneln denen, die Lee und Mitarbeiter an den magnozellulären LGN-Zellen der Makaken gefunden hat.

Par des mesures des seuils, avec des lumières papillotantes vertes et rouge de 25 Hz en phase et anti-phase et pour diverses relations d'amplitude, on a trouvé un canal de luminance pour la vision humaine ou les signaux des récepteurs M et L s'accumulent. Les lumières furent superposées à un grand champ d'adaptation (~ 4000 td) vert on rouge. Les propriétés de ce canal ressemblent à celles que Lee et al. ont trouvées pour les cellules magnocellulaires de LGN des macaques.

1. Introduction

In our detection experiments we have revealed a mechanism that responds to the linear sum of signals from the middle (M) and long wave (L) cones. (Only a brief account of this work will be given here, since a full report [1] was published after the Florence Meeting.) This summation detection mechanism presumably represents the same luminance channel as measured with heterochromatic flicker photometry. Recent work by STOCKMAN, MACLEOD and DEPRIEST [2] and unpublished work by us show that the mechanism may also receive a weak input from the short wave (S) cones, but this input is of inverted sign and thus forms a subtractive luminance signal – a positive light increment to the S cones results in a negative luminance contribution.

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* *Harvard University, Division of Applied Sciences, Cambridge, Mass.*
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2. Methods

2.1: Stimuli

With a multichannel MAXWELLian view we produced the stimulus depicted in Fig. 1. Red and green annuli and identical central test areas (1.2°) were superposed on an intense adapting field (7.2°). All lights were typically narrowband (10 nm HBW). The test and annuli were generated with light emitting diodes, with the light passing through interference filters. The red and green central test areas were flickered sinusoidally at the same frequency about their mean levels. The red and green flicker was either in phase or in antiphase. The flicker on each trial had a GAUSSian temporal envelope encompassing about 25 cycles.

2.2: Procedure

For each run the amplitude ratio of the red and green flicker was fixed and threshold was determined of 71% correct detection by varying the amplitude of the flicker with a two-temporal-alternative forced-choice staircase. Each fixed ratio of the flicker amplitudes stimulated the M and L cones in a fixed ratio, either positive or negative: the stimulus can thus be represented as a test vector in a two-dimensional cone space (Δ M/M, Δ L/L), as shown in Fig. 2. The two axes represent the WEBERian 'contrast' for the M and L cones respectively. The vertical axis represents the rate of quantal absorption in the M cones at the peak of the (AC) test flicker, normalized by the M cone quantal catch rate owing to all steady

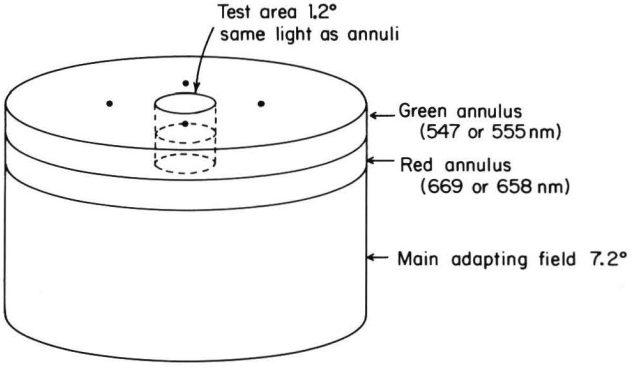

Fig. 1: The red and green central test regions were flickered at the same frequency about their mean intensities, and the amplitude ratios of the flickering lights were fixed to stimulate the M and L cones in different ratios. Thresholds for such different flicker vectors are plotted in the coordinates of Fig. 2

(DC) field components, while the horizontal axis represents the similar variable for the L cones. The flicker is approximately symmetric about the mean and is thus represented by a symmetric vector about the origin. We used the SMITH and POKORNY [3] cone fundamentals to represent our data.

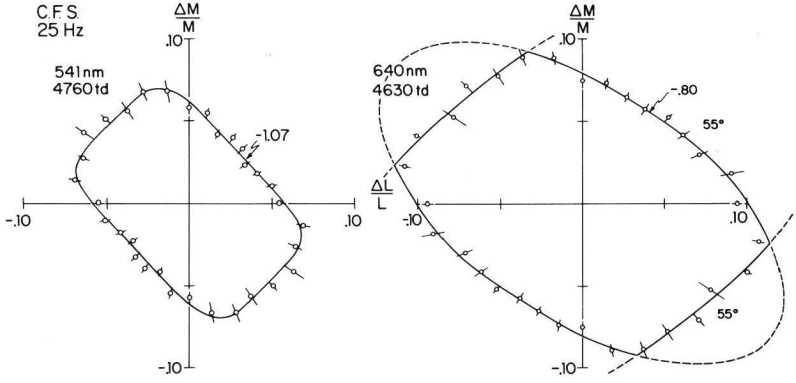

Fig. 2: Flicker detection contours for 25 Hz flicker detected on a large intense adapting field which was green (left) or red (right). Each point is the threshold for flicker that stimulates the M and L cones in different ratios. The contours fitted to the points in quadrants 1 and 3 represent a luminance mechanism that positively summates M and L cone flicker signals.

3. Results

Thresholds for the full range of test vectors at 25 Hz were measured to determine the complete detection contours for two adapting field conditions metameric with 541 nm and 4760 Td (Fig. 2, left panel) and 640 nm and 4630 Td (right panel). For the green adapting condition the detection data were fitted with straight line segments. The segments in the first and third quadrants define the sensitivity of the luminance mechanism which is represented by a weighted sum of M and L cone signals, $[a\,\Delta M/M + b\,\Delta L/L]$; a, b > 0. Thus the luminanance mechanism responds to the linear sum of M and L cone signals produced by the test flicker. The segments in the second and fourth quadrants define the sensitivity of a chromatic mechanism that responds to the difference of the M and L cone signals produced by the flicker, which can be represented by $[c\,\Delta M/M - d\,\Delta L/L]$; c, d > 0.

The results for the red adapting field (right panel) were fitted by segments of ellipses. The red light would be expected to light-adapt the L

cones considerably more than the M cones; thus the M cones would respond slower and the latency delay would causes an elliptical bowing of the otherwise straight detection contours. The depicted contours indicate a 55° phase difference between M and L cone signals.

The above results thus show isolation of a luminance detection mechanism that responds to the linear sum of the M and L cone flicker signals. We related our detection results to heterochromatic flicker photometry. Photometric matches were made by fixing the modulation of the green test flicker at a suprathreshold level and having the observer adjust the modulation of the counterphase red flicker to best null the combined flicker. The sum of the two flickering components can be plotted as a single flicker vector in our coordinates. Such a vector, representing the null, lies approximately parallel to the luminance flicker detection contours; this demonstrates that in setting the null, the observer attempts to minimize the luminance component of the vector.

4. Discussion

4.1: Implication

Our results show that rapid flicker may be detected with a luminance mechanism that summates signals from the M and L cones. Further, this mechanism would appear to underlie heterochromatic flicker photometry. As stated in the Introduction, the mechanism also appears to receive a weak S cone input of inverted sign.

4.2: Related Studies

A high degree of additivity has been measured by IKEDA [4] for heterochromatic flicker photometry using his summation index method. INGLING and TSOU [5] have claimed that the additivity of flicker photometry does not imply that there exists a luminance mechanism that summates M and L cone signals; however, our results do demonstrate such a mechanism. KAISER, VIMAL, COWAN and HIBINO [6] have also demonstrated a high degree of additivity for the nulling of apparent motion, a task which is thought to also tap the luminance mechanism.

4.3: Physiological mechanisms

LEE, MARTIN and VALBERG [7] have shown that the magnocellular cells of the macaque LGN may underlie heterochromatic flicker photometry, and DERRINGTON, KRAUSKOPF and LENNIE [8] have suggested that such cells, many of which also receive S cone inputs, form part of a specialized subsystem for motion.

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Author's address:
Dr. Charles F. Stromeyer III
Harvard University
Pierce Hall
29 Oxford Street
Cambridge, Mass. 02138, USA

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Vivianne C. Smith* and **Joel Pokorny***, CHICAGO:

Is there a Luminance Channel?**

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"Luminance" is a term which has been used in different ways in different contexts. Four distinct interpretations encompassing theoretical, physiological, operational, and psychological constructs are defined and literature examples are given for each.

„Luminanz" ist eine Bezeichnung, die recht verschieden in unterschiedlichen Zusammenhängen verwendet wird. Vier verschiedene Interpretationen einschließlich theoretischer, physiologischer, operationeller und psychologischer Auslegung werden definiert, und für jede Auslegung werden Literaturbeispiele gegeben.

Le term "luminance" est une désignation qui est utilisé très différemment dans des contextes divers. Ici on définit quatre interprétations pour les aspects théorique, physiologique, opérationel et psychologique; on présente des exemples hors de la littérature pour chaque de ces aspects.

1. Introduction

Luminance is the radiance of a source, $P_e(\lambda)$, weighted by the spectral luminosity $V(\lambda)$ of the CIE [5] standard observer:

$$F_v = k_m \int P_e(\lambda)\, V(\lambda)\, d\lambda \qquad (1)$$

where k_m relates lumens to watts. This definition requires that the luminous efficiency function obey ABNEY's Law, i. e. that is show linearity. Psychophysical data obeying ABNEY's law include heterochromatic flicker photometry (HFP), the minimally distinct border (MDB), constant criterion visual acuity, constant critical fusion frequency, apparent movement minimization, and criterion reaction times (reviewed in [41]). We interpret such functions as representing summed cone activity. Implicit in this interpretation is the concept of a luminance channel, i. e. a specific neural channel, accessible by specific techniques, encoding luminance. There are many ways in which the concept of a luminance channel has been used in vision; indeed, the concept of a luminance channel has been extended to include the idea of a channel encoding a perceptual quality such as brightness or whiteness. We can distinguish:

(1) A theoretical construct: a channel encoding the sensation of luminance, measured by certain psychophysical methods and obeying ABNEY's Law.

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* *Eye Research Laboratories, University of Chicago*
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(2) A physiological construct: a neural channel in which specific cells signal luminance at successive levels in the nervous system.

(3) An operational construct for stimulus specification: a visual stimulus may be partitioned into separable luminous and chromatic components.

(4) A psychophysical construct: a channel coding the perception of brightness or blackness/whiteness.

In this communication we review these ways in which the concept of a luminance channel has been used.

2. The luminance channel as a theoretical construct

Many stage theories of color vision partition visual stimuli into luminous and chromatic channels (e.g. [22; 46]). Modern evidence suggests that luminance is predominantly subserved by a sum of the long wavelength sensitive (LWS) and middle wavelength sensitive (MWS) cone types [14; 20; 42]. The red/green and blue/yellow channels are chromatic opponent channels, receiving the differenced input of the SWS, MWS and LWS receptors. The spatial and temporal properties of these channels are not specified. However, the luminance channel is presumed responsible for spectral sensitivity measured by the psychophysical techniques of HFP and MDB.

An operational and theoretical question is whether the luminance channel obeys global linearity, independent of adaptation level. Spectral sensitivity measured by either HFP or MDB narrows with increased luminance [26; 47]. On theoretical grounds, any channel fed by two (or more) cone types cannot be precisely linear with luminance because of receptor compression and gain mechanisms [26]. Thus a luminance channel will only approximate local linearity, even at a fixed adaptation level. Additionally a method such as HFP may show non-linearities introduced by temporal differences in cone activity [8; 44].

3. The luminance channel as a physiological construct

Physiologists have measured two major classes of receptive fields with MWS and LWS cone input in retinal ganglion cells and LGN single units (reviewed in [9; 35]). In one class, "broadband" cells MWS and LWS cones occur in both centers and surrounds [11; 17; 33; 49], which thus have similar spectral sensitivity. In a second class, "opponent" cells, one cone type (LWS or MWS) feeds the center and the other (MWS or LWS) feeds the surround. At the lateral geniculate level, the broadband receptive fields are predominant in the magnocellular layer, and opponent cells predominate the parvocellular layers. In striate cortex, the two projections remain segregated. The broadband [11], magnocellular pathway

[33] has been considered the substrate for a luminance channel [11; 33]. Lennie [35] considered the magnocellular pathway as a poor candidate for a luminance channel because of its poor spatial resolution. More recently, this has been questioned [23; 28]. However, the majority of color vision theories do not specify how spatial resolution is accomplished.

A number of investigators [12; 25; 35] have noted that the parvocellular system with receptive fields that are both chromatically and spatially opponent can carry both a chromatic and an achromatic signal. LENNIE and D'ZMURA [34] have suggested that perhaps these signals are segregated in the visual cortex. The majority of cortical receptive fields from the parvo-cellular projections respond to achromatic stimulation [36]. In this view, a physiological luminance channel *per se* does not exist, at least in the sense that at each succeeding level in the nervous system, a cell-type is devoted to signaling luminance.

4. The luminance channel as an operational construct

A large number of studies have partitioned the visual stimulus into luminous and chromatic components. In the study of chromatic discrimination, the threshold appears deteermined by probability summation of independent luminous and chromatic components [7; 18; 27; 31; 37; 38; 40; 43]. Similarly, studies of adaptation [13; 19; 30; 32; 45] and masking [2; 10] are consistent with the idea of separable achromatic and chromatic signals. Whether or not there is a luminance channel, the concept of independent achromatic and chromatic signals which combine by probability summation at the visual threshold has provided an economical view of a wide variety of threshold behaviors.

5. The luminance channel as a psychophysical construct

The final way in which the concept of a luminance channel has been used is exemplified by theories [24] in which a channel formed by the sum of all three cone types signals a perceptual code for brightness or for whiteness/blackness. It is well-established that the perception of brightness is not simply related to luminance. KAISER as Chairman of CIE Committee TC 1.4 [6] summarized the studies which show that the spectral sensitivity measured by brightness matching deviates systemtically from that measured by HFP or MDB. Many studies indicate both luminance and chromatic contributions to brightness [1; 3; 45; 50]. Brightness is known to show non-linearities, even at a fixed adaptation level [3].

Another interpretation of luminance channel is that it serves to provide a quality code for whiteness/blackness. A way of evaluating this question is to ask if blackness can be predicted from knowledge of the

luminance relations of a test spot viewed in a brighter surround, as happens when both are white. The answer depends on the spectral components of test and surround. If the test is white and the surround is chromatic (or white), then test darkening can be predicted by knowledge of their luminances [4; 15; 29; 39; 48]. If the test field is chromatic and the surround is white, then darkening of the test in not predicted by knowledge of their luminances [15; 16; 39], but depends on the test brightness. If both test and surround are chromatic, then test darkening appears better fit by a luminance than a brightness matching function [4]. These data indicate that the perception of blackness/whiteness requires a more complicated model than a simple consideration of $V(\lambda)$ as a whiteness channel.

6. Summary

The concept of a luminance channel involves the implicit assumption of at least four underlying hypotheses: namely the theoretical construct (Hypothesis 1) of a specific neural channel (Hypothesis 2), accessible by specific psychophysical techniques (Hypothesis 3), encoding a specific perceptual (Hypothesis 4) quality. While the individual hypotheses may themselves have merit or utility in guiding experimental design, there is little evidence to support the concept of a global luminance channel.

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Author's address:
Prof. Dr. V. C. Smith
Prof. J. Pokorny
Eye Research Laboratories
The University of Chicago
939 East 57th Street
Chicago, IL, 60637, USA

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Yoshimichi Ejima*, KYOTO:

Variable Tuning of the Red-Green Opponent-Color System

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Increment threshold data reveal a link among spectral, spatial and temporal variables inherent in the visual system. This linkage provides a promising notion of variable tuning of the chromatic system that emphasizes the importance of its response pattern across receptive fields in space and time.

Ergebnisse von Untersuchungen über die Zuwachsschwellen deuten auf eine Verknüpfung zwischen spektralen, räumlichen und zeitlichen Variablen innerhalb des visuellen Systems. Diese Verknüpfung führt zu der vielversprechenden Vorstellung von einer variablen Einstellung des Farbseh-Systems, die die Wichtigkeit von der Verteilung der Reaktionen über die rezeptiven Felder in Raum und Zeit betont.

Il y a des résultats d'expériences sur les seuils d'augmentation qui indiquent une liaison entre les variables spectraux, spatiaux et temporels du système visuel. Cette liaison permet, peut-être, l'idée d'un réglage chromatique variable qui soulignerait l'importance des réponses spatiales et temporelles à travers les champs réceptifs.

1. Introduction

One influential idea in visual psychophysics is that qualitatively different mechanisms underlie the transformation of luminance and color. The idea is formulated by the hypothesis that the visual signals are transformed through one luminance and two opponent-color channels, each having a unique spectral sensitivity. The formulation is based on successful isolation of the non-opponent and the opponent-color mechanisms at threshold by manipulating spatial and temporal parameters of the test stimuli. The relevant psychophysical observations fall broadly into two groups: (1) When a small and/or brief-duration test is used, the spectral sensitivity of the visual system is characterized as non-opponent nature; (2) When a large and/or long-duration test is used, the spectral sensitivity is characterized as opponent-color property. These observations apparently consist with the idea that the detection of a small and/or brief-duration light depends upon the luminance channel, which is thought to have good spatial resolution and fast responses, while the detection of a large and/or long-duration light depends upon the opponent-color channels, which are thought to have poor spatial resolution and slow responses.

* *Kyoto University, Dept. of Psychology, The College of Liberal Arts*

This apparent consistency, however, does not equivocally support the hypothesis of the three independent channels. What I am suggesting here is that the spectral sensitivity of a channel is a function of spatial and temporal variables. That is to say, the link among spectral, spatial and temporal variables is inherent in the visual system. By analyzing the increment detection sensitivity data, I address the problem of the tuning characteristics of the mechanisms subserving the detection of stimulus increments.

2. Empirical data

First, I deal with the problem of the interaction between spatial and spectral variables in the increment sensitivities. The increment spectral sensitivity functions were determined for a test stimulus consisting of a vertical grating presented on the center of a 10° circular steady uniform white background field [1]. Figure 1 shows the increment spectral sensitivities for the four spatial frequencies, measured for the four background intensities. The ordinate gives the sensitivity expressed as log reciprocal radiant intensity relative to the sensitivity at 540 nm under the condition of 0.66 c/deg and 1 Td. Here, we see three aspects of the results. (i) At the lowest white-background intensity (1 Td), there is no obvious difference in the shapes of the increment spectral sensitivity functions for different

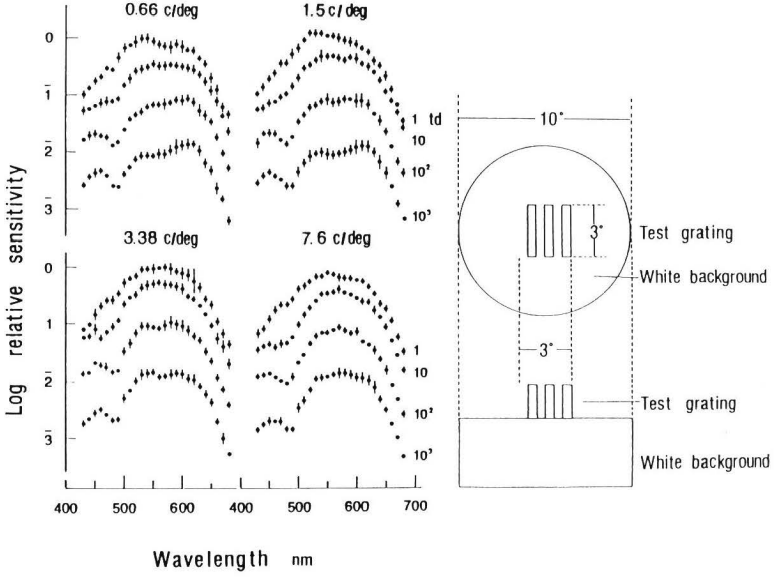

Fig. 1: Increment spectral sensitivity function

spatial frequencies: the function shows a single peak near 540–560 nm. (ii) As the background intensity is increased, a peak emerges at about 450 nm and a marked sharpening of the peak occurs in a similar manner for all the spatial frequencies employed. (iii) For the green-red region of the spectrum, the shape of the sensitivity function at a certain level of the background intensity strongly depends on the spatial frequency. For the low spatial frequencies, a clear peak emerges at 600–610 nm and the notch near 570 nm is considerably deepened in the presence of the high-background intensity. On the other hand, for the highest spatial frequency, the function remains having a single peak near 550–560 nm over the background intensity range employed.

The data shown in Fig. 1 show some features which are not coordinated with the hypothesis of the three independent channels. First, the increment spectral sensitivity curve for 7.6 c/deg remains having a single peak at high background intensity, but the function is not shape-invariant with an increase in the background intensity, becoming a norrower function. Second, when the background intensity is increased, there are unanimously a gradual lowering of the region near 530 nm and a gradual highering of the region near 600 nm. This tendency does not depend on spatial frequency. Thirdly, the sharpening of the peak in the region of 450 nm occurs in a similar manner for all the spatial frequencies. These feature are more complicated than predicted by the hypothesis. The spectral property of the non-opponent mechanism obtained at the high frequency for the high-background intensity is different from the spectral property of the non-opponent mechanism obtained for the lowest background intensity. This suggests that the lowering of the background intensity and the increasing of the spatial frequency may have different effects on the detection precess.

To identify the mechanisms responsible for the present increment spectral sensitivity functions, it may be useful to examine the nature of interaction between different receptors taking place in the detection process. Then, we tested the additivity by using a test-mixture procedure. Figure 2 shows the test mixture additivity as a function of spatial frequency of the test. Open circles represent the data for the 1 Td, and solid circles represent the data for the 1000 Td. The ordinate in the figure represents the detectability of a combined 500+640 nm test relative to the detectabilities of the monochromatic components, which is expressed by the following equation,

$$\sigma = \log\,[(E_{gm}/E_{go}) + (E_{rm}/E_{ro})]$$

where E_{gm} and E_{rm} are the intensities of the 500 and 640 nm lights in the mixture needed to detect, and E_{go} and E_{ro} are the intensities needed to detect when a 500 or 640 nm light was presented alone. A value of 0.0 means the complete linear additivity. Positive values signify subadditivity

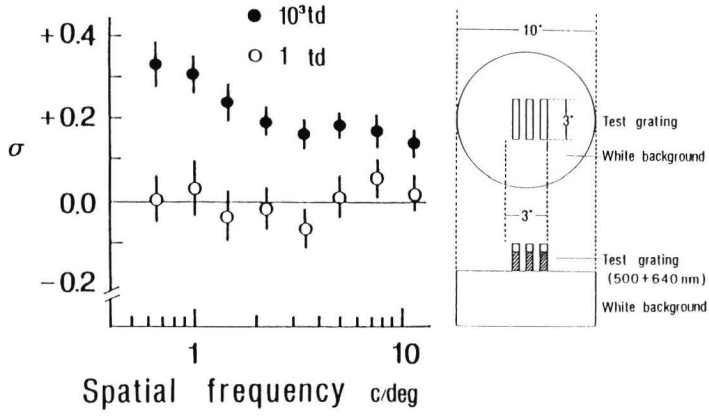

Fig. 2: Additivity failure of test mixture against spatial frequency

or partial additivity, including probability summation and/or cancellation effect. Negative values represent super-additivity. For the 1 Td background intensity, the linear additivity of test mixture approximately holds and there is no obvious dependence of the additivity on the spatial frequency and the 500 nm/640 nm ratio. On the contrary, the data for the 1000 Td show evidence for subadditivity. The additivity failure strongly depends on the spatial frequency of test stimulus: The subadditivity becomes profound with a decrease in the spatial frequency. Noto here that the probability summation cannot explain the dependence of the subadditivity on the spatial frequency, presented here; for each spatial frequency, the relative detectability of a test mixture, σ, was obtained on the basis of the detectabilities of the monochromatic components which were determined for respective spatial frequency. Then, the effect for probability summation which varied with a change in the spatial frequency is eliminated in the present index. Then, the present subadditivity data suggest that the detection of the high-spatial frequency tests superimposed on the high-background intensity may be mediated by the chromatic system, although the resultant sensitivity function is characterized as non-opponent. Thus, we can conclude that a mechanism underlies the detection of a stimulus presented on the high-background intensity involves the color-opponent process.

We further obtained evidence indicating that the subadditivity of test-mixture depends upon the temporal property of stimuli [2]. Fig. 3 shows the additivity as a function of stimulus duration. The ordinate is the same as that shown in Fig. 2. The test mixture lights consisted of 520 and 650 nm light. The background was a 570 nm light and its intensity was 1000 Td. The figure clearly shows that the test mixture additivity approxi-

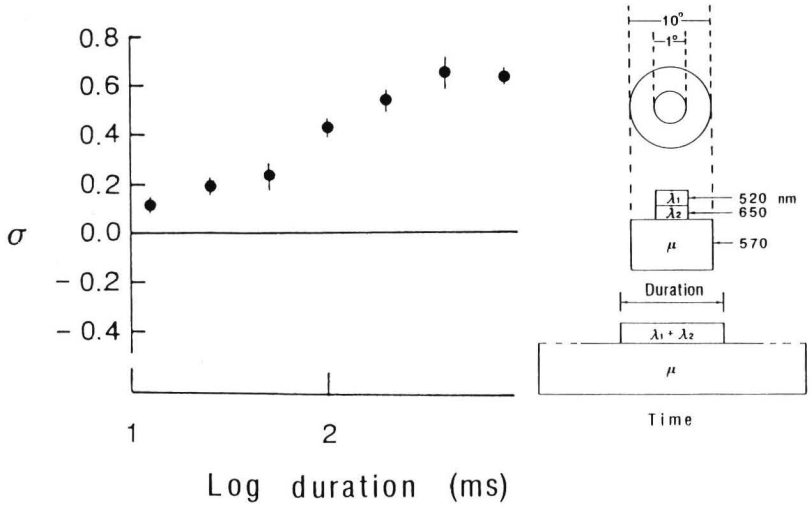

Fig. 3: Additivity failure of test mixture against exposure duration

mately holds for short duration range from 10 to 50 ms, but it does not hold for durations longer than 50 ms. The degree of the additivity failure increases with increase in duration of the test flash, and the subadditivity for durations longer than 100 ms is clearly characterized as a cancellation type. The dependence of the subadditivity on exposure duration may imply that the middle- and long-wavelength cones are temporally interact at some site in the detection process.

3. Discussion

One can imagine that the results described here are all consequences of cone-antagonism as a function of spectral, spatial and temporal variables, showing itself in different guises. Clearly these results have important implications with regard to mechanism, because the specification of the manner of the interaction may be an important guide to understanding of the successive transformations of signals in the visual system. A question arises here is what type of mechanisms that would achieve it. The present results favor the hypothesis of variable tuning of the chromatic system. The hypothesis assumes that the chromatic mechanisms change their spectral tuning with changes in stimulus parameters. Our hypothesis under consideration is that such a variables tuning of the chromatic system is mediated by the receptive field organization of the opponent-color system.

Let me give a possible model. The model is based on the two pathways model proposed by WANDELL and PUGH [3]. The response of one pathway is determined only by the rate of quantum catch of a single class of cones, and hence the response is additive. The response of another pathway is determined by antagonistic action between the middle- and long-wavelength cones, which is in series with the cone receptor site. The response of the pathway is opponent-color in nature. The antagonistic action between different types of cones is achieved by means of the center-surround antagonism, and the integration time of the opponent-color pathway is longer than that of the receptor pathway because of the time lag in the opertion of surround action. By the treatment of the spread function representation of the channel sensitivity, the spectal sensitivity is shown to be a function of the spatial and temporal frequency, and to be able to respond in different modes of non-opponent and opponent, depending upon stimulus parameters. The model can well account for the variation of the increment spectral sensitivity function and of the test-mixture additivity as a function of spatial and temporal variables.

The question arising here is, do the non-opponent and opponent-color pathways function independently? What I propose here is that these detection pathways do not function independetly but my reflect th processing of luminance and color within one neural channel. The responses of the two detection pathways are combined into a detector not by means of probalility or vector summation but through switching like an analog multiplexer. The model presented here is one of the coherent attempt to solve the problem of the interaction in a general way. The novelty lies in the idea that the pattern of responses across receptive fields in space and time might be of primary importance in the encoding of luminance and color, distinctively. It turns out that manipulations of stimulus variables produce variations in tuning characteristic of the hypothesized channel. However, it appears to share with earlier ideal a reliance on the distinction between luminance and color encoding.

There are physiological data indicating that spectral sensitivities change from opponent to non-opponent with a decrease in stimulus size. The studies by WIESEL and HUBEL [4] and GOURAS and ZRENNER [5] have shown that transition from a color-opponent hue coder to a non-opponent brightness coder occurs in individual color-opponent cells of the primate retina, depending on the antagonistic or synergistic interaction between center and surround, which is controlled by the temporal and spatial variables of stimulus. Presumably the visual mechanisms incorporate assumptions about the transformtion of cone signals so called as "variable tuning". The variable tuning of the opponent-color channels is considered as its quality of being versatile. This versatility is an intrinsic potentiality that can be brought into effect by the visual experience.

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Author's address:
Dr. Y. Ejima
Dept. of Psychology
The College of Liberal Arts
Kyoto University
Yoshidanihonmatsu-cho
Sakyo-ku, Kyoto 606, Japan

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H. G. Sperling* and **S. L Mills***, HOUSTON, Tex.:

Origins and Growth of Opponent Interactions in Normal and Blue-Blind Rhesus Monkey Retina

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ERG spectral sensitivity functions from the outer-plexiform layer (a-wave) and inner-plexiform layer (b-wave) of the rhesus retina are compared with psychophysical increment-threshold spectral sensitivity functions containing neural interactions produced at and central to the ganglion cell layer. Little inhibitory interaction occurs in the outer-plexiform layer, with no R/G interaction, but some evidence of a +G–B interaction. At the inner-plexiform layer there is pronounced +R–G and +G–R opponent processing present, which becomes greatly enhanced at and beyond the ganglion cell layer.

Die spektralen Empfindlichkeitsfunktionen im ERG aus der äußeren (a-Welle) und inneren (b-Welle) plexiformen Schicht in der Netzhaut des Rhesus-Affen werden mit denen verglichen, die mit der psychophysichen Methode der Zuwachs-Schwellen gewonnen worden sind, die die neuralen Wechselbeziehungen enthalten, die im Inneren der Ganglienzellen-Schicht entstehen. Man findet nur kleine hemmende Wechselwirkungen in der äußeren plexiformen Schicht: keine R/G-Beziehungen, aber einige Anzeichen für eine +G–B-Wirkung. Aber in der inneren plexiformen Schicht sind deutliche +R–G- und +G–R-Gegenprozesse anzutreffen, die erheblich in der Ganglienzellen-Schicht und darüber hinaus verstärkt werden.

Les fonctions de sensibilité spectrale dans l'ERG de la couche plexiforme extérieure (conde a) et inférieure (onde b) de la rétine du singe Rhésus sont comparées aux fonctions spectrales que l'on a gagnées par une méthode psychophysique et qui contiennent les interactions neurales produites en dedans la couche des cellules ganglionnaires. Dans la couche plexiforme extérieure il n'y a que des petits effects inhibitoires et pas d'interférence R/G, mais quelque interaction +G–B. Dans la couche plexiforme intérieure, les procédés +R–G et +G–R sont prononcés; ces procédés sont intensifiés considérablement dans le niveau de la couche des cellules ganglionnaires et au-delà.

Using corneal focal electroretinograms (ERGs) and behavioral testing, we have observed the growth of color-opponent interactions in the primate visual system by comparing a- and b-wave spectral sensitivity functions and psychophysical, increment-threshold spectral sensitivity.

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* *The University of Texas Health Science Center at Houston, Graduate School of Biomedical Sciences, Sensory Sciences Center*

In our focal ERGs, we employ 12° spectral test flashes on a 21°, 30 000 Td white background field. A third beam, also 21° can be added to the background to provide different chromatic adaptations. Rod intrusion is reduced by using the bright background and a relatively small test stimulus centered on the fovea. Recording a full spectral sensitivity curve allows us to easily measure the amount of rod contribution so that it is not the confounding variable it would be in ERG studies involving only waveform changes for a few wavelengths. The responses to 150 flashes of 70 ms duration, repeated every 400 ms, are typically averaged for each stimulus setting. An intensity series is run for each wavelength and the intensity for a fixed microvolt criterion, interpolated for each wavelength, becomes the basic datum for an action spectrum. We use a 5 μV criterion for the a-wave and a 10 μV criterion for the b-wave. The animal is anaesthetized with ketamine and the eye is stabilized with a retro-bulbar block using marcaine.

The psychophysical thresholds were determined with a 50 ms, 2° test flash centered on a 16.6°, 3000 Td white background.

By repeatedly measuring at frequent intervals in the spectrum, we are able to see in detail features which can be ascribed to classes of cones and their interactions. Since the a-wave of the ERG has been shown to originate in the photoreceptors and the b-wave is initiated by the depolarization of on-bipolar cells [1], it is possible to assign interactions seen in the spectral sensitivity functions to the outer and inner plexiform layers. Changes occurring at these two levels can also be compared with spectral sensitivity obtained by behavioral responses from alert animals to permit identification of changes contributed at or above the ganglion cell level.

Fig. 1 compares spectral sensitivity functions obtained at these different integrative levels on four adult, male rhesus macaques adapted to 3000 (BEH) or 30000 (A and B) Td of a neutral white background field. The two animals in Fig. 1 A, L 210 and TM 3, are normally involved in behavioral testing. Their behavioral curves are therefore quite well-determined and their ERGs less so. The two animals in Fig. 1 B, L 228 and L 38, have been exclusively used for ERG recordings and have no corresponding behavioral curves.

Each set of data points in Fig. 1 represents the mean of two to nine individual curves for each animal. The bottom row of curves represents the a-wave spectral sensitivity function for each animal. The second row from the bottom represents the corresponding b-wave curves. The top row shows the behavioral curves (in Fig. 1 A) for animals L 210 and TM 3. The solid line connecting each set of data points is the best approximation to the data generated by our model, as detailed below. The dashed lines represent, for the a-wave curves, the individual cone sensitivities, as derived from the model and summed linearly to form the solid line. For the b-wave curves, the dashed lines represent opponent functions, also

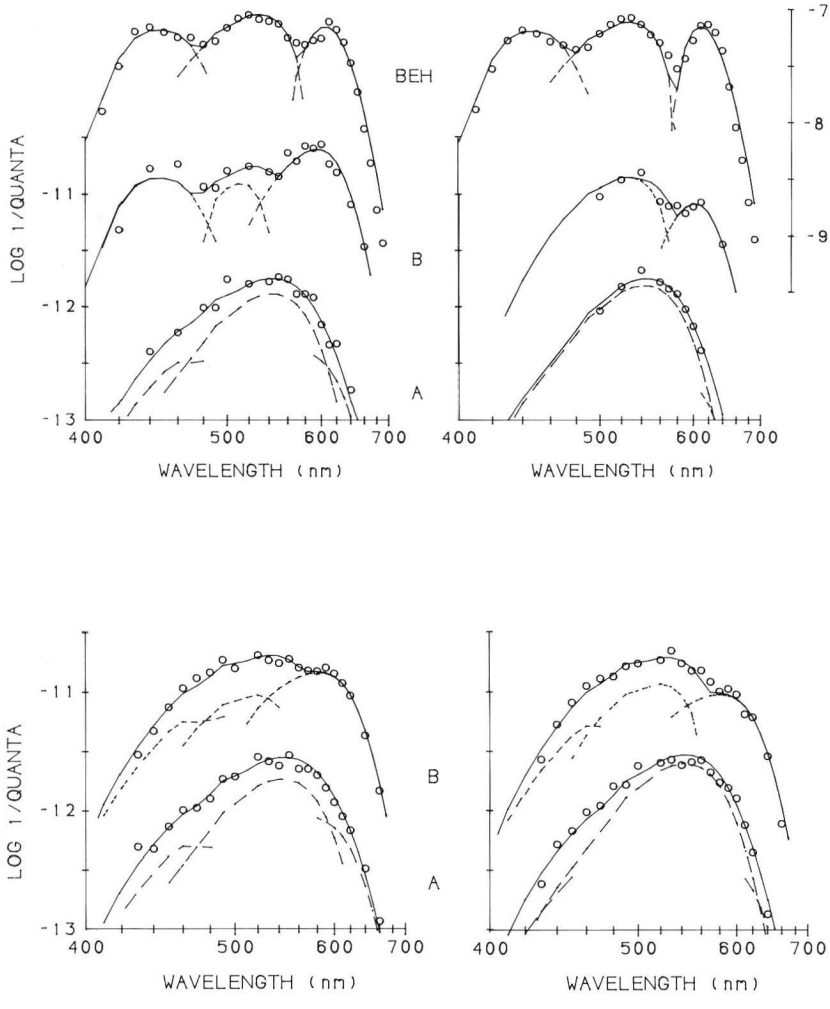

Fig. 1: A comparison for four monkeys of the a-wave (bottom), b-wave (middle), and behavioral (top) spectral sensitivities. Behavioral and a-wave curves are on a true scale; b-wave, which are on the average 0.4 log units more sensitive than the corresponding a-wave curves are placed arbitrarily for clarity.
(1A) Animals L210 (left) and TM3 (right). Refer to the righthand scale for behavioral sensitivity and to the left for ERG senitivities.
(1B) Animals L228 (left) and L38 (right). These two animals have no behavioral curves. Circles are mean data points. Solid lines represent the best fit of a model described in the text. Dashed lines are the individual mechanisms of that model.

summed to produce the solid line. For behavioral curves, the dashed lines again represent opponent functions, but the solid line is here the upper envelope of the most sensitive channel of the model at any wavelength. Both the a-wave and behavioral curves are placed correctly on the axes appearing to their left. The b-wave curves, which are arbitrarily placed between the other two curves, were always more sensitive than the corresponding a-wave curves. This difference averaged 0.4 log units; the difference in threshold criterion is corrected for and is not included in that difference. The ordinate for the behavioral curves appears to their right.

A small peak at about 570 nm has frequently appeared in our a-wave data. We have made attempts to exaggerate and isolate this effect. Fig. 2

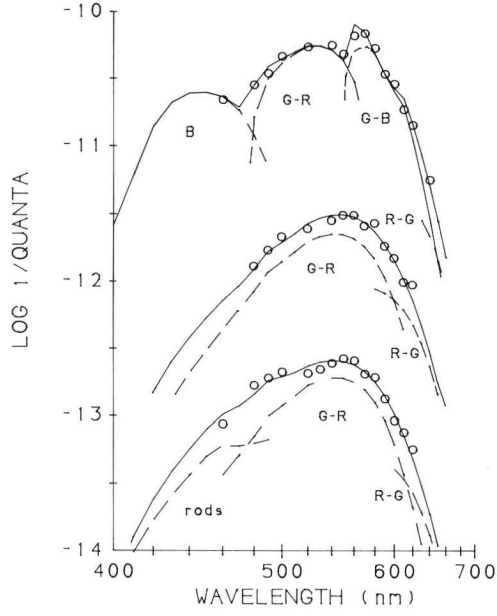

Fig. 2: Three a-wave curves taken under conditions of strong blue light adaptation. The upper curve is the mean of three curves each from animals L228 and L210 with a 90000 Td, 470 nm field spatially coincident with the 30000 td white field always present. The middle curve is the mean of three curves from these animals in the presence of 180000 Td of 470 nm light added to the white. The bottom curve is from the blue-blind eye of animal L210 in the presence of a 90000 Td, 470 nm field added to the 30000 Td white background, as in the top curve.

shows a-wave curves obtained with strong blue light adaptation. The peak in question is most pronounced when a spatially coincident 90000 Td, 470 nm field is added to the 30000 Td white background (top curve in Fig. 2). The resultant peak is poorly fit by R–G, G–R, and B interactive photoreceptor sensitivity functions. The only function we could generate to fit these data consisted of a second +G channel with a very strong inhibitory B component. While such a mechanism would be quite unusual, two further experiments lend support to it. The middle curve in Fig. 2 shows data from the same eye in the presence of 180000 Td of 470 nm light. The 570 nm peak has disappeared at this level, presumably because the blue cones are saturated. The resultant curve is well fit by +R and +G terms alone. A second test involves use of the other eye of animal L 210. This eye has been reduced to tritanopia by exposure to intense blue light using a procedure developed in this laboratory [2]. The spectral sensitivity from this eye is shown in the bottom curve of Fig. 2. Under background conditions identical to those producing the peak in question in normal eyes, no 570 nm peak is evident; the data are again well fit by R and G terms alone.

Discussion

The theoretical predicitions of the data shown in our figures have been derived using a model of spectral sensitivity which is a more complete version of the model of SPERLING and HARWERTH [3] but substituting scalar summation of ERG terms for the upper envelope combination of terms, which we retain for behavioral data. The primaries used for the cones are the response spectra of SMITH and POKORNY [4]; the absorption spectrum of rhodopsin was used for the rod channel.

The revised model for spectral sensitivity (S.S.) is summarized as follows:

S.S. =	$k_1 R - k_2 G$	I (red channel)
	$+k_3 R - k_4 R - k_5 B$	II (green channel)
	$+k_6 B$	III (blue channel)
	$+k_7$ rods	IV (rod channel)

It should be noted that only three free parameters are required to fit most of the a-wave functions which we have obtained, namely, the +R, +G, and rod mechanisms. To fit the b-wave functions, –G and –R terms must be added to the +R and +G to obtain satisfactory fits, just as they are in behavioral curves. A second green channel, +G–B, must be added to closely fit the 570 nm peak that appears in some a-wave curves (Fig. 2). This would require a model with a red, a blue, a rod, and two green channels. In addition, we have added a –B term to the +G–R channel (II). It frequently reduces systematic departures from a good fit on the short wavelength side of the center peak in both b-wave and behavioral data.

The admission of departures from scalar additivity of cone response functions in the a-wave functions such as produced by the 570 nm peak (Fig. 2) and the +G–B mechanism would require cone-specific feedback onto the photoreceptors. There has as yet been no evidence in mammals supporting the position that cone to horizontal cell to cone contacts are in fact so specific [5], although feedback of this nature has been shown in some cold-blooded vertebrates [6].

The blue mechanism can be seen as a 450 nm peak in the behavioral curves due partly to the elimination of masking by rods, but also to an increase of the sensitivity of the blue mechanism relative to the red and green. A similar shift can be seen in the relative balance of the red and green mechanisms. The dashed lines in Fig. 1 demonstrate that the relative contribution of the green mechanism to the total curve is substantially higher in the a-wave than in the b-wave or behavior. It is likely that the a-wave reflects the relative proportions of R, G, and B cones. This stage would naturally show less gain control than later stages of visual processing. This early imbalance is already being corrected by the level of the b-wave. At the behavioral level, three chromatic processes (channels I, II, and III) are essentially equally sensitive at threshold.

Comparison of the amount of inhibition in the b-wave and behavioral data can also be accomplished by examination of the dashed curves in the respective functions. It can be seen that the long-wavelength slope of the G–R mechanism, and the short-wavelength slope of the R–G mechanism are both steeper in behavioral curves than in the b-wave. This implies that the relative amount of heterochromatic inhibition is increasing as processing proceeds from photoreceptor to final output.

In summary, we have found that: (a) in macaques any inhibition present at the outer plexiform layer and presumably due to horizontal cell feedback on cones is small, as seen in the a-wave or late receptor potential. (b) By the inner-plexiform level, red-green opponency is evident and some shifting of the relative sensitivities of the cone mechanisms has begun to take place. (c) Inhibitory interactions grow larger with each afferent level of processing we have sampled. (d) A persistent small peak near 570 nm is found in our a-wave data which we can account for only as a feed-back of blue on green cones in the outer-plexiform layer.

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Author's address:
Prof. Dr. H. G. Sperling
Dr. S. L. Mills
Sensory Science Conter
University of Texas
Houston, Texas, 77030, USA

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Gershon Buchsbaum*, PHILADELPHIA, PA:

Multidimensional Signal Coding in the Visual System

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The response of receptive fields is an inseparable function of color, space and time. In particular, color is coded by antagonistic (opponent) combinations of retinal color mechanism implemented in spatially antagonistic center-surround architecture. It is suggested here that this response has correlates in the structure of natural images and its purpose is efficient coding in these three dimensions of vision.

Die Reaktion eines rezeptiven Feldes ist eine untrennbare Funktion von Farbe, Raum und Zeit. Insbesondere ist Farbe durch antagonistische Kombinationen retinaler Farbmechanismen verschlüsselt, die in einer räumlich antagonistischen Zentrum-Umfeld-Architektur ablaufen. Es wird hier vermutet, daß diese Reaktion Entsprechungen in der Struktur natürlicher Bilder hat und daß ihr Zeck die wirksame Verschlüsselung in diesen drei Dimensionen des Sehvorgangs ist.

La réaction d'un champ réceptif, c'est une fonction inséparable de couleur, espace et temps. Particulièrement la couleur est chiffrée par des combinaisons antagoniques des mécanismes rétinaux qui se déroulent dans une architecture de centre/ambiance d'une manière spatiale antagonique. Ici on présume que cette réaction corresponde à la structure des images naturelles et qu'elle eût pour but le chiffrement efficace dans ces trois dimensions du procès visuel.

1. Introduction

In this article it is argued that a relation can be established between the multidimensional properties of natural images and the multidimensional response structure of retinal receptive fields. The basic hypothesis is that the purpose of retinal signal transformations is to reduce signal-redundancy and to efficiently compress visual information before transmission to higher stages of the visual system [1]. Under this hypothesis the receptive field response structure can be related to the properies of natural images.

2. Properties of natural images

Natural visual stimuli are multidimensional signals encompassing parameters of space, time and color. Image processing methods try to

* *University of Pennsylvania, School of Engineering and Applied Science, Department of Bioengineering, Philadelphia, PA.*

capitalize on the properties of this complex signal to meet constraints of limited computational resources, signal storage, transmission resources (channel capacity) and time constraints (e.g., real-time requirements). Research in image processing seeks methods to process pictorial data so as to generate a set of signals which can be processed using minimum resources. Many of the image processing methods are designed to generate a set of signals which is uncorrelated. The source of correlation in pictorial data is in the very nature of the information. Natural images have redundancy because they exhibit some spatial temporal and chromatic regularities. Further, these signal dimensions are not independent in the sense that variations in space are correlated with variations in time and color.

The visual system is confronted with the same constraints. The visual system has to process the spatial, temporal and chromatic information in the scene employing a finite number of photoreceptors feeding after some preprocessing in the retina into a nerve fiber with limited channel capacity. The preprocessing is done in all three dimensions space, time and color and is implemented by multidimensional receptive fields. In space combinations of receptors are taken to form receptice fields. Receptive fields have a spatial concentric shape as shown in Fig. 1, the center and surround have a opposite responses. The center can be either excitatory or inhibitory. The receptive field profile is well approximated as the difference of two Gaussians. In color, antagonistic combinations of different cone types are taken to form opponent color coding. The implementation of the color antagonistic coding is through the receptive and the example in Fig. 1 has a surround and a center with different color responses. Combinations of the three cone color mechanism are taken to

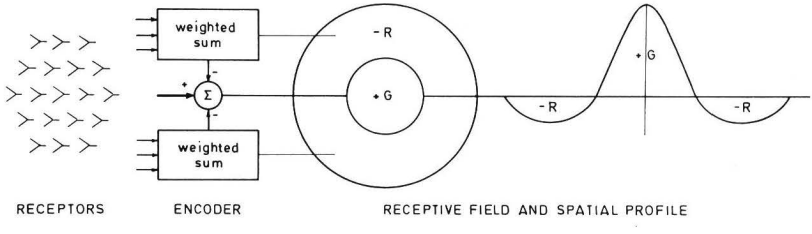

Fig. 1: Processing in the retina occurs simultaneonsly in all three dimensions, space, time, and color. In space, combinations of receptors are taken to from receptive fields, as illustrated in the figure. In this example, the surround and center have different color responses.

form an achromatic channel and two opponent chromatic channels. In time, the coding is done by receptive fields with different slow and fast time constants and by time delays between centers and surrounds.

3. Correlation of photoreceptor outputs

Because of the redundancy in natural scenes different pixels in a scene are correlated and so is the output of retinal photoreceptors. The correlation of receptor outputs may have two sources, the properties of the receptors and their position in the retina and the properties of the signal itself [2; 3]. Table 1 summarizes the sources of correlation of receptor outputs in each of the three visual dimensions.

Table 1: Sources of correlation between photoreceptors outputs

Spatial:	A. Redundancy in real-world images (correlation between picture elements)
	B. Overlap of photoreceptors spatial span
Color:	A. Redundancy in the shape of wavelength spectra in the real world
	B. Overlap of the wavelength response of different color receptor types
Temporal:	A. Regularity of motion in real-world images
	B. Eye movement (temporal overlap)

4. Application of coding methods in the retina

There are two classical methods in image processing used to reduce the correlation of pixels, transform coding and predictive coding [4; 5]. In transform coding the variables involved in the coding are transformed into a new set of variables which are uncorrelated as a means to reduce redundancy. Another factor is the signal compression capability of the transformation. Loosely speaking it is desirable to have as much of the signal energy concentrated in as few components as possible as a means to reduce error and effects of noise. Predictive coding is also designed to take advantage of correlation. The basic idea is to employ differences or weighted differences of correlated variables rather than the correlated variables themselves as a means of decorrelation and information compression.

These coding methods have been applied to the study of signal coding in the visual system. Predictive coding analysis was applied to the recep-

tor mosaic of the retina [2]. A weighted mean of the signal in receptors in the surround is taken to generate a prediction of the signal at the center. The predicted value is subtracted from the actual center photoreceptors signal minimizing the required neural dynamic range. The correlation between receptor outputs was taken to be exponentially decreasing with the distance between receptors and was based on a model for the autocrrelation of natural images which is an exponential function of distance [4]. The analysis gives rise to spatial receptive fields as represented in Fig. 1. The result suggests that the visual system employs predictive coding methods to code spatial information. In the temporal domain application of predictive coding to outputs of receptors excited by a moving target can provide an explanation for the time course characteristics of some visual cells. Application of position prediction considerations for moving targets can account for existence of slow and fast receptive fields. In another study [3] transform methods were applied to decorrelate the outputs of retinal cone color mechanisms along the wavelength axis. There are only three types of color receptors and computation of the transform is relatively simple. The result has been prediction of opponent color transformations as they happen to occur in the retina. A transformation of the outputs of the three color mechanisms is taken in the retina to decorrelate the three signals and also to obtain an energy distribution in the transformed outputs which minimizes requirements of dynamic range. Each of these schemes treates one dimension of vision only. A combined coding scheme would require hybrid coding i.e., different coding methods in each dimension. Such coding schemes have

Table 2: Simultaneous redundancy reduction and efficient coding in space, color and time in the visual system

Dimension	Solution	Combined mutidimensional Solution
Space:	Predictive coding: spatially organized center-surround receptive fields	
Color:	Transform coding: color antagonistc (opponent) transformation	Spatially organized chromatically opponent receptive fields with complex temporal characteristics
Time:	Sampling: "slow" and "fast" responses	
	Predictive coding: self inhibitory time course response	

been considered before, for their obvious combined advantages [4; 5]. In the visual system they are exemplified in receptive fields which have spatial and chromatic anatagonistic organization with complex temporal characteritics. Table 2 provides a summary of the general encoding scheme in the visual system. The response of the receptive fields can be written as a function of space-time-color, $f(r, t, \lambda)$, however, it cannot be written as the product of separate spatial temporal and chromatic responses, i.e., $f(r, t, \lambda) \neq f_1(r) f_2(t) f_3(\lambda)$, indicating the simultaneous and inseparable multidimensional nature of retinal signal processing.

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Author's address:
Prof. G. Buchsbaum
University of Pennsylvania
School of Engineering and Applied Science
Departement of Bioengineering
Philadelphia, PA., 19104-6392, USA

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Peter Gouras*, NEW YORK:

Neural Systems Distinguishing Chromatic from Achromatic Contrast**

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Color vision requires detecting chromatic contrasts across a (moving) border independently of achromatic contrasts. We have examined the responses of each functionally unique visual neuron in the macaque lateral geniculate nucleus to a moving border of maximum achromatic and strong chromatic contrasts. Using this ensemble of responses we have electronically constructed hypothetical units that respond to specific chromatic contrasts independently of achromatic contrasts. The strategies used may be relevant to color vision processing in visual cortex.

Farbensehen erfordert die Wahrnehmung eines Buntkontrastes längs einer (bewegten) Grenzlinie unabhängig von Helligkeitskontrasten. Wir haben die Reaktionen eines jeden funktional unabhängigen visuellen Neurons auf eine bewegte Grenzlinie mit höchstem Helligkeits- und starkem Bunt-Kontrast im Geniculatum von Makaken untersucht. Unter Verwendung dieser Reaktionen haben wir auf elektronischem Wege hypothetische Einheiten konstruiert, die auf spezifische Buntkontraste unabhängig vom Helligkeitskontrast ansprechen. Die hierbei angewandten Strategien könnten für das Verständnis des Farbsehvorgangs im kortikalen Bereich von Bedeutung sein.

La vision colorée exige la perception de contrastes chromatiques à travers une ligne limitante, indépendant d'un contraste achromatique. On a examiné les réponses des neurones dans le géniculate de macaques à une ligne mouvante de contraste maximum achromatique et de haute chromaticité. Sur le fondament de ces réponses, on a construit électroniquement des unités hypothétiques qui répondraient à des contrastes chromatiques spécifiques indépendamment du contraste achromatique. Ces stratégies comme y appliquées pourraient être importantes pour la compréhension du procès de la vision colorée dans l'écorce cérébrale.

We have defined a chromatic contrast detector as a neuron which responds to spectral (wavelength) contrast independently of effective energy contrast across a boundary. We have studied the responses of each functionally distinct variety of neuron in the macaque (*cynomolgus*) monkey lateral geniculate nucleus to a moving boundary of strong spectral contrast across which effective energy contrast can be altered inde-

* *College of Physicians and Surgeons of the Columbia University, New York*
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pendently to determine how similar any one of these units is to our defined hypothetical chromatic contrast detector.

In general but not in total agreement with most other laboratories we find at least ten functionally distinct types of neurons in the primate lateral geniculate nucleus. Two types exist in the magno- and eight types in the parvo-cellular layers. The magno-cells are phasically responding on- or off-center cells which appear to receive similar inputs from long (L) and middle (M) but no inputs from short wave (S) sensitive cones [1–3]. An S cone input is determined by a cell's responsiveness to a boundary of spectral contrast along a tritanopic confusion axis (white/yellow) in color space. Since they lack cone opponency we have tentatively discounted them as participating in chromatic vision.

Eight types of cells are found in the parvocellular layers. Six types show cone opponent interactions. These cells are best designated by the cone mechanisms subserving their receptive field center. The vast majority involve only the L and M cone mechanisms. There are L on- and off-center cells with antagonistic surrounds from M cones; there are M on- and off-center cell with antagonistic surrounds from L cones. These four groups of cells have the smallest receptive fields of all geniculate and presumably contribute to high spatial resolution as well as chromatic vision. There is also a population of non-opponent, i.e. broad-band L and/or M on- and off-center cells without any input from S cones. Lastly are S cone on- and off-center with antagonistic inputs from L and/or M cones; these cells are rare (3%) and have larger receptive fields without an obvious concentricity.

Fig. 1 shows a library of responses of each of the eight types of parvocellular cells to strong chromatic contrasts presented as increments (above) (black to red, yellow, green or blue) and as decrements (below) (white to red, etc) of effective energy contrast. The on-center cells subserving the L and M cones (first three columns) are excited by increments and inhibited by decrements of effective energy contrast. The off-center variety show the reverse behavior. Because of cone opponency there are considerable differences in their responsiveness to the spectral characteristics of the effective energy contrasts. Nevertheless these cells respond drastically different to the same spectral contrast when the polarity of effective energy contrast is reversed.

Fig. 2 (above) illustrates this point for L cone on-center cells which are antagonized by an M cone surround; these so-called red on-center, green off-surround cells are excited by almost all increments and inhibited by almost all decrements of effective energy contrast regardless of the spectral contrast. This class of cells alone cannot provide an unambiguous clue to the chromatic contrast across the border. A similar pattern can be seen for M cone on-center cells, so-called „green on-center, red off-surround cell" (Fig. 3, above).

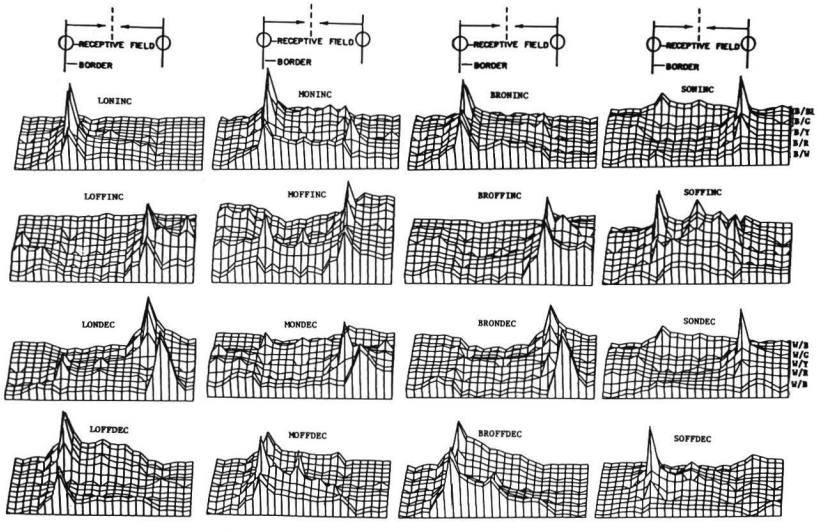

Fig. 1: A library of responses of each functionally type of parvocellular cell to the moving boundary of spectral contrasts as increments (INC suffix) and decrements (DEC suffix) of effective energy contrast. This library includes the average responses of 6 LON, 7 MON, 8 MOFF, 5 BRON, 4 BROFF, 5 SON and 3 SOFF cells. The terminology stands for long wave cone on- (LON) and off- (LOFF), middle wave on- (MON) and off- (MOFF), broad-band on- (BRON) and off- (BROFF), short wave on- (SON) and off- (SOFF) center cells. The two-dimensional surface uses a program in which two horizontal lines map the responses of each cell type to increments or decrements of effective energy contrast and chromatic contrast, designated as Black/Blue (B/Bl), Black/Green (B/G), Black/Yellow (B/Y), Black/Red (B/R), and Black/White (B/W) correspondingly (upper two rows) and as White/Blue (W/Bl), White/Green (W/G), White/Yellow (W/Y), White/Red (W/R) and White/Black (W/B) (lower two rows). The x-axis is 10° in visual angle and 3 in time, i.e. the border moves at 10°/s acros the cell's receptive field and then reverses its movement at 1.5 s to traverse the receptive field again, with the opposite contrast polarity. The y-axis indicates the response in impulses/s. The z-axis distributes each form of spectral contrast. The computer stores the standard deviation at each data point. These responses can be electronically combined in any way to produce higher order responses to the moving border (see Figs. 2 and 3).

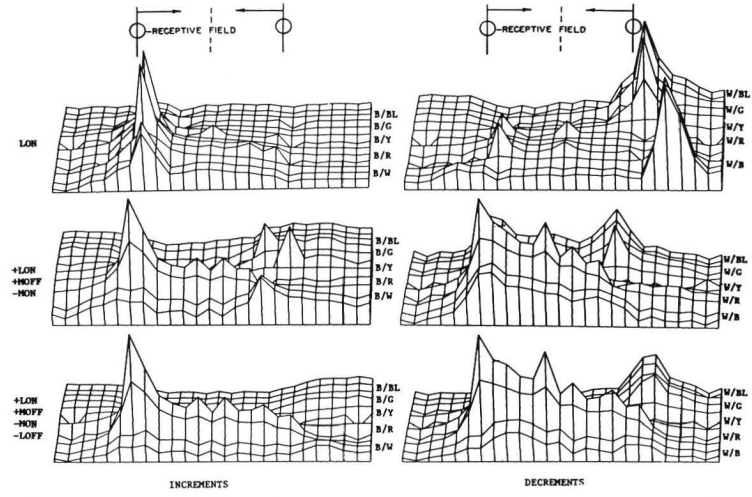

Fig. 2: The upper traces show the same responses as in Fig. 1 of a LON cell to chromatic contrasts as increments and decrements of effective energy contrast. The middle row illustrates a hypothetical cell formed by adding LON and MOFF outputs and subtracting MON outputs. The lower row shows that the additional subtraction of LOFF outputs provides an even more chromatically selective cell.

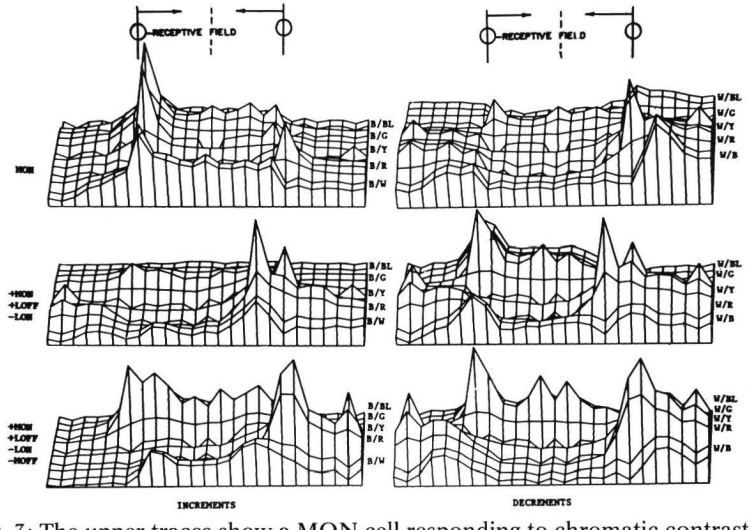

Fig. 3: The upper traces show a MON cell responding to chromatic contrasts as increments and decrements of effective energy contrast. The middle row illustrates a hypothetical cell formed by adding MON and LOFF and subtracting LON outputs. The lower row shows that the additional subraction of MOFF outputs provides an even more chromatically selective cell.

Nevertheless the brain must utilize the geniculate output to determine the color on each side of the boundary [4]. We have used the library of responses (Fig. 1) to determine what possible combinations of geniculate outputs the brain could use to determine the chromatic contrasts across these moving boundaries. In combining these inputs we assume linearity except we eliminate negative outputs in accord with the non-linearity of impulse formation. By adding L on-center (LON) with M off-center (MOFF) and subtracting M on-center (MON) responses we can construct a hypothetical cell which can detect the "red" side of the boundary (Fig. 2, middle row) much better than a LON cell, alone. If in addition we also subtract L off-cell outputs we can construct an even better cell for detecting the "red" side of the border independently of effective energy contrast across the border (Fig. 2, lower row).

A similar procedure is shown in Fig. 3 for constructing a hypothetical unit that can detect the "green" side of the border independently of the effective energy contrast across the border. It is interesting to see how important it is to use both on- and off-center opponent cells to counteract the problem of effective energy contrast. The off-center system comes into its own at relatively high ambient light levels where decrements of effective energy contrasts become common in addition to spectral contrasts. A similar need to exploit off- as well as on-center cell outputs has recently been noticed by VALBERG et al. [5] in their modeling of equidistant color space. It is interesting to see how different the logical use of these neuronal outputs are in constructing chromatic from achromatic contrast detectors. Combining the outputs of on- and off-center cells additively is not the logical way to build units sensitive to achromatic, i.e. effective energy, contrast but is obviously important for constructing chromatic contrast detectors.

These hypothetical units are single opponent cells, i.e. they are designed to detect successive but not simultaneous color contrast. Fig. 4 (above) shows schematically how they can be constructed. It would be interesting to know wheter such a hypothetical neuron exists in striate cortex. MICHAEL [6] has recently demonstrated that single opponent cells exist in layer 4 and are smooth, stellate cells; the double opponent variety are spiney, stellate cells. If there is a specific single opponent striate cortical cell, it might have proporties different than geniculate cells and more similar to those suggested here. Antagonistic interactions between such single opponent cells, as illustrated in Fig. 4, below, could lead to simultaneous color contrast detection.

In constructing the hypothetical chromatic contrast detecting cells, it has been necessary to consider some means of discounting their potential responses to small achromatic spots, because these stimuli can drive the geniculate output cells. To do this we must require that they only reach

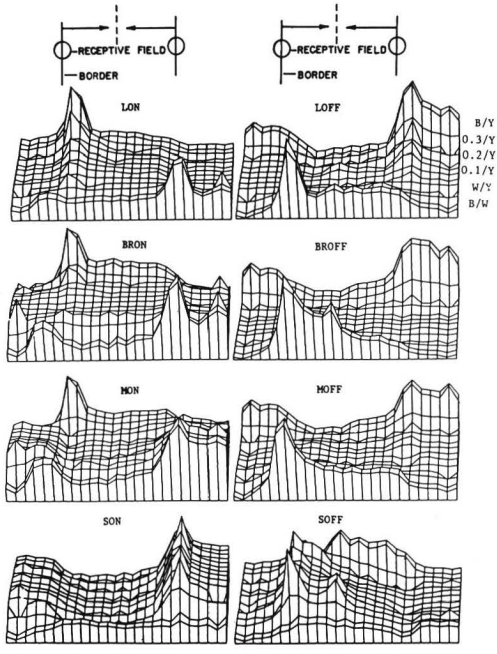

Fig. 4: The library of LGN responses of each functionally distinct parvocellular cell to a white/yellow border across which the effective energy gradient has been stepwise minimized and reversed from white/yellow through gray/yellow to a black/yellow border. All but the SON and SOFF subsystem completely reverse their response polarity as the polarity of effective energy contrast across the border reverses. Although this reversal point differs among these cell types, it is nevertheless complete with the response to yellow/black being the same as or extremely similar to white/black. SON and SOFF cells fail to reverse response polarity and respond to the spectral contrast uniquely. The format is the same as Figs. 1–5.

threshold if they integrate the responses from more than one, or perhaps even a few, cones. This requirement to increase the spatial integration may confer on them a greater contrast sensitivity and could be at the root of the observed higher contrast sensitivity of chromatic over achromatic vision [7; 8]. This is an interesting point since at the geniculate level individual parvocellular cells have a low contrast sensitivity [9]. This probably stems from the fact that each cell is subserving only a single cone. In transforming these outputs into separate chromatic and achromatic systems, spatial integration may, and as we suggest must, be altered thereby influencing their potential contrast sensitivity.

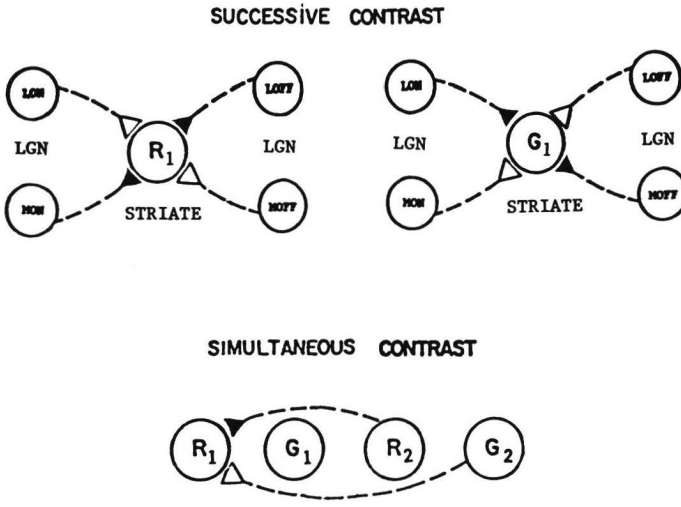

Fig. 5: The suggested interaction of LGN units to produce u*nits sensitive to specific successive chromatic contrast independently of effective energy contrast, single opponent cells (above) and simultaneous chromatic contrasts (double opponent cells) by interacting these same units across different areas of visual space. In order to make this cell insensitive to high frequency achromatic contrast we require that it will not reach threshold unless it integrates from several or more geniculate cells of the same class. This is necessary in order to eliminate any response to small achromatic spots or lines.

The S cone system affects two varieties of geniculate cells, both in the parvocellular layers (Fig. 1, right hand column). One variety is excited by S and inhibited by L and/or M cones (SON); the other is inhibited by S cones and excited by L and/or M cones (SOFF). These cells respond to chromatic contrast independently of effective energy contrast and are therefore, by definition, chromatic contrast detectors. Since they are excited not only by blue surfaces but also by white ones, especially after yellow, red, or green leaves their receptive field, they cannot be used to distinguish a "blue" surface unequivocally. They can, however, be used to distinguish the short wave reflecting side from the non-short wave reflecting side of a boundary.

An interesting question is how the brain distinguishes white, gray or black from other colors. These perceptions are more closely related to

effective energy contrast, but there is no easy way to distinguish white as a unique quality independent of effective energy contrast across a boundary by using any one type of geniculate neuron. The broad-band on-center cell is a logical candidate but this cell cannot distinguish a bright red, yellow, or green from a white side and therefore alone provides completely ambiguous information about the chromatic contrast across a border. Fig. 5 illustrates this point in showing the responses of each type of parvocellular neuron to a white/yellow border at different effective energy contrasts. The broad-band cells (BRON and BROFF) cannot distinguish the white from the yellow side of the border. If, however, a hypothetical cell were formed by having an excitatory input from BRON and an inhibitory input from SOFF cells, it would come closer to distinguishing the "white" side. The SOFF cell would always veto this cell whenever a non- short wave side crossed the receptive field. This would only allow this hypothetical cell to respond to the white side of the border. Since BRON cells have no input from S cones, the blue side of the border will always be a relatively weak stimulus.

In this research we have shown how ambiguous the responses of geniculate neurons are for distinguishing chromatic (spectral) from achromatic (effective energy) contrast. We have demonstrated, however, that it is possible to use the signals from an ensemble of functionally different parvocellular cells to construct hypothetical units that come close to simulating chromatic contrast detectors. It will be interesting to determine the heuristic value of these hypothetical units by testing neurons in visual cortex with the same moving boundary.

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Author's address:
Prof. Dr. P. Gouras
Columbia University
Dept. of Ophthalmology
630 West 168th Street
New York, N.Y., 10032, USA

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Munehira Akita*, KYOTO:

Cone-Interaction in the Yellow-Blue Opponent Process

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We describe here the non-linear contribution of the short-wavelength cone system caused by interacting operations of the middle- and long-wavelength cone signals based on (1) inverse interaction in the y–b system as changing a light-adaptation level, (2) achromatic sensations for trichromatic mixtures, and (3) non-linearity of the y–b system in normals, but no non-linearity in a deuteranope.

Hier wird der nicht-lineare Beitrag des kurzwelligen Zapfensystems beschrieben, der durch Wechselwirkungen der mittel- und langwelligen Zapfen-Signale entsteht, und zwar (1) durch inverse Wechselwirkung im Blau-Gelb-System bei Änderung des Adaptationsniveaus, (2) durch Unbuntempfindungen bei Dreifarbenmischungen und (3) durch die Nicht-Linearität des Blau-Gelb-Systems bei Farbennormalsichtigen, aber nicht bei Deuteranopen.

Ici on décrit la contribution non-linéaire du système à courtes ondes des cônes, une contribution qui est produite par les interactions des signaux des cônes à ondes moyennes et longues, (1) par une interaction inverse dans le système bleu-jaune à cause d'un changement du niveau d'adaptation, (2) par des sensations achromatiques dans les mélanges trichromatiques, (3) par la non-linéarité du système jaune-bleu chez les observateurs normaux, mais il n'y a pas de non-linéarité chez un deuteranope.

1. Introduction

There is a question whether we can ascribe the nonlinearity of the short-wavelength cone sensitivity to a nonlinear contribution of interacting operations in the middle- and longer-wavelength cone systems. The present study deals with evidence which may help answering in the affirmative this question, based on our three previous papers on which my laboratory group has worked: the effect of light adaptation [8], achromatic sensation for trichromatic mixture [3], and the comparison of normal trichromat and deuteranope [1], in terms of the yellow-blue hue cancellation function.

* *Psychology Laboratories, Kyoto Institute of Technology,* Kyoto (Japan)

2. Effect of light adaptation on the opponent-color responses

2.1: Experimental methods

A three channel Maxwellian-view optical system was used to present the stimuli. Two monochromators provided monochromatic lights for test and cancelling stimuli. Another channel provided a white background onto which the test and cancelling stimuli were presented. The size of the white background was 10° in diameter, and the size of the test stimulus was 2°. Based on light measurements, we produced the stored programmed data to control the luminance of the stimuli.

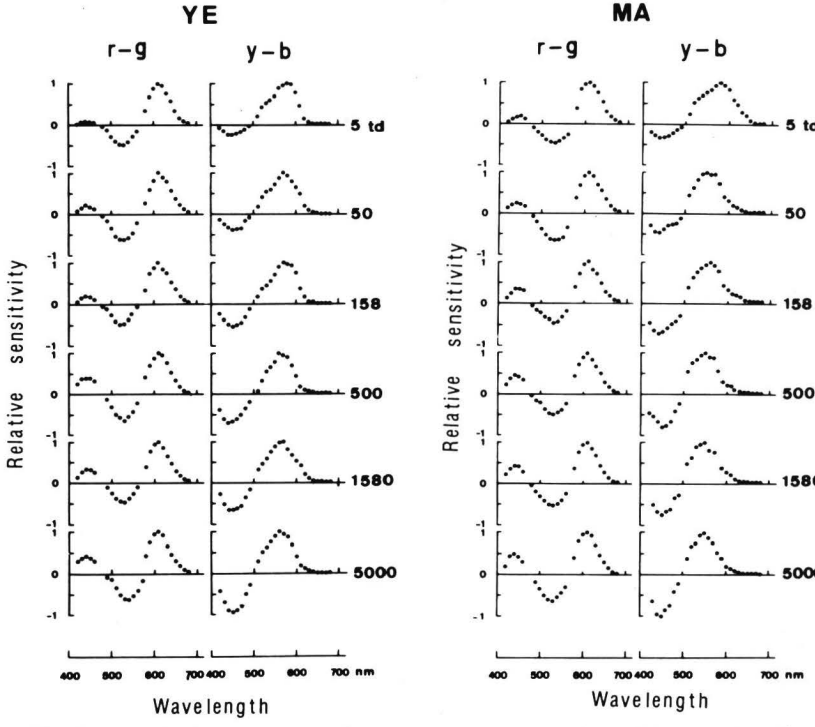

Fig. 1: r-g and y-b opponent-color responses as a function of the wavelength of the test stimulus for different levels of light adaptation. The data are based on the results of log relative chromatic valence of the r-g and y-b opponent-color system for an equal-energy spectrum for the six light-adaptation levels. A number in each graph represents the retinal illuminance of the white background. Observer was YE [8]

Fig. 2: r-g and y-b opponent-color responses as a function of the wavelength of the test stimulus. Other details as in Fig. 1; Observer MA. [8]

Four chromatic responses, i. e. red, green, yellow, and blue, were measured by obtaining the energy ratio of a cancelling light to a test light at the red-green or yellow-blue equilibrium point for each test stimulus. The canceling light was chromatic opponent to the hue to be cancelled.

The wavelength of the test light was varied from 420 to 680 nm in 10 nm steps. The cancelling light consisted of each observer's unique blue, unique green, and unique yellow, which were 470, 500, and 570 nm for observer YE and 475, 500, and 575 nm for observer MA. A 670 nm spectral light was used for the red. The retinal illuminance of the 8700 K white background was 5.50, 158, 500, 1580, or 5000 Td.

2.2: Result and discussion

As the light adaptation level was increased for the r-g system, the short-wavelength cone contribution was relatively enhanced while the middle- and longer-wavelength cone contributions were irrelevant. However, for the y-b system, the contributions of the short- and middle-wavelength cone increased while the contribution of the longer-wavelength cone decreased, as shown in Figs. 1 and 2.

To the first approximation, we evaluated the relative contributions of the three cone types to the two opponent-color response functions for each of the six light-adaptation levels by means of a linear model. We found that the coefficients of the S cones increased with the increase in the light-adaptation level for both the r-g and the y-b systems. On the other hand, the coefficients of the L and M cones were almost constant for the different levels of light adaptation for the r-g system. Our solution of the linear model support the view that S-cone signals affect the r-g system. Although the role of the S cones in the transformed r-g system is in dispute, there is other evidence for signals from S cones in the r-g system [5; 6; 7; 9].

3. Achromatic sensation for trichromatic mixture

3.1: Experimental methods

An achromatic color 2° field, viewed with a dark surround, was determined for trichromatic mixtures as a function of stimulus intensity. The observer's task, in the Maxwellian view through a 2-mm-diameter artificial pupil, was to adjust the intensities of two lights so as to obtain an achromatic appearance of the test field, for a fixed intensity of the third light.

The wavelength combinations employed were divided into the three groups, GY–V, BG–R, and BR–G condition for each achromatic setting.

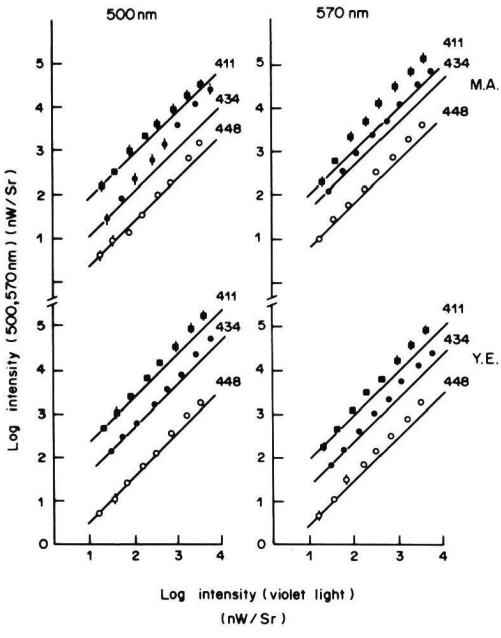

Fig. 3: Result for the GY-V condition. The log relative radiant intensities of the 500 nm (left panel) and the 570 nm (right panel) are plotted against the log radiant intensity of the violet light [3]

In the GY–V condition, the intensity of the 500 nm or the 570 nm light and violet lights were adjusted, while the fixed intensity of the third light was set at 570 nm or 500 nm respectively. In the BG–R condition, the intensity of the 467.5 nm or the 500 nm light and reddish lights were adjusted, while the fixed intensity of the third light was set at 500 nm or 467.5 nm respectively. In the BR-G condition, the intensity of the 467.5 nm or the 640 nm light and greenish lights were adjusted, while the fixed intensity of the third light was set at 640 nm or 467.5 nm respectively.

Each session began with 5 min of dark adaptation, followed by the presentation of one component light at predetermined illuminance levels. The observer then adjusted the intensities of the other two component lights until the rest of the field appeared achromatic. The presentation of the stimulus was 500 ms every 2 s. Overall illuminance levels convered the range from 2 to 2000 Td.

3.2: Result and discussion

The results for the two observers, MA and YE, are given in Figs. 3, 4, and 5. In all the figures, the intensity is expressed as log radiant intensity in nW/sr. Each set of data points represents the result for each wave

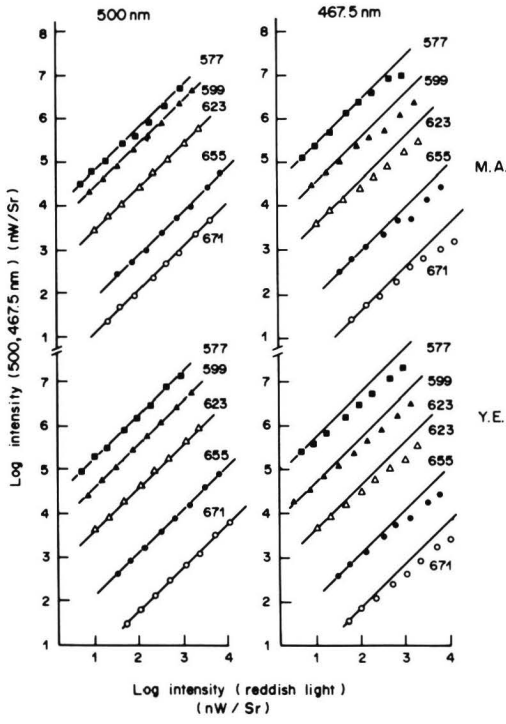

Fig. 4: Result for the BG-R condition. The log relative radiant intensities of the 500 nm (left panel) and the 467.5 nm (right panel) are plotted against the log radiant intensity of the reddish light [3]

length combination. The numeral value to the right of each set of data points indicates the wavelength of the third component light. To facilitate display, the sets of data points have been vertically displaced by one logarithmic unit. Each data point represents the mean of nine settings for each condition. Error bars give $\pm$ 1 SE. For any data with the standard error smaller than 13%, the error bar is omitted, since the standard error is smaller than the plotting symbol. The results showed that the change in the achromatic locus with stimulus intensity can be described in terms of a linear relation between the middle- and longer-wavelength components and of a non-linear relation between the short- and longer-wavelength components.

An asymmetry in the contributions of the short- and longer-wavelength cones in the yellow-blue opponent system may be responsible for producing the apparent compression of the contribution of the short-wavelength mechanism with an increase in stimulus intensity (2 and 4). The compression at high luminance levels implies the acceleration of the sensitivity of the short-wavelength mechanism which may also be related to the non-linear property of achromatic loci found in the present study.

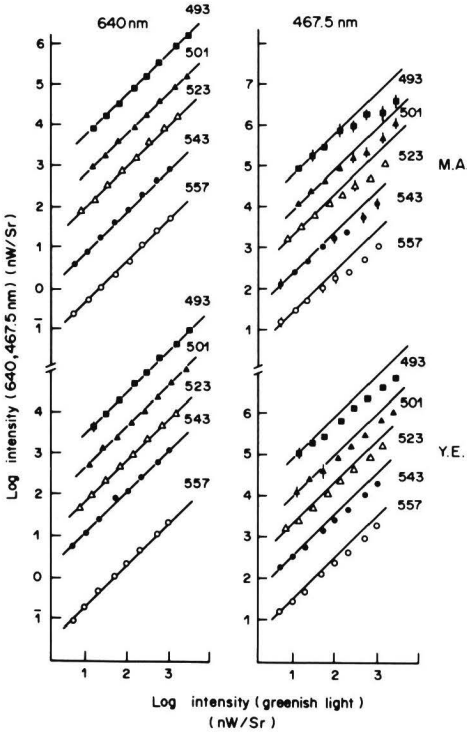

Fig. 5: Result for the BG-G condition. The log relative radiant intensities of the 640 nm (left panel) and the 467.5 nm (right panel) are plotted against the log radiant intensity of the greenish light [3]

4. Yellow-blue cancellation equilibria of a deuteranope

4.1: Experimental method

A two-channel Maxwellian-view optical system was used to present stimuli. One channel provided various yellow lights and the other a 465 nm blue light. The two beams which were presented for 500 ms every 2 s were combined to form a 2° test field on the fovea.

In the first experiment, the y–b equilibrium was determined as a function of retinal illuminance of the 465 nm light which varied from 5 to 1000 Td for four wavelength combinations. The wavelengths containing the yellow light were either 520, 540, 600, or 660 nm.

In the second experiment, the y–b equilibrium was determined as a function of the wavelength of the yellow component for four illuminance levels of the 465 nm light. The wavelength of the yellow component was varied from 510 nm to 660 nm. The retinal illuminance of the blue light was either 1.05, 5, 25, or 105 Td.

4.2: Result and discussion

The data for all the wavelength combinations in the first experiment lay in straight lines with a gradient or unity, as shown in Fig. 6, for a deuteranope. This implies that the yellow-blue equilibrium displays scalar invariance for the present illuminance range while the normal trichromat's function varies in shape with illuminance being depressed in the long-wavelength region of the spectrum with an increase of illuminance.

The result for the second experiment, given in Fig. 7, showed that the energy ratio of the 465 nm light to the yellow light at the y–b equilibrium is the shape invariance with illuminance, and the shape of each curve was quite similar to the spectral sensitivity curve of long-wavelength cones with the deuteranope, whereas the normal trichromat's curve could not be fitted by the spectral sensitivity function of one type of cone. The comparison between normal trichromat and deuteranope is shown in Fig. 8. The cone-interaction assumed between the short- and the long- and middle-wavelength cones which is responsible for the non-linearity of the yellow-blue opponent-color system in normal trichromat seems not to be operative in the case of the deuteranope because of having a deficiency of the middle-wavelength sensitivity.

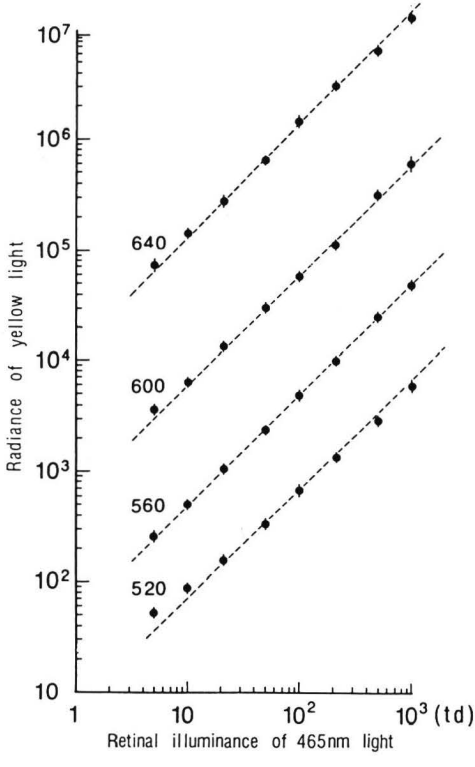

Fig. 6: Energy of yellow components in radiance required to obtain the yellow-blue equilibrium is plotted against the retinal illuminance of the 465 nm blue component [1]

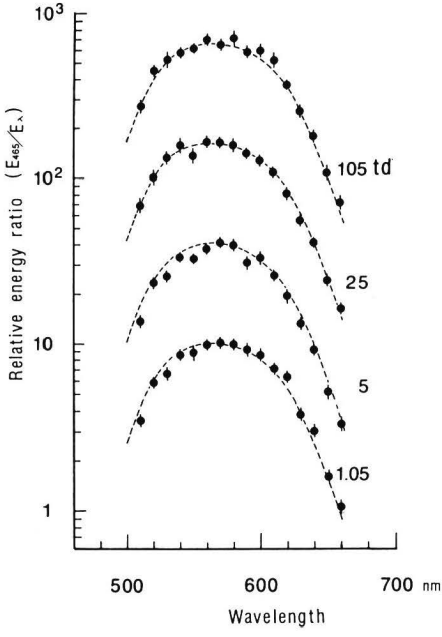

Fig. 7: Relative energy ratio as a function of the wavelength of yellow component for the four illuminance levels of the 465 nm light. The ordinate denotes the energy ratio of the 465 nm light to yellow lights. The dotted lines represent the spectral sensitivities of the long-wavelength cones [1]

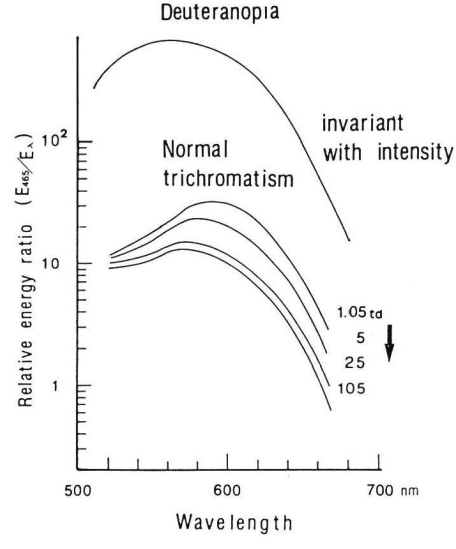

Fig. 8: Comparison of normal trichromat and deuteranope of the yellow-blue hue cancellation function [1]

5. Conclusion

Assuming a site in post-receptoral level at which signals originating from the middle- and longer-wavelength cones converge, we can ascribe the non-linear contribution of the short-wavelength cone system to the interacting operations of the middle- and longer wavelength cone signals at the site.

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Author's address:
Dr. M. Akita
Kyoto Institute of Technology
Psychology Laboratories
Matsugasaki, Sakyo-ku
Kyoto 606, Japan

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Y. Nayatani*, **K. Takahama**** and **H. Sobagaki****, NEYAGAWA and AMAGASAKI

Nonlinearity of Visual-Receptor Responses

DK 612.843.2/.3

Cone responses postulated in the authors' color appearance model consist of two kinds of nonlinear components. The first component reflects the adapting luminance and the second component reflects a change of the target object color. The effectiveness of the nonlinear responses is confirmed by various psychophysical experimental results reported so far. In addition, the color-appearance model has a special feature very similar to the concept of Land's retinrx theory.

Die im Farbwahrnehmungsmodell der Autoren angenommenen Zapfen-Reaktionen setzen sich aus zwei nicht-linearen Komponenten zusammen. Die erste entspricht der Adaptations-Leuchtdichte, und die zweite gibt den Wechsel der betrachteten Körperfarbe wieder. Die Wirksamkeit der nicht-linearen Reaktionen wird durch die Ergebnisse verschiedener psychophysischer Versuche bestätigt, über die bereits berichtet wurde. Außerdem hat das Modell eine besondere Eigenschaft, die es der Retinex-Theorie von Land ähnlich macht.

Le modèle d'apparence des couleurs dans lequel les auteurs avaient proposé de certaines réponses des cônes se compose de deux composantes non-linéaires. La première rend la luminance d'adaptation, la seconde réflet le changement de la couleur d'objet. L'efficience des réponses non-linéaires est affirmée par les résultats de beaucoup d'expériences psychophysiques déjà référées. De plus, le modèle de l'apparence possède une propriété spéciale qui le fait très semblable à la théorie Retinex de Land.

1. Introduction

Color perception of object colors changes by changing its adapting illuminant and luminance as exemplified by the following phenomena: an increase of whiteness-blackness contrast of nonselective samples by raising the adapting luminance [1; 2], an increase of colorfulness of chromatic samples by raising the adapting luminance [3], and hue perception of nonselective samples illuminated by a colored illuminant [4]. Using a set of specified nonlinear responses of the visual receptors, the present authors have developed a model for predicting color appearance of object colors including the above phenomena, and showed that the model could well predict various phenomena of color appearance [5–7]. This paper reviews the nonlinearity of visual-receptor responses adopted in the model, and discusses the reasons to select it. In addition, a relation is discussed between the color appearance model by the present authors and the retinex theory by LAND [8].

* *Osaka Electro-Communication University*, Neyagawa
** *Electrotechnical Laboratory, Life Electronics Research Center*, Amagasaki

2. Characteristics of nonlinearity

We consider the color perception of an object color on a nonselective background with MUNSELL Value 5/. To predict the color perception, the following nonlinear outputs are postulated for the three receptors:

$$
\begin{aligned}
U_{\mathrm{R}} &= \left[\frac{R_{\mathrm{o}}^{0.4495}+1.038^{0.4495}}{R_{\mathrm{o}}^{0.4495}+63.66^{0.4495}}\right]\cdot\log\left[\frac{R+R_{\mathrm{n}}}{R_{\mathrm{o}}+R_{\mathrm{on}}}\right]\\
U_{\mathrm{G}} &= \left[\frac{G_{\mathrm{o}}^{0.4495}+1.038^{0.4495}}{G_{\mathrm{o}}^{0.4495}+63.66^{0.4495}}\right]\cdot\log\left[\frac{G+G_{\mathrm{n}}}{G_{\mathrm{o}}+G_{\mathrm{on}}}\right]\\
U_{\mathrm{B}} &= \left[\frac{B_{\mathrm{o}}^{0.5128}+1.079^{0.5128}}{B_{\mathrm{o}}^{0.5128}+63.66^{0.5128}}\right]\cdot\log\left[\frac{B+B_{\mathrm{n}}}{B_{\mathrm{o}}+B_{\mathrm{on}}}\right]
\end{aligned}
\tag{1}
$$

where R_{o}, G_{o}, B_{o} are the absolute tristimulus values of the background, and R, G, B are those of the object color under consideration [9]. These tristimulus values correspond to the luminance units. The quantities R_{on}, G_{on}, B_{on} and R_{n}, G_{n}, B_{n} are the absolute tristimulus values of the noise components existing in the receptor outputs for the background and for the object color, respectively. The formulae of these tristimulus values are given in the Appendix.

The quantities U_{R}, U_{G}, U_{B} are logarithms of the 2nd step responses **R**, **G**, **B** in the nonlinear model of chromatic adaptation [10] apart from proportional coefficients:

$$
U_{\mathrm{R}} = \log \mathbf{R},\quad U_{\mathrm{G}} = \log \mathbf{G},\quad U_{\mathrm{B}} = \log \mathbf{B}. \tag{2}
$$

The Q, T, P responses in the nonlinear color appearance model [7] are given in terms of U_{R}, U_{G}, U_{B} as

$$
\begin{aligned}
Q &= k_{\mathrm{Q}}\left[\frac{2}{3}\,e(R)U_{\mathrm{R}}+\frac{1}{3}\,e(G)U_{\mathrm{G}}\right]\\
T &= k_{\mathrm{c}}e_{\mathrm{s}}(\theta)\left[U_{\mathrm{R}}-\frac{12}{11}\,U_{\mathrm{G}}+\frac{1}{11}\,k_{\mathrm{B}}\,U_{\mathrm{B}}\right]\\
P &= k_{\mathrm{c}}e_{\mathrm{s}}(\theta)\left[\frac{1}{9}\,U_{\mathrm{R}}+\frac{1}{9}\,U_{\mathrm{G}}-\frac{2}{9}\,k_{\mathrm{B}}U_{\mathrm{B}}\right]
\end{aligned}
\tag{3}
$$

where the coefficients $e(R)$ and $e(G)$ are

$$
\begin{aligned}
e(R) &= 1.75 \text{ for } R \geqq R_{\mathrm{o}},\\
&= 1.00 \text{ for } R < R_{\mathrm{o}},\\
e(G) &= 1.75 \text{ for } G \geqq G_{\mathrm{o}},\\
&= 1.00 \text{ for } G < G_{\mathrm{o}}.
\end{aligned}
\tag{4}
$$

These coefficients were introduced to obtain a high correlation between the Q response and the MUNSELL Values [6]. The coefficient $e_s(\theta)$ is a weighting factor on hue, originally introduced by HUNT [11]. The coefficients k_Q, k_C, k_B are constants.

The first term of the right-hand side of eq. (1) gives a nonlinear-receptor response reflecting a change of adapting luminance, and the second term gives a nonlinear response reflecting a change of the object color and the relative spectral power distribution of illuminant. We call the first term the S-type function, and the second term the logarithmic function.

Now, we discuss the structure of eq. (1). The S-type function is the same as the following structure already reported from the physiological point of view [12]:

$$L^n/(L^n + \sigma^n). \tag{5}$$

The only difference between eqs. (1) and (5) is the existence of the terms of $1.038^{0.4495}$ and $1.079^{0.5128}$ in the numerators of the S-type functions. These terms are the noise components. The introduction of these components may be reasonable by considering the spontaneous discharges in the cells under dark adaptation. The value 63.66 in the denominators of the S-type functions is the luminance (cd/m^2) of the background with reflectance of 0.20 at 1000 lux: $L_0 = 1000 \times 0.20/\pi = 63.66$.

In the S-type nonlinearity, the exponent is 0.4495 for R_0 and G_0, and 0.5128 for B_0. This suggests that the response of the B receptor varies steeper than that of the R or the G receptor for the same change of the adapting level of each receptor. These S-type functions are similar to the power functions $R_0^{1/6}$, $G_0^{1/6}$, $B_0^{1/6}$. Figure 1 shows the S-type functions together with the power function plotted against the effective adapting level R_0, G_0, or B_0 of each response system.

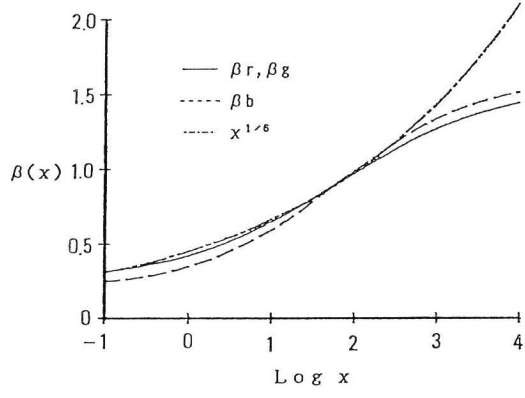

Fig. 1: The S-type functions of eq. (1). The dot-dash curve corresponds to the power function $x^{1/6}$, where x on the abscissa stands for R_0, G_0, or B_0.

The logarithmic function in eq. (1) corresponds to the perception of the object color under consideration. This is always defined by the ratio between the responses to the object color and to the background. Therefore, the logarithmic functions are reduced to

$$\begin{aligned} &\log[(R_{\mathrm{rel}} + 1)/20\xi + 1)], \\ &\log[(G_{\mathrm{rel}} + 1)/20\eta + 1)], \\ &\log[(B_{\mathrm{rel}} + 1)/20\zeta + 1)], \end{aligned} \tag{6}$$

where R_{rel}, G_{rel}, B_{rel} are the relative tristimulus values in the fundamental system transformed from the CIE 1931 tristimulus values of the object color. The value 20 corresponds to the background reflectance 0.20. The quantities ξ, η, ζ are the transformed values in the fundamental system from the chromaticity coordinates of the adapting illuminant x_0, y_0. The constant terms of unity in both the numerators and the denominators correspond to the noise components. Equation (6) is easily derived by referring to the Appendix.

The logarithmic function of eq. (6), for example in the red system, is positive for $R_{\mathrm{rel}} > 20\xi$, negative for $R_{\mathrm{rel}} < 20\xi$, and zero for $R_{\mathrm{rel}} = 20\xi$. This means the logarithmic function is zero when the red component of the object color is the same as that of the surround. This relation also holds in the other systems, the green and the blue, and gives a basis for the opponent-color system consisting of whiteness-blackness, redness-greenness, and yellowness-blueness.

When the adapting luminance of a specified object color is changed, its color-perception change is predicted by the *S*-type function. On the other hand, when the object color is changed under a specified adapting luminance, its color perception is specified only by the logarithmic function. The structure of eq. (1) well divides the receptor responses into the components reflecting the adapting luminance, the object color, and the illuminant color, and puts all of them together.

3. Reasons of selecting the nonlinear characteristics

Now, we describe the reasons of selecting the nonlinear characteristics found in eq. (1).

3.1: *Nonlinearity on adapting-luminance change*

The reasons of selecting the *S*-type function are as follows.

3.11: Requirement from BRENEMAN's study

BRENEMAN [13] studied a chromatic-adaptation effect between D_{65} and A, in which the adapting luminance was kept at the same value under each illumination. Accordingly the study, the observed results deviated appreciably from the predictions by the VON KRIES law for an intermedi-

ate adapting luminance. However, raising the adapting luminance to 1,500 cd/m^2, the observed results agreed well with the predictions by the VON KRIES law. The *S*-type nonlinearity was needed to illustrate these results [14].

Figure 2 (a) and (b) show the predictions of chromatic-adaptation effects between D_{65} and A for a low and a high adapting luminance based on the *S*-type functions. The corresponding predictions by the VON KRIES law are shown in Fig. 2 (c). The results of Fig. 2 (b), which correspond to the high adapting luminance of about 1,900 cd/m^2, approach the predictions by the VON KRIES law of Fig. 2 (c).

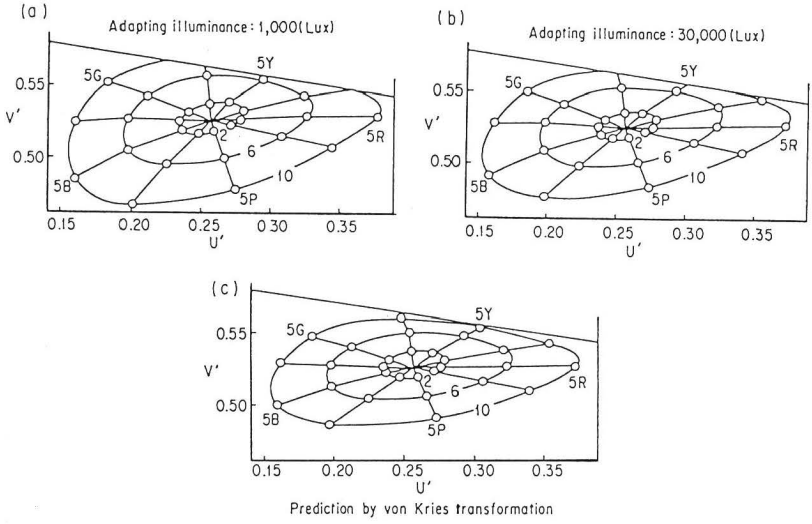

Fig. 2: Chromatic adaptation effect between D_{65} and A predicted by use of the S-type exponent: (a) case of 64 cd/m^2, (b) case of 1,900 cd/m^2, (c) case of the VON KRIES law [14]

3.12: Requirement from HUNT's experiment.

HUNT [3] studied a relation between the colorfulness *M* of chromatic color and its adapting luminance L_o. He derived the relation as $M \simeq s_{uv} L_o^{1/6}$, where s_{uv} is the metric saturation of a colored stimulus [15]. This result directly requires the receptors to have the nonlinearity with the power function of $R_o^{1/6}$, $G_o^{1/6}$, $B_o^{1/6}$ on the change of adapting luminance [14]. This power function is already compared with the *S*-type functions in Fig. 1. The *S*-type functions closely coincide with the power function of the exponent 1/6.

3.13: Difference between the *S*-type functions of *B* response and of *R*, *G* response.

HUNT [3] also made the experiments on the color perception of chromatic colors with the same chromaticity but with different Y_{rel} values by only raising their adapting luminance. The experimental results showed that the blueness in the chromatic colors increases with an increase of their Y_{rel} values. This effect also increases with the adapting luminance. In order to predict these facts, the *S*-type function of the *B* response was needed to make steeper than those of the *R* and the *G* response for the change of adapting luminance [14]. The predicted examples are shown in Fig. 3.

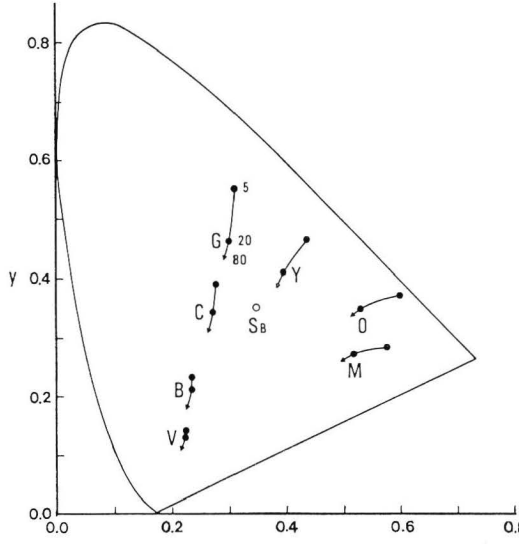

Fig. 3: Predictions of the second HUNT effect. The tip of the arrow correponds to the reflectance 80% and starting point to the reflectance 5% [14]

3.14: Values of exponents in the *S*-type functions.

In the *S*-type functions, the exponents used are 0.4495 for R_0, G_0 and 0.5128 for B_0. These values are almost similar to 1/2. This naturally corresponds to 1/2 of the exponent of *L* in eq. (5). However, BOYNTON and WHITTEN [16] reported that the nonlinear response of the receptor physiologically measured was well predicted by using $n = 0.7$ in eq. (5) for a fixed pupil size and no bleaching of the receptor. Further, BOYNTON [17]

gave the following equation by introducing the parameters for pupil size A and bleaching coefficient p:

$$Res. \propto (LAp)^{0.7}/[(LAp)^{0.7} + 631] \quad (7)$$

where Res. is the nonlinear output of the receptor and L the luminance of adapting field. By using the numerical values of L, A, p in BOYNTON's Table 6.1 [17]. eq. (7) is computed and plotted in Fig. 4.

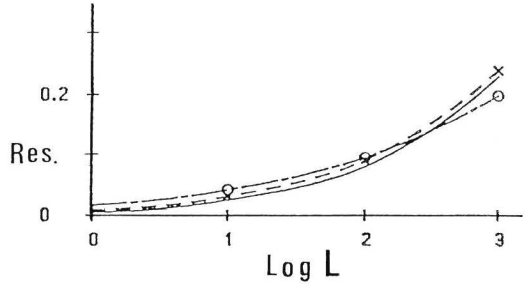

Fig. 4: A comparison between eq. (5) and eq. (7). Real line shows response values computed by eq. (7). Open circles correspond to the response values computed by eq. (5) for $n = 0.4$, and crosses to $n = 0.5$.

When eq. (7) is approximated by the function of eq. (5), what value of n should be used? The value of n was estimated by a trial and error method, and found to be around $n = 0.4$ to 0.5. In Fig. 4, the computed results are shown for $n = 0.4$ by open circles, and those for $n = 0.5$ by crosses. In a practical adapting-luminance range, the agreement between eq. (7) and the approximations to it by eq. (5) is quite excellent. The exponents of about 1/2 of R_0, G_0, B_0 in eq. (1) are estimated to be reasonable.

3.2: *Nonlinearity on object color perception*

The logarithmic function reflects object color perception. This structure does not include the adapting luminance, but only takes the spectral characteristic or color of the adapting illuminant into account. It also considers the object color under illumination. This is a kind of VON KRIES transformation. This structure was chosen by the following reasons.

3.21: Requirements from the color constancy of object colors.

In a series of nonselective samples, the white sample is whiter and the black sample is blacker by raising their adapting luminance [1; 2]. However, the gray sample with MUNSELL Value 5/ keeps its grayness unchanged in spite of the change of adapting luminance. In addition, when nonselective samples are illuminated by a colored illuminant, the

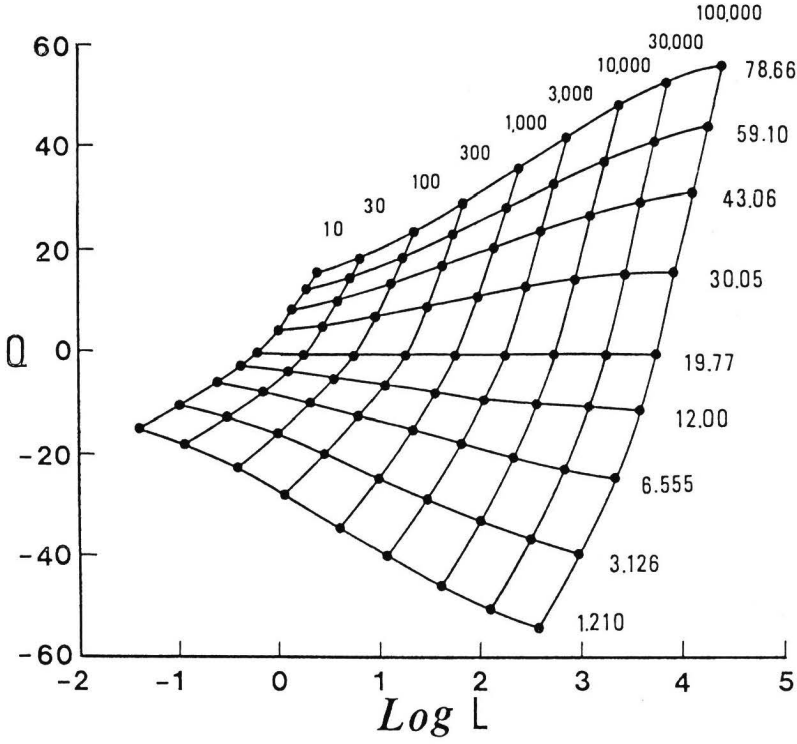

Fig. 5: Metric whiteness-blackness Q of a series of nonselective samples for different adapting illuminance. The ordinate shows metric whiteness-blackness, and the abscissa the luminance of samples. Number 1.210 to 78.66 correspond to the reflectance (%) of samples. Numerals 10 to 100,00 correspond to the adapting illuminance (lux) [6]

samples lighter than the background are perceived as having the illuminant hue and those darker than the background as having the complementary hue of the illuminant [4]. In order to predict these effects, it is necessary to normalize the tristimulus values of object color by those of the background.

Further, it is necessary that the normalized value is tranformed by logarithmic operation in order to generate the opponent responses. By this transformation, the resultant responses change their signs to positive or negative for redness vs. greenness, yellowness vs. blueness, and whiteness vs. blackness. Thus, opponent-color responses are generated. Refer to ref. [7] on its details.

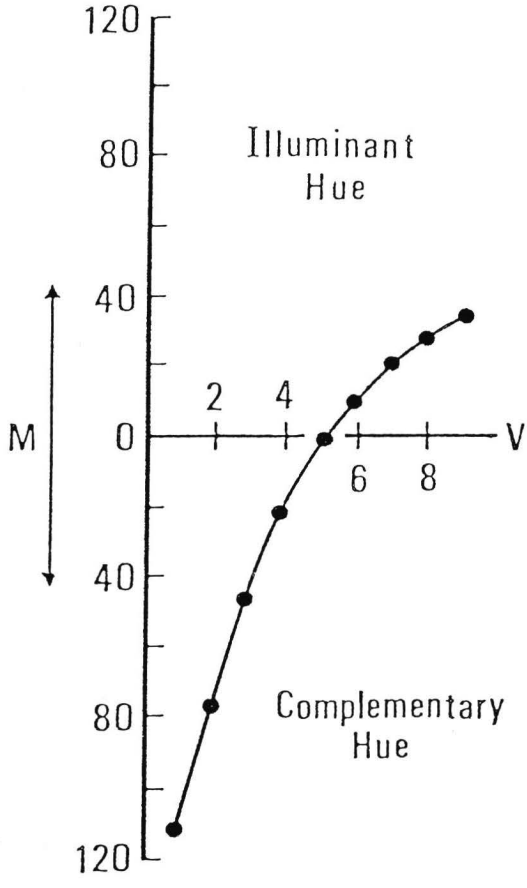

Fig. 6: HELSON-JUDD effect on a series of nonselective samples under yellow illuminant with highly saturated color. The ordinate shows the values of metric colorfulness and the abscissa shows the Munsell Values of the test samples (from ref. 5).

Based on this stucture, an increase of white and black contrast [5] is predicted by raising the adapting luminance and shown in Fig. 5. The predicted results is shown in Fig. 6 for nonselective samples under a highly saturated yellow illuminant [5].

Figure 5 shows that the Q value changes more significantly for the change of reflectance than for the change of illuminance. This is a daily experience. In order to take account of this fact, it is needed that the reflectance dependence and the illuminance dependence of lightness of an object color are governed by different functions. Our model of color appearance uses two different types of functions: S-type function and logarithmic function. If the same S-type functions are used for the reflectance dependence and the illuminance dependence, their values of exponent must be widely different from each other.

3.22: Similarity to the retinex theory.

In spite of significant change of illuminant and luminance, the perceptions of object colors well keep their color appearances under daylight illuminant. In the retinex theory, the effective luminance values in the fundamental system are measured or predicted for each of the component colors in a MONDRIAN figure, and then the values are normalized by deriving the luminance-value ratio between all the adjacent colors found in the figure [18].

The normalization to the background in eq. (6) shows an excellent similarity to the retinex theory. Let us consider the responses of the color appearance model of an area (t) in the MONDRIAN figure on a gray background of N5/:

$$U_T = \beta(L_T) \log \frac{T_t + 1}{T_o + 1} \qquad (T = R, G, B) \tag{8}$$

If we consider any pathway from the target area to the background as shown in Fig. 7, eq. (8) is rewritten by use of a chain of responses T_i (i=1, 2, . . ., n) in the pathway as

$$U_T = \beta(L_T) \left[\log \frac{T_t + 1}{T_1 + 1} + \log \frac{T_1 + 1}{T_2 + 1} + \cdots + \log \frac{T_n + 1}{T_o + 1} \right] \tag{9}$$

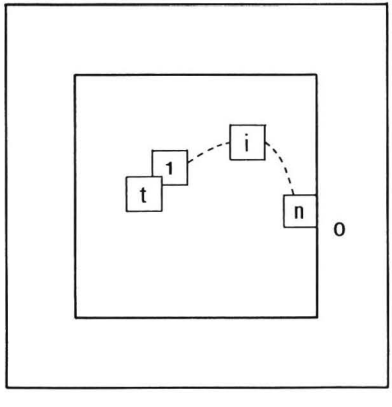

Fig. 7: A MONDRIAN figure. Label t shows a target area, and label o shows a background of a medium gray. A series of areas shown by labels t, 1, . . ., i, . . ., n is a pathway from the target area to the background.

Equation (9) corresponds to the successive sum of response-ratio between adjacent areas from the target to the background. This shows that the above algorithm of our model is very much similar to that of retinex theory. This suggests that good similarities exist between the retinex theory and the model of eq. (1).

Anyway, it should be noted that the normalizations and the succeeding logarithmic transformations are needed to assure the color constancy of object colors under various changes of adapting-illuminant color and adapting luminance.

4. Conclusion

A nonlinear structure of receptor response is proposed by considering various psychological information for predicting color perception of object. The model has various features in the prediction of color perception including the various psychological effects already stated. The model can be thought that the nonlinear change of receptor response for changing adapting luminance is added to the usual VON KRIES law.

Appendix: Tristimulus Values in the Fundamental System

The absolute tristimulus values of the object color R, G, B are given by

$$\begin{bmatrix} R \\ G \\ B \end{bmatrix} = \frac{E}{100\pi} \mathrm{M} \begin{bmatrix} X_{\mathrm{rel}} \\ Y_{\mathrm{rel}} \\ Z_{\mathrm{rel}} \end{bmatrix} \tag{A1}$$

where E is the adapting illuminance, M is the transformation matrix from the CIE system to the fundamental-primary system, and X_{rel}, Y_{rel}, Z_{rel} are the CIE tristimulus values of the object color under consideration. It is given by eq. (A2), when the ESTÉVES-HUNT-POINTER primaries are used as the fundamental primaries and when standard illuminant D_{65} is used as the normalizing white stimulus [7]:

$$\mathrm{M} = \begin{bmatrix} 0.38920 & 0.68917 & -0.07871 \\ -0.22977 & 1.18321 & 0.04640 \\ 0 & 0 & 1.21346 \end{bmatrix} \tag{A2}$$

The maximum value of Y_{rel} is normalized to 100. The absolute tristimulus values of the background R_o, G_o, B_o are given by

$$\begin{bmatrix} R_o \\ G_o \\ B_o \end{bmatrix} = \frac{E}{100\pi} \mathrm{M} \begin{bmatrix} X_{0rel} \\ Y_{0rel} \\ Z_{0rel} \end{bmatrix} \tag{A3}$$

where X_{0rel}, Y_{0rel}, Z_{0rel} are the CIE tristimulus values of the background.

The values of ξ, η, ζ are given by

$$\begin{bmatrix} \xi \\ \eta \\ \zeta \end{bmatrix} = \mathrm{M} \begin{bmatrix} x_0/y_0 \\ 1 \\ z_0/y_0 \end{bmatrix} \tag{A4}$$

where x_0, y_0, z_0 are the chromaticity coordinates of adapting illuminant. For the nonselective background with $\varrho_0 = 0.20$, eq. (A3) is rewritten by introducing eq. (A4) as

$$\begin{bmatrix} R_o \\ G_o \\ B_o \end{bmatrix} = \frac{E}{100\pi} \begin{bmatrix} 20\xi \\ 20\eta \\ 20\zeta \end{bmatrix} \tag{A5}$$

The quantities R_{rel}, G_{rel}, B_{rel} are given by

$$\begin{bmatrix} R_{rel} \\ G_{rel} \\ B_{rel} \end{bmatrix} = \mathrm{M} \begin{bmatrix} X_{rel} \\ Y_{rel} \\ Z_{rel} \end{bmatrix} \tag{A6}$$

where X_{rel}, Y_{rel}, Z_{rel} are the CIE tristimulus values of object colors.

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Author's address:
Dr. Y. Nayatani
Osaka Electro-Communication University
18-8 Hatsu-cho, Neyagawa
Osaka 672, Japan
Dr. K. Takahama and H. Sobagaki
Electrotechnical Laboratory, Life Electronics Research Center
3-11-46 Nakoji, Amagasaki
Hyogo 661 , Japan

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Donald C. Hood*, NEW YORK, N.Y.:

Non-linear Response Functions and Adaptation

DK 612.843.317.3
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Instanteneous non-linear response functions of the visual system can be inferred from a psychophysical detection paradigm. Data are summarized that argue: 1. The psychophysically measured non-linear response functions are not receptoral in origin, and 2. these functions are modified by a multiplicative adaptation mechanism within milliseconds after the onset of an adapting light.

Unmittelbar einsetzende nicht-lineare Wirkungsfunktionen des Sehsystems lassen sich von einem psychophysischen Wahrnehmungsmuster ableiten. Hier werden Daten zusammengestellt, die Gründe dafür anführen, daß 1. eine psychophysisch gemessene nicht-lineare Wirkungsfunktion nicht aus den Rezeptoren der Netzhaut stammt, und daß 2. solche Funktionen durch einen multiplikativen Adaptationsvorgang innerhalb von Millisekunden nach dem Einsetzen eines umstimmenden Lichtes modifiziert werden.

On peut dériver les fonctions d'efficacité non-linéaires instantanées dans le système visuel d'un paradigme de détection psychophysique. Ici on a compilé des données qui arguent (1) que les fonctions d'efficacité non-linéaires mesurées d'une manière psychophysique ne proviennent pas des récepteurs dans la rétine, et (2) que ces fonctions sont modifiées par un procès multiplicatif d'adaptation, dans l'espace de quelques millisecondes après que que la lumière d'adaptation a commencé.

1. Introduction

No single model of color vision can either quantitatively predict both detection and appearance data or integrate psychophysical and physiological data into a unified theory. Although secondary texts often give the impression that a unified model of color vision exists, the "textbook model" of color vision can be shown to have serious problem [1]. In general, current attempts to quantitatively account for aspects of color vision predict more limited sets of appearance and/or detection data. Some of these models incorporate explicit non-linearities. Here I summarize a line of research, unfamiliar to many color scientists, designed to describe an instantaneous non-linearity of the visual system and the mechanisms of adaptation thought to modify it.

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* *Columbia University New York, Dept. of Psychology*

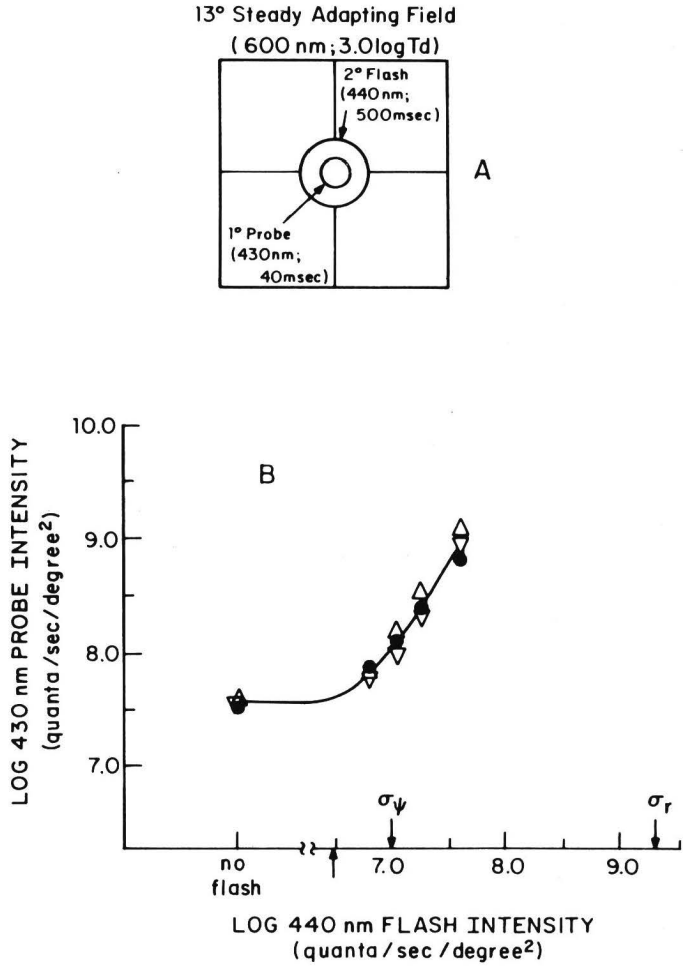

Fig. 1: A. A detection (probe-flash) paradigm used to study cone system non-linarities.
B. Log probe intensity is plotted against log flash intensity. The data points are for three individual observers. The average flash threshold for the three obervers is indicated by the upgoing arrow on the abscissa. The smooth curve is a theoretical prediction based on the model in Fig. 2. The value of the semi-saturation constant estimated from the model, is shown for comparison to the estimated from physiological recordings (5, 6). (This figure is modified from an figure in HOOD and GREENSTEIN [3])

Over the last ten years a few laboratories have been using a flash-on-flash (aka probe-flash) detection paradigm to study non-linear response functions of the visual system and to explore how these non-linearities change with adaptation. The non-linear response functions and the adaptation mechanisms described in this work are not unlike those in some of the models in the color literature, including models described by two of the speakers in this session. Although these two lines of research share non-linear functions and similar adaptation mechanisms, that is about all that is shared. In general, this work has ignored the color literature and, by and large, has been ignored by those working on color problems.

I will introduce the probe-flash approach by considering a non-linearity of a short-wave sensitive cone pathway. Then I will briefly summarize a class of models of sensitivity control and mention points of contact between these models and models of color vision.

2. The detection paradigm

Fig. 1 A shows the spatial and temporal paradigm. Notice that there are three lights; one is steady and two are brief. The observer's task is to detect the 40 ms probe light when it is presented with a 500 ms background flash. The probe is briefer than the flash and they are presented simultaneously. You can think of the paradigm as an increment threshold paradigm in which the background is brief rather than steady.

3. Results

In this experiment, a short-wave sensitive pathway (STILES π_1) was isolated by using a 3.0 log trol orange field and violet probes and flashes. Threshold intensity for detecting the violet probe is measured in the presence of violet flashed backgrounds. Panel B of Fig. 1 shows data for three observers. The log probe threshold is plotted against log flash intensity.

The arrow indicates the threshold for the flash. Notice that flash intensities barely above threshold elevate probe threshold. Also note that these data are steeper than traditional increment threshold curves.

4. Theoretical framework

Fig. 2 is a schematic of a simple theoretical framework. The first box represents the site of light absorption; we assume that the number of molecules absorbed is a linear function of intensity. The second box is the site of the major non-linearity of the visual system. The non-linearity is instantaneous; it does not take time to develop.

The output of the system is given by

$$R(I) = \frac{I^n}{I^n + \sigma^n} \cdot R_{max} \quad (1)$$

and for detection:

$$R(I_f + I_p) - R(I_f) = \xi \quad (2)$$

σ in eq. 1 is the semi-saturation constant. When the intensity I of the light is equal to σ, then the response R of the system is one half of its maximum. We call this model a single site model because in principle it could be describing a single cell. We can fit a model based on the response function of eq. 1 by adding a detection assumption (see eq. 2). In eq. 2, I_f and I_p are the flash and the probe intensity, and ξ is the criterion response needed for detection. The smooth curve in Fig. 1 B is the best fit of the model. (See HAYHOE, HOOD, and BENIMOFF [2] for a review of this general approach, and HOOD and GREENSTEIN [3] for more details about this experiment.)

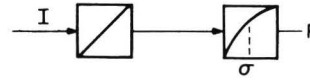

Fig. 2: A single site model (See the text and HOOD and GREENSTEIN [3] for more details)

The non-linearity we are studying is not at the receptors. There are two lines of evidence to support this statement. First, the psychophysical estimate of the semi-saturation constant, σ, is smaller than the σ estimated for the receptors. In fact, the psychophysically estimated σ is over two hundred times smaller than that estimated for the receptors [3]. In Fig. 1 B our psychophysical estimate is shown along the abscissa with the estimate of σ for the monkey cones [4; 5; 6]. Secondly, you can show psychophysically that the non-linearity we measure occurs beyond an opponent interaction among different receptor types. STROMEYER et al. [7], for example, has added yellow flashes to violet flashes and decreased the threshold for the probe. FINKELSTEIN and HOOD [8] have done a similar experiment for a red-on-red condition. Thus, the major non-linearity we measure is beyond the receptors.

5. Models of adaptation

In this section I will briefly summarize a class of models of sensitivity control developed to explain the effects of steady fields. Similar models have been proposed by GEISLER [9], HAYHOE, HOOD, and BENIMOFF [2], and WALRAVEN and VALETON [10], for the photopic system, and by ADELSON [11] for the rod system.

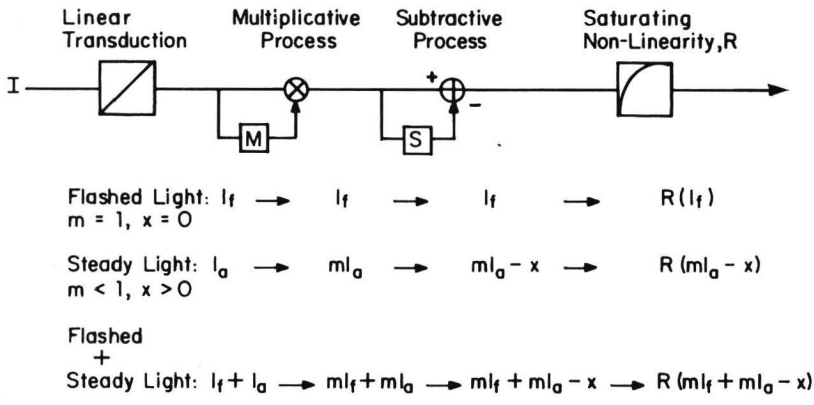

Fig. 3: A single site model of adaptation incorporating a linear transduction mechanism, multiplicative and subtractive adaptation mechanisms and a single saturating non-linearity. The non-linarity is instantaneous; the adaptation mechanisms develop with time. (See the text, and HAYHOE et al. [2] for more details)

Fig. 3 shows the single site model with two mechanisms of adaptation added. Each of these mechanisms develops with time. Consider a brief flash of intensity I_f presented in the dark. The peak response to this flash will be relatively unaffected by the mechanisms of adaptation. When a steady field, I_a, is presented, the two adaptation mechanisms are brought into action. Unlike the instantaneous non-linearity, these mechanisms take time to develop. Notice that the multiplicative mechanism acts to scale the intensity by multiplicative constant. This is a VON KRIES type of adaptation. This mechanism is followed in the model by a subtractive mechanism that removes most of the remaining signal from the background. In the color literature, this is sometimes referred to as complete, or nearly complete, discounting of the background. Models like the one in Fig. 3 have been fitted to the probe – flash data collected on different adapting fields [2; 9; 10; 11].

Fig. 4 shows an extention of this model to two sites, a first site with characteristics matching the receptors and a second site following the interaction among different receptor types. The semi-saturation of the second site is lower than that of the first. Note that both the receptor site and the post-receptor site are shown to have multiplicative mechanisms. We have been working on a two site model of a 'blue-yellow' pathway, extending the work of PUGH and MOLLON [12]. We find that most of the multiplicative changes are taking place before the second site [13]. However, you can demonstrate that multiplicative changes are occuring beyond the

receptors and beyond a site of an opponent interaction. In other words, a VON KRIES type adaptation is needed at least at two sites, at the receptors and at a site beyond an opponent interaction among receptors.

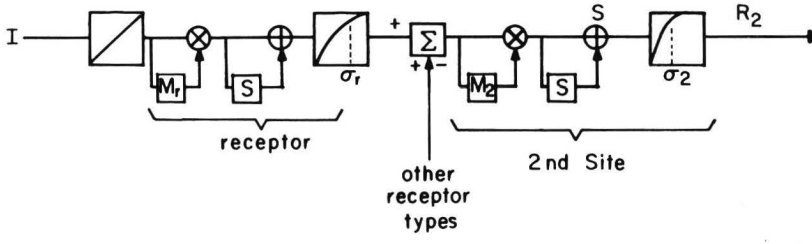

Fig. 4: A two site model. Each site is shown with multiplicative and subtractive mechanisms. The existence of multiplicative and subtractive mechanisms at the receptor is still open to debate [4; 5]

6. Fast von Kries type adaptation

A final point concerns the time course of the mechanisms of adaptation. Although these mechanisms take time to develop, they can develop very quickly. HAYHOE, HOOD, and BENIMOFF [2] estimated that following the onset of a 2.7 log trol adapting field the multiplicative changes were complete within 50 ms. And most, but not all the subtractive changes, were over within 200 ms. The non-linear response functions that are inferred from some of the paradigms used in the color literature are less steep than we measure. For example, when using a 500 ms light, as in some of the studies reported in this session, a more shallow function is needed to fit the data. The reason for this discrepancy is that the non-linearity examined by these paradigms is, in our terms, a function of both the instantaneous non-linear function and the multiplicative and subtractive mechanisms.

7. Summary

Models of adaptation developed to explain probe-flash detection data suggest the following for models of color vision. One, if you need a non-linear response function to describe the data, these functions are probably not describing receptor non-linearities. Second, the non-linear response functions you measure are probably not instantaneous non-linearities, they are already changed by fast acting adaptation mechanisms. And third, multiplicative changes (VON KRIES type adaptation) can occur beyond the receptors.

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Author's address:
Prof. Dr. D. C. Hood
Dept. of Psychology
Columbia University
Schermerhorn Hall
New York, N. Y., 10027

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Robert W. G. Hunt*, NORTHWOOD, MSX.:

A Visual Model for Predicting Colour Appearance under Various Viewing Conditions

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A previously published model of color vision has been extended to provide predictions of hue, brightness, colorfulness, lightness, saturation, and chroma, for stimuli of any luminance and chromaticity in adapting fields of any luminance and chromaticity. Factors allowing for the Helson-Judd effect and for induction by surrounds are also included.

Eine schon früher entwickelte Modell-Vorstellung vom Farbensehen wird hier erweitert, um Voraussagen für Buntton, Leuchtdichte, Helligkeit, Sättigung und Buntheit für Farbvalenzen beliebiger Leuchtdichte und Farbart in Umfeldern beliebiger Leuchtdichte und Farbart machen zu können. Dabei sind auch Faktoren zur Berücksichtigung des Judd-Helson-Effektes und des Simultankontrastes eingebaut.

Un modèle de la vision des couleurs que l'auteur a publié déjà autrefois est ici étendu pour rendre possible de prédire la teinte, luminance et luminosité, saturation et chroma des couleurs, de luminance et chromaticité quelconques si l'on les voit dans des ambiances de luminance et chromaticité quelconques. Aussi on a incorporé des facteurs qui tiennent compte de l'effet Judd-Helson et du contraste simultané

1. Introduction

A previously published model of color vision [1] predicted the hues, lightnesses, saturations, and chromas of colours seen under a medium photopic level of illumination; this model has now been extended to provide, in addition, predictions of brightness and colourfulness, at any level of illumination.

2. Stimulus response function

The curvature of lines of constant hue in chromaticity diagrams is predicted well on the basis that the responses produced by the cones in the retina are proportional to the square-root of the amount of radiation usefully absorbed by them [1]. However, a simple square-root relationship cannot be a true representation for all levels of stimulus intensity. At very low intensities, noise in the visual system must prevent extremely small

* *Department of Optometry and Visual Science, The City University,* Dame Alice Owen Building, 311–321 Goswell Road, London EC1V 7DD

Table 1: Criteria and measures for related colours

Achromatic colours	$C_1 = C_2 = C_3 = 0$
Constant hue	$C_1 : C_2 : C_3$: in constant ratio
Unique red	$C_1 = C_2$
Unique green	$C_2 = C_3$
Unique yellow	$C_1 = C_2/11$
Unique blue	$C_1 = C_2/4$
Hue angle	$h_s = \arctan \{[-\frac{1}{2}(C_3 - C_2)/4.5]/[C_1 - C_2/11]\}$
Hue	$H = H_1 + 100 \dfrac{[(h_s - h_1)/e_1]}{[(h_s - h_1)/e_1 + (h_2 - h_s)/e_2]}$
Blueness-yellowness	$M_{BY} = N_c(\frac{1}{2})\ (10/13)\ (C_3 - C_2)\ (e_s/4.5)\ F_t$
Redness-greenness	$M_{RG} = N_c\ (10/13)\ (C_1 - C_2/11)\ e_s$
Colourfulness	$M = (M_{BY}^2 + M_{RG}^2)^{1/2}$
	$M_c = 100\,M$
Relative blueness-yellowness	$m_{BY} = M_{BY}/(R_a + G_a + B_a)$
Relative redness-greenness	$m_{RG} = M_{RG}/(R_a + G_a + B_a)$
Saturation	$s = 50\,M_c/R_a + G_a + B_a)$
Brightness	$Q = (A + M)N_1 - N_2$
Lightness	$J = 100\ Q/Q_w$
Chroma	$C = sJ/100$

where $N_1 = A_w^{0.5}/(5.33\ N_b^{0.13})$ and $N_2 = A_w^{1.9}\ N_b^{0.362}/2080$; A_w *and* Q_w are the values of A and Q, respectively, for the reference white; and e_s, e_1, e_2, h_1, h_2, H_1, N_c, N_b, F_t are defined in Table 2. In the expression for s, the constant 50 and M_c (instead of M) are used to give convenient numbers; and, although Q could have been used as the divisor, $R_a + G_a + B_a$ is used because it results in good predictions of the saturations of spectral colours [1].

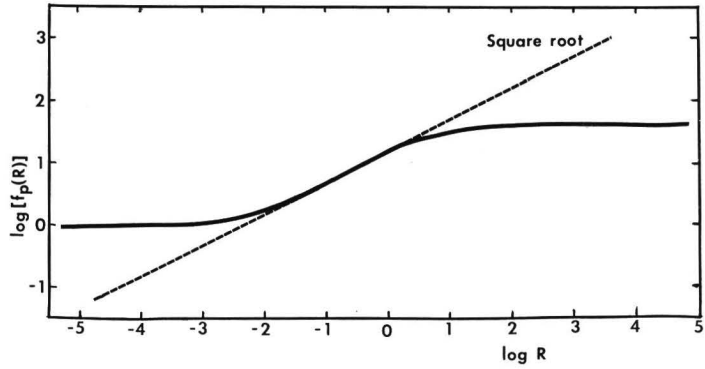

Fig. 1: Stimulus response function, $f_p(R)$, for cones in a given state of adaptation. Log $[f_p(R)]$ is plotted againt log R, where R is the amount of radiation usefully absorbed by the cones per unit retinal area.

responses being significant; and, at very high intensities, a point must eventually occur where a maximum level is reached, representing an inability of the visual mechanism in question to produce any more response. For these reasons, it is necessary to use limiting functions to represent visual responses [2; 3]. Following SEIM and VALBERG's suggestions, functions for the three cone types are formulated as follows:

$$f_p(R) = 40\,[R^{0.73}/(R^{0.73} + 2)] + 1 \qquad \text{where } R = 0.4002X + 0.7076Y - 0.0808Z$$

$$f_p(G) = 40\,[G^{0.73}/(G^{0.73} + 2)] + 1 \qquad \text{where } G = -0.2263X + 1.1653Y + 0.0457Z$$

$$f_p(B) = 40\,[B^{0.73}/(B^{0.73} + 2)] + 1 \qquad \text{where } B = 0.9182Z$$

R, G, B are the amounts of radiation usefully absorbed by each cone type per unit area of the retina in a given state of adaptation. The log of the function, $f_p(R)$, is plotted against log R in Fig. 1, and it can be seen that, over its central region, the curve has a slope of about ½, thus providing an approximately square-root relationship as required. Similar curves apply for $f_p(G)$ and $f_p(B)$. There is a striking similarity between the function f_p and that found by BOYNTON and WHITTEN [4] for the respone of monkey cones:

$$b\,[R^{0.7}/(R^{0.7} + k')]$$

where R is the radiation usefully absorbed in the cones, and b and k' are constants.

3. Adaptation

The cone responses after adaptation are formulated as:

$$R_\alpha = f_p\,(F_L F_R R/R_w) + R_D$$
$$G_\alpha = f_p\,(F_L F_G G/G_w) + G_D$$
$$B_\alpha = f_p\,(F_L F_B B/B_w) + B_D$$

where R_w, G_w, B_w are the values of R, G, B for a suitably chosen reference white in the effective adapting illuminant, and F_L, F_R, F_G, F_B, R_D, G_D, B_D are parameters that make allowance for the extent of the adaptation.

The parameter, F_L (a luminance-level adaptation factor) is defined as:

$$F_L = [100\,(5L_A)/(5L_A + 10^5)]^{1/3} + 0.001$$

where L_A is the luminance of the adapting background in cd/m^2. In this formula, $5L_A$ is used because, in typical viewing conditions, the luminance of the reference white is often about five times that of the adapting background. In Fig. 2, log F_L is plotted against log $(5L_A)$.

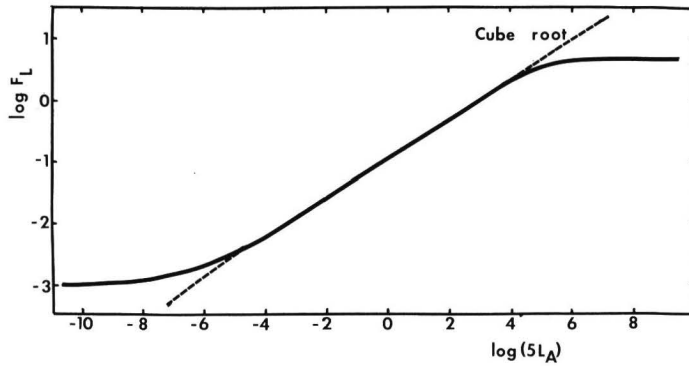

Fig. 2: Luminance-level adaptation factor, F_L. Log F_L is plotted against log ($5\,L_A$), where L_A is the luminance of the adapting field in cd/m^2, and $5\,L_A$ is the luminance of a typical white.

If F_R, F_G, F_B were all equal to unity, and R_D, G_D, B_D were all equal to zero, then the terms R_w, G_w, B_w would provide a VON KRIES type of allowance for chromatic adaptation; by using different values, reduced levels of chromatic adaptation, and the HELSON-JUDD effect (illuminant-coloured highlights and complementary-coloured shadows) can be modelled. Let us assume for the moment that $F_R = F_G = F_B = 1$ and $R_D = G_D = B_D = 0$. Then $R_a = f_p(F_L R/R_w)$, and when $R = R_w$, it follows that $R_a = f_p(F_L)$. If log ($5\,L_A$) = 3.5, then log R_a = 1.23; this value is shown by the circled point at the extreme right in Fig. 3, in which log R_a is plotted

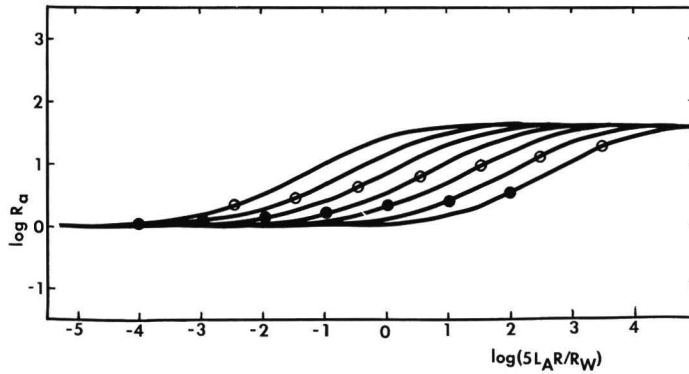

Fig. 3: Cone response functions, R_a, for various states of adaptation. Log R_a is plotted against log ($L_A R/R_w$) for log L_A = 3.5, 2.5, 1.5, 0.5, –0.5, –1.5, and –2.5. L_A is the luminance of the adapting field in cd/m^2; R_w is the value of R for the reference white. Whites: ●; blacks: ○.

against log ($5 L_A R/R_w$). The curve passing through this point shows the values of R/R_w at the same value of L_A; and the filled point on this curve shows the value of log R_a when $R/R_w = 0.0316$ (that is, 1.5 less on the log scale). Thus the extreme right-hand circled and filled points represent a white and a 3.16% black. The other points and curves in Fig. 3 represent the values of log R_a for values of log ($5 L_A$) equal to 2.5, 1.5, 0.5, −0.5, −1.5, and −2.5.

It is clear from Fig. 3 that, as the luminance of the adapting background is reduced (represented by the curve moving towards the left), the points for the white and the black gradually approach the minimum level, and this represents the fact that colours, especially if dark, are difficult to discern in low levels of illumination. Sets of curves similar to those shown in Fig. 3 have also been found in physiological studies on monkeys [5]. The circled points of Fig. 3 lie on a line of slope approximately 1/6, thus representing the approximate proportionality of the colour responses to the one-sixth power of the adapting luminance (at least for light colours) as reported from haploscopic studies [6]. In Fig. 4, experimental results from these studies (points) are compared to predictions (curves) using this formulation for R_a, G_a, B_a; it is seen that the predictions and experimental results are in approximate agreement.

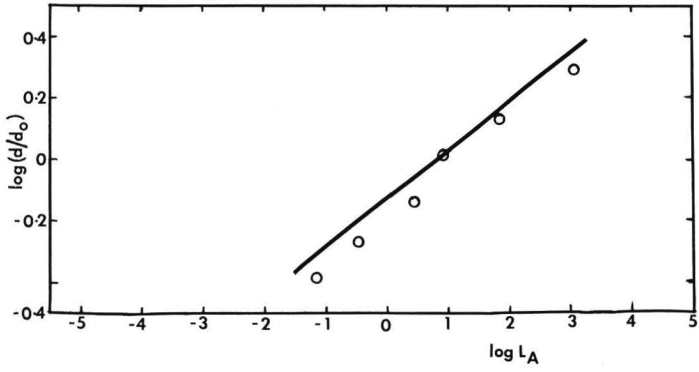

Fig. 4: Relationship between the average distance, d, on the u', v' chromaticity diagram, from the white point to points representing colours that, when seen in a reference adapting field, had the same appearance as a set of colours seen at one of the six different levels of illumination to which the observer was adapted. Log (d/d_o) is plotted against log L_A, the adapting luminance in cd/m^2, where d_o is the value of d for the case where L_A was the same as for the reference field (8.1 cd/m^2). Points: experimental results (6). Curve: predictions.

4. Colour responses

By analogy with the relationships in the earlier model [1; 7], the following signals, and the criteria given in Table 1, are adopted:

Photopic achromatic signal	$A = 2R_\alpha + G_\alpha + B_\alpha/20$
Color difference signals	$C_1 = R_\alpha - G_\alpha$
	$C_2 = G_\alpha - B_\alpha$
	$C_3 = B_\alpha - R_\alpha$

The proportions of R_α, G_α, B_α used in the photopic achromatic signal are chosen to reflect the plausible assumption that the relative abundancies of the *R*, *G*, *B* cone types are in the ratios of 40 to 20 to 1 respectively.

5. Brightness response

The brightness response in vision is generally regarded as being a function of the achromatic signal together with a small contribution from the colour difference signals. The photopic contribution to the brightness response, by analogy with the earlier model, is taken as $A_a + M$, and to this has to be added the scotopic achromatic signal, S_a. The stimulus response function adopted for the rods is the hyperbolic function:

$$f_s(S) = 30.5\,[30/(S + 30)]\,[S^{0.56}/(S^{0.56} + 0.16)] + 0.61$$

where *S* is the radiation usefully absorbed by the rods per unit area of the retina in a given state of adaptation. The log of this function, plotted against log *S*, is shown in Fig. 5. The term $30/(S + 30)$ results in the response reducing to the minimum level at very high intensities to allow for overstimulation of the rods resulting in loss of response (as occurs with stabilized retinal images). The function f_s was chosen to give a combined rod and cone response that increases smoothly with stimulus intensity, as shown in Fig. 6. In this figure, the responses of Figs. 1 and 5 have been added together linearly, as $f_s(I) + 3.05\,f_p(I)$, and the log of this sum has been plotted against log *I*, where *I* can be regarded as a measure of the stimulus intensity. The factor 3.05 (which is equal to $2 + 1 + 1/20$) is introduced so that the cone response is representative of that for colours for which $R_\alpha = G_\alpha = B_\alpha$. The broken line in the figure has a slope of 1/3 and shows a cube-root relationship.

To allow for adaptation to the level of illumination by the rods, a luminance-level adaptation factor, F_{LS}, similar to that used for the cones, is included in the following expression for S_α, the rod response after adaptation:

$$S_\alpha = f_s\,[F_{LS}(S/S_w)]$$

where S_w is the value of *S* for a suitably chosen reference white, and

$$F_{LS} = [100(5L_{AS}/2.26)/(5L_{AS}/2.26\ 6\ 10^5)]^{1/3} + 0.001$$

where L_{AS} is the scotopic luminance of the adapting background in scotopic cd/m^2; S, S_w, and L_{AS} are evaluated using the CIE $V'(\lambda)$ function. $L_{AS}/2.26$ is used instead of L_{AS}, because $L_{AS}/2.26$ and L_A are equal for the equi-energy stimulus, S_E.

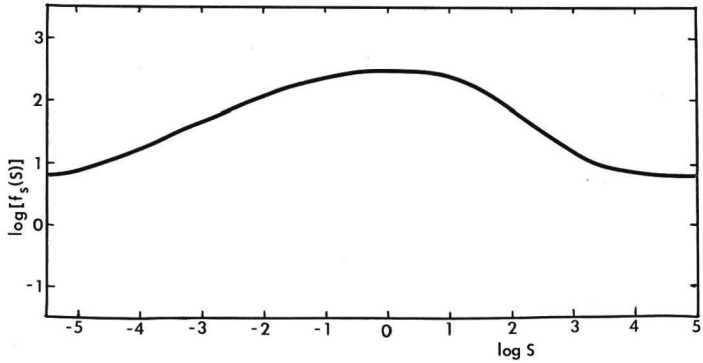

Fig. 5: Stimulus response function, $f_s(S)$, for rods in a given state of adaptation. Log $[f_s(S)]$ is plotted against log S, where S is the amount of radiation usefully absorbed by the rods per unit retinal area.

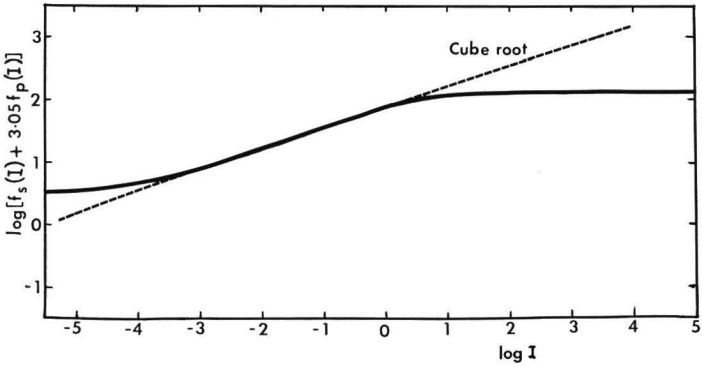

Fig. 6: Combined stimulus response function for rods and cones, $f_s(I) + 3.05 f_p(I)$. Log $[f_s(I) + 3.05 f_p(I)]$ is plotted against log I, where I is the intensity of the stimulus.

The total achromatic response is then given by:

$$A = A_\alpha + S_\alpha$$

and the parameter on which brightness depends by

$$A + M = A_\alpha + S_\alpha + M$$

In Fig. 7 are shown the relationships between log $(A + M)$ and log $(5 L_A I/I_w)$, for the case where $F_R R/R_w = F_G G/G_w = F_B B/B_w = S/S_w = I/I_w$ and $M = 0$. I can be regarded as a measure of the stimulus intensity of the colours, and I_w that of the reference white. $L_{AS}/2.26$ is assumed to be equal to L_A. As in Fig. 3, the relationship is shown for the range of values of log $(5 L_A)$ equal to 3.5, 2.5, 1.5, 0.5, – 0.5, – 1.5, and –2.5, and the circled and filled points represent reference whites, and 3.16% blacks, respectively. Fig. 7 shows that the addition of the scotopic component has lifted the blacks above the minimum level, as compared to the situation shown in Fig. 3, indicating that dark objects in low illuminations may be discernible in brightness, but not in colour.

A correlate of brightness, Q, is then derived as:

$$Q = (A + M)\, N_1 - N_2$$

where $N_1 = A_w{}^{0.5}/(5.33 N_b{}^{0.13})$ and $N_2 = A_w{}^{1.9} N_b{}^{0.362}/2080$.

This formula is based on the work of BARTLESON [8]. As the illuminance increases, N_1 provides the correct representation of the increase in brightness and N_2 in contrast. A_w is the value of A for the reference white, and N_b is an induction factor for brightness.

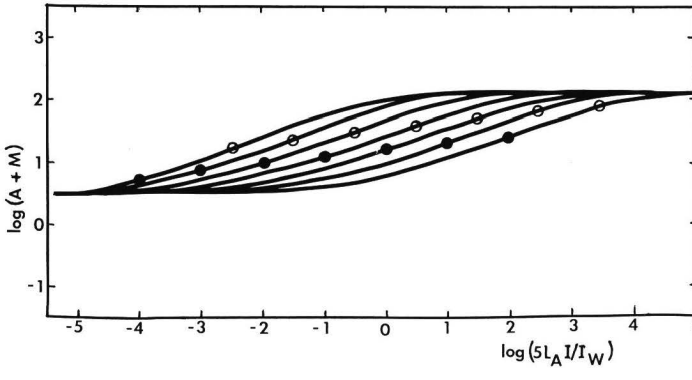

Fig. 7: Relationship between the total achromatic response, A, plus the colourfulness response, M, and the luminance of stimuli, for various states of adaptation. Log $(A + M)$ is plotted against log $(5 L_A I/I_w)$ for log $L_A = 3.5, 2.5, 1.5, 0.5, -0.5, -1.5$, and -2.5. L_A is the luminance of the adapting field in cd/m^2; I is the intensity of the stimulus, and I_w that of the reference white. Whites: ●; blacks: ○.

In Fig. 8 are shown relationships between the brightness measure, Q, and stimulus luminance, for uniform colours of 1° angular subtense, seen against uniform white surrounds of different luminances to which the observer was adapted. Log Q is plotted against log $(5L_AI/I_w)$. The experimental results obtained by BARTLESON are shown by the circles; the predictions by the above formula for Q, with $I_w = 5L_A$, $M = 0$, and N_b put equal to 370, are shown by the curves. In Fig. 9 a similar comparison is shown for elements of reflection prints of real scenes viewed with typical surrounds; in this case N_b was put equal to 75. In Fig. 10 a similar comparison is shown for elements of slides of real scenes viewed when projected with dark surrounds; in this case N_b was put equal to 9.3. It is clear from Figs. 8, 9, and 10 that the quantity, Q, gives predictions in very satisfactoy agreement with the experimental results. In all these cases it is assumed that $L_A = L_{AS}/2.26$. In these figures, equal differences in log Q represent approximately equal perceived differences in brightness.

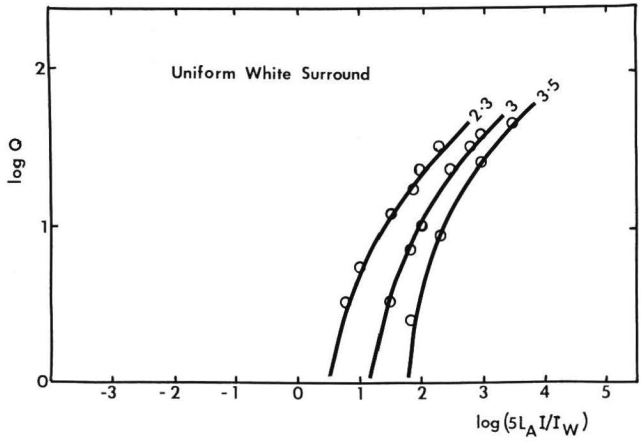

Fig. 8: Relationships between brightness, Q, and stimulus intensity, for colours in white surrounds. Log Q is plotted against log $(5L_AI/I_w)$. Circles: experimental results (8). Curves: predictions using $N_b = 370$. Surround luminances such that log $(5L_A) = 3.5, 3, 2.3$, with L_A in cd/m^2.

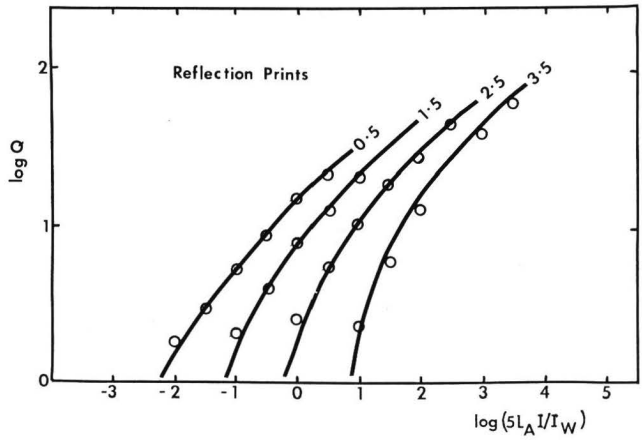

Fig. 9: Same as Fig. 8, but for elements of reflection prints viewed in typical conditions. $N_b = 75$. Illumination levels such that $\log(5L_A) = 3.5, 2.5, 1.5$, or 0.5, where $5L_A$ was the luminance of the reference white in cd/m^2.

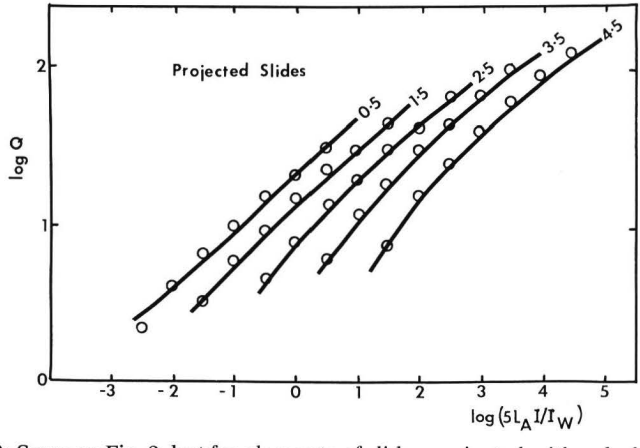

Fig. 10: Same as Fig. 9, but for elements of slides projected with a dark surround. $N_b = 9.3$. Screen luminances such that $\log(5L_A) = 4.5, 3.5, 2.5, 1.5$, or 0.5, where $5L_A$ was the screen luminance of the reference white in cd/m^2.

Table 2: Definitions of variables

$$e_s = e_1 + (e_2 + e_1)\ (h_s - h_1)/(h_2 - h_1)$$

where e_1, h_1 are the values of e_s, h_s, respectively, for the unique hue having the nearest lower value of h_s, and e_2, h_s are the values of e_s, h_s, respectively, for the unique hue having the nearest higher value of h_s. The values of e_s and h_s for the four unique hues are:

	Red	Yellow	Green	Blue
h_s	20.14	90.00	164.25	237.53
e_s	0.8	0.7	1.0	1.2

H_1 is either 0, 100, 200, or 300, according to whether red, yellow, green, or blue, respectively, was the hue found as having the nearest lower value of h_s.

N_c = 1.0 for average normal scenes
0.95 for television displays in dim surrounds
0.9 for projected slides in dark surrounds
0.75 for arrays of adjacent colours in dark surrounds
0.5 for isolated uniform colours in dark surrounds

N_b = 370 for small uniform areas in white surrounds
100 for average normal scenes
75 for reflection prints
9.3 for projected slides in dark surrounds

$F_t = B_L/(B_L + 0.5)$ where B_L is the value of B obtained when X, Y, Z are expressed such that Y is the luminance in cd/m^2.

$$F_R = (1 + L_A^{1/3} + h_r)/(1 + L_A^{1/3} + 1/h_r)$$
$$F_G = (1 + L_A^{1/3} + h_g)/(1 + L_A^{1/3} + 1/h_g)$$
$$F_B = (1 + L_A^{1/3} + h_b)/(1 + L_A^{1/3} + 1/h_b)$$

where
$$h_r = (3R_w/R_E)/(R_w/R_E + G_w/G_E + B_w/B_E)$$
$$h_g = (3G_w/G_E)/(R_w/R_E + G_w/G_E + B_w/B_E)$$
$$h_b = (3B_w/B_E)/(R_w/R_E + G_w/G_E + B_w/B_E)$$

and R_E, G_E, B_E are the values of R, G, B for the equi-energy white, S_E.

$$R_D = f_p\ (0.2F_LF_G) - f_p\ (0.2F_LF_R)$$
$$G_D = 0$$
$$B_D = f_p\ (0.2F_LF_G) - f_p\ (0.2F_LF_B)$$

hence $R_a = G_a = B_a$ for colours for which $R/R_w = G/G_w = B/B_w = 0.2$; lighter colours then exhibit the illuminant hue, and darker colours the complementary hue.

$$R = 0.4002X + 0.7076Y - 0.0808Z; \quad X = 1.85995R - 1.12939G + 0.21990B$$
$$G = -0.2263X + 1.1653Y + 0.0457Z; \quad Y = 0.36119R + 0.63881G$$
$$B = 0.9182Z; \quad Z = 1.08906B$$

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Author's address:
Prof. Dr. R. W. G. Hunt
10 Kewferry Road
Northwood, Mddsx., HA6 2NY, England

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Thomas E. Frumkes* and **Noreen Denny***, FLUSHING, N.Y.:

Types of Rod-Cone Interactions**

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Simple flicker experiments were used to illustrate both a quasi-linear (facilitatory) and highly non-linear (inhibitory) influence of rods upon the long-wavelength cone mechanism. The implications of multiple forms of rod-cone interaction for color theory are discussed in relationship to these data.

Mit Hilfe einfacher Flimmer-Experimente werden sowohl ein quasi-linearer (begünstigender) als auch ein höchst nicht-linearer (hemmender) Einfluß der Stäbchen auf den langwelligen Zapfen-Mechanismus aufgezeigt. Der Zusammenhang zwischen den vielfältigen Formen der Stäbchen-Zapfen-Wechselbeziehungen mit der Theorie des Farbensehens wird in Beziehung zu den hier mitgeteilten experimentellen Daten diskutiert.

On montre, par des expériences simples de papillotement, qu'il y a une influence quasi-linéaire (facilitante) aussi bien qu'une influence extrêmement non-linéaire (reprimante) des bâtonnets sur le mécanisme des cônes à longues ondes. On discute les connections entre les diverses formes de réactions réciproques entre les cônes et les bâtonnets pour la théorie de la vision colorée en relation aux donnés expérimentales.

1. Introduction

Modern zone theories maintain that human color vision is processed by three types of cones referred to here as red, green, and blue: these funnel information into a red-green, blue-yellow, and luminosity mechanism. The existence of rod-cone interaction provides three interrelated questions. First, which type(s) of cone interacts with rods? Second, do rods interact at the trichromatic and/or at the opponent-process-luminosity stage? Third, is rod-cone interaction summatory and linear, and/or is it inhibitory and non-linear?

The answer to these questions must be complex. For example, fig. 1 summarizes current retinal information obtained from cat [12; 15] and to a lesser extent, cold-blodded vertebrates [3; 13] probably applicable to humans. The retina of higher mammals probably includes at least six different types of rod-cone interaction pathways. In the distal retina, these

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* *City University of New York, Queens College, Dept. of Psychology*

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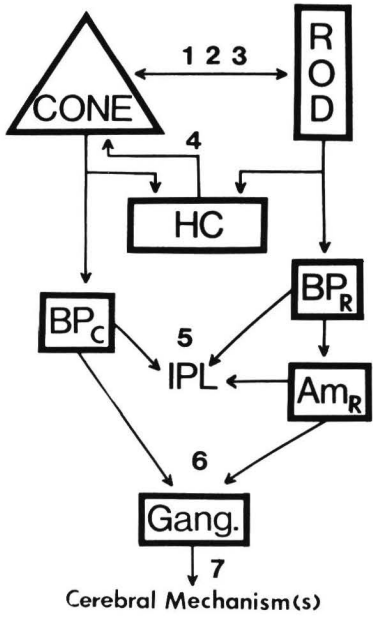

Fig. 1: Diagram of neural pathways which are likely to mediate rod-cone interaction in humans, as inferred from anatomical and physiological study in cat and lower vertebrates [3; 4; 6; 12; 13; 15]. The post-receptor neurons indicated are a horizontal cell (HC), a cone bipolar cell (BP) and rod bipolar cell (BP), a rod amacrine cell (Am), a ganglion cell (Gang.), as well as the possibility of cerebral mechanisms; IPL refers to the inner plexiform layer of the retina. The arabic numerals stand for different possible pathways which are: 1. electrical synaptic connections between photoreceptors; 2. chemical synaptic connections between photoreceptors; 3. non-synaptic interaction between photoreceptors; 4. horizontal cell mediated rod-influence upon cones; 5. multiple types of interaction between rod- and cone-related amacrine and bipolar cells within the IPL; 6. convergence of rod- and cone-pathways upon the same ganglion cell; 7. postretinal (cerebral) mechanisms.

include direct electrical and chemical synaptic connections (pathways 1 and 2), and possibly several forms of non-synaptic interaction (pathway 3) discussed elsewhere [4]. At least in lower vertebrates, there is a mechanism involving horizontal cell feedback onto cones (pathway 4). In mammals, there are multiple interactions between rod- and cone-related pathways within the inner plexiform layer represented here by the number 5, and a convergence of rod- and cone-bipolar information (via amacrine cell intermediaries) onto the same ganglion cell (pathway 6). Finally, psychophysical research in humans [6] suggests a cerebral meachanism (pathway 7).

Fig. 1 emphasizes one point. It is highly improbable that there is only one type of rod-cone interaction. The brief experiment described below illustrates the two we know best.

2. Summatory (quasilinear) rod-cone interaction

This mechanism posits that rods and cones summate their like polarity influence on some common neural pathway. Based upon physiological and anatomical data in cat, this could be at virtually any level of the neuroretina from photoreceptors through ganglion cells [12; 15]. The first

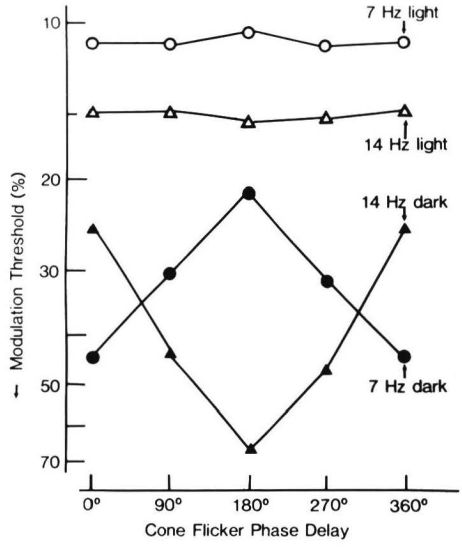

Fig. 2: Modulation threshold (along ordinate increasing in the downward direction) as a function of phase delay of the cone (red LED) flicker stimulus in respect to the rod (green LED) flicker stimulus. Data were obtained in the dark adapted eye (filled symbols) or in the presence of a rod-stimulating background field (open symbols). The circles and triangles represent, respectively, 7 and 14 Hz sinusoidal flicker.

clear psychophysical evidence was published by MACLEOD [10]. For our replication summarized in fig. 2, two spatially superimposed stimuli of 2°20′ diameter were presented 7° in the parafoveal retina. These stemmed from red and green light emitting diodes (LEDs) with maximum emittance at 660 and 545 nm respectively. Both provided sinusoidal flicker at either 7 or 14 Hz which was ganged together in modulation depth, but varied in temporal phase relationship. Average illuminance provided by the red and green LED in log trolands was +0.6 photopic (−1.4 scotopic) and −0.5 photopic (−1.0 scotopic) units respectively. For exposition purposes, we refer to flicker stemming from the green LED as the rod flicker stimulus as it was too dim to appreciably influence cones. Similarly, we ignore the influence of the red LED stimulus upon rods (which in fact, is considerably less than provided by the rod stimulus) and refer to it as the cone flicker stimulus. The observer increased the modulation depth of the combined rod-cone stimulus until flicker could just be perceived.

Fig. 2 plots modulation threshold as a function of the phase delay of the cone- in respect to the rod-flicker stimulus. An upward shift on the ordinate indicates a decrease in modulation threshold, i.e., an increase in flicker sensitivity. Consider at first data obtained in the otherwise dark-adapted eye (the closed symbols). For 7 Hz flicker (the circles), modulation sensitivity is greatest when stimul are 180° out of phase and is less at other phase angles; for 14 Hz flicker (the triangles), modulation sensiti-

vity is highest when the stimuli are in phase. MACLEOD [10] interpreted such data as follows. Flicker signals mediated by rods and cones converge at some common locus. Due to about a 70 ms longer latency for the rod signal, these will either be in phase and enhance one another, or out of phase and cancel each other out. Since the periods corresponding to 7 and 14 Hz approximate 140 and 70 ms respectively, 7 Hz flicker sensitivity is greatest when 180° out of phase and is least for in-phase stimuli: just the reverse is true for 14 Hz flicker. MACLEOD's interpretation was supported by VAN DEN BERG and SPEKREIJSE [17] who used many more flicker frequencies between 1 and 18 Hz. Their data show a frequency dependent phase shift amounting to a 70 ms longer rod latency. Summatory rod-cone interaction has also been more directly implicated: subliminal rod- and cone-signals add nearly perfectly together to produce a threshold sensation, providing experimental procedures taken into account the longer latency of the rod-signal [8]. Although recent speculation stresses the importance of direct rod-cone electrical coupling (e.g., [3; 15]), no direct evidence implicates any neuronal type for these psychophysical data.

We believe that such a summatory mechanism accounts for the majority of psychophysical demonstrations of rod-cone interaction. But one warning for color vision. Although many colorimetrists considering a role for rods think in terms of such a mechanism, they usually consider the interaction to be between rods and the blue cone mechanism (e.g. [16]). It is highly probable that in normal subjects, data such as fig. 2 and similar experiments involve an interaction between the red-cone mechanism and rods.

3. Suppressive rod-cone interaction (*SRCI*)

Over the past five years, several different laboratories have described a considerably different mechanism (e.g., [1; 2; 9]), which we [7] call suppressive rod-cone interaction *(SRCI)*. Cone mediated flicker sensitivity most obviously to high flicker frequencies, decreases during the rod recovery stage of dark adaptation and increases if rods are selectively light adapted. In fig. 2, this is indicated by comparing data obtained in the dark adapted eye (closed symbols) with data obtained in the presence of a continuously presented, rod stimulating background field of 28° diameter, 512 nm wavelength, and 0.1 log scotopic (−0.6 log photopic) tds illuminance. Regardless of phase angle and flicker frequency, sensitivity is greatly increased by this dim background. A very large number of control experiments (e.g., see [5; 9]) indicate that these data must reflect a tonic inhibitory influence of dark-adapted rods upon cone-mediated signals which is removed by rod light adaptation. Intracellular recordings from amphibian [7] and cat [14] retina, as well as *ERG* data

(2) indicate that *SRCI* takes place in the distal retina, and is most probably mediated by retinal horizontal cells. Data from patients with restricted distal retinal pathology [1; 2] and from individuals with hereditary color deficiencies (COLETTA and FRUMKES, in preparation) support this conclusion.

We now stress four features of *SRCI*. First, in normals it is an interaction involving only red cones and rods [5]. Second, it is much greater in magnitude than summatory rod-cone interaction as indicated in fig. 2. In fact, it is greatest in magnitude at flicker frequencies >20 Hz which exceed the flicker following characteristics of rods and excludes the possibility of summatory rod-cone interaction. Third, NAARENDORP [11] has recently shown in our laboratory that *SRCI* can be obtained with non-flickering stimuli: the visibility of high spatial frequency gratings can be enhanced >1 log unit by presenting large, rod-stimulating backgrounds. This spatial effect is almost as great for foveal as parafoveal stimuli, and action spectra show it involves an enhancement at the red end of the spectrum. Finally, we mention one subjective feature of this spatial effect. High spatial frequency, monochromatic gratings enhanced by rod backgrounds appear very desaturated and often completely colorless. We have yet to formally study this desaturation but it is extremely reliable. Unless theorists are content with descriptions of high-luminance, foveal vision, non-linear rod-cone interactions such as *SRCI* provide an important challenge for color theory.

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Author's address:
Prof. Th. E. Frumkes
Noreen Denny
City University of New York
Queens College, Dept. of Psychology
Flushing, N.Y., 11367, USA

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Pat W. Trezona, CAMBRIDGE (Engl.):

Is the Retina Trichromatic or Tetrachromatic?

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In a field of 10° subtense, trichromatic colour matches lead to incorrect predictions, unlike the tetrachromatic match where rod activity is additionally balanced. Anomalies in 10° trichromatic matches suggest that rod activity elicits a blue sensation.

Trichromatische Farbgleichungen mit 10° Gesichtsfeld ergeben unrichtige Aussagen im Gegensatz zu tetrachromatischen Gleichheits-Einstellungen, wenn nicht die Stäbchen-Mitwirkung zusätzlich ausgeglichen ist. Gewisse Anomalien bei trichromatischen 10°-Einstellungen deuten darauf hin, daß die Stäbchentätigkeit eine blaue Farbempfindung bewirkt.

Les équations trichromatiques produites dans un champ visuel de 10° donnent des résultats incorrects contrairement aux équations tétrachromatiques que l'on a gagnées en balançant l'activité des bâtonnets additionnellement. Certaines anomalies que l'on trouve dans le contretypage dans le champ de 10° font supposer que les bâtonnets produisent une sensation bleue.

1. Introduction

The question of the way in which we match colours in often posed in the form "Is the retina trichromatic?" – colour normal being implied. The present discussion is not dealing with fields of view of just a few minutes of arc, nor with some exceptional reports of greater match dimensionality which have not been substantiated in experiments by other investigators. These apart, can we answer this question from considering the number of receptor types? There are three cone types but a total of four receptor types if rods also are included. So is the retina trichromatic (based on cones only) or tetrachromatic (including rod function)? The answer is "both" but from different points of view.

2. Simple trichromacy

First we should consider what is meant by (Simple) Trichromacy, defined as follows:

1. Any colour can be matched by a mixture of three primaries, provided:
   a) No one of them can be matched by a mixture of the other two,
   b) Negative quantities are allowed.
   (The primaries need not be red, green and blue although these are normally used to minimise negative quantities and improve precision.)
2. Matches can be made over a wide range of conditions.

3. A match (at a given luminance level) is unique. Four matching stimuli provide one too many, leading to a wide range of possible matches; two is one too few, and satisfactory matches cannot be made in general.

In the central 2° of the retina rod receptors are absent and so one expects and gets trichromacy. But what happens for extrafoveally fixated fields, and for large (say, 10°) fields viewed centrally where rod activity must also participate? Not only can a trichromatic match still be made, but the 10° central match is more precise than the 2°. So it would appear that the retina is trichromatic.

3. Full trichromacy

But is this so for another aspect of trichromacy? For this we must consider the "Strong" or "Full" Trichromatic Theory which is also concerned with correct colour match predictions being made. Additivity[1] of Trichromatic Colour Equations (sometimes known as GRASSMANN's Laws) occurs if equation (3) follows from equations (1), (2):

$$(C_1) = r_1(R) + g_1(G) + b_1(B) \quad (1)$$

$$(C_2) = r_2(R) + g_2(G) + b_2(B) \quad (2)$$

$$(C_1) + (C_2) = [r_1+r_2](R) + [g_1+g_2](G) + [b_1+b_2](B) \quad (3)$$

A special case of this principle is the invariance of a trichromatic colour match with luminance level as the whole field is attenuated neutrally. Such an additivity test was made by STILES [10], his results being shown in Fig. 1, where a horizontal line indicates no match change with level. This investigation shows, as do others, that while the 2° field is broadly additive, large deviations occur in the 10° field, especially for the blue primary and at lower luminance levels. Although it is possible to find colour stimuli combinations which are exceptions, in general a large-field trichromatic match is non-additive. (N. B. A match can be retained at reduced levels even if the colour appearance changes.)

4. Distortion of the trichromatic colour match by rod-cone interaction

Thus although a large field trichromatic colour match can be made it is a distorted match: the distortion arises from rod-cone interaction, the effects being greatest at low levels where rods become more active relative to cones. At a given luminance level the effect is greatest when the particular stimuli give a large scotopic discrepancy between the fields.

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[1] This should not be confused with ABNEY's Law of Additivity of Luminances

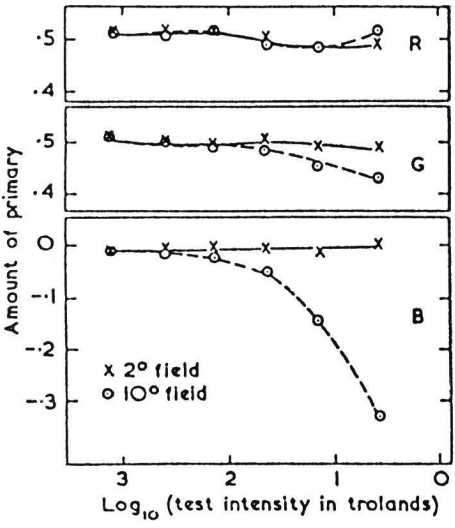

Fig. 1: Effect of changing field intensity on mixture quantities of a match on a yellow of wavelength 581 nm. STILES [10].

The distortion arises because the field with the lesser scotopic content requires extra "rod colours" and this can only be derived from the three matching stimuli, in practice mainly the "blue" one (Fig. 2).

Because of this distortion incorrect predictions will be made, leading to an invalid system of colorimetry. Then linear transformation to another set of stimuli is not permissible, and the trichromatic match is valid only under conditions of its measurement.

5. Achieving the tetrachromatic match

To obtain an undistorted large-field match a fourth primary must be introduced to allow for the extra receptor type: but then one matching stimulus is superfluous, resulting in a non-unique match. This is because rods introduce no new colour sensation, rod activity feeding into the

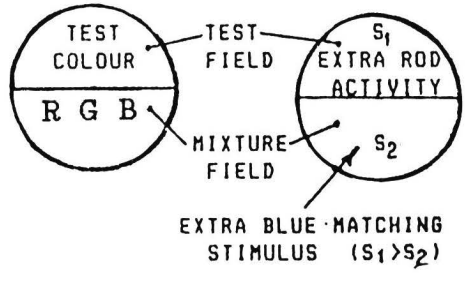

Fig. 2: Diagrammatic representation of the colorimeter field. If $P(\lambda)$ is the spectral power distribution $S_1 = \int P(\lambda)\, V'(\lambda)\, d\lambda$ and S_2 is similary defined, Scotopic Discrepancy (11) $= S_1 - S_2) / \sqrt{S_1\, S_2}$

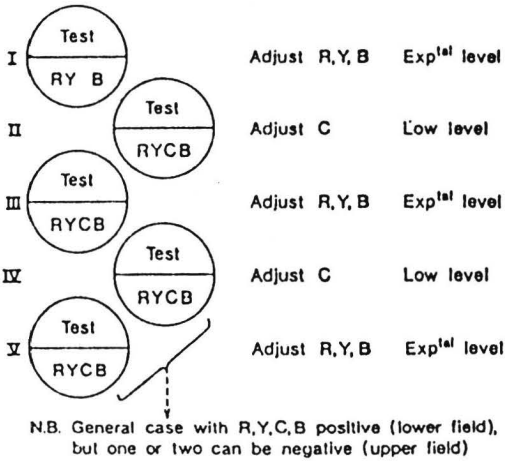

Fig. 3: Diagrammatic representation of approach to the tetrachromatic colour match

cone processes. A new way of equating rod activity is needed and BONGARD et al. [2] used a trial-and-error method to find the four-variable match most stable to changes in luminance level and coloured adaptation. TREZONA's [14; 15] method is the two-luminance level, convergent technique for reaching the tetrachromatic match systematically and precisely. The second luminance level is the "low level", normally below cone threshold (see Fig. 3). First a trichromatic match is made at the luminance level of the experiment (usually photopic), using red (R), yellow (Y) and blue (B) primaries. The whole field is then attenuated neutrally with a sector disk to a level below cone threshold, when the cyan (C) stimulus only is varied for this colourless, brightness match. A return to the experimental level necessitates a re-adjustment of (R), (Y), and (B), followed by a return to the "low level" with a re-adjustment of (C). This procedure is repeated a few times, the required changes becoming less each time. When the match is fully acceptable at both levels, typically after three or four iterations, the values of (R), (Y), (C), (B) are those for the tetrachromatic match. Of the wide range of possible colour matches with four variables the tetrachromatic c.m.fs. is the only one which is additionally rod-balanced.

6. Properties of the tetrachromatic match

TREZONA showed the tetrachromatic match to be a unique match independent of the starting conditions [15], and invariant with luminance level [16], for each of several test stimuli. The same test stimuli gave large trichromatic changes (shown in Fig. 4, where a horizontal line indicates no change of match with level). This technique allowed measurement of the tetrachromatic colour matching functions (c.m.fs.) [17], shown in

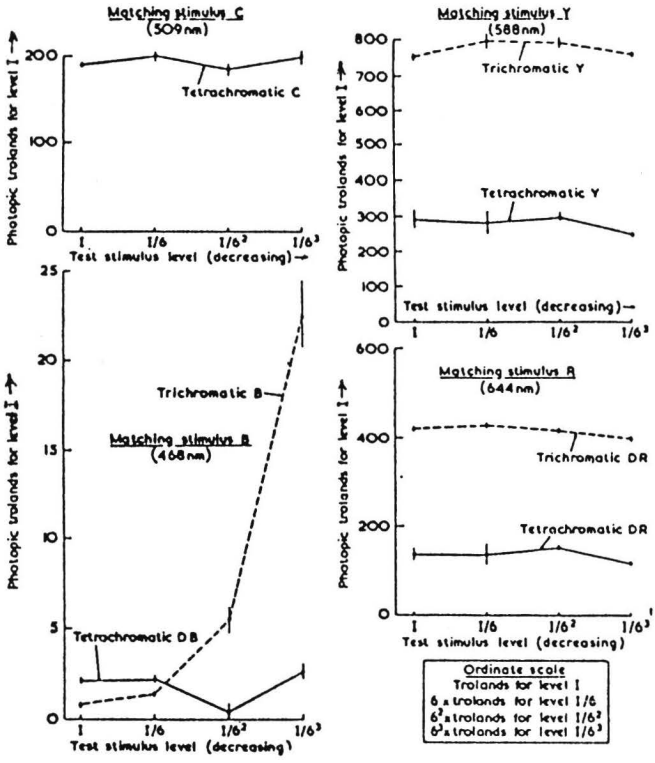

Fig. 4: Trichromatic and tetrachromatic matches on a 10° field for one observer at 4 luminance levels. Test colour 530 nm of 400 at level I. Lines shown ± 2 × stan dard error of mean

Fig. 6 and defined similarly to the trichromatic. Unlike the trichromatic, tetrachromatic c.m.fs. are valid at all luminance levels.

But if conditions are such that rods are not contributing appreciably to the colour match, the easier-to-use trichromatic c.m.fs. become allowable [17]. It is then possible to reduce the tetra- to the tri-c.m.fs. by use of a "reduction equation" (see Fig. 7) obtained from the horizontal part of a plot of the trichromatic match between the four matching stimuli (Fig. 5), used in conjunction with linear algebra. Fig. 7 has the same data points as Fig. 6, the improved precision resulting from removal of the "noisy" rod-component. Fig. 7 compares "reduced" functions for one observer with the CIE 10° trichromatic functions, derived from measurements by STILES and BURCH [13] and SPERANSKAYA [8]. The above indirect technique is a way of deriving the trichromatic c.m.fs. free of rod-intrusion

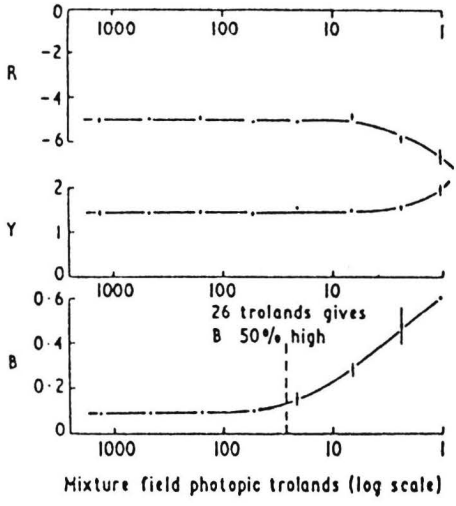

Fig. 5: Effect of a decrease in luminance level on a trichromatic colour match between the four matching stimuli. Powers of R (644 nm), Y (588 nm) and B (468 nm) required to match unit power of C (509 nm). Error lines as Fig. 4.

because rods, though present are balanced out: as rod-cone interaction does not distort the match, no special matching precautions need be taken. On the other hand STILES [11] had to work at very high luminance levels, change a matching stimulus from green to yellow during the course of the experiment, and add some green to both fields to diminish

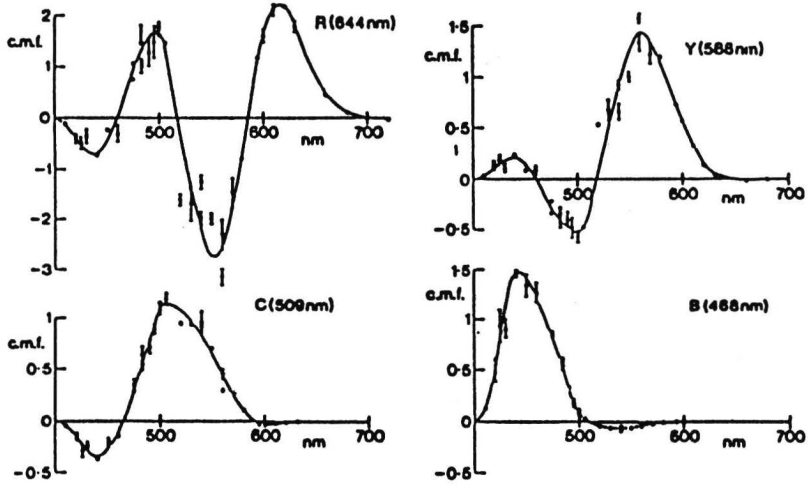

Fig. 6: Tetrachromatic colour matching functions, required to match unit power of test colour for one observer. Error lines as Fig. 4

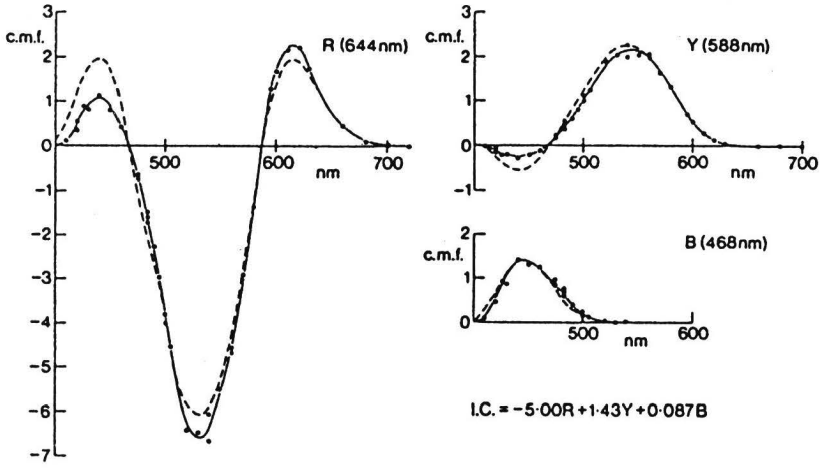

Fig. 7: Trichromatic c.m.fs., using same data as Fig. 6, together with the reduction equation, derived from the horizontal part of Fig. 5. The CIE 10° trichromatic c.m.fs. are shown dashed

rod-activity. Although rod-activity can often be ignored at high luminance levels, leading to a valid trichromatic system, it is difficult to be certain that this is valid for all stimuli.

Thus, for all fields other than a foveally-viewed one subtending $<2°$ there are two kinds of matches, the trichromatic which is possible but which could give rise to wrong predictions and the tetrachromatic which predicts correctly. In the latter, but not the former, there is equal quantum absorption in the two fields for each receptor type. The term "physiological identity" [3] is sometimes used to cover the case of colour defectives e.g. for a dichromat three stimuli are required.

7. Applications of the tetrachromatic system

The trichromatic can be regarded as a system for colour specification and the tetrachromatic for colour calculation. A proposal for making all calculations in the tetra- followed by emergence into a tri-system for colour specification [5] has not yet been developed. Of what other practical use is a tetrachromatic system? Firstly, it is the most effective way of obtaining trichromatic c.m.fs. free of rod distortion and without loss of precision. Secondly, for a small field dichromat who shows some trichromacy with a 10° field, one can distinguish between the cause being rod participation and some activity of a third receptor type. Thirdly, just as the tetrachromatic match is a match of cones without rod intrusion, is also embodies rod matches without cone intrusion, even for

long wavelengths where rod and cone sensitivities are comparable. Such a derivation of the scotopic sensitivity curve in now under consideration: an added advantage is that it need not be carried out at very low levels with the consequent reduced precision.

8. Rods and "blue cones"

Similarities between rods and "blue cones" have long been realised. WILLMER [18] considered them synonymous: however, this cannot be so as an extra variable is involved where rods also are matched, and this would not be the case if they were one and the same. But in all cases I have examined [14] discrepancies have been in the blue direction, either towards or away from it. Furthermore, the direction is always such that an extra quantity of the blue primary is required on the side of the field deficient in rod content (see Fig. 2), and the effect is greater the lower the level. This suggests that under a wide range of conditions "rod colour" is blue. (Although a neutral "rod colour" might explain certain results, it could not explain the movement in the blue direction for, say, a green test stimulus.)

Tab. 1 shows differences and similarities between rods and "blue cones". These could be reconciled if rods and "blue cones" existed as different receptor types but shared a common neural pathway [14].

The blueness of rod-receptors provides an alternative explanation of the Maxwell Spot to that of a central yellow pigment [14]. Adaptation to peripheral blueness would give rise to a yellowness in the central rod-free area, until that too is removed by adaptation.

Tab. 1: Rods and "blue cones"

Similarities:

1. In fovea rods absent and "blue cones" scarce (small field tritanopia).
2. Peripheral sensititity greater than foveal in rod and "blue cone" spectal regions [3; 6].
3. High WEBER Fraction for rods and "blue cones" [12], and low luminosity sensation for both.
4. Poor visual acuity for both [4; 9].
5. Spatial integration for both [9].
6. Many night-blind people are tritanopic [7].
7. Many "rod monochromats" have "blue cones" [1].
8. Apparent blue colour of rods in colour match distortion (see above).

Dissimilarities:

1. STILES-CRAWFORD Effect for all cones, but not rods.
2. Different spectral absorption characteristics for rods and "blue cones", and the unlikelihood of deriving the latter from the former and its bleaching products.

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Author's address:
Pat. W. Trezona
33, Field View, Bar Hill
Cambridge CB3 8SX, England

Manuscript received:
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Françoise Viénot*, PARIS:

What Are Observers Doing when Making Color Matches?

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When making color matches, subjects do not, as is often believed, make quantum matches, but rather make assessments of cone excitation ratios (i.e. of the color valences).

Bei Farbabmusterungen nehmen die Versuchspersonen nicht, wie oft angenommen wird, Vergleiche von Quanten vor, sondern eine Bewertung von Verhältnissen der Zapfenerregung (d.h. der Farbvalenzen).

Ce ne sont pas les quantités de photons absorbés qui déterminent les égalisations de couleur des observateurs (comme on suppose souvent), mais plutôt les rapports d'excitation des cônes (c.à d. des valences chromatiques).

1. Introduction

The answer an observer is required to give in a color match is composed of the three tristimulus values, which express the trichromatism of color vision. But in order to give a response, the observer has to face a complex situation, especially when matching color on large fields in a free viewing mode, for which inhomogeneity of the retinal structure and modifications of the density of the photopigments yield additional variables.

The question "What are observers doing when making a color match?" includes two different aspects: The first would be: "When facing a complex situation, how does the observer deal with the composing features of the situation?" The second: "Assuming that the complexity of the situation was to be reduced to a minimum and that a true trichromatic condition was to be established, how does the observer handle the various pieces of information carried by the stimulus in order to achieve a match? Which criteria does he refer to? Does he have a strategy?" The latter questions are the ones that are addressed in this paper.

In searching for an answer, we proceeded in two steps.

- First, the complexity of the situation was reduced in order to approach the true trichromatic case. This was done by strictly controlling the spatial, temporal and luminous parameters of the test field.
- Secondly, in such a "reduced" situation, the observer was invited to

* *Centre National de la Recherche Scientifique (CNRS)* et *Muséum National d'Histoire Naturelle, Laboratoire de Physique Appliquée, Paris*

give his answer, that is, to adjust the three primary fluxes. The mean amounts of the primary fluxes depend upon the selected reduced situation; however, slight variations of the fluxes appear from trial to trial, and thus allow the standard deviations and correlations between the tristimulus values to be established.

Therefore, discarding the mean values and considering only the statistics of variance and correlation, in a given reduced condition, we can ask ourselves: „Is there any scheme that yields these results and leads an observer to choose one color match among others?"

2. Methods

Two methods were used for analysing the results of color-matches.
- The first consists in converting the amount of matching stimuli required in a color match into cone excitation [1] and tracing the input signals at the retinal level. Given an *a priori* set of fundamentals, such as SMITH and POKORNY's [2], it is easy to compute the cone excitation level for each side of the bipartite field. The macular pigmentation of the observer on the stimulated retinal area should be taken into consideration.
- The second method consists in discounting our knowledge of color mechanisms and in examining variations in data by factor analysis in order to find the underlying factors of variability. Identification of the factors could be achieved later on.

In order to illustrate our point, a few results are presented [3]. All color-matches were obtained by the maximum saturation method at clearly photopic levels. Results of three observers were analysed. The first observer performed color matches at several wavelengths on a 1°45′ field, that was steadily presented. The other two observers performed color matches at two wavelengths (green, 506 nm, and blue, 432 nm) on several spatial configurations that ensured spatial homogeneity and that were selected in a 20° field. Observation was either *ad libitum* or time-controlled.

3. Results

3.1: Conversion into cone excitation

For each cone type, the ratio (Q) of the cone excitation level of the left half-field is compared to that of the right half-field. Theoretically, according to the equal quantum catch criterion, there is a match for each cone type, and the cone excitation ratios should be equal to unity. When the ratios deviate from unity, one could expect that their values be distributed at random around unity and that the matches related to each of the three cone systems be independent (Fig. 1). Yet, a graph is drawn having

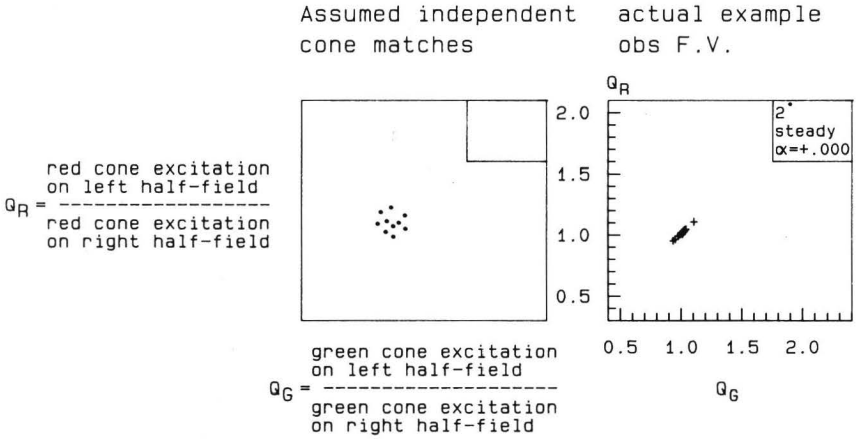

Fig. 1: Presentation of the cone excitation level ratios

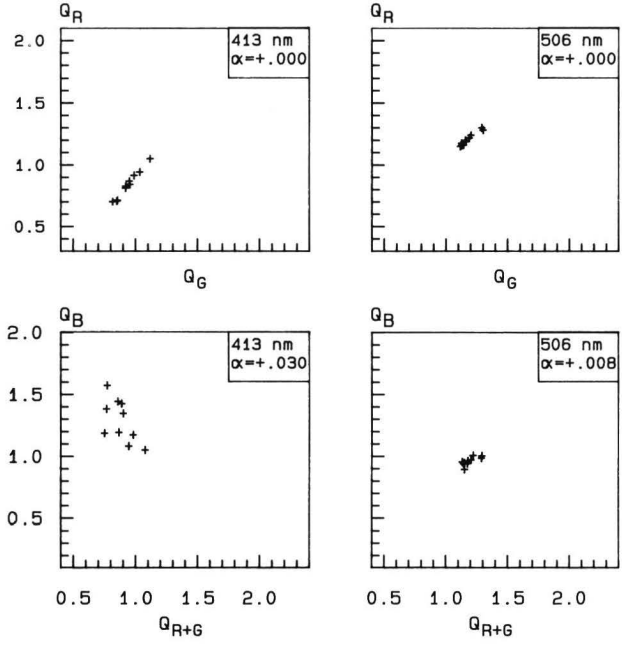

Fig. 2: Cone excitation level ratios for various wavelengths. Obs. E. P.

the Q-ratios respectively plotted on each axis, in most cases, a correlation appears. Such a feature means that in the case of a positive correlation between the ratios Q_R and Q_G, for example, the cone excitation level of the red cones on the right side of the field cannot be raised without entailing an increase in the cone excitation level of the green cones. Or, for the same example, color matching means adjusting the red/green ratio of the cone excitation level rather than adjusting the cone excitation level itself. Thus, we are close to an antagonism between the two cone types.

The examination of a series of color matches made for various wavelengths or performed on various fields, shows that the correlation between Q_R and Q_G is mainatained; but a progressive change occurs in the strength and shape of the correlation between Q_B and Q_{R+G} (Fig. 2).

Nevertheless, some data indicate that the inclusion of the fovea in the stimulating field favours the correlations between the cone excitation ratios (Fig. 3). As far as the control of the duration of the match is concerned, no definite influence could be determined, since the two observers tested for this modality did not behave similarly.

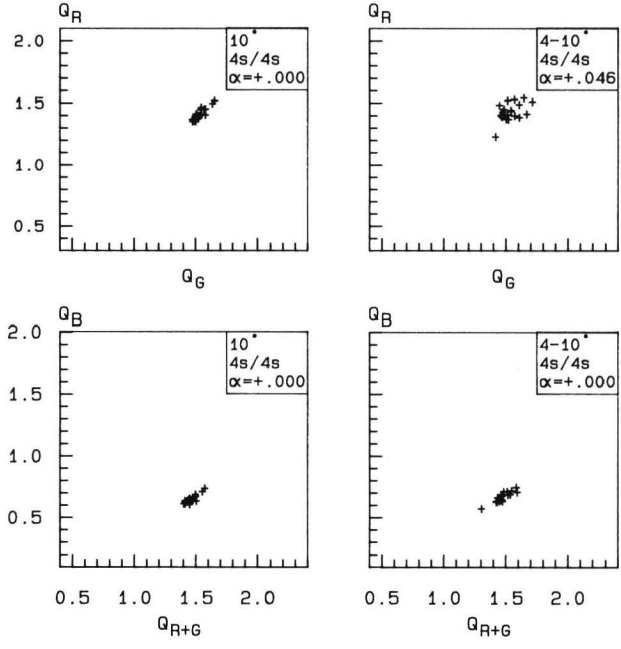

Fig. 3: Cone excitation level ratios for various configurations (unweighed results). Obs. M. J., 506 nm

3.2: Controlling some parameters

- Randomizing the primary fluxes

An artificial observer is produced, the color-matching functions of which have the same variances as a real observer, but the artificial one is assumed to adjust the three primary fluxes at random. When presented on a cone excitation diagram, the cone excitation ratios of the artificial observer appear correlated, but not as highly as the genuine data of the real observer. In fact, inside a polygone covering the cone excitation ratio domain for random matches, the points representing the actual matches achieved by the observer are less variable and are clustered along a line (Fig. 4). This could provide an explanation for the correlations between color-matching functions.

- Investigating the role of macular pigmentation

Various densities of macular pigmentation were simulated in order to correct the action spectra. The sign of the correlation between Q_B and Q_{R+G} was sensitive to the correction for macular pigmentation. Nevertheless, the corrections based on the mean values of the tristimulus values are the best for bringing the cone excitation ratios back to unity (Fig. 5).

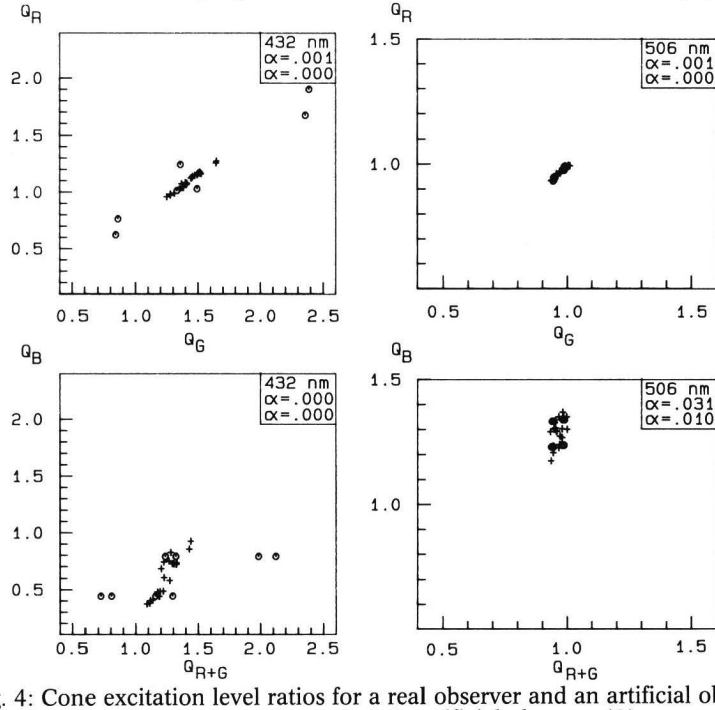

Fig. 4: Cone excitation level ratios for a real observer and an artificial observer (20°, 2s/2s). Obs. F. V. (+); artificial observer (⊙)

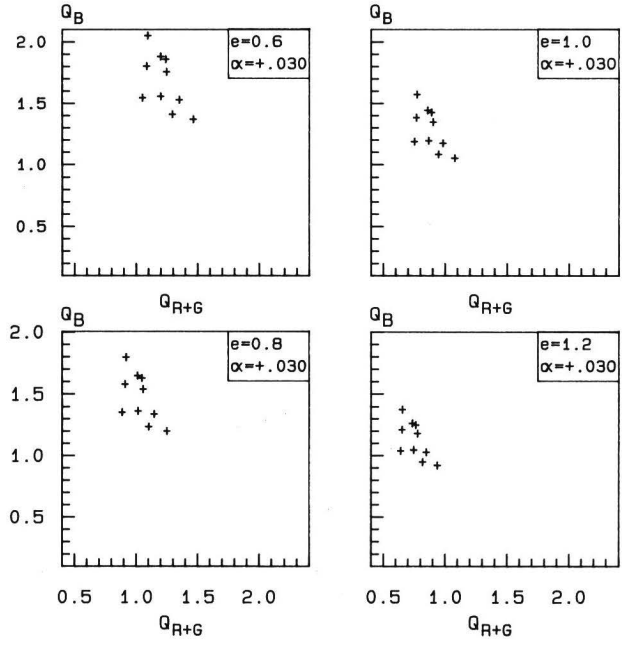

Fig. 5: Cone excitation level ratios; weighed results. Simulation of various densities of macular pigmentation. Obs. E. P.; 413 nm

3.3: Factor analysis

The technique of factor analysis does not require any precise knowledge of the cone action spectra and it does not concern the mean matches but rather concentrates on intra-individual dispersion.

The analysis is based on the logarithmic values of the spectral tristimulus values, in order to get rid of the effects of macular pigmentation and the density of photopigments. For green matches, as well as yellow or orange ones, the first two factors are statistically significant: the first one accounts for about 60% of the variance and both together for 90% of the cumulative variance (Fig. 6a). Of course, the artificial observer matches yield no principal axis of inertia. Since the percentage of eigenvalues remains high regardless of the configuration tested, it is questionable, when there is no straightforward relation between the Q-values, whether a concealed structure would not exists.

For blue matches, the first factor is a scaling factor denoting that the three tristimulus values increase or decrease together at every trial. This results from the matching method in which the blue test flux is varied in

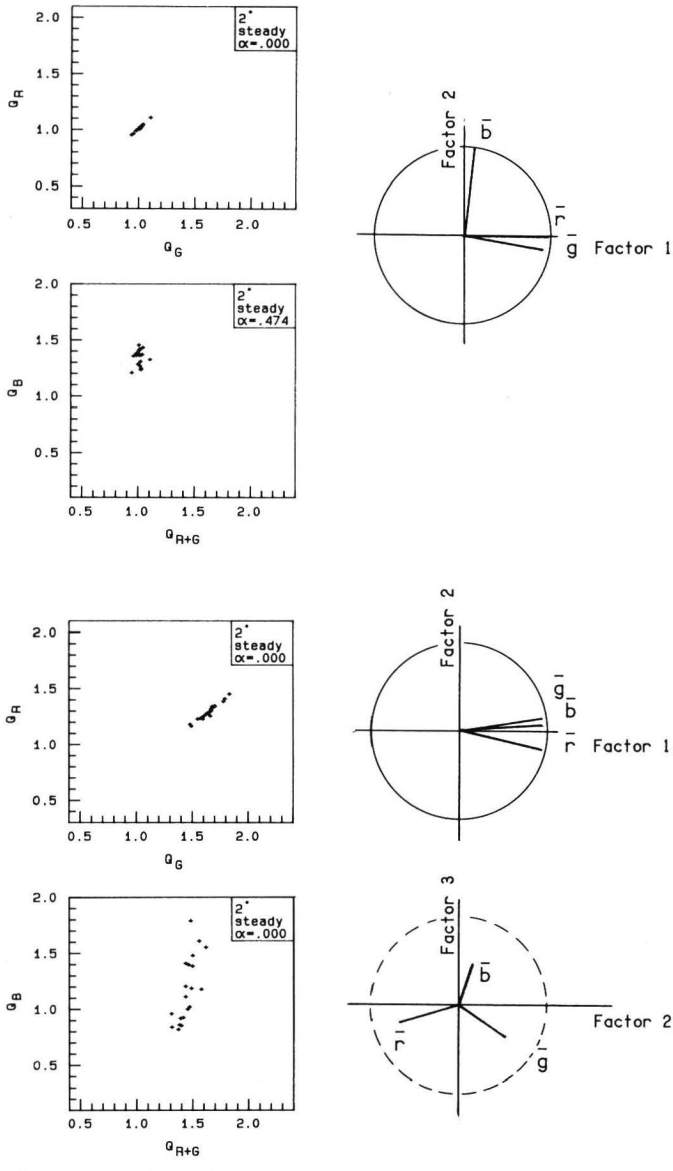

Fig. 6: Joint presentation of cone excitation ratios (left) and of the plot of the instrumental tristimulus values on the factorial axes (right). Obs. F.V. a: 506 nm matches (above), b: 432 nm matches (below).

order to keep the final match in a limited range of luminance. This factor accounts for more than 96% of the proportion of inertia and makes it difficult to find another structure (Fig. 6b).

3.4: Summarized results

So far, factor analysis reflects the role of an operative factor. The results based on cone excitation can be summarized as follows:
- There is a high correlation between the cone excitation ratios when the observer achieves several matches. This shows that the observer does not adjust the matches randomly around the mean match, but that he uses a strategy.
- The observer does not make his choice by refering to a specific cone signal but to a combination of these signals.
- Although the reproducibility of matching may be rather low, the correlation is very high.
- The strength of the correlation becomes higher as the fovea is included in the stimulating field.

4. General conclusions

1) When asked to achieve a color match, an observer makes his decision on the basis of post-receptoral signals rather than on the cone signals themselves. The combination of cone signals, which resembles an antagonistic combination, is obvious for the red/green pair, but somewhat questionable for the blue cone signals.

2)Such a mechanism restrains the spread of color matches to those which obey the afore-described correlations. Thus, notwithstanding the variability of the results, the variance is controlled and limited in range. The decisive signal is actually less variable than the stimulating signals and there is a structuration of the signal which is ensured by the observer himself.

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Author's address:
Françoise Viénot
Muséum National d'Histoire Naturelle
Laboratoire de Physique Appliquée CNRS ER 257
43, Rue Cuvier
F-75231 Paris Cedex 05

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Arne Valberg*, **T. Seim*** and **Barry B. Lee**, OSLO:

A Three-Stage Model of Colour Perception

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616.843.318.1

Besides reconstructing an equidistant color space, it is possible, by an integration and a linear combination of outputs of color-opponent cells, to derive responses that correlate well with changes in the perception of chroma and hue that occur when the relative intensity of monochromatic lights is changed (Bezold-Brücke phenomenon).

Es ist möglich, durch Integration und lineare Kombination der Signale von Gegenfarbneuronen einen gleichabständigen Farbenraum aufzubauen und gleichzeitig eine gute Korrelation zu den Änderungen in Buntheit und Buntton abzuleiten, die bei Änderung der relativen Strahldichte von monochromatischen Lichtern entstehen (Bezold-Brücke-Phänomen).

Il est possible à construire un espace des couleurs uniforme, par une intégration et une combinaison linéaire des signaux des cellules à couleurs-opposées. De cela, on peut dériver une correlation satisfaisante aux changements du chroma et de la teinte qui se montrent si l'on change l'intensité relative des lumières monochromatiques (phénomène de Bezold-Brücke).

1. Introduction

Colour discrimination and scaling cannot be adequately described within the framework of trichromatic theory *(first stage of the model)* because of the non-linear nature of cell responses. Further progress is therefore dependent on a better understanding of neural processing of colour information. To gain insight into this processing, we have recorded the responses of cone-opponent cells in the retina and lateral geniculate nucleus (LGN), *(second stage of the model)* of the macaque monkey to a variety of light stimuli [1; 2]. The predictions of the physiological model integrating the outputs of LGN cells on a cortical level *(third stage)* are here compared with uniform color systems, and with estimates of chroma changes and the BEZOLD-BRÜCKE hue shift as a function of stimulus intensity. We demonstrate that it is possible, from a linear combination of responses of ON- and OFF-opponent cells of the visual system of the primate to account for the dependency of these attributes on luminance and to reconstruct a uniform colour space.

* *Department of Physics, Section of Biophysics, University of Oslo*

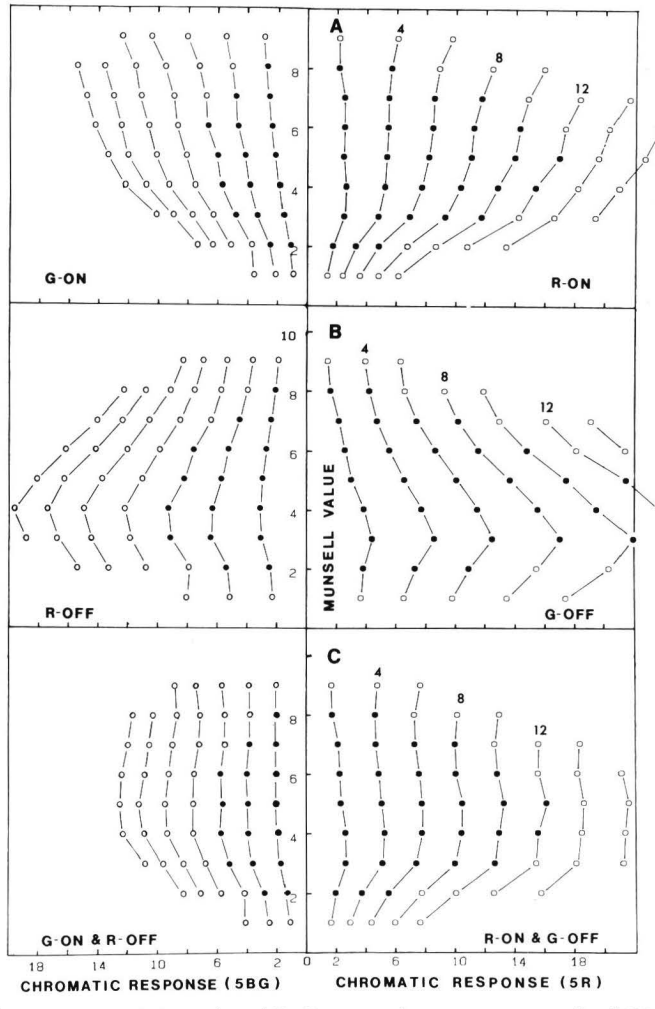

Fig. 1: Cone-opponent stage. A and B: Computed response sums of red ON-centre and green OFF-centre cells (L–M cone inputs) and of green ON-centre and red OFF-centre cells (M-L cone inputs) of the LGN to opposite red and green colours of the Munsell System (Chroma 2 to 14, and Value 1 to 9). A shows that ON-cells respond with increasing firing rate as luminance (value) increases, whereas in B OFF-cells have larger responses to darker colours. In Fig. 1 C is demonstrated that the combined responses of ON- and OFF cells yield Chroma loci parallel to the achromatic axis, with about equal spacing for each hue. The Chroma spacing is however smaller for 5 BG than for 5 R, indicating that a further transformation is necessary to obtain a uniform colour space.

2. Cone opponency

The ON- and OFF-centre, cone-opponent cells share the task of representing the entire scale of bright and dark colours. ON-cells are best suited for coding the brighter colours of self-luminous objects, and OFF-cells for coding the colours of darker, passively reflecting surfaces.

It is possible by a linear combination of the outputs of these cell-systems, to account for scaling of colour differences, as found in the OSA-UCS and Munsell systems [3; 4]. Mathematical transformations between the CIE X, Y, Z coordinates of each sample and the responses of single cells have been made for typical cells [5].

Fig. 1 A shows the chromatic response obtained when combining the responses of a red ON-centre cell (with L–M cone input) and a green ON-centre cell (with M–L cone input) to opposite red and green hues. In Fig. 1 B is shown the result for a green OFF-centre (L–M) and a red OFF-centre cell (M–L), and in Fig. 1 C the averaged combined response of these cells has been computed [5].

Physiologically, chromatic responses may be derived by subtracting outputs of cells with the same receptive field location, but opposite cone inputs (i. e. subtracting outputs of red and green ON-centre cells, and of green and red OFF-centre cells). The coding of the third dimension, lightness for objects and brightness for light sources, may be provided by adding the activities of ON-centre cells to yield a "brightness" signal and of OFF-centre cells to provide a signal for "blackness" of surface colours [1].

At this first opponent stage, the combined responses of ON- and OFF-centre cells of Fig. 1 C yield chroma lines parallel to the achromatic axis, and with about equal spacing for each hue. The chroma spacing is, however, smaller for hue 5 BG that for 5 R, and constant chroma loci for all hues are situated on ellipses, not circles, about the achromatic point [5].

3. Cell opponency

With the result of Fig. 1 C, the simplest way to obtain a uniform colour space throughout, with chroma ellipses transformed into circles, and the same geometrical distance representing the same sensory colour difference, is by a linear second stage cell-opponent transformation [5]. This transformation, leading to the new "red-green" opponent coordinate F_1 and "yellow-blue" coordinate F_2, is assumed to take place in the visual cortex receiving inputs from LGN cells. Constant ratios of these opponent processes F_1 and F_2 lead to approximately constant hue percepts, as is displayed in Fig. 2 A for Munsell Value 5.

We have also computed the F_1 and F_2 coordinates for OSA-UCS colours of constant OSA lightness $L = 0$ (close to Munsell Value 5). The

results presented in Fig. 2B demonstrate a close to optimal equidistant representation of the OSA (g,j) coordinates, which represent the most recent attempt to establish a uniform colour space for surface colours.

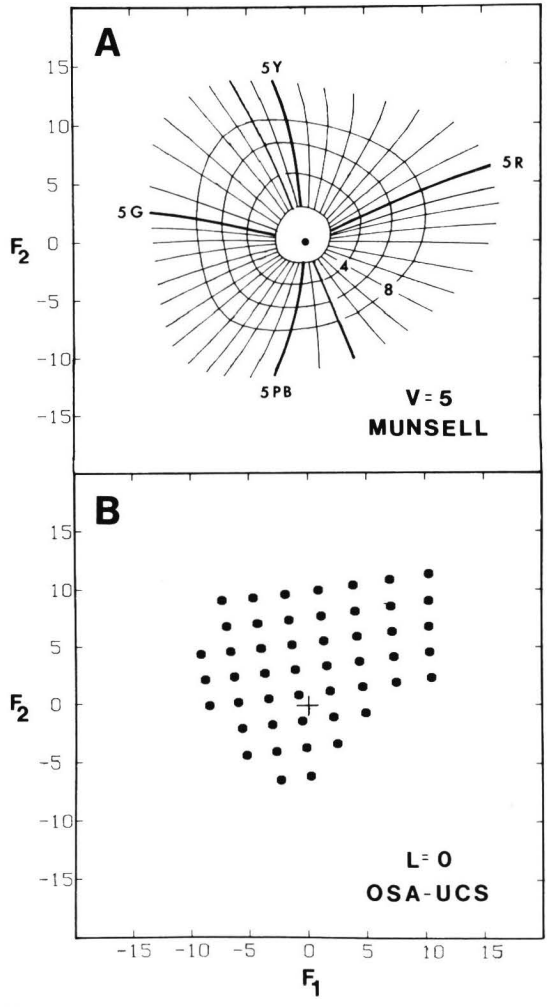

Fig. 2: A: Cell-opponent stage. The F_1 and F_2 coordinates are linear combinations of outputs of LGN cone-opponent cells. The uniformity of hue circles, spacing of equal Chroma steps, and the linearity of hue lines is comparable to, or better than, that of the CIE color-difference formulae.
B: The same transformation as in A yields a close to ideal equidistant spacing of the OSA-UCS scale for lightness $L = 0$ (Value 5).

It is a common observation that when the luminance of a light of constant chromaticity is increased from zero, the perceived colour strength (chroma) increases to a maximum and then decreases again. This chroma change is accompanied by a change in hue where, for instance, long-wavelength lights become more yellowish as luminance increases (BEZOLD-BRÜCKE effect). On the assumption that chroma and hue percepts are both related to the relative activities of opponent cells, one would expect that the same second stage transformation F_1 and F_2 also predicts the dependency of these attributes on intensity.

Fig. 3 compares these predictions made by our model with magnitude estimations of colour strength and hue. The radial distance from origo, $F = (F_1^2 + F_2^2)^{1/2}$, is proportional with Munsell chroma, and the angle of

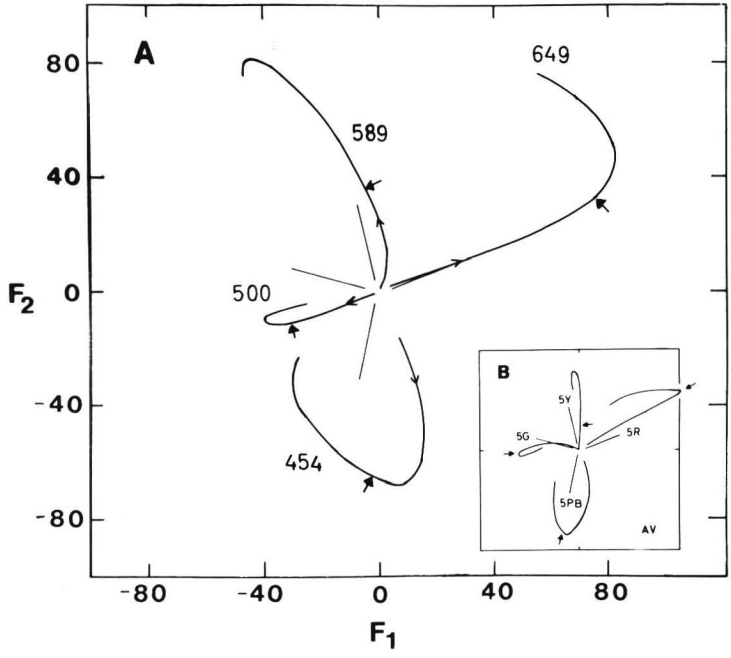

Fig. 3: A: The model prediction of the combined change of hue (BEZOLD-BRÜCKE effect) and chromatic strength (chroma) that would occur when close to spectral stimuli of the dominant wavelengths indicated increase in luminance. B: The scaling of hue and relative chromatic strength for the same stimuli as in A. Observer A. V. Both hue and Chroma changes are well predicted by the model. Chroma initially increases with increasing luminance to reach a maximum and then decreases. This Chroma change is accompanied by a BEZOLD-BRÜCKE hue shift towards yellow for long wavelength lights and towards blue-green for short wavelenghts.

this radius vector relative to the coordinate axes represents hue. Predictions in Fig. 3 A are similar to the subjective ratings in Fig. 3 B. This indicates that the non-linear response behaviour of LGN opponent cells, and their combination at a higher level, may be a common source for both the observed BEZOLD-BRÜCKE hue shift and the non-monotonic dependency of colour strength on luminance.

4. Conclusion

Although psychophysical performance is constrained by the receptors at the very first stage, trichromatic theory fails to account for discrimination and scaling, and the dependency of perceptual attributes on physical parameters. It is therefore necessary to consider transformations of cone signals in different types of neurones.

We have demonstrated that an improved account of some colour attributes and of chromatic scaling results from combining cell outputs from the retina and the LGN by linear equations. This result [1; 2; 5] suggests that a study of the diversity of cone pathways and consequent parallel processing may lead to a better understanding of human colour perception. The result also indicates that other perceptual attributes are implicit in the activity of these systems. Cortical mechanisms may be able to derive perceptual attributes form the retinal image by analysing multiple parallel streams of spectral information and interactions between these pathways.

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Author's address:
Arne Valberg
Dept. of Physics
University of Oslo
Box 1038 Blindern, N-0315 Oslo

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Mitsuo Ikeda* and **Yasuhisa Nakano***, YOKOHAMA:

A Mechanism that Determines Luminous Efficiency for Brightness

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By analysing the energy of mixtures of two monochromatic lights needed to maintain a certain brightness level, the underlying mechanism to determine the brightness was investigated. It is composed of three sub-mechanisms: a non-opponent type, R+G, and two opponents, +R−G and −R+G, where R and G represent the amounts of energy absorbed by the R and G cones respectively. The level is maintained by the largest response of the three.

An Mischungen aus je zwei monochromatischen Lichtern wurden die Strahldichten untersucht, die bei gegebenem Sehmechanismus nötig sind, um ein bestimmtes Leuchtdichte-Niveau zu erzielen. Dieser Mechanismus setzt sich aus drei Unter-Mechanismen zusammen, einem einfachen Typ R+G und zwei Gegenfarben-Mechanismen, +R−G und −R+G, wenn R und G die Einzelbeträge sind, die durch die R- bzw. G-Zapfen absorbiert werden. Das Helligkeits-Niveau wird durch die größte dieser drei Erregungen bestimmt.

Avec quelques mélanges de deux paires de lumières monochromatiques on a étudié les intensités de rayonnement dont on a besoin à obtenir un certain niveau de la luminance chez un mécanisme visuel donné. Ce mécanisme se compose de trois sous-mécanismes: d'un type simple R+G et de deux mécanismes opposés, + R−G et −R+G, R et G étant les quantités d'énergie qui sont absorbées dans les cônes R resp. G. Le niveau de la luminance est déterminé par la majeure de ces quantités.

1. Introduction

As a part of activities of the CIE Technical Committee 1-02: *Luminous Efficiency functions*, a table was recently completed where luminous efficiency functions determined by the heterochromatic brightness matching is tabulated for monochromatic point sources, 2°, and 10° field [1; 2]. Fig. 1 illustrates the function for the 2° by open circles. This is the luminous efficiency curve for brightness and can be used to evaluate monochromatic lights for their brightness. How to utilize this curve for lights with compound spectra is the next problem that we encounter with, and some basic researches are still needed. One of the most important is certainly to investigate the physiological mechanism to produce this curve.

* *Tokyo Institute of Technology, Dept. of Information Processing*

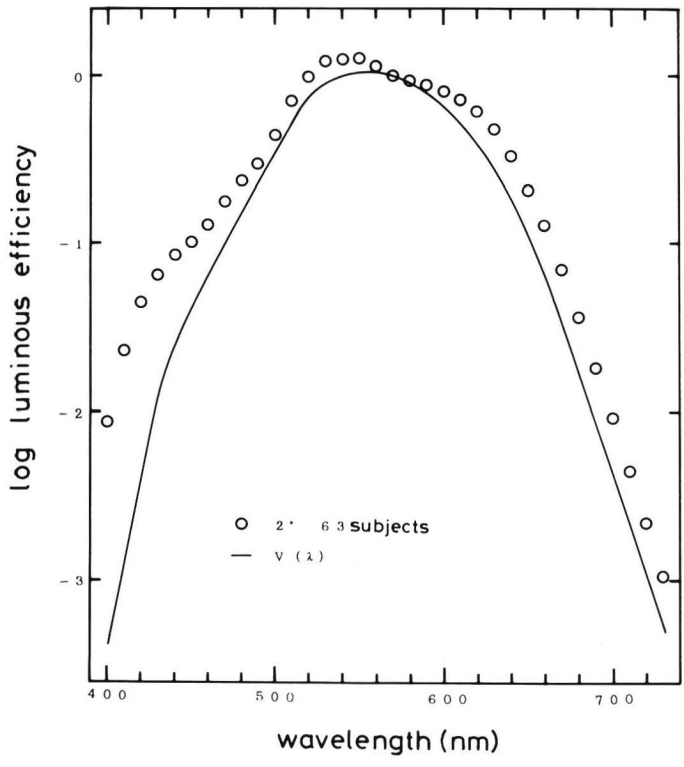

Fig. 1: Spectral luminous efficiencies determined by the heterochromatic brightness matching for 2° field compared with the CIE $V(\lambda)$

GUTH and his colleagues [3] noticed that the increase in efficiency compared to $V(\lambda)$ resembles the saturation function, and the proposed a vector model for brightness in which the vector sum of achromatic (A) and two opponent chromatic (T, D) responses determined the brightness as shown by the following equation.

$$L^{**} = (A^2 + T^2 + D^2)^{1/2} \tag{1}$$

GUTH's model was modified by YAGUCHI and IKEDA [4] such that three responses (A, C_1, C_2) add nonlinearly to yield brightness expressed as

$$1 = (A/L_b)^2 + (C_1/L_b)^{2p} + (C_2/L_b)^{2q} \tag{2}$$

where L_b is the luminance of the stimulus that maintains a certain level of brightness, an p and q are some non-linear coefficients. Either of the two

can predict the efficiency curve of fig. 1 very nicely, and no superiority or inferiority can be noticed in the curve fitting. A difference becomes quite apparent when these models are applied to the additivity experiement of two lights, λ_1 and λ_2. The experiment is composed of several heterochromatic brightness matchings, namely between λ_1 and a fixed reference white, W, to obtain L_1, between λ_2 and W to obtain L_2, and between mixtures of λ_1 and λ_2 with various ratios and W to obtain $L_{1,m}$ and $L_{2,m}$. We often exhibit the results in a ϱ_1 versus ϱ_2 plot, where $\varrho_1 = L_{1,m}/L_1$ and $\varrho_2 = L_{2,m}/L_2$. Any model is required to explain the results of this kind of additivity experiment.

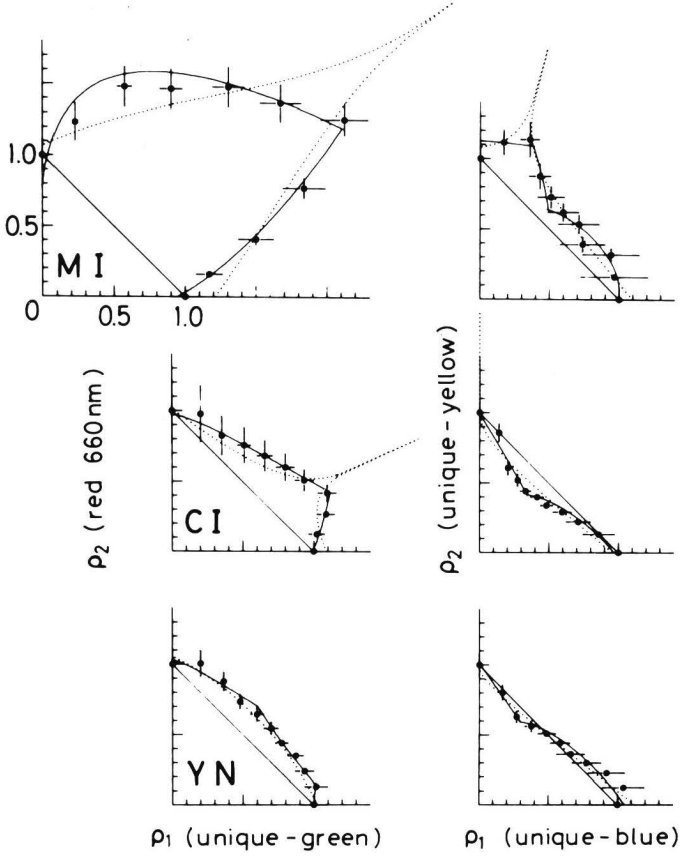

Fig. 2: Results of additivity experiment for pairs of red-green and yellow-blue. Three subjects, MI, CI and YN. Dotted curves: Yaguchi-Ikeda model, solid curves: Nakano-Ikeda-Kaiser model

2. Additivity experiments and comparison of models

NAKANO, IKEDA and KAISER conducted the additivity experiment for ten subjects and for two pairs of λ_1 and λ_2, namely the wavelength for unique green of each subject against 630 nm, and the unique blue against the unique yellow [5]. Examples from three subjects are shown in fig. 2. Visual field size was of 2° of arc and the retinal illuminance of the reference white was 100 Td. Nine different ratios of λ_1 and λ_2 were investigated. Bars at each experimental point indicate 90% confidence intervals after fifteen matchings. The experimental points in each graph constitute a contour of an equal brightness corresponding to 100 Td white. Thus the subject MI requires a more light to maintain the brightness, when a red and green stimuli are mixed, than predicted from the additivity law which should give a straight line connecting $\varrho_1 = \varrho_2 = 1$.

Now the GUTH's vector model fails to explain the asymmetrical contour exhibited in almost all ten subjects as in three subjects of fig. 2, because the model always predicts a symmetrical and elliptical curve. The YAGUCHI-IKEDA model, on the other hand, foresees asymmetrical contour if the non-linear coefficients p and q are properly chosen. The coefficients p and q are determined for each subject to fit the results as much as possible and the theoretical contours are shown by dotted lines in fig. 2. The model explains results of some subjects fairly well but there remain some serious problems unexplained. A very sharp loss of brightness is predicted with a mixture when it is mostly desaturated in subjects MI and CI. This kind of phenomenon is quite unlikely to take place in reality. Another problem, although not shown here, is a prediction of a very large enhancement of brightness for a mixture of certain lights such as a green and a yellow light, or a yellow and a red light in subjects such as CI in whom extremely small values of p and q are derived. Some other model seems to be needed.

3. A new model

In seeking for a new model that might predict the results of additivity experiment we decided to work with a plot other than the ϱ_1–ϱ_2 plot of fig. 2, namely a plot in terms of cone responses so that we can see how much each cone is responding to stimulus to maintain the brightness. The new plot of log R versus log G is shown in fig. 3, where R and G are amount of lights absorbed by R and G cones calculated by the SMITH-POKORNY's fundamentals, $\bar{r}_\lambda$, $\bar{g}_\lambda$, $\bar{b}_\lambda$ [6; p. 404], as defined by the following equations:

$$R = \int L_{e,\lambda} \bar{r}_\lambda \, d\lambda \qquad G = \int L_{e,\lambda} \bar{g}_\lambda \, d\lambda \qquad B = \int L_{e,\lambda} \bar{b}_\lambda \, d\lambda, \tag{3}$$

where $L_{e,\lambda}$ is the spectral radiance of the stimulus. The bottom three graphs in fig. 3 are replots of fig. 2 for the red and green combination, and the top three are for the yellow and blue combination.

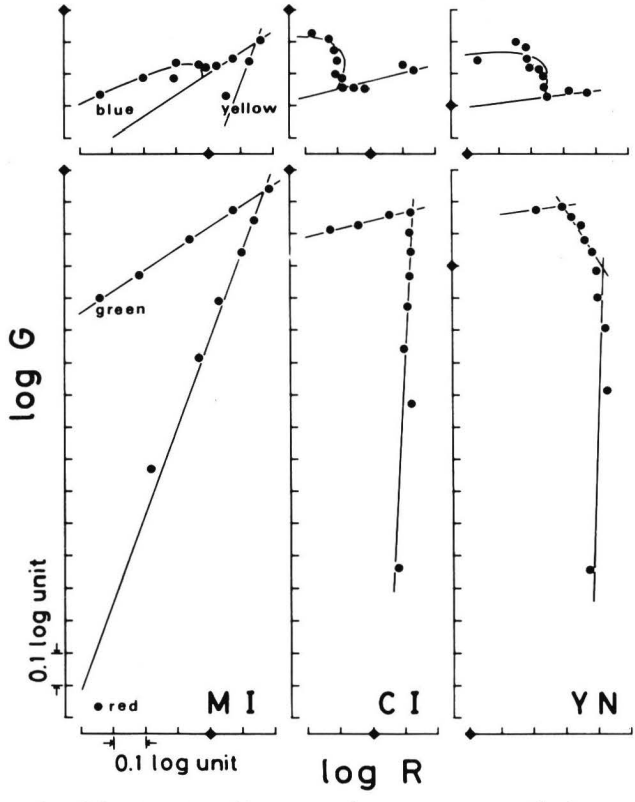

Fig. 3: Results of fig. 2 replotted in terms of cone responses. The bottom three are from the red-green pair, and the top from the yellow-blue pair. Straight lines are theoretical.

It seems now clear what is determining the brightness. The experimental points for the red-green pairs lie on straight lines, or they are expressed by

$$\log G = m \log R + K$$

where m and K are some constants. The equation can be written as follows without losing generality,

$$\alpha \log R + \beta \log G + \gamma \log B = \text{const} \qquad (4)$$

where α, β and γ are constants with the restriction, $\alpha + \beta + \gamma = 1$. We obtained these three constants for each curve and for each subject, and results are shown for the subject MI at the bottom of fig. 4. Two underly-

ing mechanisms, $(R-G)$ and $(-R+G)$ are revealed. The same formulae can be used for another pair of yellow and blue as seen at the top of this figure. For this pair, however, the blue cone must be taken into account and a system $(-R+G-B)$ is introduced, which replaces the straight line of the $(-R+G)$ system with a curved contour at a certain point in the entire curve. Because of the similarity of constants α and β for R and G of these two lines, we suppose the two curves belong essentially to the same system, and the blue cone comes in when a stimulus has short wavelength composition.

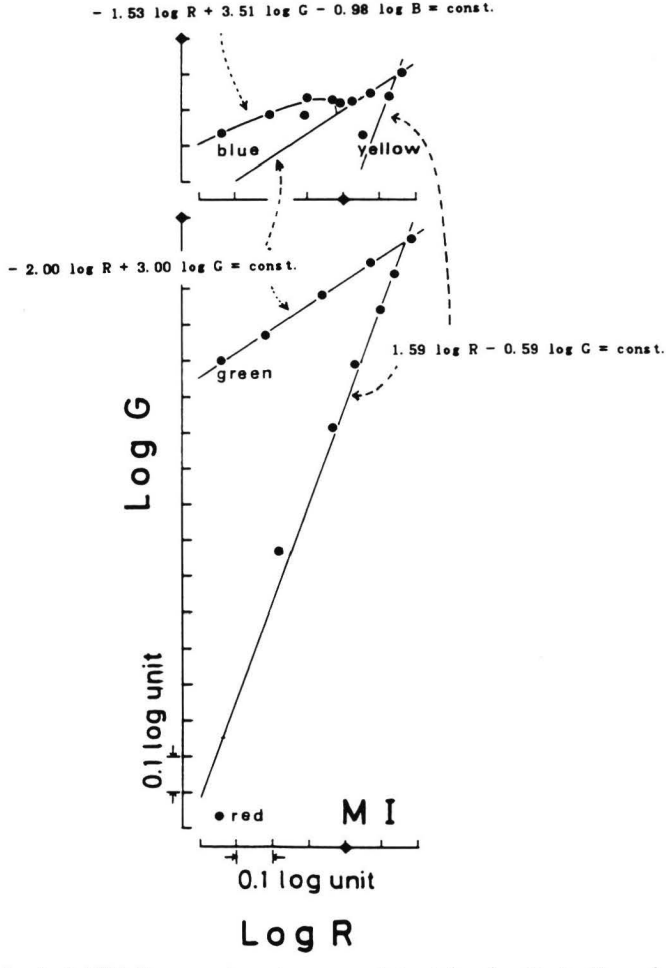

Fig. 4: Additivity experiments are explained by the N-I-K model

The same analysis can be applied to other subjects as to MI and the theoretical solid curves are given in fig. 3. In the subject YN the third straight line is evident in the red-green pair and it is explained by a $(R+G)$ system.

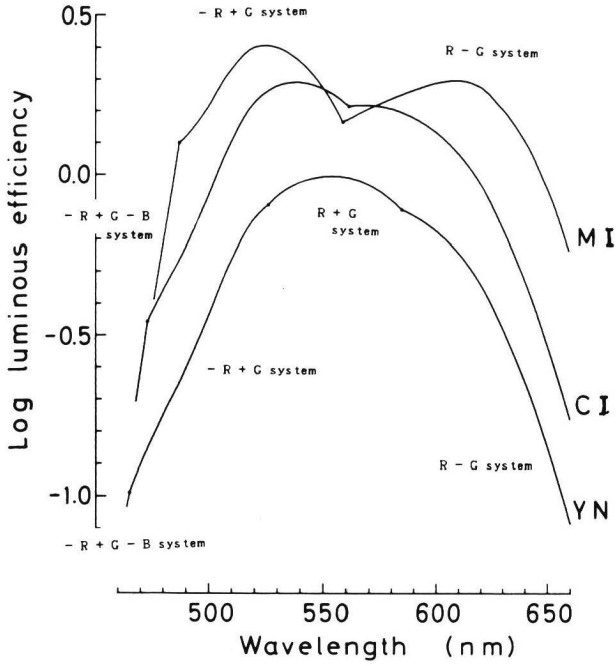

Fig. 5: Predicted luminous efficiency functions for brightness bases on the N-I-K model for three subjects

4. Conclusion

The whole story seems to have become very simple as to the question what is determining the brightness. A certain level of brightness is reached when either of the following three systems

$$\begin{matrix} R-G \\ -R+G \text{ (or } -R+G-B) \\ R+G \end{matrix}$$

produces a certain amount of response according to eq. [4].

By returning to the $\varrho_1 - \varrho_2$ plot the experimental results can ne nicely explained by the systems as shown by solid curves of fig. 2. No sharp decrease of brightness is predicted, and asymmetrical nature of the contours is explained. The luminous efficiency curve for brightness is also explained by these systems as shown in fig. 5. These theoretical curves are nicely correlated in shape at least qualitatively with the experimental results of these subjects that are shown elsewhere [7].

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Authors' address:
Dr. M. Ikeda
Dr. Y. Nakano
Tokyo Institute of Technology Graduate School
Dept. of Information Processing
4259 Nagatsuta, Midori-ku
Yokohama 227, Japan

Manuscript received:
October 30, 1987

Horst Scheibner*, DÜSSELDORF:

Opponent-Color Vision in Relation to Perceptual Criteria

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It is shown how opponent-color vision may be founded on four perceptual criteria determining an opponent color space. Direct additive decomposition of any color into chrominance and luminance is stressed as well as the privotal role of the "blue" mechanism concerning postreceptoral and (phylo-)genetic phenomena.

Es wird gezeigt, wie das Gegenfarbensehen auf vier Wahrnehmungskriterien gegründet werden kann, die ihrerseits einen Gegenfarbenraum bestimmen. Das Prinzip der direkten additiven Zerlegung einer Farbe in Chrominanz und Luminanz wird betont, ferner die zentrale postrezeptorale und (phylo-)genetische Stellung des „Blau"-Mechanismus.

On montre comment on peut baser la vision des couleurs opposées sur quatre critères de la perception; ces critères définissent un espace des couleurs opoosées. On souligne le principe de la directe décomposition additive d'une couleur en chrominance et luminance, aussi bien que le rôle central du mécanisme „bleu" post-réceptoriel et (phylo-)génétique.

1. Introduction

The ultimate purpose of any useful color vision model should be to conform to perceptual color phenomena. As it seems impossible to encompass all chromatic attributes in one color vision model, there hat to be some reduction onto a small number of features. In the following, I will restrict my statements on linear, color vision, and present a linear color vision model [10; 11] which claims a certain degree of completeness and thereby hopefully reveals some places where future refinements and extensions my take place.

2. Perceptual criteria

I claim that four perceptual criteria are necessary and sufficient to establish a linear color vision model. Fig. 1 shows the four criteria between quotation marks. They are: a) indistinguishably equal, i.e. the complete color match, b) neither blue nor yellow, c) neither green nor red, and d) heterochromatically equally bright, i.e. the heterochromatic brightness match.

* *Physiologisches Institut II der Universität Düsseldorf, Abt. für Neuro- und Sinnesphysiologie*

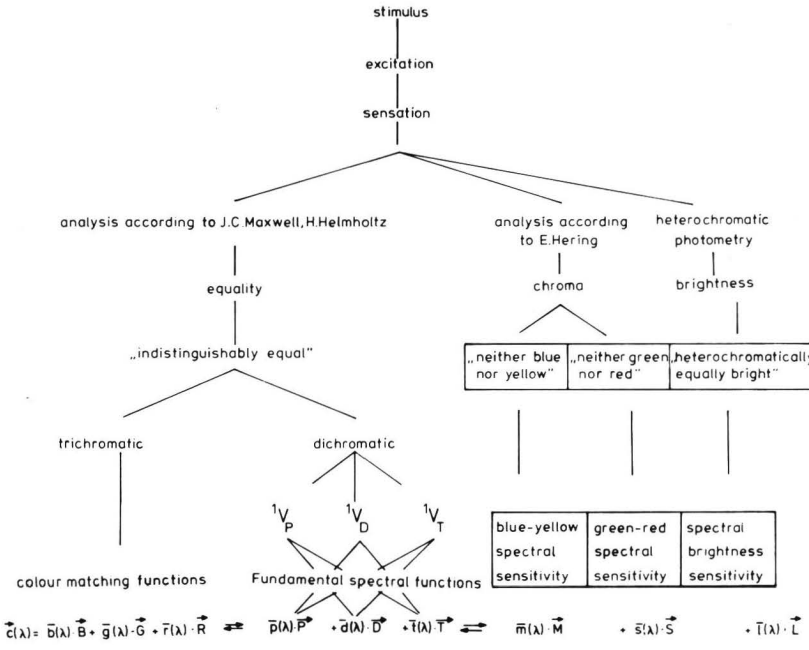
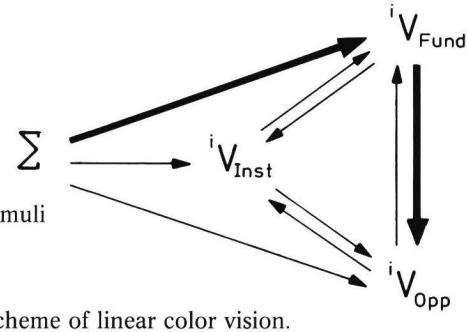


Fig. 1: Color theory through four perception criteria. Bipartite scheme of color sensation analysis. The perceptual criteria are indicated between quotation marks.

I will show that these four perceptual criteria define subspaces of the color space, preferably the color space in which one performs measurements, i.e. the instrumental color space. Similar to many theories, the essential statements made by the model are expressed by mappings between color spaces; therefore, we need more than one color space.

3. General scheme of color vision

Fig. 2 shows the general scheme. It consists of a set of visual stimuli, an instrumental color space, a fundamental color space, an opponent-color space and the mappings between them. The mappings are indicated by arrows, double arrows for invertible mappings, onesided arrows for non-invertible mappings. The heavy arrows can be interpreted as physiological transfer in two steps.



Σ = Set of visible radiation stimuli
$^{i}V_{Inst}$ = Instrumental color space
$^{i}V_{Fund}$ = Fundamental color space
$^{i}V_{Opp}$ = Opponent-color space

Fig. 2: General scheme of linear color vision.
V: vector space; superscript i: dimension of vector space; one-sided arrows: non-invertible mappings; double arrows: invertible mappings; heavy arrows: phsiologically interpretable mappings. Trichromacy for i = 3; Dichromacy for 1 = 2.

4. Opponent-color space

In order to make clear what is meant in particular by an opponent-color space, a schematic picture of it is shown in Fig. 3 [9; 16].

Characteristic of it is that primaries ($\vec{M}$ and $\vec{S}$) are imaginary and together carry the chrominance, which correlates with the sensation of chroma. The third primary ($\vec{L}$) has its locus within the region of real colors and carries the luminance, which correlates with the sensation of brightness. As a consequence of such a configuration, the opponent tristimulus values are partly positive, partly negative, and two of the pertaining spectral opponent functions exhibit both positive and negative branches. The trichromatic formulation of opponent-color vision in the form shown in Fig. 3 is due to SCHRÖDINGER [14].

5. Direct additive decomposition of color

An important property of the opponent-color space, often neglected, is the following: The two chromatic primaries $\vec{M}$ and $\vec{S}$ span a two-dimensional space, the so-called chrominance space [8][1]; the achromatic primary $\vec{L}$ spans a one-dimensional space, the so-called luminance space. In other words, we have a direct additive decomposition of the whole color space into chrominance and luminance:

$$^{3}V_{Opp} = {}^{2}V_{Chrom} \oplus {}^{1}V_{Lum};\ {}^{2}V_{Chrom} \cap {}^{1}V_{Lum} = \vec{O}$$

[1] The chrominance space is a special equiluminant plane, namely of luminance zero. SCHRÖDINGER's original denotation for equiluminant plane was "isolychne"; hence the chrominance space is an "alychne" [14].

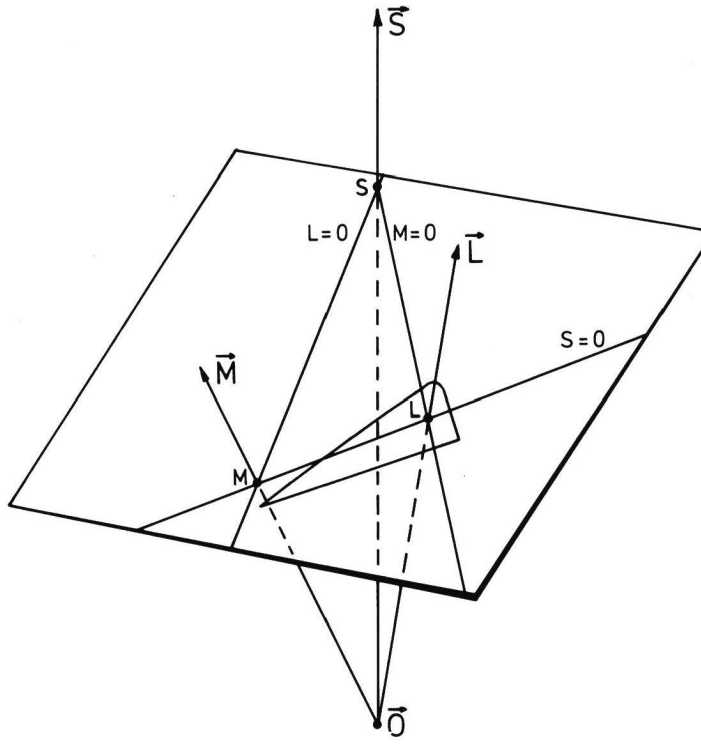


Fig. 3: Spatial representation of the opponent-color spae and its pertaining chromaticity chart. Only part of the real colors lies inside the opponent-color triangle.

If this property is not taken into account, the pertaining spectral opponent response functions together with the spectral brightness function do not obey this additive decomposition either, and thus do not really deserve the name of opponent-color theory. Hence the assertion: Every proper opponent-color theory must obey the principle of direct decomposition into chrominance and luminance.

This assertion must be seen against the background that a color space founded on color matches possesses merely affine properties, no metric, euclidean ones [13; 10]. Thus, before introducing any orthogonalizations into the color space, one should exhaust the concept of direct additive decomposition.

6. Mappings and perceptual criteria

In pursuing the scheme of Fig. 2 (double arrows), the invertible mappings may be considered as mappings from the instrumental color space in itself. In this case, determining the mappings onto the fundamental and opponent color spaces is tantamount to determining these two color spaces themselves. This can be done with the help of the four perceptual criteria mentioned, in conjunction with the laws of additive color mixture. The criteria effectively single out subspaces of the color space. Depending on how they single out such subspaces, the criteria can be subdivided in two categories, category A: equivalence relation, category B: zero relation, Fig. 4. For details, I refer to [12]. The important idea is that a subspace singled out by means of a perceptual criterion is taken to be the kernel of a linear mapping. This simply means that the mapping vanishes on this subspace, or in other words, it assigns the property zero to the colors in the subspace. The properties are a) blue-yellowness (blue-

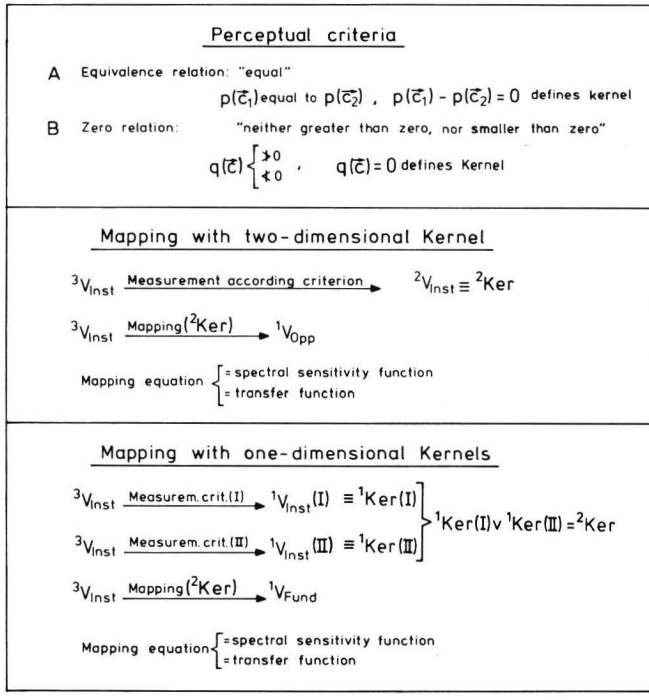


Fig. 4: Types of perceptual criteria allowing to measure subspaces, which, when identified as kernels, establish homomorphic mappings from the instrumental color space onto the fundamental respect. opponent-color spaces.

yellow chrominance) denoted by M in Fig. 3, b) green-redness (green-red chrominance) denoted by S in Fig. 3, c) brightness (luminance) denoted by L in Fig. 3. Since we are mostly interested in spectral functions that pertain to one vector component, i.e. to a one-dimensional subspace, two-dimensional kernels – within a three-dimensional original space – are the simplest case. This is indicated in the middle of Fig. 4.

At the bottom of Fig. 4, the handling of one-dimensional kernels is exemplified – e.g. the dichromatic missing colors in the fundamental color space: Two of them are pairwise joined (symbol v) to form a two-dimensional kernel. The mapping equation resulting from this two-dimensional kernel describes that component that is not contained in this kernel. In such a way the absence of orthogonality in a space possessing solely affine properties [13] may be compensated for, and spectral functions are obtained derived from ones measured in the instrumental space.

7. Results

Fig. 5 shows the results of determining one- and two-dimensional mapping kernels performed by trichromats, protanopes, deuteranopes and tritanopes with the help of the four perceptual criteria. They are presented as loci – points or straight lines – in the chromaticity chart of the fundamental color space. By appropriately assembling the traces of the various kernels, i. e. points and straight lines, we recognize the fundamental color triangle TDP[2], the opponent color triangle MSL and the three dichromatic neutral zones (dash-dotted straight lines). The only line not being the locus of a two-dimensional kernel is the one connecting the points S and P. The experiments on which these results are based are summarized in [10].

Fig. 6 shows the graphs of the pertaining spectral functions, i.e. the spectral fundamental functions as well as the spectral opponent functions. In the center are shown the mapping equations connecting ${}^3V_{\text{Inst}}$ with ${}^3V_{\text{Fund}}$ (Fig. 2) and at the bottom those connecting ${}^3V_{\text{Fund}}$ with ${}^3V_{\text{opp}}$. The latter are of the type of opponency response functions.

8. Discussion

The foregoing outline and results have much in common with the work of KRANTZ (3; 4], although I have not striven for an axiomatic representation at all. From my point of view, KRANTZ's opponent-colors theory [4] is incomplete in that the perceptual criterion of the heterochromatic brightness match is not used. Consequently, KRANTZ does not make use of

[2] The fundamental primaries used may be assumed to possess the following CIE 1931 chromaticity coordinates (x, y) [16]: P(0,7602; 0,2419); D(1,3886; – 0,3802); T(0,1577; 0,0000).

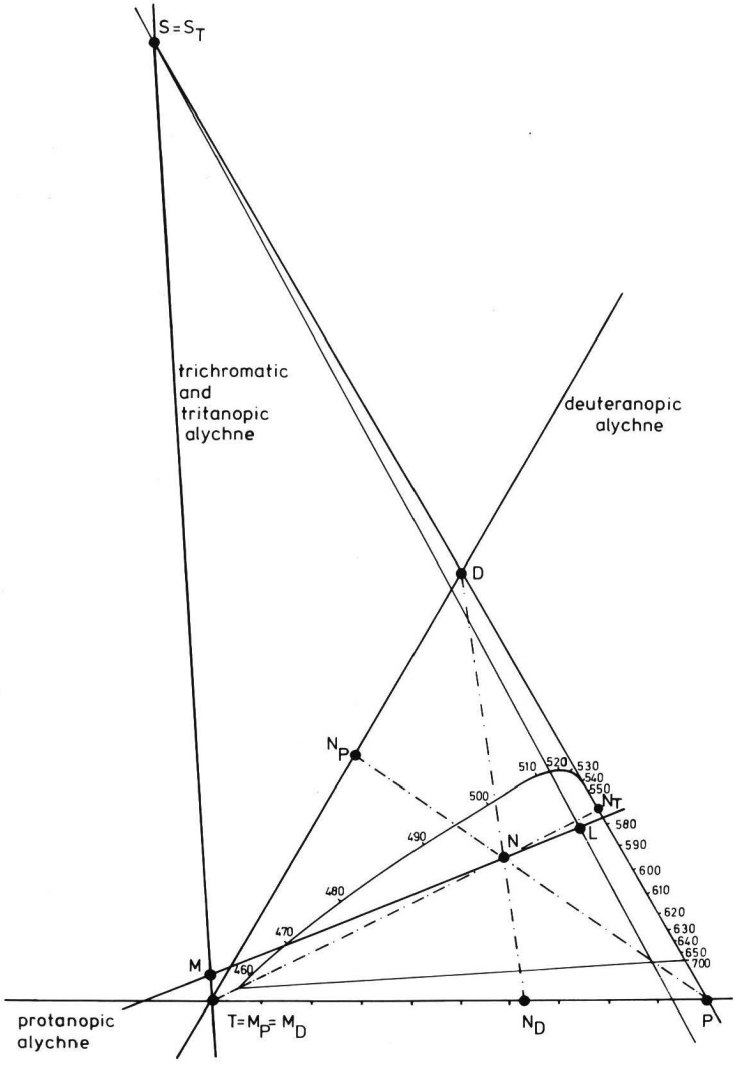


Fig. 5: Fundamental color triangle PDT and, related to it, the opponent-color triangle MSL. The neutral zones of the dichromats are dash-dotted. The equation of the trichromatic alychne reads $D+1.8P=0$; the equation of its trace reads $d = -1.8\ p$.

the concept of alychne or alychne trace (the line L = 0 in Fig. 3), and he shows no opponent-color space at all. This situation always appeared strange to me, since those concepts introduced by SCHRÖDINGER were – as is well known – incorporated into the color system CIE 1931. In the sequel, KRANTZ [4] does not observe the direct decomposition of any color into chrominance and luminance, even violates it by positioning his

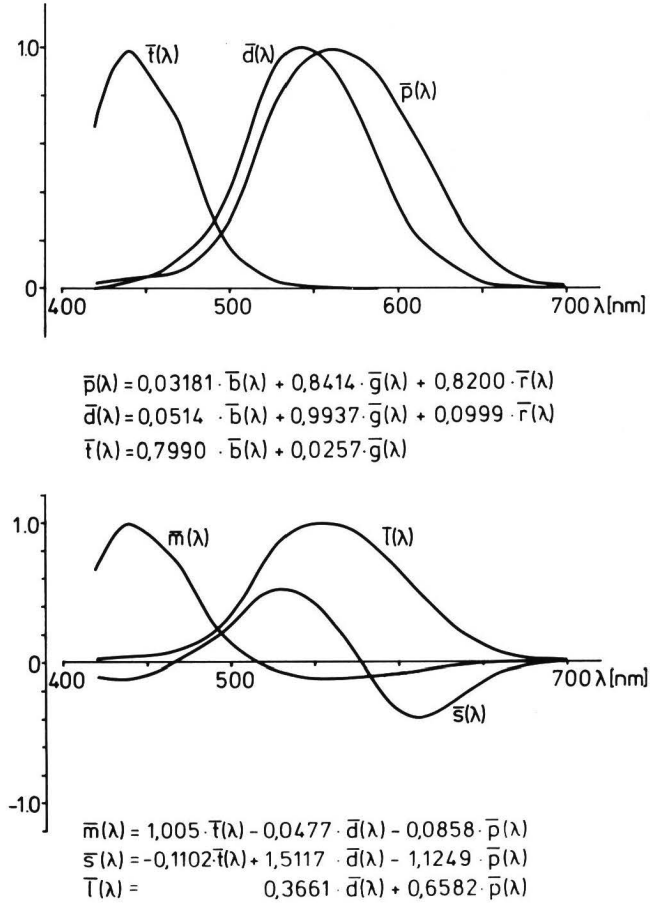


Fig. 6: The upper part shows the trichromatic spectral fundamental functions together with their connection to the color matching functions pertaining to the instrumental color space. The lower part shows the trichromatic spectral opponent functions together with their connection to the trichromatic spectral fundamental functions.

equilibrium colors (in our Fig. 3 the loci M and S) not on the alychne trace (Ref. [4], p. 311, Fig. 3). Chromatic opponent-response functions thus derived necessarily contain luminance, and vice versa, a brightness function contains chrominance. One may, of course, ask how strict the human visual system obeys the principle of decomposition in question. But this is a question of higher order. Technical compatible color television seems to indicate that the principle works quite well [8].

The outline presented here is, at first, confined to strict linear relations. In reality, the mapping that connects $\sum$ with ${}^3V_{\text{Fund}}$ (Fig. 2) and describes the primary receptor process (a more detailed description is given in [10] and [11]) is strongly non-linear. An extension of the theory should replace the linear equations by non-linear ones.

While the non-linearities that exist between the set of visual stimuli $\sum$ and the fundamental color space ${}^3V_{\text{Fund}}$ are hardly observable in color mixture, the ABNEY effect [1; 2; 5] is an expression of non-linear relations between the fundamental and opponent-color spaces. Here, a first extension of the linear theory by means of piecewise linearizations seems promising.

A striking feature to be seen in Fig. 5 is the fact that the alychne traces of all four types of observer intersect in a common locus, namely the locus T of the blue color mechanism. Studies on protanomalous observers [15] indicate that the same locus T plays the same part as a central pivot also with anomalous trichromats. Altogether this suggests that the "blue" cones play a key role in the postreceptoral color processing as well as in the phylogenetic and genetic evolution of human color vision [6; 7].

Finally, the direct operational identification of subspaces through the perceptual criteria attributes a significance to these subspaces at least as important as the usual psychophysical "channels". Singling out the subspaces does not touch the affine structure of the color space. Insofar do the three "opponent" criteria (right branch in Fig. 1) not refine the affine structure imprinted originally by the color match. This leaves possibilities open.

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Author's address:
Prof. Dr.-Ing. H. Scheibner
Physiologisches Institut
der Universität Düsseldorf
Moorenstraße 5
D-4000 Düsseldorf 1

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Tarow Indow*, IRVINE, CAL.:

Psychologically Unique Hues in Aperture and Surface Colors

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As unique hues of surface colors, a minimum of poles of three opponent processes are necessary, which include black-white. Perceptual decomposition of each surface color into these components or one more component (purple) and its implications for color order systems and color vision theories are discussed.

Für Urfarben bei Körperfarben ist ein Minimum an Polarität in den drei Gegenfarbenprozessen erforderlich, eingeschlossen Schwarz-Weiß. Die empfindungsgemäße Aufspaltung einer jeden Körperfarbe in diese Komponenten oder eine weitere Komponente (Purpur) und deren Bedeutung für Farbordnungssysteme und Farbensehtheorien werden diskutiert.

On a besoin d'un minimum de pôles de trois procès-opposés des couleurs pour les couleurs uniques de couleurs superficielles, blanc/noir inclus. La décomposition perceptuelle d'une couleur superficielle dans ces composantes ou une autre de plus (pourpre) et son importance pour les systèmes d'ordre des couleurs et pour les théories de la vision colorée sont discutées.

1. What are psychologically unique hues?

It seems to me that the most fundamental criterion to define this rather vague concept is non-reducibility of each unique hue to any other hues. Other criteria sometimes implied should be regarded as possible properties of a psychologically unique hue. A hue cannot be defined unique for the reason that it remains invariant for change of the intensity (no BEZOLD-BRÜCKE shift), but we can ask whether a unique hue has this property and/or invariance for change of its purity (no ABNEY shift), etc.

1.1: *Poles of three opponent processes*

The spectrum appears to the human eye as divisible into some regions. According to the definition given above, the discontinuities of a minimum number should be unique hues. There are studies (e.g. [1]) based upon appropriate behavioral indices which show that infants see the same discontinuities as adults; *R, Y, G, B.* Observation of the spectrum tells us unique hues in aperture colors; colors which change only from dim to bright. On the other hand, surface (object) colors have a definite impression of being black or white, either of which cannot

* *Dept. of Cognitive Sciences, Irvine, University of California*

be reduced to any other hues. Hence, this achromatic change is opponent and psychologically unique as *R–G* and *Y–B* are. These six poles of three opponent processes are also color terms which appear at the earliest stages of the development of the basic color vacabulary in 98 different languages studied by BERLIN and KAY [2].

1.2: *Components discernible in colors*

The above definition implies that non-unique colors consist of more than one components. How a color is analysed into components may not be unique. No doubt, however, that the decomposition is most natural when the components correspond to unique hues. All cancellation experiments have been performed with regard to *R, Y, G, B* in aperture color, in spite of that, if requested, the subject is able to cancel, for example "purpleness" or "orangeness" in aperture color. The subject is able to perceptually decompose surface colors into gray and chromatic components and in turn the former into blackness (*Bl*) and whiteness (*W*) whereas the latter into *R, Y, G, B*, or more. The experiments in the next section are concerned with this problem.

2. Spatial representation of Munsell colors

2.1: *Results of multidimensional studies*

Colors in the main part of the MUNSELL solid can be represented as a configuration of points $\{P_j\}$ in a 3-D space with locally Euclidean metrics in the following way [3].

1. The input data d_{jk} and the result d_{jk} in I of Fig. 1, inter-point distances in $\{P_j\}$, are proportional, provided that perceptual differences between colors (j, k) are matched with perceptual differences between two grays (hence d is given in terms of the MUNSELL value scale V) and pairs (j, k) are limited in the range in which color differences are intuitively palpable ($d<3.5$ V).

2. Points P_j for colors of the same V are on a plane and the axis corresponding to V is orthogonal to the plane.

3. The structure of P_j in each plane is topologically in agreement with MUNSELL notation of H and C.

4. Many quantitative deviations from MUNSELL notation are noticeable with $\{P_j\}$. For example, 5*PB* colors are too closely located to 5*B* colors, etc.

2.2: *Vectors representing principal hues*

When we have the additional data, $\xi_{\alpha i}(j)$, degree of a principal hue α perceived by a subject i in a color j, then it is possible to define vectors $f_{\alpha i}$ in the same space in which $\{P_j\}$ is constructed. The subject was asked to divide a line segment in proportion to degrees of grayness, $N(j)$, and prin-

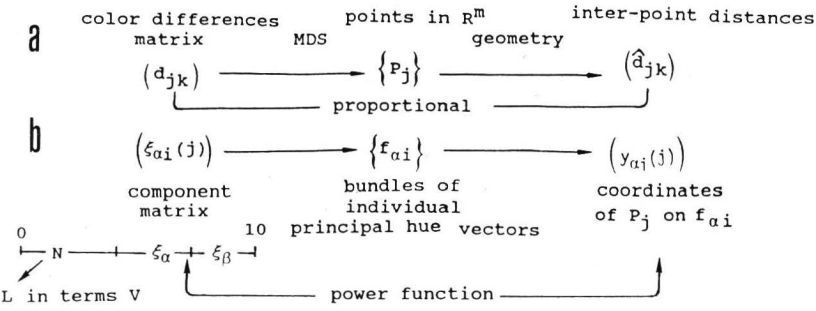

Fig. 1 Judgments and processing of the data by two programs of MDS, DMRPD (Direct mapping in RIEMANNIAN Space through powered distances), in a and DMPC (Direct mapping through powered components) in b

cipal hues (α, β) and also match the lightness L of the gray with MUNSELL Value scale (II of Fig. 1). Then, for α and i being fixed, $\xi_{\alpha i}(j)$ are defined to be a power function of coordinates of P_j on $f_{\alpha i}$, $y_{\alpha i}(j)$ (contravariant components). Fig. 2 shows the synthesized result based upon two experiments (5 subjects each) in which one $\{P_j\}$ was constructed for all the subjects but individual differences were allowed for $f_{\alpha i}$. Hence, bundles (α) of 5 individual vectors are given on the outer circles for two cases, one for 4 unique hues and the other for 5 principal hues including purple (P) as in MUNSELL notation. Individual differences in how to interpret respective principal hues are small in R, G, B and considerably large in Y and P. Exactly the same results have been obtained in [3] also. Because Y does not have its counterpart in retina and P is not psychologically unique, each of these must be based upon a multichannel process and individual differences in each channel involved are superimposed. When P is not included, individual differences in R and B become much larger. Though P is not unique, it seems to help sharpen concepts of pure red and pure blue.

2.3: *Chromatic response functions in surface colors*

Ratios $h_\alpha(j) = \xi_\alpha(j)/[10-N(j)]$ are plotted against H in I of Fig. 3, where $\xi_\alpha(j)$ and $N(j)$ denote the respective means over individuals. Broken curves represent $h_\alpha(j)$ when P is included. It is evident that P is decomposible to R and B. Whether P is included or not, the subject sees in each color essentially two principal hue components only. Points or short intervals can be defined on the abscissa of I in Fig. 3 at which 10 MUNSELL H notations are best located. Unique B is not at $5B$ but closer to $5P$, which explains the deviation stated in 4 in 2.1. We can regard the four curves, R, Y, G, B, as being equivalent to chromatic response functions which are obtained with spectral light by the cancellation method. Curves of HURVICH and JAMESON [5] and the synthesized result by WERNER and WOOTON [6] are given in II, the abscissa of which has been trans-

formed to H on the basis of dominant wavelength of the most saturated color stimulus of respective hue in our experiments. Except G, curves are similar in two plottings, I and II. Frequency curves in a color naming experiment with aperture color [7] are given in III, G-curve of which is also sharply different from that in II.

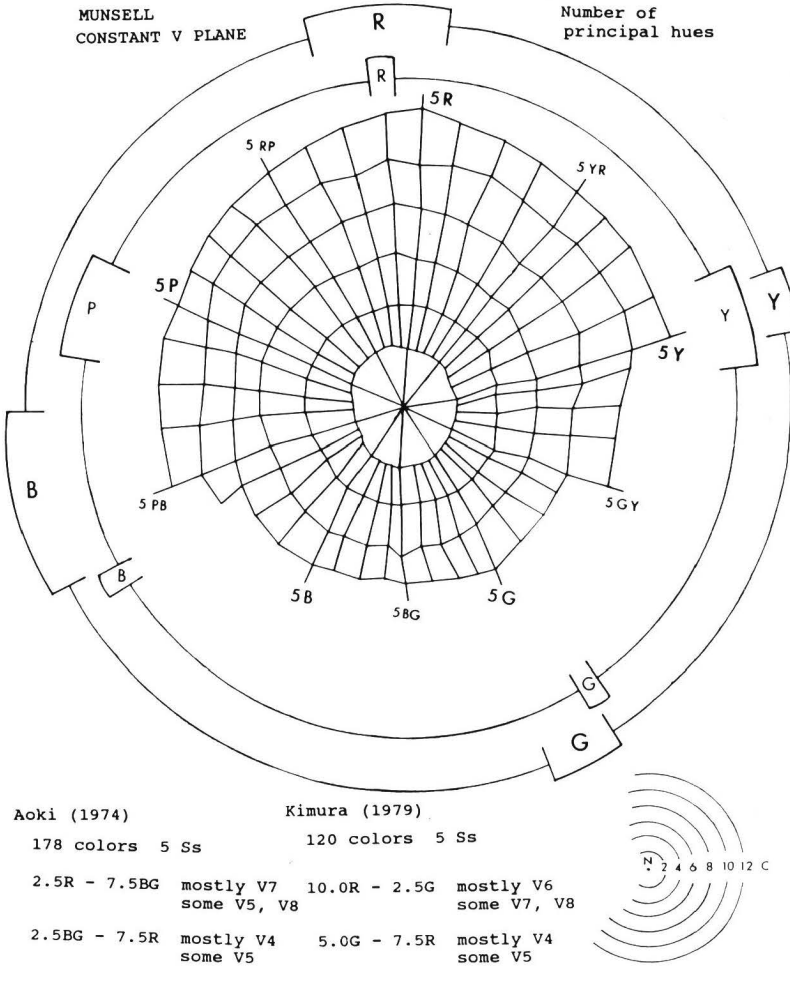

Fig. 2: Configuration $\{P_j\}$ and bundles (α) of individual vectors $\{f_{\alpha i}\}$ of MUNSELL colors. Processed in 1987

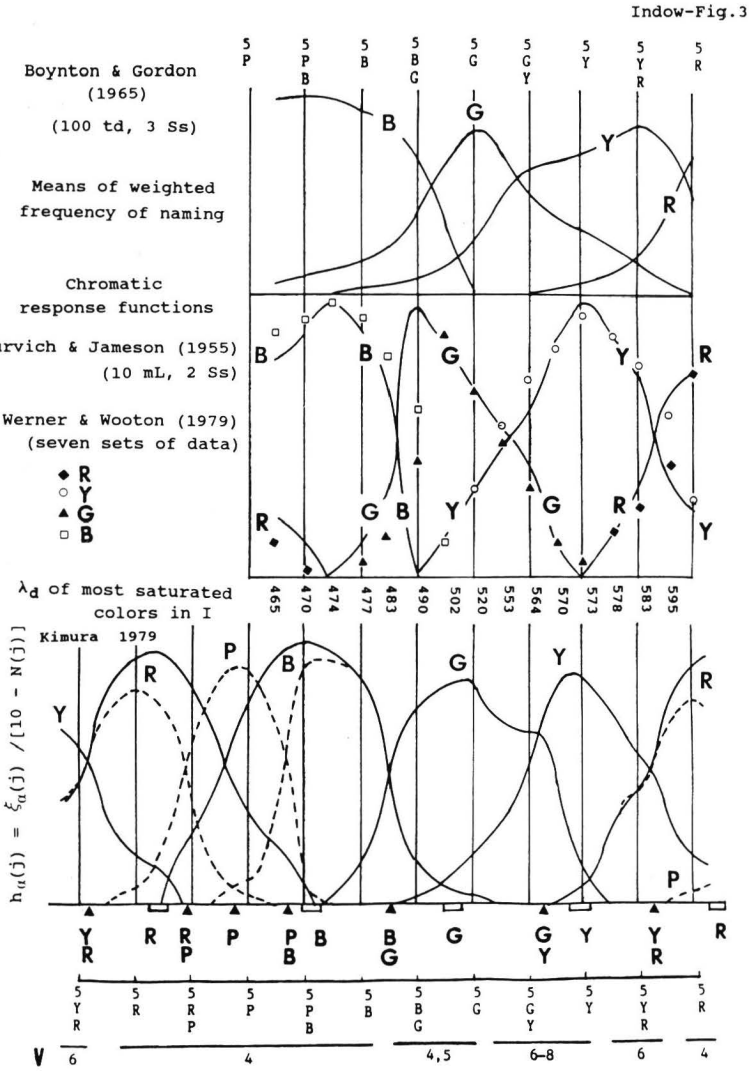

Fig. 3: Chromatic response and related curves for MUNSELL colors and monochromatic lights

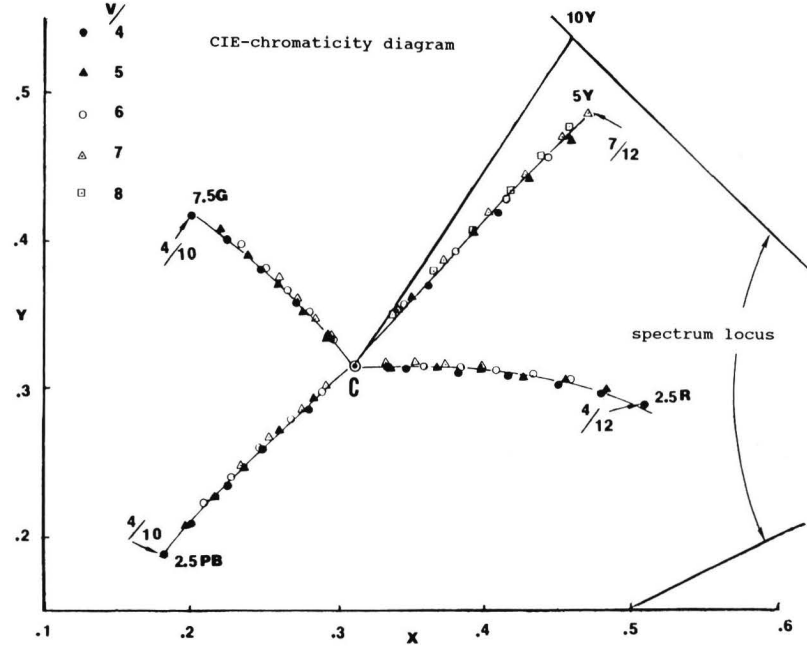

Fig. 4: MUNSELL 5 H colors in CIE chromaticity diagram as functions of C and V

Chromatic response functions lose their meaning unless, when the intensity of light is changed, only their amplitudes change while their forms remain constant. This is also true for h_α-curves. In fact, $h_\alpha(j)$ are fairly independent of V and C of color j and effects of V and C are of the order that can be regarded as perturbation around h_α-curves. The perturbation is largest around h_y-curve. In the master chart for H plotted in the chromaticity diagram, one may have the impression that effects of V and C are apparent in all loci of constant H, except $10\,Y$. The chart is somewhat misleading, however. If the plotting is limited in the gamut under discussion, one may understand why h_α-curves can be fairly independent of V and C. BEZOLD-BRÜCKE and ABNEY shifts are not too conspicuous, especially in the Y–B process (Fig. 4).

3. Comments on neural processes

3.1: *Roles of psychologically unique hues*

Both in spectral and surface colors, unique hues act as poles of opponent processes. Surface colors are richer in the sense that they have various degrees of grayness (N_j) and can be spatially represented in which distance $\hat{d}$ of modest size corresponds to perceptual color difference. We can define such radial and oblique coordinate axes f_α, 4 or 5 in number, that coordinates $y_\alpha(j)$ of P_j correspond to $\xi_\alpha(j)$. H of the color j is primarily determined by $h_\alpha(j)$, the amount of $\xi_\alpha(j)$ in the chromatic part. If P is included, $h_p(j)$ can be rewritten in terms of R and B. Saturation C and lightness V of the color j are captured in $N(j)$ and its matched MUNSELL value L. N is decomposible into black (Bl) and white (W), the third opponent process. Evidently, a measure $\hat{d}_{ik}$ of perceptual difference is related to differences in coordinates $|y_\alpha(j) - y_\alpha(k)|$ where α represents components common to two colors. In short, perceptual color differences and principal components, both obtained through subjective judgments, approximately behave as a linear system [8]. To serve this purpose, R–Y and G–B cannot be two orthogonal axes, as adopted in some color systems. The opponent process Bl–W is orthogonal to the other unique hues. So far, the color space is assumed to be locally Euclidean. I have tried to embed $\{P_j\}$ and $\{f_{\alpha i}\}$ in some non-Euclidean spaces, but no particularly interesting additional information was obtained. Difference of geometry matters only for the functional relationship between $\hat{d}_{ik}$ and $|y_\alpha(j) - y_\alpha(k)|$.

3.2: *Neural processes underlying unique hues*

Though oversimplified, the above stated quantitative and compact systematization of perceptual facts of surface colors may be taken as a challenge to neuroscientists. In the past, theories and neurological studies of color vision have been focussed upon aperture colors, especially data based upon monochromatic light. The purpose of this presentation is to make explicit that MUNSELL color solid, if analysed appropriately, is a source of useful information for theories of color vision as data based upon spectral light. As to neural processes at the end of the visual system, a number of questions will be raised.

1. What neural processes are involved for changing aperture color mode to surface color mode? How does the Bl–W process come to exist? Inhibition from the surrounding seems to be a necessary condition.

2. It seems unlikely to have separate groups of (gnostic) cells for R, Y, G, B (Bl, W). A necessary condition for perceiving a unique hue seems to be that the other hue opponent process, but not necessarily the achromatic Bl–W process, is in equilibrium (e.g. [9]).

3. How does color difference emerge from the neural processes for unique hue components?

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Author's address:
Prof. Dr. T. Indow
Dept. of Cognitive Sciences
University of California
Irvine, CA., 92717, USA

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Steven K. Shevell*, CHICAGO:

Processes Mediating Color Contrast**

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The color appearance of a light depends on other lights that surround it. Three processes by which a chromatic surround can affect perceived color are evaluated: scattered light, receptoral sensitivity change, and induction. When the light and its surround are both steadily presented or briefly flashed, sensitivity change and induction are the dominant processes.

Das farbige Aussehen eines Lichtes hängt von anderen Lichtern ab, die es umgeben. Drei Prozesse, durch die ein buntes Umfeld die Farbempfindung beeinflussen kann, werden untersucht: Streulicht, Änderung der Rezeptor-Empfindlichkeiten und Induktion. Werden das Licht- und sein Umfeld stetig oder als kurze Blitze dargeboten, sind Änderung dr Empfindlichkeit und Induktion die hauptsächlichen Prozesse.

L'apparence d'une lumière depend des autres lumières ambiantes. On a étudié trois procès qui peuvent influencer la couleur: la lumière diffusante, le changement de la sensibilité des récepteurs, et l'induction. Si l'on présente la lumière et son ambiance continuellement ou par des éclairs brefs, on trouve que le changement de la sensibilité et l'induction sont les facteurs dominants.

1. Introduction

When a small patch of light is viewed alone in an otherwise dark field, its color appearance can be predicted from the spectral energy distribution. Hue, saturation and brightness of the patch become difficult to specify, however, when the same light is part of a more complex visual scene. The other lights in view can alter the perceived color of the patch, a property of human vision appreciated for nearly 150 years [1] but still understood only in part.

What is responsible for one light's influence on the color of another? WYSZECKI's recent review [2] describes a number of mechanisms. In the case of chromatic contrast, at least three distinct processes can be identified. First, quanta from a light in one part of the visual field may fall on a part of retina corresponding to a separate area of the field, because the image on the retina is not a precise geometrical image of the stimuli. Diffraction, the eye's optics, and scatter all contribute to the spread of light within the eye. Second, nearby lights may selectively alter the sensitivity

* *The University of Chicago, Dept. of Behavioral Sciences* and *Dept. of Ophthalmology and Visual Science*

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of photoreceptors, leaving one type of receptor relatively less sensitive than normal. Changes in gain can affect color appearance by altering the relative strength of neural signals from the three types of cones. Third, a neural process can induce a color shift in a nearby field; for example, a long-wavelength reddish surround can induce greenness within its center. The three processes can be distinguished by a nearby light's quantitative effect on the color of a small test patch. Under particular conditions each of the three processes can affect color appearance, though the present measurements show that one or two of them sometimes dominate.

2. Methods and procedures

The observer views a circular test field of diameter 1.1°. The test is an admixture of 540 nm and 660 nm lights (denoted T_{540} and T_{660} respectively); the retinal illuminance of the 660 nm light is held fixed while the observer adjusts the level of the 540 nm test component so that the color of the test is neither reddish nor greenish. This is a reliable and subjectively easy task: the standard error of the mean of each measurement, based on repeated observations over four days, always was less than 0.1 log unit. Measurements are taken at 660 nm test-light levels ranging from 1.3 to 2.9 log Td.

During most sessions the test is surrounded by a 660 nm field with outer diameter 6.8°. The surround, denoted S_{660}, is contiguous with but not overlapping the test. Two surround levels are tested (1.5 and 2.2 log trolands); surround retinal illuminance is varied between sessions.

3. How do the three processes affect measurements of color appearance?

Changes in color appearance caused by the surrounding 660 nm field are assessed by comparing 540 nm test-light (T_{540}) measurements when the surround is present to baseline measurements when the surround is absent (dark adaptation). Because the wavelength of equilibrium yellow does not vary with luminance [3], with no surround the required amount of 540 nm test light (T_{540}) is a constant proportion of the retinal illuminance of the 660 nm test field, T_{660}. Therefore the dark adapted measurements fall along a 45° line in log-log coordinates (dashed line, left panel of Fig. 1).

Conceptually, the measurements are then repeated with the surround in view (actually, the experimental condition for any given session is chosen randomly, to avoid ordering artifact). The change in the amount of 540 nm test light set by the observer is the measure of color shift caused by the surround. The different processes of color contrast are distinguished by varying the level of the test field. The following sub-sections consider the theoretical effect of each process, as a function of test-field retinal illuminance.

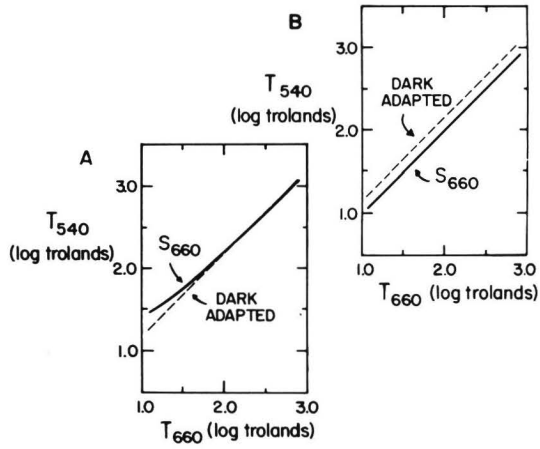

Fig. 1: A: Center and surround both steady or both flashed. Scattered light adds to the central field
B: Surround steady, center flashed. Scattered light in central area acts as a steady adapting field

3.1: *Light spread and scatter*

Light from the surround falling in the part of retina corresponding to the central test is, of course, real light and thus affects color appearance as would additional 660 nm light stimulating the test area. When the center and surround are both presented steadily or both flashed briefly at the same instant, the scattered light adds physically with the test light. In this case there is more 660 nm light in the test area than the level of T_{660} set by the experimenter, so at lower test levels the observer should set the 540 nm test component, T_{540}, higher than he does under dark adaptation. At higher test levels, the amount of scattered 660 nm light is negligible relative to T_{660}, so the measurements converge to dark adapted results (Fig. 1, left panel).

When the surround is presented steadily but the test flashed briefly once every few seconds, the effect of scattered light is quite different. Except for the short period when the test is present, scattered light alone stimulates the central area and thus acts as a steady adapting field. Scattered light from the surrounds used here causes selective gain changes primarily [4], resulting in levels of T_{540} proportionally smaller than the corresponding dark adapted measurement. This implies the results fall on a 45° line parallel to and below the dark adapted values (Fig. 1, right panel).

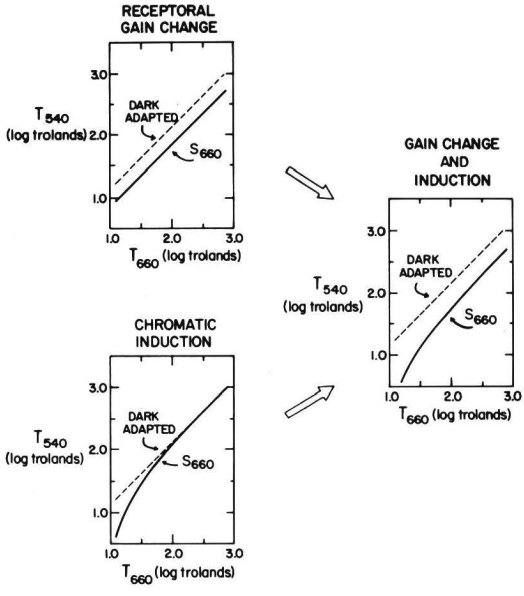

Fig. 2: Combination of receptoral gain change and chromatic induction

3.2: *Gain changes*

Light absorbed in the retinal area corresponding to the surround may desensitize nearby receptors in the central area. The long-wavelength surround would affect long-wavelength-sensitive (LWS) cones more than middle-wavelength-sensitive (MWS) receptors so, compared to measurements without a surround, less 540 nm test light (T_{540}) would be required at each level of the 660 nm test field (T_{660}). Gain changes multiply receptor signals, so the empirical implication is again a proportional change in T_{540}, implying results that fall on a 45° line below the dark adapted values (Fig. 2, top panel of left).

3.3: *Chromatic induction*

The long-wavelength surround also may induce greenness in the central field. The amount of induced greenness can depend on the radiance of the surround but not on the level of the test. Because induced greenness reduces the amount of greenness needed from the 540 nm test light, induction tends to reduce the level of T_{540} set by the observer, compared with the no-surround results. For a given surround the induced greenness is a fixed amount, so its *relative* contribution to the color of the central area becomes smaller as the test level is increased, and becomes negligible when the test level is high. This implies the measurements of T_{540} will be lower than the no-surround values with less intense test fields, but that

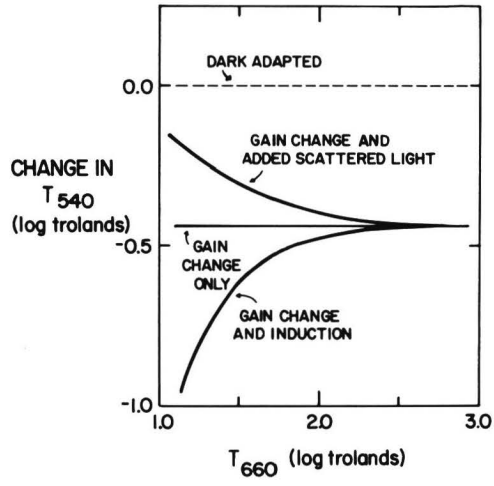

Fig. 3: Change in measurements caused by 660 nm surround

the measurements will converge to the no-surround results at higher test levels. This is shown schematically in Fig. 2 (bottom panel on left).

Chromatic induction and gain changes may occur simultaneously, in which case the line through the T_{540} measurements has curvature determined by chromatic induction and vertical position determined by gain changes (Fig. 2, right panel).

3.4: *The specific effect of the chromatic surround*

Fig. 1 and 2 show the theoretical impact of scattered light, gain changes and chromatic induction, and from these figures the theoretical differences from the no-surround condition can be noted. The differences are drawn schematically in Fig. 3. The dashed horizontal line at zero (no difference) is by definition the dark adapted (no-surround) results. Gain changes alone result in a vertically displaced horizontal line; scattered light (with center and surround both steady or both flashed) implies a curve that bends upward at lower test levels; and induction implies a curve that bends downward at lower test levels.

4. Results

Measurements for two observers are in Fig. 4, plotted in the format of Fig. 3. Left panels are data from observer M.A., right panels from observer L.Y. (both paid undergraduate volunteers). The top panels show results when both the central test and the surround are viewed steadily. Squares and triangles are values with 1.5 log Td and 2.2 log Td surrounds, respec-

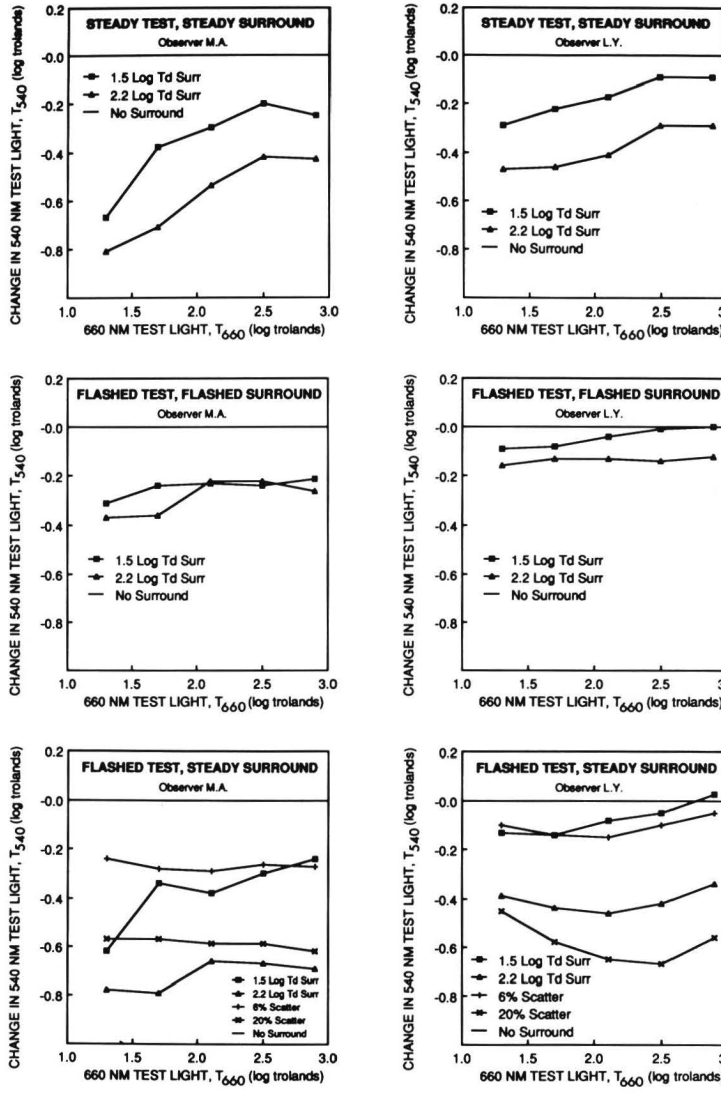

Fig. 4: Changes in the 540 nm test light T_{540} (log Troland)

tively. Results for both observers at each adapting level follow the pattern expected from chromatic induction and gain changes. The shift from no-surround values is large at the left of each panel, and gradually declines as test level is increased until it approaches a horizontal asymptote at the right of the plot. Any possible effect of scattered light is compensated and dominated by substantial chromatic induction.

When the central test and surround are flashed simultaneously (for 500 ms once every 7 s), the effect of the surround is smaller than when the fields are presented steadily. This is shown in the middle panels, where the points fall closer to the horizontal reference line at zero that indicates no effect of the surround. Compared to results with steady center and surround fields (top panels), both the induction and gain-change effects are reduced with flashed presentation. Weaker induction is implied by less curvature in the plots, which deviate relatively little from a horizontal line; smaller gain changes are indicated by the horizontal asymptotes that are closer to the zero line.

Measurements with a steady surround and briefly flashed central test (500 ms once every 7 s) are plotted in the botton panels of Fig. 4. Scattered light acts primarily as an adapring field in this case and thus may alter gains (see Fig. 1, right panel). The effect of scattered light is assessed by replacing the surround with a solid steady 6.8° adapting field, which covers the central test, at a level equal to the scattered light. The scattered-light level, calculated from the point-source light profile [5] for the field sizes used here, is about 11%. As this is a typical value that is not precise for every observer, steady fields were chosen to bracket the calculated value for the 2.2 log Td surround: 6% (1.0 log Td) and 20% (1.5 log Td). For observer M.A., even 20% scatter cannot account for the measurements, which deviate from no-surround results more than can be due to scattered light; further, the shape of the line through his measurements is characteristic of induction and not of scattered light. Conclusions from the other observer, L.Y., are less clear; although 6% scatter cannot account for her measurements, a solid steady background at 20% of the surround level shifts results from dark adaptation more than the steady surround (triangles). In summary, scattered light might account for observer L.Y.'s results, in accord with WALRAVEN [6], but scatter cannot explain the measurements of observer M.A.

5. Conclusion

Scattered light, receptoral gain change and chromatic induction all affect color appearance. When the complete stimulus field is viewed steadily or is briefly flashed, induction and gain changes predominate. When the surrounding field is steady and the central test briefly flashed, scattered light contributes significantly to changes in color appearance.

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Author's address:
Dr. St. K. Shevell
Dept. of Behavioral Sciences and
Dept. of Ophthalmology and Visual Science
The University of Chicago
5848 S. University Avenue
Chicago, IL, 60637, USA

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Jan Walraven*, **T. L. Benzschawel**** and **B. E. Rogowitz****, SOESTERBERG:

Color-Constancy Interpretation of Chromatic Induction

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Changes in illumination of Munsell color chips were simulated on a monitor, and shifts in color appearance were studied by dichoptic matching. The results support the idea of chromatic induction as a misdirected attempt of the visual system to obtain color constancy.

Wechsel der Beleuchtung von Munsell-Farbmustern wurde auf einem Monitor nachgeahmt, und die beobachteten Farbverschiebungen wurden durch beidäugig getrennten Vergleich untersucht. Die Ergebnisse unterstützen die Meinung, daß die Farbumstimmung ein mißlungener Versuch unseres Sehapparates zur Erzielung einer Farbenkonstanz ist.

Le changement de l'illumination des échantillons de Munsell était simulé sur l'écran d'un moniteur. On a étudié les changements des couleurs à l'aide d'une observation haploscopique. Ces résultats appuient l'idée que l'adaptation chromatique n'est qu'un essai mal venu de notre système visuel à obtenir une constance des couleurs.

1. Introduction

The color of an object is (physically) determined by both its spectral reflectance and the spectral power distribution of the illuminant. Nevertheless, object colors tend to appear quite invariant in spite of considerable changes in illuminant color, a phenomenon known as "color constancy".

Although the visual system may truthfully signal the "real" color of an object under illuminant changes, it may completely fail to maintain invariance of a color stimulus when the color of its surrounding area is varied. The color that is perceived, then, will usually be shifted in the direction of

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* *TNO Institute for Perception*, Soesterberg (Netherl.)
** *IBM T. J. Watson Research Center*, Yorktown Heights, New York

the complementary color of the surround. This phenomenon, generally referred to as chromatic induction, was treated by HELMHOLTZ [1] as some kind of psychological bias (Täuschung des Urteils) triggered by the dominating presence of the surround.

Chromatic inducation may indeed be interpreted as an error of the visual system, but we would prefer, more in line with current thinking, to treat it as a misdirected attempt of the visual system to maintain color constancy. That is, the induction effect occurs because the system attributes the change in surround color to a change in illuminant rather than a change in reflectance.

We were able to test the above linking hypothesis of chromatic induction and color constancy in a study [2] in which both phenomena were measured in the same experimental paradigm.

2. Experimental methods

2.1: Stimulus

The stimulus pattern was generated on a computer-driven monitor. It consisted of an array of 35 one degree square color samples separated by a neutral grid (one degree width). The display simulated Munsell chips (50% reflectance) "illuminated" by standard white (D 65) or colored light (13 cd/m^2). The pattern was presented successively to the left and right eye, either in a test mode (colored illuminant) or matching mode (white illuminant). In the matching mode all chips were achromatic (80% reflectance) except for the one that was to be matched to the same chip presented in the test mode.

2.2: Simulation of illuminant changes

The "illuminants" that we simulated were mixtures of three lights, i.e. the lights emitted by the display phosphors (R, G, B). The color samples were characterized by their "reflectances" within the R, G and B wavebands. For example, a white test patch reflects approximately 10% B, 30% R and 60% G. In the standard condition, for which $R = G = B$, the white patch will indeed emit light with the same chromaticity as (standard) white light (D 65). However, when the ratio of $R : G : B$ is changed from unity to some other ratio, the white sample, which will still reflect 10, 30 and 60% of whatever amounts of R, G and B are used, will now appear to be illuminated with colored light.

The colored illuminants we used were created by shifting the $R/G/B$ ratio from its white setting in the direction of either more R, G, B or $R + G$ (= yellow). In this communication we shall only discuss results obtained with the green illuminant ($x = 0.279$, $y = 0.480$, $Y = 13$ cd/m^2).

2.3: Experimental conditions

The intervening space between the test samples, the grid, was either white (100% reflectance) or black (no reflectance). In the "dark grid" condition, the illumination changes were confined to the test samples. In addition, we studied the condition in which the illuminant change (from white to colored light) was applied only to the grid, that is, the light surrounding the samples: this was called the "induction" condition. In this way we could separate the effect due to local (sample) illumination from that produced by surround illumination. These effects combine in the third condition tested, the "constancy" condition in which the whole test pattern was illuminated.

3. Results and discussion

Only part of the results can be shown here, that is, the data (means of the three authors) obtained in the conditions employing the green illuminant. Fig. 1 shows the (physical) chromaticity shift of the test samples due to the change from white to green illuminant (open symbols), and also the matching samples obtained under the "constancy" condition. Note that the latter match the chromaticities of the samples under white rather than green illumination, thus indicating a fair degree of color constancy.

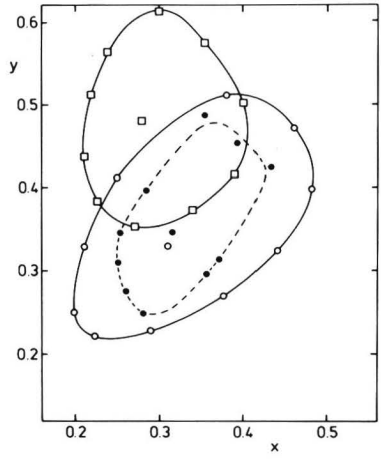

Fig. 1: Data from "constancy" condition. Open circles and squares: chromaticities of the color samples under white and green illumination, respectively. Closed circles: chromaticities of the matching samples. Coincidence of open and closed circles would indicate perfect color constancy

Fig. 2a shows the matches (again) of the results obtained for the "constancy" condition, together with those that apply to the "induction" and "dark grid" condition. Note that in the "dark grid" condition (no surround illumination) the matching samples are shifted towards the chromaticity of the green illuminant (compare with Fig. 1). Apparently, the compensatory action from the constancy mechanism is almost absent here. The opposite effect, a chromatic shift away from the illuminant, is observed in the "induction" condition. It is clear that this induced response is mainly responsible for the more complete illuminant discounting observed in the "constancy" condition. In other words chromatic induction is functional in preserving color constancy, but can show up as an artefact when inappropriatly triggered by just a surround change, as in the "induction" condition.

If chromatic induction is actually a (misdirected) attempt to obtain color constancy, it should be possible to describe it in that context. Color constancy models usually incorporate a so-called VON KRIES tranformation [3]. One of the best known models based on that principle is LAND and MCCANN's Retinex model. We used one of its most recent versions [4] to describe the results shown in Fig. 2a. As can be seen in Fig. 2b, the predictions do not, as yet, exactly reproduce the data, but they certainly support an unitary explanation of chromatic induction and color constancy.

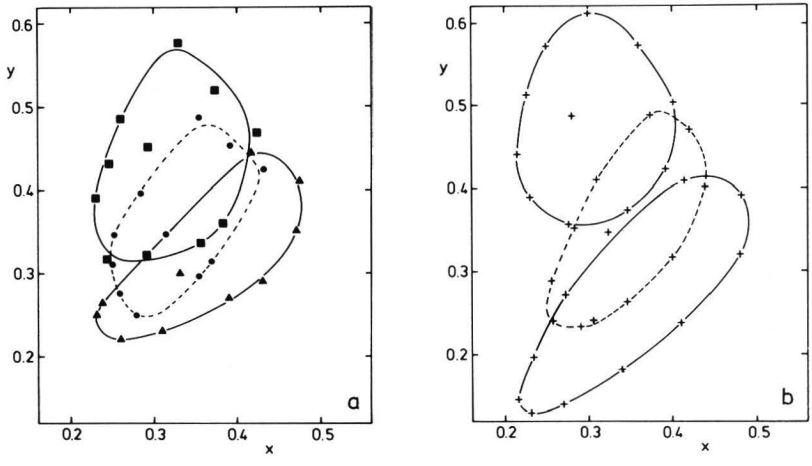

Fig. 2a: Chromaticities of matching stimuli for the conditions "dark grid" (squares), "constancy" (circles), and "induction" (triangles)
Fig. 2b: Predictions of the data shown in Fig. 2a on the basis of a VON KRIES-type color transformation (Retinex algorithm)

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Authors' address:
Dr. Jan Walraven
TNO Institute for Perception
Kampweg 5
NL-3769 DE Soesterberg
T. L. Benzschawel, B. E. Rogowitz
IBM T. J. Watson Research Center, P.O. Box 218
Yorktown Heights
New York 10598, USA

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John J. McCann*, CAMBRIDGE (Mass.):

Local/Global Mechanisms for Color Constancy

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This paper attempts to identify the signature of color constancy mechanisms from experimental measures of departures from "perfect" color constancy. Color matching experiments provide data consistent with nearly global normalization of independent long-, middle-, and short-wave mechanisms with corrections for absolute intensity. The evidence for this conclusion is the very high correlation between quantitative computer model predictions and quantitative color-matching experiments for a very large variety of images.

In dieser Arbeit wird versucht, die Merkmale des Farbenkonstanz-Vorgangs mittels experimenteller Messungen der Abweichung von der „perfekten" Farbenkonstanz herauszufinden. Farbvergleichsversuche liefern Werte, die in nahezu allgemeingültigem Grade der lang-, mittel- und kurwelligen Mechanismen bei Korrektur der absoluten Helligkeiten übereinstimmen. Die Berechtigung zu dieser Schlußfolgerung leitet sich aus der hohen Korrelation zwischen den Computer-Modell-Vorhersagen und den Farbvergleichsversuchen für eine sehr große Mannigfaltigkeit der Bildmuster her.

Dans cet article, nous tentons d'identifier les caractéristiques du mécanisme de la constance des couleurs en utilisant des mesures expérimentales de déviations par rapport à la constance "parfaite". Des expériences de comparaison de couleurs ont produit des résultats en accord avec une normalisation presque globale des mécanismes indépendants d'ondes longues, moyennes et courtes accompagnée d'une correction des intensités absolues. Cette conclusion est justifiée par la forte corrélation entre les prédictions de l'ordinateur et les expériences quantifiées de comparaison de couleurs faites sur une très grande variété d'images.

1. Introduction

Color constancy experiments show that very large spectral changes in illumination cause only small changes in the appearance of objects. There is universal agreement that the magnitude of color-constancy corrections is very large. There is universal agreement that the constancy is never perfect. When one makes a substantial global change in the illuminant, one finds that the appearance of the object is nearly constant, but never absolutely constant [1–6]. One computational modeling approach to color constancy assumes that the constancy mechanism embodies a global correction. A second computational approach is that color con-

* *Polaroid Corporation, Cambridge, Mass.*

stancy is a local calculation [7; 8]. Many investigators use the discrepancies between observed constancy and perfect constancy to identify the underlying mechanisms that account for color constancy. Since objects have nearly constant appearance, then the signature of the underlying mechanism has to be teased out from small departures from "perfect constancy". Furthermore, constancy experiments have multiple parameters that can affect experimental results. For example, when one changes the amount of the long-wave component of the illuminant, one changes both the relative amounts of long-, middle-, and short-wave illuminants, and the absolute amount of the long-wave illuminant. Both relative and absolute intensity changes have small, characteristic effects on the appearance of objects [5]. In evaluating mechanisms for color constancy one needs to consider the local, the global, the spectral sensitivity, and the absolute sensitivity properties of any hypothetical mechanism.

2. Color matching experiments

Work in our laboratory has emphasized the quantitative measurements of departures from "perfect" color constancy. The data show the need for both a strong global component and local interactions to model the results of color constancy experiments. The experimental procedure used for all of the data presented here was first described in McCann, McKee, and Taylor [5]. The idea was that the *Munsell Book of Color* in constant illumination and with a constant surround is a "standard catalog" of color sensations. The observer was asked to find a match to the test object in the standard catalog. In all the experiments desbribed in this paper, we asked the observer to use one eye to study the test images, and the other eye to study the catalog. All matches were made sequentially. The object of these procedures was to let each eye reach its own independent state of dark adaptation and to prevent the image content of either the test or the catalog image from having an effect upon the other.

The McCann, McKee and Taylor (MMT) experiment measured the color appearance of 18 areas in a single Mondrian, in each of five different proportions of long-, middle-, and short-wave illuminants. Color appearance showed very poor correlation with the light absorbed by the long-, middle-, and short-wave cones. Color appearance showed very good correlation with *Scaled Integrated Reflectance* of the Mondrian papers. *Integrated Energy* is the integral of the spectral distribution of the light coming to the eye from a particular paper and the spectral sensitivity function of one of the cone pigments. In other words, *Integrated Energy* is the quantum catch of a cone mechanism. *Integrated Reflectance* is the ratio of the *Integrated Energy* coming from a particular paper, divided by the *Integrated Energy* coming from the highest reflectance paper in that waveband in the Mondrian. *Scaled Integrated Reflectance* is *Integrated*

Reflectance shaped by an equal-lightness function such as GLASSER et al. [9]. In each case, these Energies, Reflectance and Integrated Reflectance are calculated independently for each cone type. The experimental data showed strong correlation between Scaled Integrated Reflectance and observer matches [5]. This result can be considered support for three major color constancy hypotheses:

1. Color constancy involves a global correction.
2. Gobal correction is made independently for each of the long-, middle-, and short-wave mechanisms.
3. Global correction is made with respect to the maximum in each waveband, not the average of the image.

In many ways these assumptions are very similar to those of the ideas of VON KRIES [10] with one important difference. Here we are arguing that the computational mechanism is the independent normalization of the long-, middle-, and short-wave mechanisms by the maximum in each cone mechanism. This idea follows directly from the fact that the colors chosen to match in color constancy show a very high correlation with reflectance measured with cone sensitivity response. These scaled integrated reflectances in MCCANN, MCKEE and TAYLOR were computed using maxima, not averages.

3. Other parameters affecting color-constancy experiments

Three parameters have measurable effects on color appearance data. They are: spatial effects, absolute intensity effects, and spectral effects due to integrating under cone sensitivity functions. These parameters contribute to the lack of "perfect" constancy and may have variable importance depending on the particular experiment, but nevertheless must be evaluated in a quantitative model of color constancy.

3.1: Spatial effects

Spatial effects represent the most interesting part of the color constancy puzzle. Human vision exhibits properties that are fundamentally different from those of image reproduction technologies, such as photography and electronic imaging. In image reproduction technologies the output of a point in the image depends on the different color records at that point in the image. In vision, the color of a point is a function of the color response at that point, the response by the local environment, and the response everywhere in the image.

An extension of the MCCANN, MCKEE and TAYLOR experiment provides an interesting insight into the mechanisms of color-constancy.

There are many alternatives to normalizing the flux in an image by the maximum in each waveband. The visual system's color-constancy mechanism could normalize to the global average of all the light in the field of view, the local average of an image segment or any number of alternative normalization mechanisms. The fact that normalization by the maximum in each wave band successfully predicts color in Mondrians does not mean that an alternative color constancy computational mechanism cannot predict the same results. Individual experiments are necessary to test the viability of alternative color constancy mechanisms.

We began by experimenting with the average of all the light in the field of view. In the following experiments we further tested the hypothesis that the visual system's color-constancy mechanism normalizes the scene to the global average of all the light in the field of view [11]. We made a new Mondrian in which all dimensions for individual papers were half the original McCann, McKee and Taylor Mondrian dimensions. We added a very large, uniform surround around the Mondrian to make the total display the same size as the MMT Mondrian. We started with a gray surround. We measured the flux from a gray paper and calculated the integrated flux from the entire display. We repeated the MMT experiment and changed the intensities of the three narrow-band illuminants such that a red paper sent to the eye the same flux that previously came from the gray paper. We measured the integrated change in flux from the entire display. The data showed an increase in middle- and short-wave light, and a decrease in long-wave light. In the next part of the experiment we used a second Mondrian with a red surround. The surround paper's spectrum was carefully chosen to exactly offset the illuminant change, i. e. to preserve constant average flux over the whole display. We repeated the three other MMT experiments by changing the illuminant intensities and choosing a surround paper that exactly compensated the illuminant change. If the color constancy mechanism uses the average of the entire image to normalize the entire image, then this experiment should produce dramatic results. Here all five Mondrians have the same average flux and the particular patches have the same triplets of fluxes. The five different papers should look identical because the stimuli at a point are identical and the integrated-average values are identical. If the color constancy mechanism uses normalization by the maxima, this experiment should produce the same results reported in MMT. The five different papers should not be identical, but should look different as they did in MMT since the experiment did not alter the maxima.

The color matching data showed considerable indifference to changes in the average reflectance. In other words, observers reported matches very similar to those in the original MMT experiment. This supports the normalization by the maxima.

In a second experiment we changed the local-average flux as much as we could with papers. In the previous experiment we compensated for substantial changes in illumination with changes in the surround paper spectra. These papers had to be very saturated to compensate for large illumination changes. The papers were N6.25/, Color-Aid RVR Hue, 5.0G 6.0/8, 5.0 Y8/14, Color-Aid BT2. How influential are the most saturated papers we can find in changing the appearance of the 18 papers in the Mondrian? We made new targets that resemble exploded-parts diagrams. These Mondrians were exactly the same in size, and global average properties as in the previous experiment. However instead of the entire Mondrian being totally enclosed within a surround, now each and every patch of Mondrian was embedded within a large local area of surround. If the color-constancy mechanism uses the local-average of each image segment to normalize the image, then the surrounds in this experiment should change the appearence of individual papers quite substantially. Here four Mondrians have maximal departures of local-average from gray. The five different Mondrians should look very different from each other, because the local-average values are different. If the color-constancy mechanism uses normalization by the maximum in each wave band this experiment should produce the same results reported in MMT. The five different Mondrians should look the same. This experiment changed the local-average values, but did not alter the maximum in each waveband. Fig. 1 is a photograph of all five targets.

We see small changes in appearance, despite the fact that we changed the local average as much as we could with papers. The average change is of the order one to two chips in the Munsell book. Local calculations alone cannot account for the magnitude of the color constancy corrections because color appearance is insensitive to changes in local surround. Why is it that changes in local surround had such a small effect on these Mondrian observations? All of us have seen simultaneous contrast demonstrations in which change of a background has produced large changes in the sensation of a center patch. The most dramatic departures from constancy are due to global normalization. GELB's classical experiment is the most dramatic I know [12]. Here a black piece of paper is the only object in the field of view, by itself it looks a dim white, but unquestionably white. When a white paper is put beside the black paper then white looks white and black looks black. This is an example of a global normalization process – one that changes a single object from white to black. Another familiar spatial experiment gives us important information about the limits of global normalization. Consider the gray-square-on-white and gray-square-on-black demonstration of simultaneous contrast. If global normalization of the entire field of view were complete, we would expect that observers would report the two gray squares with identical reflectances would have the identical appearance. If local mecha-

nisms were the only consideration, then the gray square in the black surround should mimic the results found in the GELB experiment, and should appear a white, since it is the maximum intensity in the local area. Observer results give important information about the relative importance of global and local interactions. The gray square in the black surround is one lightness unit out of nine lighter than the same gray in the white surround. If local spatial calculations were the only consideration, the gray in black should appear a 9.0. If global spatial considerations were the only consideration, the gray in black should appear a 5.0. The observer matched the gray in black to a 6.0. In other words, the spatial normalization mechanism is an imperfect global mechanism. Alternatively, it is a local mechanism that is significantly influenced by information from the entire image. The conclusion one draws from both sets of experiments is that the most powerful examples of local influence of a surround are found in situations in which the extent of the surround is large enough to influence the global normalizing mechanisms. The best examples of simultaneous contrast, such as GELB, involve changes in the maxima in the image. Experiments that change only the properties of local portions of the image produce only small changes in an observer's match – only one or two chips in the Munsell Book.

3.2: Overall brightness effects

MCCANN, MCKEE and TAYLOR showed a small but consistent shift in the color matches due to changes in overall illumination. Their data showed that a change in intensity by a factor of 4 caused a change in lightness (on a scale of 0 to 10) of 0.8 units for long and middle-wave lights and 0.6 for short-wave light. As well, numerous other experiments show a corresponding shift in lightness as a function of overall illumination [13; 14]. Compared to the color shifts created by color constancy mechanisms, those created by overall brightness are small. Nevertheless, compared to the imperfections in color constancy they can be significant.

3.3: Spectral integration effects

MMT data show that the Integrated Reflectance of a particular paper changes with changes in spectral energy in the illuminant. Changes in the relative amounts of three narrow-band illuminants can cause changes in the Integrated Reflectance of papers because of the overlap in cone sensitivity functions. Obviously, the paper's reflectance does not change. Nevertheless, the ratio of light integrated by a cone intensity function for two papers with very different reflectances can be changed by large changes in the illuminant. In five illuminants the 5R5/12 paper had the following triplets (L, M, S) of scaled integrated reflectance: 6.5, 3.6, 3.6; 4.3, 3.1, 3.7; 6.9, 4.1, 3.7; 7.1, 4.3, 3.6; 5.9, 3.5, 3.7. The long-wave scaled

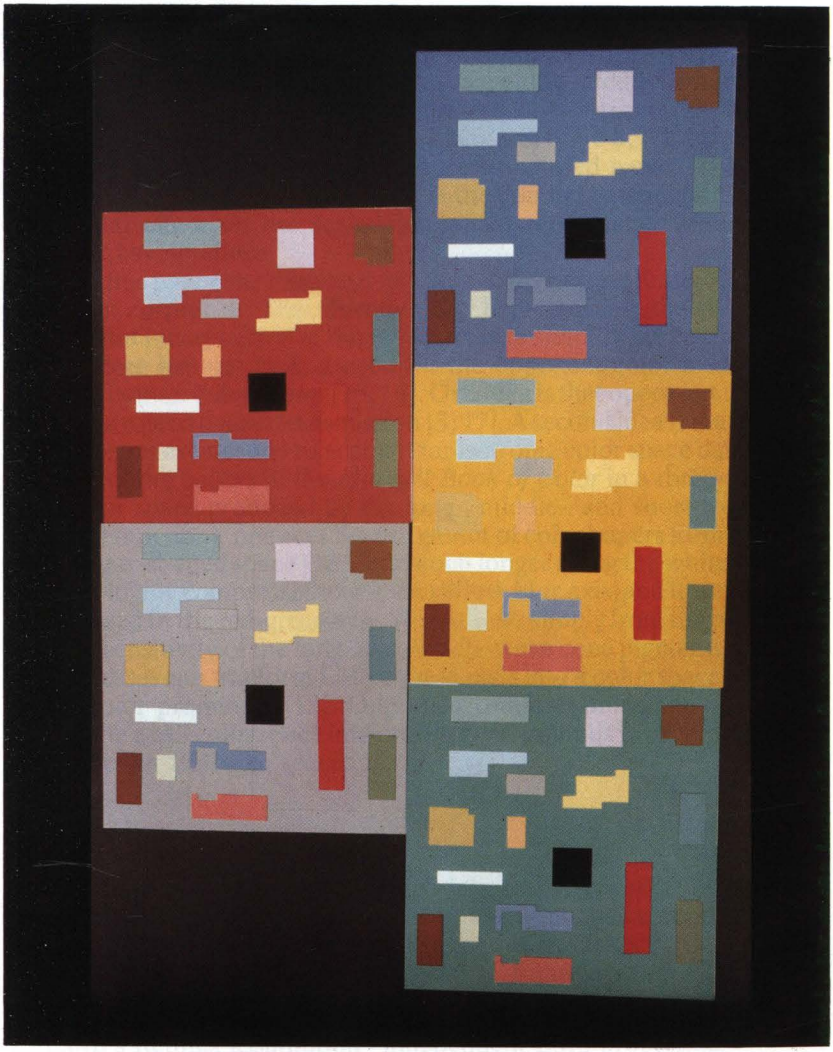

Fig. 1: The five Mondrians changed the local-average flux as much as possible with papers. Four Mondrians have maximal departures of local-average from gray. If the color-constancy mechanism uses a global normalization by the maximum in each wave band, then each of the 18 Mondrian papers in the five different Mondrians should look the same as its corresponding paper. This experiment changed the local-average values, but did not alter the maximum in each waveband.

integrated reflectances varied from 6.9 to 4.3; the middle-wave varied from 4.3 to 3.1; the short-wave varied from 3.7 to 3.6. This can be compared with the very small changes in scaled integrated reflectance with neutral gray papers. In five illuminants N6.75 had triplets (L, M, S) of scaled integrated reflectances: 6.7, 6.7, 6.6; 6.8, 6.7, 6.8; 6.7, 6.7, 6.8; 6.7, 6.7, 6.8; 6.7, 6.7, 6.8. With highly saturated colored papers, changes in illumination have substantial effect on the quantal catches and hence a substantial effect on the scaled integrated reflectance. With neutral papers it has no effect.

So far this paper has restricted its scope to the narrow limits of explaining color constancy. The objective has been to limit the number of mechanism incorporated in the model so as to simplify the computation. So far there has not been a need for the opponent-color mechanisms found in human color vision [15; 16]. One idea is that opponent mechanism play a role in neural transmission [5; 17]. A second idea is that opponent processes are needed to account for isotropic color space data. If one plots all of the papers in the *Munsell Book of Color* in a three-dimensional color space produced by the long-, middle-, and short-wave cone response functions, one sees the full gamut of color papers form an elongated, cigar-shaped space [18]. It is much longer along the white to black axis; it is highly compressed along the yellow-blue axis, and it is extremely compressed in the red-green axis. This follows simply from the overlap in spectral sensitivity of the long- and middle-wave cone pigments. Opponent processes can tranform LMS cone signals into a color space with isotropic color properties [19]. Opponent tranformations can effectively stretch the LMS color space into one that corresponds to experimentally-defined color isotropic spaces.

4. Conclusion

The color-constancy experimental data are very well fit by a simple global normalization of long-, middle-, and short-wave cone response functions combined with appropriate quantitative corrections for spatial, absolute intensity, and spectral effects. In summary, our approach to modeling color constancy incorporates a number of assumptions:

1. LAND's Retinex assumption – independent LMS processing.
2. GELB's global normalization combined with non-global propagation that accounts for local spatial effects.
3. Secondary dependence on overall intensity.
4. Variation of scaled Integrated Reflectance with changes in the spectra of the illumination.
5. Importance of opponent processes become important for isotropic color space and neural transmission properties.

The test of successful color-constancy models is the range of different experimental images – complex and simple – for which it can quantitatively predict color matches [20].

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Author's address:
J. J. McCann
161 Claflin Street
Belmont, MA. 02178
USA

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Eberhart Zrenner*, MÜNCHEN:

Are there Separate Channels for Luminance and Color?

DK 612.843.36

The paper points out that the shape of the daylight luminosity function (V_λ-function) depends, to a great extent, on stimulus variables and on the strength of adaptation. Consequently this function is not well suited to describe brightness sensation in the human visual system. Especially temporal variables such as flicker alter the processing in color-opponent neurons which contribute to the daylight luminosity function.

Die Arbeit legt dar, daß der Verlauf der Tageslichtempfindlichkeitsfunktion (V_λ- Funktion) sehr stark von Reizvariablen und Adaptationszustand abhängt. Folglich ist diese Funktion nicht gut geeignet, die Helligkeitsempfindung im menschlichen visuellen System zu beschreiben. Speziell die zeitlichen Variablen, insbesondere Flimmerreize, verändern die Verarbeitung der Farbopponenz-Neurone, die an der Tageslichtfunktion beteiligt sind.

Ici on montre que la forme de la fonction V_λ photopique dépend extrêmement des variables d'excitation et de l'état de l'adaptation. Pour cela cette fonction n'est pas propre à la description de la sensation lumineuse dans le système visuel de l'homme. Ce sont particulièrement les variables temporelles, notamment les excitations du papillotement, qui changent le processus dans les neurones des couleurs opposées participant à la fonction photopique.

1. Introduction

The last two decades of neurophysiology of the visual system are marked by the discovery of distinct classes of cell types in the retina and geniculate [7; 3; 2]. These cell types differ in their spectral, spatial and temporal properties. There have been numerous speculations to assign special tasks to certain cell groups for coding particular psychophysical properties. Although some of these hypotheses look very appealing, none of them could be proven yet.

Having assembled a group of experts from all visual disciplines and representing different "schools", we wanted to take the opportunity of

* *Laboratorien des Max-Planck-Instituts für Physiologische und Klinische Forschung in der Augenklinik der Universtität München*

hearing their opinion on the existence of a presently widely discussed luminance channel. This question was extensively discussed in a mini-debate and in a subsequent general discussion, following the papers of RONCHI, LEE, STROMEYER, SMITH and EJIMA (published in this volume). As chairman of the session, I was asked to provide a summary of the outcome of the discussions. A preliminary draft of this summary was handed out to all participants during the meeting. The subsequently received additional comments led to the present form of the following statements.

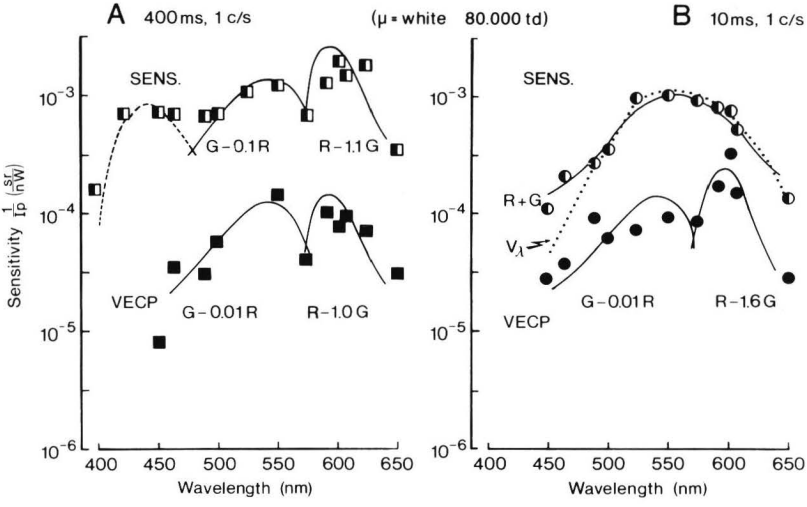

Fig. 1: Spectral sensitivity function obtained by determination of the subjective threshold sensation for single flashes (left 1 c/s, 400 ms duration) and a flickering field (right 30 c/s, 33 ms duration) of 6° in diameter in presence of white background (20,000 td, 20° in diameter). Average values of four normal trichromatic observers (mean ± S.D.). Dotted line represents the CIE V_λ function. Note that the increment threshold for single flashes follows a three-peaked function, where each peak is narrower than individual cone action spectra. Flickering stimuli reveal a function closer to the V_λ function. (From ZRENNER [8].)

2. Results

There is clear consensus that the photopic luminosity function V_λ is a rather robust function, indeed useful for standardization and determination of units of luminance, as an estimation of the effectiveness of light on the human visual system under certain photopic conditions. There is agreement that the luminance function can be described by an additive

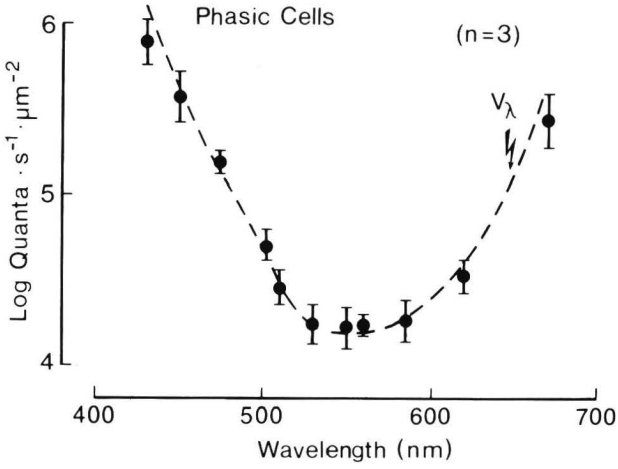

Fig. 2: Action spectra of three phasic ganglion cells of the magnocellular system; mean S.D. Photopic relative luminous efficiency function (V_λ) indicated by broken line most probably projecting to the magnocellular layer. (From ZRENNER [8].)

action of two or three spectrally different cone types. However, there is also strong evidence that under certain conditions subtractive interaction between cones alters the shape of the photopic luminosity function [6; 5]. An example of the influence of temporal parameters on the detection threshold of monochromatic light is shown in Fig. 1 (from ZRENNER, 1983).

Although a small population of neurons in the visual system closely follows the V_λ function (Fig. 2), there is a widely expressed, strong reluctance, if not opposition, to postulate a luminance "channel", where information about luminance is carried separately from other information. Although cells of the magnocellular layer of the primate geniculate (*M*-cells, phasic cells, Y-cells, Alpha-cells) follow the V_λ function and have a response minimum under heterochromatic flicker conditions (LEE et al., this volume), there is no physiological evidence for a unique pathway for luminance. Additionally, it was pointed out that a subset of cells that project to the parvocellular layer (*P*-cells, tonic cells, *X*-cells, Beta-cells) follows the V_λ function as well (Fig. 3). Moreover, there are very convincing psychophysical and physiological data that luminance is carried not independently from spatial and temporal information, as shown in Fig. 1. ZRENNER and GOURAS [9] and GOURAS and ZRENNER [4] have shown that individual colour-opponent ganglion cells can change their action

spectra from spectrally broadband luminance coders to spectrally double-peaked opponent cells, rendering the V_λ curve a special case, applicable only under certain conditions. There was clear agreement that the V_λ function fails to reliably describe the visual system's properties in "measuring" the physiologically and psychophysically effective radiance throughout the spectrum under conditions other than flicker photometry or minimal distinct border techniques (to name more common methods, see BOYNTON [1]).

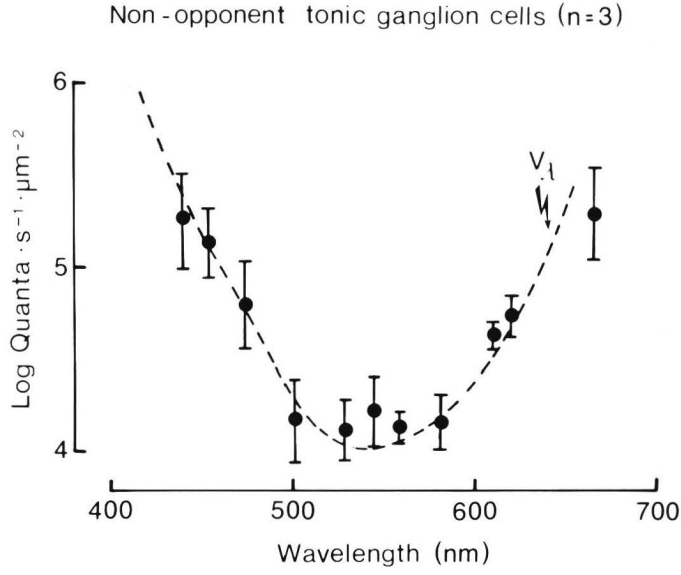

Fig. 3: Action spectra of three non-opponent tonic ganglion cells (mean and S.D.) of the parvocellular system. Photopic relative luminous efficiency function (V_λ) indicated by broken line. (From ZRENNER [8].)

3. Discussion

Luminance as a function of wavelength alone is a very restricted measure, usually not applicable in most situations of stimulation where temporal and/or spatial parameters are varied, especially when increment threshold techniques are involved. This common failure of the V_λ function to reliably describe the physiologically effective radiance under a wider range of conditions limits its use as a normative function, having a very limited resemblance to physiologically and psychophysically determined processes. There is no evidence that a single subset of neurophy-

siologically described cells can form a "luminance channel", nor is there evidence that any neuronal assembly can signal luminance independently of other parameters. Consequently the term "luminance channel" should be avoided.

There seems to be a strong need to reserve the term "luminance" to an historically grown technique of standardization and to develop physiologically more relevant and more widely applicable terms and units for the psychophysically effective radiance that leads to achromatic sensations, such as e.g. brightness, lightness, whiteness and blackness.

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Author's address:
Prof. Dr. E. Zrenner
Laboratorien des Max-Planck-Instituts
für Physiologische und Klinische Forschung
Mathildenstraße 8
D-8000 München 2

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Oscar Estévez*, AMSTERDAM:

The Florence Meeting on Color Vision Models**

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612.843.3

The Florence Symposium was wide in scope and mainly focused on problems of color vision. In all, thirty papers were given and followed by discussions from the sixty participants. For the purpose of this report, we shall follow the subjects handled in Florence in chronological order of the symposium and by the questions handed at each session.

The opening paper was given by J. D. MOLLON, from Cambridge, on general questions concerning vision models and modelling. After defining a 'model' formally as either a) and analogy, b) a scheme or c) a formula, MOLLON proceeded to sub-divide the visual model specifications into five 'stages' approximately corresponding to different levels of physical or physiological processes. Perhaps the most significant contribution of MOLLON was his clarification of the concept of 'opponency': Retinal opponency, that is to say the opponency that occurs at or near receptor level, is not the same as 'perception' opponency or HERING-opponency, he stated, but rather a result of the optimalization of signal coding early in the system. This same concept received later strong support in the paper of BUCHSBAUM, when handling the question "transformation of spatial and temporal information". Another important concept in MOLLON's paper was that the L/M-cone system represents a relatively 'new' addition to vision: it is a system that evolved from one and the same type of receptors after these developed two different pigments, but maintained their original role, namely that of subserving form and contrast vision. The S-cone system represents, in MOLLON's view, an older system

* *Dept. of Medical Informatics, University of Amsterdam.*

** This report originally was written for the use of the CIE. It is printed here instead of the summary of the Florence Symposium Dr. ESTÉVEZ gave at the closing session. This summary was highly appreciated by the participants. Unfortunately, Dr. ESTÉVEZ had no manuscript of his summary, so he could not submit it to the redaction of these Proceedings. But on advice of Prof. KAISER and Prof. TERSTIEGE he was kind enough to let us his report for reproduction – for the benefit of the participants of the Symposium and of the readers of these Proceedings. The Editor is very indebted to Dr. ESTÉVEZ for his kind cooperation.

properly encoding chromaticity, albeit a primitive form of it as it concerns only differences in colors that arise from different proportions of short vs. long-wavelength light.

The first question *"Cones: what are the factors that determine cone action spectra? and How do the details of cone action spectra affect models of cone vision?"* was tackled by J. Vos. His most substantial contribution is very relevant. He proposed a new set of fundamentals of human color vision – jokingly called by the audience *"the Dutch fundamentals"* – that obtain by using ESTÉVEZ approach as exposed in his PhD Thesis and several key concepts from the original VOS and WALRAVEN papers. The most significant gain of the new set is that it appears to give a much better fit to known dichromatic data while also providing a much improved fit to the luminance function. This is an important new addition because it is an aspect that was left out in ESTÉVEZ's original treatment. VOS's approach appears to circumvent ESTÉVEZ's objections and it can be an important step forward in the attempt to achieve a more satisfactory integration of luminance with color standards.

J. POKORNY's and C. CICERONE's papers in the next session *"How are models affected by he numerosities and spatial distributions of different cone classes"* took opposite points of view on the question of 'unique yellow': POKORNY concluded that there is no correlation between numerosities and 'unique yellow' – when numerosities have been estimated by heterochromatic flicker photometry methods, while CICERONE finds that numerosities do predict unique yellow. In a note prepared for this paper she wrote: "We estimated the relative numbers of *L* to *M* cones in the following way. Probability detection functions were measured with a tiny (1′) and brief (50 ms) red (or green) target on a green (or red) background (3°). The functions describing probalility detection were evaluated using a psychometric model which relates the steepness of the function to the number of cones detecting the flash." From these experiments CICERONE and co-workers estimated ratios of L/M-cones to lie around 2 to 1. She goes on to say: "We demonstrated that measurements of heterochromatic flicker photometry and the variations among individuals in unique yellows can be accounted for by our estimate of the relative numbers of L and M cones as weighing factors on their contributions."

The 3rd session was on early transformations of cone signals and the concept of opponent channels. H. YAGUCHI, in the first paper, showed that a linear combination of a subject's color matching functions set can fit well his own red-green opponent functions but this is not the case for the blue-yellow set: this can't be linearly fitted by combinations of color-matching functions. Important in his work is that he measured both 'maximum saturation' and 'MAXWELL-matches' type of c.m.f. and both appear to yield a satisfactory fit to opponent functions. R. DEVALOIS

paper was more general in scope: he made a critical survey of concepts of opponency and the possible reasons why it might have evolved. Again, his considerations agreed with those of MOLLON and BUCHSBAUM: opponency is an answer of the organism evolution to efficiently encode color information. However, he stated, the real controversy is whether there is nothing but opponent coded cells (thus no luminance information is separately coded). He proposed that magnocellular layers of the lateral geniculate nucleus (LGN) are not concerned with luminance, but with movement – they also have a different projection to the cortex. The continuation of question 3 involved more technical and physiological problems of retinal encoding by H. SPERLING, A. KANEKO and A. REEVES. The most significant results argued by these workers is the overwhelming evidence for very early opponency processing in the retina: as early as the receptor's response – as found by SPERLING on the basis of A-wave measurements in the ERG – and/or via horizontal cells back to the cones, as argued by KANEKO. K. DEVALOIS argued, in the session around question 4: *"To what extent is color information analyzed independently of spatial and temporal information?"*, that indeed no psychophysical evidence points to a separation of the analysis of these percepts, but nevertheless there appear to be important interactions in the processing pathways.

Question 5: *"Is there a luminance channel"* is perhaps the single more relevant subject for the CIE-Workshop. In all, five speakers formally and many of the audience, participated in the debates. The speakers were L. RONCHI, B. LEE and C. STROMEYER during the first session and V. SMITH and Y. EJIMA during the second. The best account of the results are those of the chairman E. ZRENNER, who wrote: "The photopic luminosity function V_λ is a rather robust function indeed useful for standardization as an estimate of the efficiency of light on the human visual system. There appears to be agreement that this function can be modelled by an additive action of two or three cone types. However evidence has been given that at some levels of adaptation subtractive cone interactions can also take place. Although a small population of neurons follow the V_λ function, there was strong reluctance – if not opposition – to postulate a 'luminance channel' as carrier of separate information. This despite the fact (already pointed out by R. DEVALOIS) that magnocellular cells follow the V_λ response under conditions of heterochromatic flicker stimulation. However, there is no convincing evidence that these cells form an unique pathway for luminance. Moreover, there is overwhelming psychophysical and physiological evidence that luminance is not independently carried from other forms of information, e.g. spatial and temporal information." He closed his remarks with the statement: "There seems to be a strong need to reserve the term 'luminance' for the historically established special application represented by the CIE standard and to find more

relevant terms applicable to the more specifically physiological and psychological processes that are studied by vision researchers."

The next sessions were dedicated to a cluster of problems around questions 3, 4, 5 and 6: *"Transformation of spatial and temporal information."* G. BUCHSBAUM and G. GOURAS participated in the first session and M. ATIKA, Y. NAYATANI, D. HOOD, R. HUNT and H. SCHEIBNER participated in the second. BUCHSBAUM's paper is significant because it shows that, as often argued at the meeting, opponency can be formally demonstrated to obtain when one sets constraints in the transformation of information from receptors to the upper levels. In particular, a simple set obtains when one searches for the most efficient compressing scheme such that the available 'dynamic' range is optimally used. The functions that BUCHSBAUM arrives at by mathematical methods greatly resemble those measured using psychophysical methods GOURAS paper, like R. DEVALOIS' one, was more general in scope and provided a brilliant survey of the main results and current concepts in cell physiology, as relates to color vision. He examined the transformations, the observed and deduced, that occur at different neural levels and stages: Retina, Lateral Geniculate and Cortex.

In the second part of the session, AKITA presented his results on opponency using the cancellation method. He agreed that red/green opponency can be thought of as a linear transformation while yellow/blue opponency cannot. HOOD's paper was intriguing in that he proposed that observed non-linearities are dynamic in nature, not static or pre-set, and thus depend in every case on the exact nature of the stimulus configuration being used. The most significant papers for CIE related work were those of NAYATANI, HUNT and SCHEIBNER. Each of them presented a very detailed model of color transformation with NAYATANI's being the most 'practically' oriented (but still firmly based on psychophysics), HUNT's more guided by physiological and psychophysical findings and SCHEIBNER's more theoretical and mathematical in nature. All these models are well represented in the published literature, as these workers have evolved their models after many years of study and their work is widely known. All three gave the audience an account of their newest developments and ideas. Notably, HUNT's and NAYATANI's model appear to be very similar in concept – although different in actual realization – and they are converging more and more. SCHEIBNER's latest work is important because he has shown a clear cut formal relation between 'opponent' and 'fundamental' color spaces such that these are derivable from dichromatic color spaces. During the session on *"How do rods interact with cone signals"* P. TREZONA presented her more recent work on the tetrachromatic color matching system she has developed. Most signifi-

cant is her discovery of the changes in the stability of color matches under varying conditions of adaptation.

Question 8: *"What are observers doing when making a) color matches, b) color discriminations and c) heterochromatic brightness matches"* was handled by F. VIENOT, A. VALBERG and M. IKEDA in that order. VIENOT argued persuasively that subjects do not, as is usually believed, make quantum matches, but rather make assessments of cone excitation ratios when making color matches. This is a very important distinction and one that must be taken into account for both theoretical and practical colorimetry. VALBERG shoned a very elegant transformation to a 'MUNSELL' color space that follows in a very straightforward way the response characteristics of chromatically encoded cells. The agreement between the derived - from physiology - and the uniform color space was very good. IKEDA showed that brightness matches can be transformed to - or fitted by - a set of human color fundamentals (those of SMITH and POKORNY) by using logarithmic combinations. The basic concept is one of 'alternation': subjects are using or attending to either one or another 'channel' combining L, M and S cone outputs. This concept elaborates on one originally proposed by ESTÉVEZ at an O.S.A. meeting and later presented during a visit to Japan in 1980 at several lectures. However, in the ESTÉVEZ's original alternation concept it was the Long or Medium cone signals themselves that were alternating, while IKEDA has clearly shown that this cannot be the case: the functions obtained can only be fitted using no-linear cone combinations.

Questions 9 and 10 were *"What is the nature of the neural processes that correspond to unique hues?"* and *"How is color constancy to be explained"*. Both themes entangled nicely during the two sessions. T. INDOW and S. SHEVELL participated in the first and J. WALRAVEN, J. MCCANN and E. ZRENNER participated in the second. INDOW's most significant statement was that unique hues need not be represented or considered as opposite poles of orthogonal axes; SHEVELL presented some very interesting results on hue or chromatic induction, and HUNT asked "What is unique 'blue' or 'yellow'?". Both WALRAVEN and MCCANN amply discussed the problems of estimating the physical spectral distributions from the cone outputs. In particular WALRAVEN posed whether the Retinex concept is a 'VON KRIES' machine and nothing else. ZRENNER argued that there may be a physiological basis for different psychological percepts in the 'zero-detector' cell responses, although this bought about a discussion from participants about who, then, would look at the 'zero-detectors'.

In general the Symposium results were very positive, and this was again highlighted at the closing paper by ESTÉVEZ. Specially important is the general finding that to understand color vision one must include

form, movement, brightness, etc.... to bear upon the results. Color Vision must not, and indeed cannot, be studied in isolation but only as an integral part of the Visual Apparatus. Furthermore, concepts that appear to be simple at first, such as 'luminance', seem to have been grossly oversimplified by workers in the past: it now seems clear that no 'luminance channel', or indeed any other 'channel' is at work in the visual system, but rather a coordinated and highly elaborated set of transformations is taking place simultaneously in a very dynamical interaction with each other.

Author's address:
Dr. O. Estévez
Dept. of Medical Informatics
Faculty of Medicine
University of Amsterdam
Meibergdreef 15
NL-1105 AZ Amsterdam

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INTERNATIONL COLOR MEETINGS 1989-1991

[In brackets Addresses for more informatio]

November 28 - December 1, 1989, in Williamsburg, VA (USA):

Color Discrimination Psychophysics Conference
[Inter-Society Color Council, c/o J. Grady, 7187 White Pine Drive, Birmingham MI 48210]

March 26-28, 1990, in Tokyo, Japan:

Regional Symposium of the Intern. Research Group on Color Vision Deficiencies
[Medical View Co. Ltd., 1-21, Yotsuya, Shinjuku-ku, Tokyo, 160, Jap.]

September 3-5, 1990, in Berlin (West), Germany:

AIC Interim Symposium „Instrumentation for Color Measurement"
[Deutsche farbwissenschaftliche Gesellschaft, Unter den Eichen 87 (BAM), D-1000 Berlin 45]

September 16-22, 1990, in Nice (Nizza), France:

20th Congress FATIPEC "Progress achieved in the Coating Industry"
[AFTPV; 5, rue Etex, F-75018 Paris]

June 26-28, 1991, in Sidney, Australia:

AIC Interim Symposium "Light and Color"
[The Color Society of Australia, P.O. Box 63, Concord West, NSW, 2138, Australia]

June 29-30*, 1991, in Sidney, Australia:

Symposium of the Intern. Research Group on Color Vision Deficiencies
[IRGCVD General Secretary, Prof. Dr. J. D. Moreland, University of Keele, Keele, Staffs. ST5 5BG (U.K.)]

July 2-12, 1991, in Melbourne, Australia:

22nd CIE Congress
[CIE Central Bureau, Dr. J. Schanda, Kegelgasse 27, A-1030 Wien]

(Note: The next regular AIC Congress will be held 1993 in Budapest, Hungary.

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* This date is not yet quite certain; may be the meeting will be held immediately *before* the AIC Interim Symposium.

Content

of the Proceedings of the Florence Symposium

Commercial Note

Re: Spectral cone response functions

It is well known among physiologists, ophthalmologists, and colorimetrists that a world-wide re-determination of the cone-sensitivity functions is desirable. Yet some scientists have undertaken careful research work in this direction, but it seems necessary that the knowledge of these functions should be based on the greatest possible number of subjects, in order to get a reliable average over the total color-normal population. Last not least this is desirable for the application of these functions in industry.

Doubtless the well-known international standard functions of the CIE 1931 (2°) and 1964 (10°) have been proved successful, but in unusual cases (e.g. strange spectral distribution of the stimulus), amendments are felt necessary. Besides this technical aspect, an easy way to examine the diverse kinds of color deficiencies by measuring the spectral cone responses of the patients would be welcome. – By the way, such investigations would be very useful in the pharmaceutical industry as a mean to test new products on secondary effects on color vision.

The main difficulty which made interested scientists abstain from these investigations, was the lack of a suitable simple (and low-priced) instrument. Those used in the classical measurements were complicated and expensive, if at all available. To meet this difficulty, a comparatively simple apparatus has been developed in the meantime[1].

This new device works on the classical basis of spectral color matches. It is operating with a set of interference filters with very narrow spectral transmission bands (5 – 7 nm), it has electronic reading, and its bipartite viewing field can be varied between 2 and 10 degrees. By its optical construction it is warranted that all errors due to internal selective absorptions in the optical pathway and the influence of the spectral power distribution of the light source are eliminated.

After a long period of retention the production of the new instrument (called „*Spectrotest*") is now tackled. For more information please contact

OCULUS GmbH, Dutenhofen, D-6330 Wetzlar 17

or PD Dr. med. H. KRASTEL, Universitäts-Augenklinik,
Im Neuenheimer Feld 400, D-6900 Heidelberg

or Prof. Dr.-Ing. M. RICHTER,
Unter den Eichen 87, D-1000 Berlin 45.

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[1] RICHTER, M., Ein neues Gerät zur Bestimmung der Spektralwert-Funktionen. Farbe **28** (1980), pp. 1–28

Papers which will appear in the forthcoming volume of the journal DIE FARBE

ARTIGAS, J. M., A. PEREZ and A. FELIPE: Color variation in textile samples when the illuminant changes

ARTIGAS, J. M., A. PEREZ and A. FELIPE: On the importance of the colour space used in the studies about colour constancy

BRIDGEMAN, T.: Two-flux formulae for the total and directional reflectance of a semi-infinite diffuser

BRUCKWILDER, R., and H. SCHEIBNER: Bestimmung der protanopischen Spektralwerte bei maximaler und minimaler Sättigung

BUERA, M. D. P., and S. L. RESNIK: Colorimetric measurements in a turbid medium: hydrolyzed concentrated cheese whey

DONG, T., and W. JIN: A chronicle of the discoveries of elementary color science in ancient Chinese literature

DÖRING, G., Rezeptierung von tiefmatten Farbmustern mit für Hochglanzlack bestimmten optischen Konstanten

EMBRECHTS, J. J.: The colour rendering index of mixed high-pressure sodium and mercury lightings

FRY, G. A.: Analyzing color mixture data at the blue end of the spectrum

HEROLD, R.: Forderungen an Farbmeßgeräte für die Druckfarbenindustrie

KALISCH, M.: Der Einfluß der erworbenen Linsentrübungen auf die Buntton-Unterschiedsempfindlichkeit

KLUXEN, G.: Experimentelle Untersuchungen über Ursache und Wesen der Blendungs-Erythropsie

DE MATTIELLO, M. F.: Matching techniques for the study of visual functions

MOLLON, J. D., and G. JORDAN: Eine evolutionäre Interpretation des menschlichen Farbensehens

MORGAN, G., and A. E. MOSS: The two blues of Russian. The referents of "sinij" and "goluboj"

PLENDL, H.: Visuell evozierte Potentiale nach Farbreizung

SCHLÄPFER, K.: Übereinstimmung von Farbmeßgeräten

WAGNER, H. G.: Projektive Koordinaten zur Darstellung der Farbarten in einer Farbtafel